



# Changes to butterfly phenology versus elevation range after four decades of warming in the mountains of central Spain

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## Abstract

Shifts over time (phenology) and space (latitude and elevation range) represent common ecological responses to climate change. However, the factors determining how changes in phenology and distribution interact, and the consequences for conservation, remain uncertain. Here, we assess how phenology responded to temperature over four decades of warming across the elevation ranges of 18 univoltine butterfly species in four mountain regions of Spain. Using count data from intermittent surveys in 166 sites between 1985 and 2022, we tested for (1) effects of monthly temperature and elevation on mean annual flight date; (2) changes to flight dates between 1985–2005 and 2017–2022; and (3) whether shifts in flight date were related to shifts in the average elevation occupied. Mean flight dates were later in years with cooler springs, and at higher sites, with a mean delay of nearly twenty days per km elevation increase. As conditions warmed over time, average flight date advanced for two thirds of species, especially those whose average elevation was stable over time. Species with stable flight dates showed greater indication of upward range shifts, although only one species showed a significant shift in average elevation. Implications for insect conservation: We show that spring temperatures influence mountain butterfly phenology, and that shifts in phenology and elevation range could compensate for each other in determining population exposure and responses to climate change. Monitoring these changes over time, including by employing evidence from historical surveys and scientific collections, can help to understand constraints on species adaptive capacity to climate change.

**Keywords** Lepidoptera · Entomology collections · Altitude gradient · Emergence time · Growing season · Iberian peninsula

## Introduction

Understanding how species are responding to climate change is crucial for effective conservation and ecological management (Parmesan et al. 2022). Two primary responses to climate change are distribution change and phenology change (Parmesan 2006; Leech and Crick 2007; Bertin 2008). Both responses reflect how species' life cycles and population dynamics respond to changing conditions through the effects of temperature on development rates and survival. As a result, species may exhibit earlier activity in the year or change their ranges to higher elevations or latitudes, enabling them to remain active during suitable conditions while avoiding excessive heat (Waldock et al. 2018). However, the ways in which changes in distribution and phenology interact remains uncertain. Do both changes occur simultaneously? Do some species show more pronounced changes in one aspect than the other? Some studies suggest

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that species experiencing greater phenology changes also exhibit more pronounced distribution shifts (Forister and Shapiro 2003; Macgregor et al. 2019; Hällfors et al. 2021). However, the degree to which these changes compensate for or amplify each other's effects remains an open question. Moreover, it is still unknown whether the responses depend on specific life history traits, and the implications for climate change adaptation and conservation.

An important consideration in understanding how phenology, abundance, and distribution respond to climate change is that the environmental factors driving the responses can vary among species (Colom et al. 2022) and even within different parts of a species' geographic range (Mills et al. 2017). This variation can result from prevailing environmental conditions or local adaptation. Furthermore, the pace of climate change varies across different locations (Maclean et al. 2017). The influence of changing conditions can also differ based on whether climate changes at similar rates throughout the year and the developmental stages occupied by a species at those times (Ubach et al. 2022). These factors contribute to variations in the magnitude and timing of phenological change among species, with some species exhibiting more rapid phenological shifts compared to others, depending on specific life history traits. This aspect is particularly relevant for ectothermic organisms (Buckley et al. 2012), whose development, growth rates, and survival depend critically on ambient temperatures (Paaijmans et al. 2013). The overwintering development stage and the period during which a species is most sensitive to temperature conditions play a crucial role in phenological responses (Hällfors et al. 2021). These differences in sensitivity can have implications for species distributions and abundance. For example, Colom et al. (2022) suggested that species whose phenology is more sensitive to climatic conditions have suffered reduced declines in abundance.

Mountain populations of ectothermic species are excellent systems to understand the ecological effects of climate change, because climatic conditions change rapidly over short geographic gradients due to the effects of elevation (Feldmeier et al. 2020). Hence, the phenology of species often occurs earlier in the year at lower elevations where conditions are warmer (Gutiérrez Illán et al. 2012). Also, many species have lower and upper limits to their distributions which are thought to be linked to climatic conditions, and there is strong evidence that the elevation ranges of species have shifted upwards as the climate has warmed (Moritz et al. 2008; McCain and Colwell. 2011; Tingley et al. 2012; Vítasse et al. 2021). Understanding these ecological responses in mountain environments is important because temperatures at high altitudes have generally increased at a faster rate than in nearby lowlands (Pepin et al. 2022).

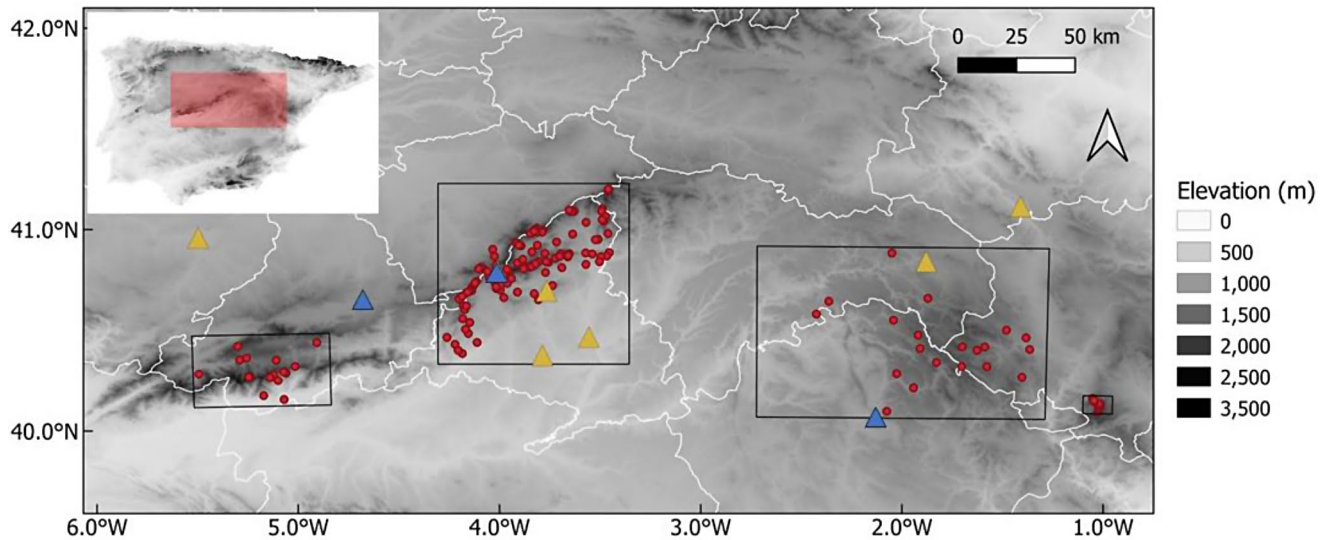
In this study we assess the effects of temperature on the phenology of butterfly populations occurring in mountain ranges in central Spain, and how these are related to the elevation ranges of the species in the past four decades. Previous studies have provided evidence of changes in altitudinal distributions of mountain butterflies in the Sierra de Guadarrama since the 1960s (Wilson et al. 2005). In this region, butterfly species tend to fly later in cooler years and at higher elevations, although data from transects monitored consistently from 2004 onwards do not provide evidence of general advancements in flight periods (Gutiérrez Illán et al. 2012; Stewart et al. 2020; Gutiérrez and Wilson 2021). For the present study, we extend the time period available to test for phenology change by conducting new transects between 2017 and 2022 across a wider set of locations that were sampled intermittently between 1985 and 2005. These include locations sampled in the Sierra de Gredos (Viejo and Martín 1988), Sistema Ibérico Meridional (Baz 1987), and Sierra de Javalambre (Sanchez-Rodríguez and Baz (1995)). For these latter sites, the preserved, labelled specimens from the historical surveys allow dates of capture and identity to be confirmed, demonstrating the value of natural history collections for research into ecological responses to global change (Belitz et al. 2022). In addition, temperature is changing at different rates during different times of the year and in the different survey regions (Gómez-Vadillo et al. 2022). This potentially leads to differences in phenology change among species and regions, helping to elucidate the factors influencing these changes.

Therefore, taking advantage of this broader geographic and longer term information we ask (1) Has the phenology of these species advanced as climatic conditions have warmed? (2) Do the different rates of climatic change during different times of the year and sensitivity periods of the species influence their phenology responses? (3) Are the changes in phenology and altitudinal distribution of these species related? These results are relevant to understanding the factors influencing the responses of insects to climate change, and their sensitivity and limits to adaptive capacity.

## Methods

### Research system and data collection

The study system includes 166 sites from four mountain ranges in the Iberian Peninsula, from west to east: 16 in the Sierra de Gredos, 120 in the Sierra de Guadarrama, 20 in the Sistema Ibérico Meridional and 10 in the Sierra de Javalambre (Fig. 1). Site elevations varied from 395–1955 m in Gredos, 928–2252 m in Guadarrama, 1066–1622 m in Meridional and 1114–2010 m in Javalambre. Nearest



**Fig. 1** Map of the study system showing elevation and the four mountain ranges where sampling took place. Mountain ranges are indicated within a black box, from west to east: Sierra de Gredos, Sierra de Guadarrama, Sistema Ibérico Meridional and Sierra de Javalambre. Each sampling transect is indicated with a red dot and meteorological

stations with triangles. Blue triangles indicate meteorological stations with continuous data throughout the entire time series (1985–2022): Ávila, Pto. Navacerrada and Cuenca (from west to east). Yellow triangles correspond to meteorological stations with complete data for the butterfly sampling years

neighbouring sites were separated by  $5.62 \pm 1.36$  km in Gredos,  $1.99 \pm 0.15$  km in Guadarrama,  $10.75 \pm 1.32$  km in Meridional, and  $0.97 \pm 0.08$  km in Javalambre. The species included in this study are not migratory but form local populations: hence, study populations generally represent independent populations and the measures of flight period for each site will not be overly influenced by individuals moving between sites, although there is likely to be some movement by some of the species (e.g. *Argynnis pandora* and *Aporia crataegi*) between near-neighbour sites, especially in Javalambre and Guadarrama.

Historical data from the 1980 and 1990s were taken from Viejo and Martín (1988) in Gredos between the years 1985–1986, Baz (1987) in Meridional in 1986, and Sanchez-Rodriguez and Baz (1995) in Javalambre in 1991. The sampling in these historical surveys was carried out by capturing butterflies encountered during visits to the sites. In the case of Gredos, there were unequal numbers of visits to each field site and in each of the two sample years; whereas in Meridional captures were conducted in a total of four 15-minute visits to each site each month from May to August 1986, and in Javalambre captures were conducted in eight visits each two weeks from May to the end of August 1991. In order to obtain information on the dates on which each individual was observed, the original specimens in the entomological collections of the Autónoma University of Madrid (UAM) and the University of Alcalá de Henares (UAH) were reviewed, confirming species identification and recording dates of capture.

Data since 2004 were obtained using transects approximately every three weeks at each of the field sites. Transects of 500 m crossed open areas occurring in accessible natural or semi-natural habitats (usually woodland clearings, scrub or pasture). Butterflies were counted following the methodology described by Pollard and Yates (1993), counting butterflies 5 m in front and 2.5 m on each side of the observer while walking the transect at a constant speed. Data from Guadarrama in 2004 and 2005 were collected by Gutiérrez Illán et al. (2010). Recent surveys, between 2017 and 2022, were carried out in the four mountain ranges following the transect methodology, in the same locations where the historical samplings were carried out. Each transect was visited every three weeks during survey years between May and August, avoiding rainy or windy days (see Supplementary Table 1 for the differences in sampling between different years and regions).

Several filters were applied to ensure that, despite differences in sampling between regions and years, the calculation of mean flight dates per site and year were consistent. First, to avoid difficulties in separating different generations of multivoltine species, we restricted analyses to species that are univoltine (one generation per year) (Gutiérrez and Wilson 2021). Second, we only calculated flight dates for sites that included counts of the respective species on at least two sampling dates in a given year. We also limited analyses to years in which a species had been recorded twice in at least four sites, for a minimum of two years in each period (historical, 1985–2005 / recent, 2017–2022). Additionally, a requirement was set for a minimum of two

years of sampling per species in each of the four regions. As a result, the final number of butterfly species included in the analyses was 18 species.

### Meteorological data

Meteorological data of the maximum, minimum and monthly average temperatures for the 9 years of phenological data (Historical: 1985, 1986, 1991, 2004, 2005; Recent: 2017, 2020, 2021, 2022) was obtained from AEMET (State Meteorology Agency; [aemet.es](http://aemet.es)) using *climaemet* R package (Pizarro et al. 2023). For this, we selected 9 meteorological stations within the study region that had complete climatic information for the nine study years (Fig. 1). Three out of the 9 stations had complete data from 1985 until 2022 (Ávila, Pto. Navacerrada, and Cuenca, from west to east) (see Supplementary Table 2). Annual mean temperatures from the three meteorological stations with continuous data demonstrate that conditions during the years of butterfly sampling in the respective regions were representative of a general increase in temperature in recent decades, rather than the result of atypical extreme weather years (Fig. 2a).

Butterfly species in Mediterranean Europe exhibit sensitivity periods for peak emergence that stretch from the previous autumn to the summer of flight (Colom et al. 2022). For this reason, the climatic data were grouped in such a way that each study year began in the autumn before field sampling and ended in the summer of the sampling year. Temperature means for each meteorological station were calculated for three-month periods for each year, representing autumn from October to December of the previous year, winter from January to March, spring from April to June, and summer from July to September of the survey year. For each meteorological station and year, the temperature anomaly of each season was calculated, subtracting the average for that season over the nine years from the observed seasonal temperature from the respective year and meteorological station (Fig. 2b).

In order to assess climate differences between historical (1985–2005) and recent periods (2017–2022), as well as between seasons, a linear mixed model was conducted for each season (spring, summer, autumn, winter). The dependent variable was the temperature anomaly, while the independent variable was the period (historical/recent). The year of study and the meteorological station were included as random factors.

### Analysis of mean flight date

To determine phenological sensitivity to climate in different seasons, and phenological variation over the elevation gradient, mean flight dates were calculated for each

year and site. Mean flight dates summarise the timing of the annual flight period for each species and are weighted by the number of individuals counted per visit (Brakefield 1987). Dates were measured as the inclusive number of days elapsed since 1 January (1 = 1 January). Linear mixed models were conducted for each species. The mean flight date was the dependent variable, while mean temperatures of the four seasons for the year in question, site elevation, and their interactions were treated as independent variables. The region and sampling site were included as nested random factors. The model with the lowest Akaike Information Criterion (AIC) value was selected.

### Analysis of change in phenology and distribution

We tested whether there were differences between the mean flight dates of each species between the historical and recent periods, as well as between the elevations where phenological data for each species were recorded in the historical and recent periods. For these tests, the sample data were any site/year combinations that fulfilled the criteria of at least two counts for the species in the respective year, grouped into historic (1985–2005) and recent (2017–2022) periods. The sample sizes were unequal between the two periods, and were not Normally distributed (Shapiro-Wilks tests,  $p < 0.05$ ) so we conducted unpaired non-parametric tests (Mann-Whitney / Wilcoxon Signed Ranks test). To account for multiple comparisons of species we applied the Bonferroni correction. Note that some species were recorded in additional sites in each year, but this analysis is restricted to sites with sufficient annual counts to enable calculation of the mean flight date, which are also likely to represent the most established populations of the species in each period (and hence provide a sample of the main elevation range).

Finally, we tested whether species flight periods had generally advanced or delayed, and whether possible phenological changes were related to changes in the elevation range. The differences in mean flight date and elevation for each species between the historical and recent periods were calculated, based on the sites fulfilling the criteria for analysis. Given that species tend to fly later at higher elevations, we expected that there would be a positive relationship between elevation change and flight date change: as temperatures increase, species shifting to higher elevations could maintain their flight dates, whereas species whose elevation ranges were stable or shifted downwards might show advances in flight date (i.e., negative changes in date) because of warming temperatures. If significant, the intercept of the model could be used to estimate the shift in mean flight date between historical and recent periods for a species whose mean elevation remained unchanged. To do this, as traits of related taxa may be similar due to

common ancestry and therefore not statistically independent in comparative analyses (Harvey and Pagel 1991), we consider phylogenetic relationships among species in a Phylogenetic Least Squares (PGLS) model using the ultrametric phylogenetic tree published by Dapporto et al. (2019). We performed two PGLS models. In one of them, the branch length transformations were left at their raw values of 1, as the default assumption in the PGLS analysis. In the other model, maximum likelihood (ML) estimation was used to estimate the lambda parameter of the branch length transformations. Again, selection of the best model was based on the Akaike Information Criterion (AIC).

All statistical analyses were performed using R (R Core Team 2022) with packages *ape* (Paradis and Schliep 2019), *lme4* (Bates et al. 2015), *caper* (Orme et al. 2018), *nlme* (Pinheiro et al. 2014) and *MuMIn* (Bartoń 2020).

## Results

### Temperature variation among survey years

There was an overall trend for increasing annual mean temperature over the 38 year period (1985–2022) encompassing the years of butterfly sampling across the survey region (Fig. 2a). Seasonal temperatures were generally warmer in the four recent survey years (2017, 2020, 2021, 2022) than the historic years (1985, 1986, 1991, 2004, 2005) (Fig. 2b). The models for the effects of survey period on the temperature of each season were highly significant ( $p < 0.001$ ), showing that there were differences between historical and recent temperatures. According to the coefficients of the models, in all cases, the recent temperatures were higher than the historical temperatures. The season showing the most change was spring (+2.03°C), followed by autumn (+1.99°C), winter (+1.13°C), and finally summer (0.65°C). (Table 1)

### Butterfly mean flight dates

Species' global mean flight dates in the historical period ranged from 18 May to 11 September (138–254). The average mean flight date in that period was 196, which corresponds to 15 July. In the recent period, species' global mean dates ranged from 9 May to 21 August (129–233). The average mean recent flight date was 187, which corresponds to 6 July.

For mean date, the best models contained effects of temperature in at least one of the seasons for all species, and effects of elevation for 16 of the 18 species (89%) (Table 2). Effects of seasonal temperature were generally negative and effects of elevation were positive, indicating that species flew earlier when conditions were hotter, and later at higher

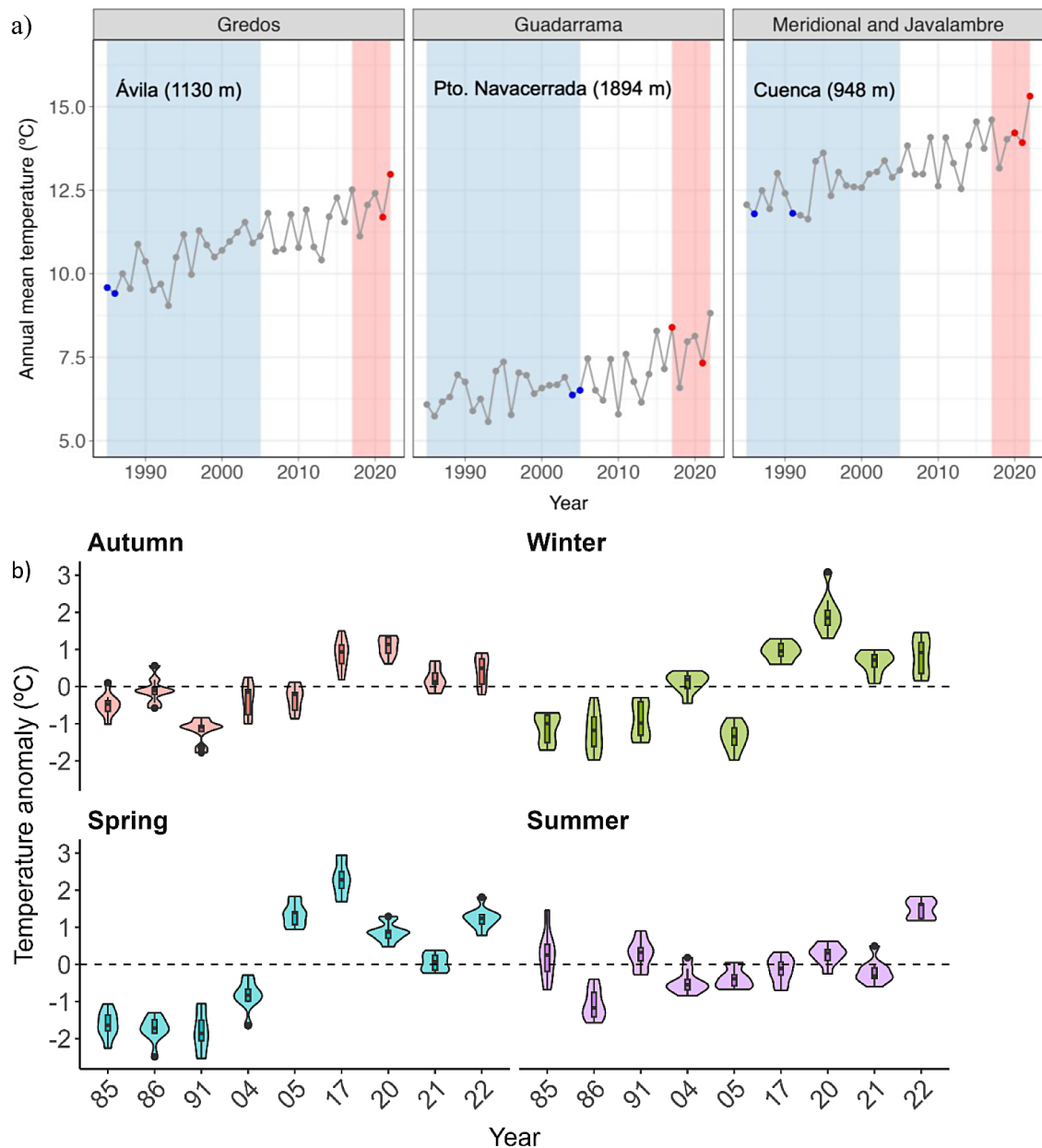
elevations. Models for 11 species (61%) contained interactions between elevation and at least one of the seasons; however, only in 6 species (33%) were these interactions significant. The only two species that did not include elevation in the model were *Hyponephele lycaon* and *Argynnis paphia*. Based on the positive coefficient values, the number of days delayed in flight date per km increase in elevation ranged from 6 (*Speyeria aglaja*) to 37 (*Pyronia bathseba*). The average estimated delay including only those species with significant relationships was 19.93 days per 1 km increase in elevation (Fig. 3; Table 2).

Spring was the season that appeared most frequently in the models (16 species, 89%). The species which did not include spring in the model were *Pyronia cecilia* and *Pyronia tithonus*. For the remaining species, all showed negative coefficients except *Fabriciana adippe* and *Aporia crataegi* but in these cases there were negative interactions between the effect of elevation and spring temperature. The significant negative coefficients for 12 species (67%) indicate an earlier mean flight date in years with hotter springs. According to the coefficient values, the number of days the flight date changes per degree increase in spring temperature ranged from -20.4 (*Argynnis pandora*) to -1.7 (*Hipparchia hermione*). The average estimated advance including only those species with significant relationships and negative coefficients was 6.8 days per 1 degree increase in spring temperature (Table 2).

Winter was the second most frequently represented season among the selected models (13 species, 72%). However, although it was significant for 61% of species, there was no clear pattern observed for the coefficients across species. Summer and Autumn appeared in the lowest number of species models, generally with negative coefficients (i.e. warmer temperatures led to earlier mean flight date) (Table 2).

### Shifts in phenology and elevation

The difference between historic and recent mean flight dates for each species was negative for 17 out of 18 species (94%), indicating an earlier recent flight date (Fig. 4). Only *Pyronia bathseba* showed a delay in the mean flight date between periods (Fig. 5). The results for the Mann-Whitney/Wilcoxon tests showed that there were significant differences for mean flight date between periods for 13 species (72%,  $p < 0.05$  after Bonferroni correction). The five species that did not show differences between periods for mean flight date were: *Brintesia circe*, *Pyronia cecilia*, *Pyronia bathseba*, *Melitaea phoebe* and *Maniola jurtina*. On the other hand, the difference between the historic and recent periods for the average elevation of each species was positive for 10 species (56%) and negative for 8 species (44%), indicating



**Fig. 2** Annual mean temperature of three meteorological stations with continuous data throughout 1985–2022 (**a**) and temperature anomalies at the nine meteorological stations for the nine years when butterfly phenology data were collected (**b**). (**a**) Blue dots represent years with butterfly sampling in the historical period (1985–2005; blue background) and red dots represent years with samplings in the recent

period (2017–2022; red background). (**b**) Temperature anomaly is the subtraction of observed seasonal temperature for each meteorological station and year, from the average temperature for that season over the nine years. Each violin plot represents variation across meteorological stations (central line = median). The horizontal dashed line at zero distinguishes between negative and positive temperature anomalies

upward and downward shifts respectively. However, significant differences in elevation between periods were only observed as a positive (upward) shift for *Pyronia bathseba*.

In summary, the following changes were observed: *Pyronia bathseba* did not change flight date but shifted to higher elevation; *Maniola jurtina*, *Pyronia cecilia*, *Brintesia circe* and *Melitaea phoebe* (22%) did not modify either flight date or average elevation; and finally, *Pyronia tithonus*,

*Hyponephele lycaon*, *Hipparchia semele*, *Hipparchia hermione*, *Melanargia lachesis*, *Coenonympha arcania*, *Fabriciana niobe*, *Fabriciana adippe*, *Speyeria aglaja*, *Argynnis paphia*, *Argynnis pandora*, *Aporia crataegi*, and *Thymelicus sylvestris* (72%) advanced flight date and did not shift in elevation (Fig. 4).

The best model for the relationship between phenology shift and elevation shift according to the AIC criterion was

**Table 1** Coefficients ( $\pm$ SE) of environmental parameters obtained in the linear mixed model for the mean temperature of each season. AIC is the Akaike Information Criterion of the model and AIC null is the AIC of the null model. Significance level is indicated using asterisks (\*\*\*)  $p < 0.001$ ). The coefficient for Recent indicates the temperature difference ( $^{\circ}$ C) between Historic and Recent years

Season	Intercept	Recent	AIC	AIC null
Spring	-0.915 ( $\pm 0.166$ ) ***	2.032 ( $\pm 0.249$ ) ***	251.356	298.773
Summer	-0.29 ( $\pm 0.105$ ) ***	0.645 ( $\pm 0.156$ ) ***	176.546	190.415
Autumn	-0.894 ( $\pm 0.077$ ) ***	1.986 ( $\pm 0.116$ ) ***	118.824	179.986
Winter	-0.507 ( $\pm 0.100$ ) ***	1.133 ( $\pm 0.149$ ) ***	169.263	262.236

the one with an estimated lambda of 0, indicating no evidence of phylogenetic dependence in the data, and that all evolutionary changes in the dependent variables occurred independently of the phylogenetic relationships (Brownian model). In this model, the phenological changes were related to changes in average elevation ( $p < 0.001$ ) with a positive slope, indicating that species which shifted their elevation more upwards experienced reduced advances in flight period (Table 3; Fig. 5). The intercept of -8.14 from this model suggests that there was an average advance of 8.14 days in flight date for a species that did not change its elevation between the historic and recent periods. The more conservative model in which the lambda value is 1 (taking into account the phylogenetic relationships between species), showed a similar but marginally non-significant advance of 7.5 days in flight date for a species maintaining its average elevation (Table 3; Fig. 5).

## Discussion

Phenology and distribution shifts are two main responses to changes in climatic conditions (Parmesan 2006; Leech and Crick 2007; Bertin 2008), but few studies have considered how these two ecological changes interact with each other (Macgregor et al. 2019; Hällfors et al. 2021). Responses are expected to vary among species and across geographic distributions depending on environmental factors and life history traits in different populations (Mills et al. 2017; Colom et al. 2022). Based on information from four decades and four mountain regions in central Spain, we show that spring temperature has a strong effect on mean flight date for the vast majority of 18 univoltine butterfly species. As spring temperatures warmed, two thirds of species advanced their

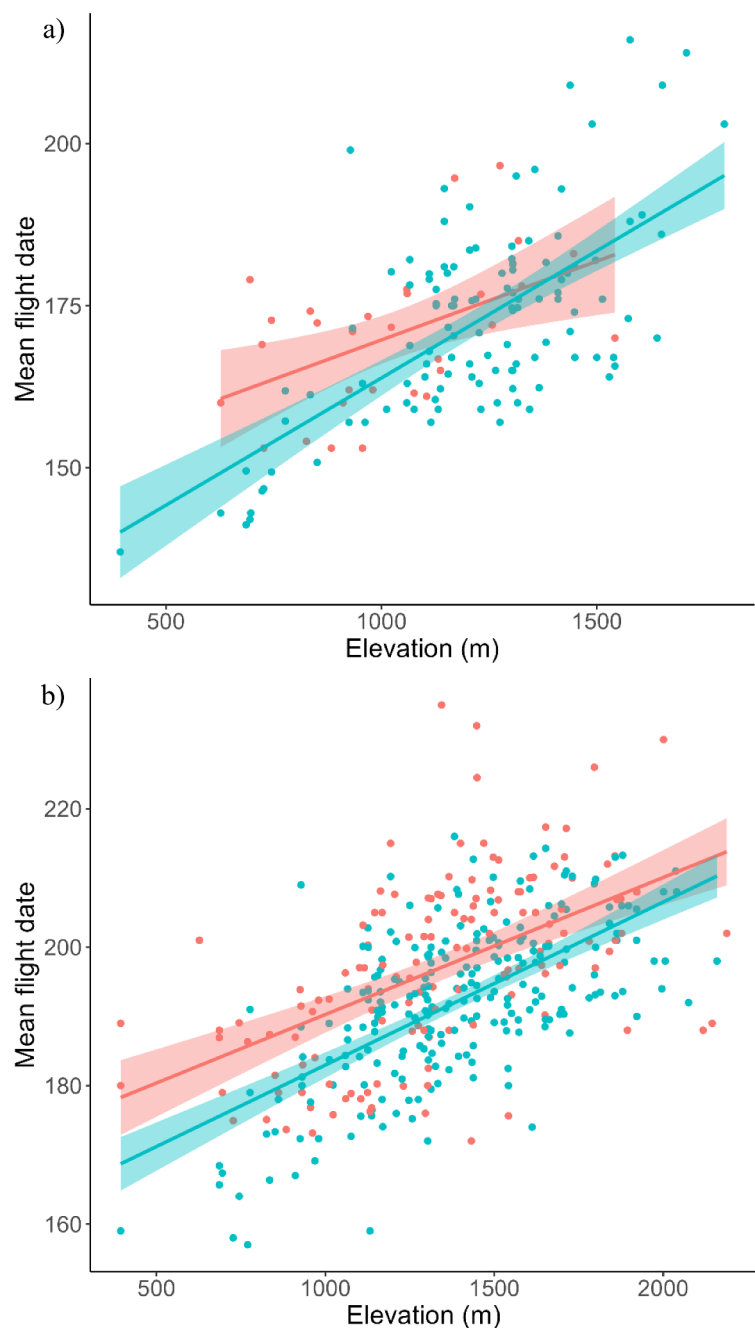
flight date (mean 6.8 days per  $1^{\circ}$ C increase). Elevation had a strong effect on phenology for 83% of species, with a delay in mean flight date of nearly twenty days per km increased. Between historical (1985–2005) and recent (2017–2022) survey periods, most species (72%) advanced their flight date but did not shift the average elevation occupied. In contrast, there was an indication that species whose elevation ranges shifted upwards showed reduced or non-significant changes in flight date (Fig. 5). Here we consider the causes and consequences of the advances in flight date for species maintaining their elevation range, and of the evidence that elevation shifts can compensate for changing phenology.

## Effects of temperature on flight period

Species mean flight dates showed significant delays with elevation for 83% of species. These results are consistent with a well-established and widely documented pattern that annual periods of insect activity tend to occur later higher up (Hopkins 1938; Whittaker and Tribe 1996; Gutiérrez and Menéndez 1998). We found a mean delay of 19.93 days per km increased in elevation. Temperature is known to decrease about  $0.5$ – $0.6^{\circ}$ C with every 100 m increase in elevation (Coulson et al. 1976), and as a consequence of this decrease at higher elevations, growth and development are delayed (Kovanci and Kovanci 2006; Nufio et al. 2010). The delay we recorded based on intermittently sampled sites supports previous evidence based on bi-weekly transects in this geographical area of 15–22 days of delay per km (Gutiérrez Illán et al. 2012). *Hyponephele lycaon* and *Argynnis paphia* are the two only species that did not show an effect of elevation on mean flight dates. These results are consistent with those obtained by Gutiérrez Illán et al. (2012) who found that species flying later in the year and restricted to higher elevations tended to show reduced elevational delays in phenology. Both of these species occur mainly from the end of July onwards and at elevations above 1000 m, which means that shorter flight seasons are available than for species occurring earlier in the year or at lower elevations: possibly imposing selection pressure to speed up development rates at higher altitude sites (Gutiérrez Illán et al. 2012), or to select hotter microhabitats for egg-laying at higher sites, as seen for some butterfly species in the region (Merrill et al. 2008; Ashton et al. 2009).

We detected that recent (2017–2022) temperatures were higher than historical (1985–2005) and that spring was the season that warmed the most between historical and recent sample years. We also found that temperature during the spring season had the strongest influence on mean flight date for the study species. This result is consistent with other articles that have observed that spring temperature is the primary determinant of butterfly phenology (Colom et al.

**Fig. 3** Relationship between mean flight date and elevation for *Pyronia bathseba* (a) and *Melanargia lachesis* (b). The Historical period is represented in red and Recent period in blue



2022; Stewart et al. 2020). Spring coincides with the larval (March-May) or pupal phase (May-June), for the majority of univoltine species studied. The timing of flight in these species may be especially sensitive to spring temperature variation because increased temperatures accelerate growth rates and consequently advance adult emergence (Buckley and Kingsolver 2012). Species with significant effects of spring temperature on mean flight date showed a mean advance of 6.8 days per 1°C increase, consistent with studies that have also detected advancing phenology of butterflies linked to

an increase in spring temperatures (Macgregor et al. 2019; Stewart et al. 2020).

### Changes over time in phenology and elevation range

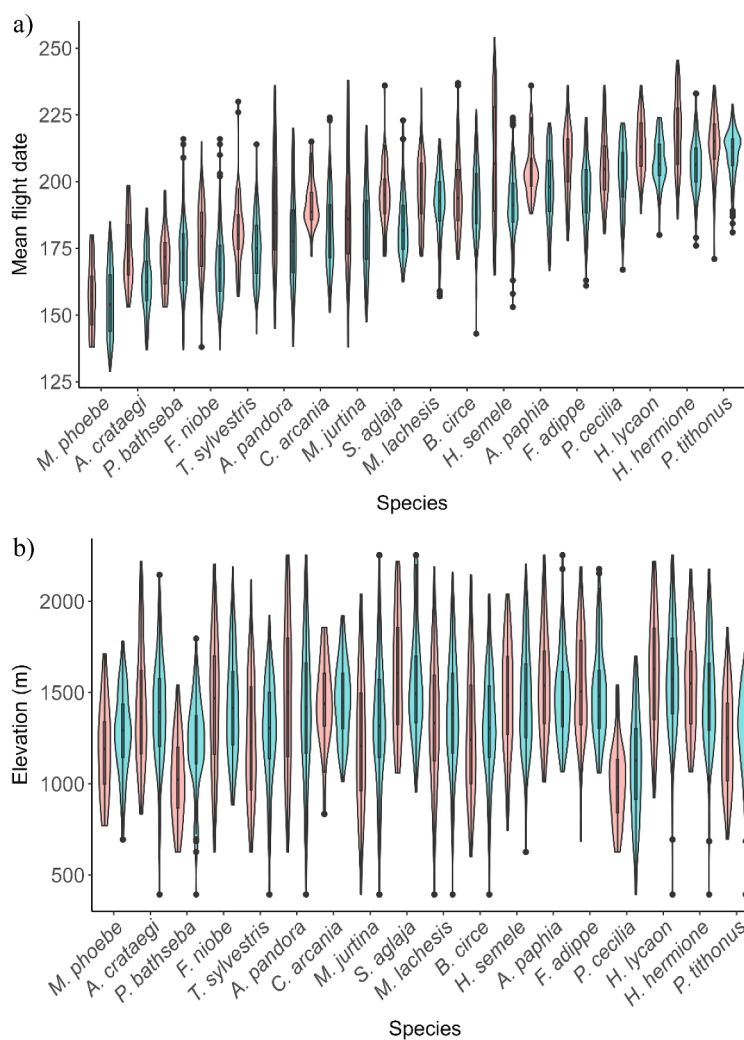
Following the increase in spring temperature, 72% of the species advanced their flight date between historical (1985–2005) and recent (2017–2022) periods, without changing the average elevation of their populations. 22% of species did not modify either flight date or their average elevation,



**Table 2** Coefficients ( $\pm$ SE) of environmental parameters and interactions between them in the best linear mixed model for each species based on the Akaike Information Criterion (AIC).  $R^2$  is the coefficient of determination and significance level is indicated using asterisks. Species are arranged phylogenetically

Species	Intercept	Elevation	Spring	Summer	Autumn	Winter	Elev.:spring	Elev.:summer	Elev.:autumn	Elev.:winter	$R^2$
<i>Maniota juritina</i>	162.78 ( $\pm 4.44$ )	0.02*** ( $\pm 0.003$ )	-3.96 ( $\pm 2.54$ )	2.36 ( $\pm 1.49$ )			-0.003 ( $\pm 0.002$ )				0.42
<i>Pyronia cecilia</i>	176.24 ( $\pm 4.08$ )	0.03*** ( $\pm 0.004$ )			-16.53 ( $\pm 4.09$ )	5.04* ( $\pm 1.94$ )					0.57
<i>Pyronia tithonus</i>	186.85 ( $\pm 2.72$ )	0.02*** ( $\pm 0.002$ )			-15.42*** ( $\pm 2.24$ )	4.98*** ( $\pm 1.07$ )					0.41
<i>Pyronia bathseba</i>	132.69 ( $\pm 5.51$ )	0.04*** ( $\pm 0.004$ )	-3.49 ( $\pm 2.82$ )		6.68** ( $\pm 2.6$ )		-0.004 ( $\pm 0.002$ )				0.83
<i>Hyponephele lycan</i>	210.92 ( $\pm 1.49$ )		-3.75*** ( $\pm 0.77$ )		-4.69 ( $\pm 3.08$ )	2.92* ( $\pm 1.18$ )					0.39
<i>Hipparchia semele</i>	185.0 ( $\pm 5.54$ )	0.01*** ( $\pm 0.004$ )	-4.76*** ( $\pm 1.18$ )	-3.91* ( $\pm 1.61$ )	14.87 ( $\pm 15.05$ )	-22.72** ( $\pm 8.55$ )			-0.02* ( $\pm 0.01$ )	0.02 ( $\pm 0.006$ )	0.65
<i>Hipparchia hermione</i>	199.71 ( $\pm 3.66$ )	0.01*** ( $\pm 0.002$ )	-1.74** ( $\pm 0.58$ )	-3.97*** ( $\pm 0.97$ )	-29.57*** ( $\pm 7.52$ )	3.18** ( $\pm 1.14$ )			0.01* ( $\pm 0.005$ )		0.47
<i>Brintesia circe</i>	174.01 ( $\pm 3.05$ )	0.02*** ( $\pm 0.002$ )	-7.03*** ( $\pm 0.5$ )			1.65* ( $\pm 0.65$ )					0.82
<i>Melanargia lachesis</i>	171.4 ( $\pm 2.42$ )	0.02*** ( $\pm 0.002$ )	-7.39*** ( $\pm 1.17$ )			0.75 ( $\pm 0.46$ )	0.002 ( $\pm 0.001$ )				0.79
<i>Coenonympha arcania</i>	165.22 ( $\pm 8.51$ )	0.01** ( $\pm 0.005$ )	-10.55*** ( $\pm 0.95$ )		19.25* ( $\pm 4.74$ )	-4.55*** ( $\pm 2.05$ )					0.84
<i>Melitaea phoebe</i>	128.29 ( $\pm 6.14$ )	0.03*** ( $\pm 0.004$ )	-3.51*** ( $\pm 0.92$ )								0.80
<i>Fabriciana niobe</i>	144.77 ( $\pm 4.19$ )	0.02*** ( $\pm 0.003$ )	-4.58*** ( $\pm 0.96$ )	-5.99 ( $\pm 8.59$ )	-8.92** ( $\pm 3.33$ )			0.01 ( $\pm 0.006$ )			0.72
<i>Fabriciana adippe</i>	184.8 ( $\pm 6.36$ )	0.01** ( $\pm 0.004$ )	10.16* ( $\pm 5.11$ )	-2.65* ( $\pm 1.36$ )	-36.59** ( $\pm 12.31$ )	4.24* ( $\pm 1.83$ )	-0.009** ( $\pm 0.003$ )		0.02* ( $\pm 0.008$ )		0.66
<i>Speyeria aglaja</i>	184.3 ( $\pm 5.25$ )	0.01* ( $\pm 0.003$ )	-4.43*** ( $\pm 0.75$ )	-17.36 ( $\pm 10.51$ )		-3.32** ( $\pm 1.1$ )		0.01 ( $\pm 0.007$ )			0.59
<i>Argynnis paphia</i>	207.97 ( $\pm 1.99$ )		-7.19*** ( $\pm 0.75$ )			-1.95* ( $\pm 1.00$ )					0.56
<i>Argynnis pandora</i>	201.78 ( $\pm 5.55$ )	-0.01 ( $\pm 0.004$ )	-20.4*** ( $\pm 2.87$ )	19.97** ( $\pm 7.51$ )			0.008*** ( $\pm 0.002$ )	-0.01* ( $\pm 0.005$ )			0.56
<i>Aporia crataegi</i>	134.69 ( $\pm 4.53$ )	0.03*** ( $\pm 0.003$ )	2.62 ( $\pm 3.06$ )		-6.67 ( $\pm 8.67$ )	-2.47* ( $\pm 1.27$ )	-0.009* ( $\pm 0.002$ )		0.01** ( $\pm 0.005$ )		0.76
<i>Thymelicus sylvestris</i>	149.94 ( $\pm 3.07$ )	0.03*** ( $\pm 0.002$ )	-6.13*** ( $\pm 0.71$ )		-8.1 ( $\pm 9.51$ )	7.54 ( $\pm 4.75$ )			0.01 ( $\pm 0.007$ )	-0.009* ( $\pm 0.004$ )	0.72

**Fig. 4** Historical and recent species mean flight dates and elevations. Violin plots show variation across all sites and years within each period for mean flight date (a) and elevation (b). Red and blue plots correspond to historical and recent periods respectively. Date is the inclusive number of days elapsed since 1 January. Species arranged from earliest to latest mean flight date



**Table 3** Coefficients ( $\pm$ SE) of environmental parameters obtained in the Phylogenetic Least Squares (PGLS) models relating change in phenology to change in mean elevation. AIC is the Akaike Information Criterion of the model and  $R^2$  is the coefficient of determination. Three asterisks indicate  $p < 0.001$ . The Intercept estimate indicates the amount of days advanced (if negative) or delayed (if positive) of the flight date for a species that does not change its elevation between historic and recent periods. Elevation difference indicates the average change in phenology per m increase in mean elevation

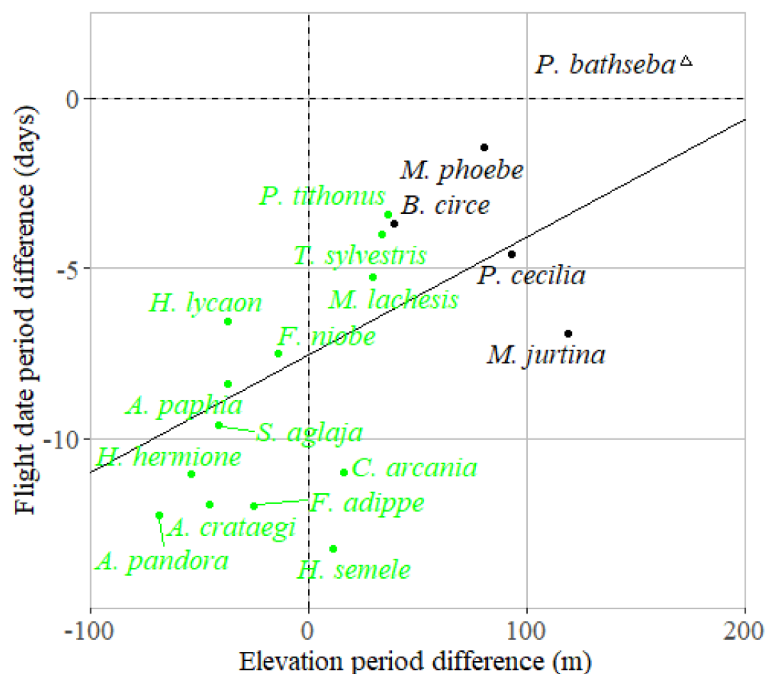
Model	Intercept estimate	Elevation difference	AIC	$R^2$
Lambda 0	-8.14 ( $\pm 0.682$ ) ***	0.05 ( $\pm 0.010$ ) ***	89.961	0.575
Lambda 1	-7.51 ( $\pm 3.787$ ) ( $p = 0.06$ )	0.03 ( $\pm 0.017$ ) ( $p = 0.05$ )	104.471	0.733

whereas only one species maintained its average flight date but shifted to higher elevations. Generally, species showing greater indications of a shift to higher elevations showed a reduced or non-significant advance in flight date (Fig. 5).

What appears to be occurring is that the increase over time in temperature (particularly during spring), which causes an advance in flight period, is partially compensated for if a species shifts its range upwards and therefore experiences reduced temperatures and consequently can maintain its flight date over its new, higher elevation range.

Many articles have provided evidence of changes in elevation range and phenology (Macgregor et al. 2019; Hällfors et al. 2021; Parmesan et al. 2022). In our system, advancing the phenology by approximately 6–8 days over forty years appears to have been the most common pattern for summer-flying, univoltine butterflies (Fig. 5). Phenology advancement is likely to be a direct response to temperature increases (in our study especially in spring), but could also depend on sufficient availability and quality of resources for existing populations, and that the resources do not lose phenological synchrony with their consumers. Recent studies have provided evidence of phenological advances in plant species in many regions of the planet (Crimmins et al. 2010; Ovaskainen et al. 2013; Vitasse et al. 2021). With the

**Fig. 5** Relationship between changes to mean flight date and elevation across species. Green indicates significant changes in mean flight date; black indicates non significant changes. Triangle indicates significant change in elevation; dots indicate non-significant. The black line represents the PGLS model with a lambda value of 1. Dashed black lines at the zero values on axes distinguish between negative and positive values, indicating the direction of the change: negative values indicate an advance in mean flight date and a downward shift in elevation; positive values indicate a delay in flight date and an upward shift



exception of *Aporia crataegi*, whose host plants are shrubs and trees, the larval food plants for all of the 18 univoltine species analyzed here are herbs and grasses (Middleton-Welling et al. 2020). In all cases, spring-feeding larvae may need to be synchronized with their host phenology to ensure that fresh leaves are eaten before their physical defences become too strong during summer, and the observed phenology shifts may help maintain populations in response to changing climatic conditions (Teder 2020).

The intermittent butterfly sampling years were generally warmer in a recent period (2017–2022) than historically (1985–2005), and hence enabled detection of phenological responses to an observed warming trend over four decades (Fig. 2). However, caution is needed in attributing population differences between snapshot surveys to longer term environmental trends, because observations could depend on extreme, outlying years (Stuble et al. 2021). Butterfly phenology tends to respond more directly and predictably than population abundance to interannual variation in seasonal temperatures (Stewart et al. 2020). Hence, impacts of temperature on phenology may be amenable to analysis using data from intermittent survey years, but the impacts of climate change on species distributions (e.g. elevation range) may reflect climatic conditions and ecological responses over longer periods of time.

Whereas phenology change within a population may represent a direct response to changing local temperature conditions or resource availability, an upward elevational range shift requires either the loss of populations at low elevations, or the colonization of additional, higher sites. Colonizations would require both sufficiently large numbers of colonizing

butterflies to emigrate from populations in the existing elevation range of a species, and for suitable habitat to be available for colonization at higher altitudes. Most of the species studied are not highly mobile and form local populations, although in the mountain ranges studied, there is likely to be sufficient habitat availability and connectivity to allow colonization of higher-elevation sites in response to local abundance increases (e.g. see Caro-Miralles and Gutiérrez 2023). However, the specific larval host plants used by some of the species may not reach elevations far above the current upper range limits of the species concerned (Merrill et al. 2008; Gutiérrez et al. 2016), limiting possible upward expansions of the species and their ability to track climatic conditions in space rather than time.

An upward range shift appeared to occur for *Pyronia bathseba* which did not experience an overall advance in its average flight dates between historical and recent surveys. In this case, *P. bathseba* was recorded at a greater number of sites in the recent than the historical surveys (Fig. 3a), especially above its historical upper range limit. Colonization of sites which experience cooler conditions on average than those in its historical range is likely to have resulted in a buffering effect on the spring temperatures experienced by *P. bathseba* populations in the region, despite warming conditions overall. Hence, the average regional flight dates of the species have not changed.

Nevertheless, a compensatory effect between phenology and distribution on temperatures experienced may not be the only explanation for the observed patterns in butterfly phenology and elevation range. It is also the case that vegetation communities are changing in the studied mountain

systems: García-Romero et al. (2010) showed that herbaceous communities of high elevation areas of some Mediterranean mountains have been replaced by shrubs. These vegetation changes impose constraints on habitat availability over the altitudinal range, but also modify the microclimatic conditions experienced by the adults and juvenile stages of the species concerned (Gutiérrez et al. 2016; Carro-Miralles and Gutiérrez 2023).

In 22% of species, no significant change either in flight date or average elevation was observed, despite warming especially in spring. Among this group, *Brintesia circe* and *Maniola jurtina* are two species in which aestivation has been observed during peak summer temperatures in Europe (García-Barros 1987; Birch et al. 2021). Populations of aestivating species could shift from exhibiting a single peak of abundance in midsummer to displaying two abundance peaks (in May and September, respectively), separated by an aestivation period (Birch et al. 2021). This could imply that the mean flight date obtained for the entire period remains the same, whether there is a single abundance peak or two, leading to a false impression of no change in flight date. However, most butterfly samples in our study were carried out before mid-August. Therefore, if there is a second peak after aestivation, we may not be able to detect it, and the observed mean flight date would likely be advanced. In our data the butterfly *Hipparchia semele* advanced its mean flight date but did not shift the average elevation occupied: this species appears to show delayed ovarian maturation in central Spain to avoid oviposition during hot, dry summer conditions (García-Barros 1988).

The fact that some species did not show any significant change in flight date nor average elevation could indicate that these species have greater dietary plasticity (e.g., Parmesan and Singer 2022; Stewart et al. 2020), exhibit greater tolerance to temperature increases (e.g. through life-history adaptations such as aestivation; Birch et al. 2021), or that temperature conditions have not changed so much during their periods of phenological sensitivity (Colom et al. 2022). However, if they are not able to adjust either their phenology or elevation range, or to show other plastic or adaptive responses including the ability to exploit heterogeneous microclimates, we can hypothesize that these species may show declines in abundance compared to the rest of the species as conditions continue to warm (Colom et al. 2022).

### Implications for butterfly monitoring and conservation

The risk of phenological mismatch between butterflies and their host plants could be particularly severe for species with a single annual reproductive opportunity (univoltine) (Ubach et al. 2022). Thus, while advancing phenology is

a common response that may enable butterflies and their young stages to maintain activity periods when temperatures are favourable, other climate-related consequences could impact population viability. For example, water availability in spring and summer plays a key role for host plant quality during the larval phase: warming may advance or exacerbate summer droughts, but rainfall patterns and hence food quality may also change unpredictably relative to temperature increases, impacting resource quality and development (Crimmins et al. 2010; Jamieson et al. 2012; Gutiérrez and Wilson 2021; Ubach et al. 2022). The ability of butterfly populations to persist will be influenced by their flexibility to changing climatic conditions and resource availability. Supporting this notion, Colom et al. (2022) show evidence that species with lower phenological sensitivity may show greater declines in the current context of climate change.

Our study contrasts with Colom et al.'s (2022) research on butterfly phenology in North-East Spain, where many species did not shift their flight dates because temperatures during their spring sensitivity periods did not increase. In our system, one species appeared to maintain similar flight dates over time by shifting to higher elevations, but advancing phenology over the historical range was the most common response to spring temperature increases: species that did not change their altitude range advanced by approximately one week. The fact that most species stayed where they were whilst shifting their phenology (perhaps because of constraints on expansion of the range) emphasizes the importance of in situ conservation to combat the effects of climate change (Greenwood et al. 2016). Extant populations may be vulnerable to increasing interannual climatic variability (Stewart et al. 2020), although exposure could be buffered to some extent by the effects of local habitat heterogeneity on microclimate (Nieto-Sánchez et al. 2015; Scherer and Fartmann 2022). Local maintenance of high-quality and heterogeneous habitats are therefore important to help populations persist in a changing climate (Greenwood et al. 2016), with extensively used uplands exemplifying a refuge habitat for butterflies (Löffler et al. 2023). In mountain regions, provision of nearby suitable habitats over elevation gradients may enable spatial spreading of climate risk, either through asynchronous population dynamics in different localities, or small-scale redistributions via colonizations and local extinctions (Mingarro et al. 2021).

Monitoring population responses also represents a key component of conservation adaptation. Many robust studies of Mediterranean butterfly phenology include evidence based on intensive weekly or bi-weekly transect counts repeated in consecutive years (e.g. Gutiérrez and Wilson 2021; Colom et al. 2022). Our study shows that surveys conducted in intermittent years, with tri-weekly surveys in the majority of sampled years and sites, can still provide

evidence of the effects of temperature variation on phenological variation in space (elevation) and time. This study also demonstrates that utilizing information on date of capture and abundance from recent-historical natural history collections can extend the time period to determine responses of butterflies to climate change (see also Belitz et al. 2022). Phenological monitoring from a wide range of sites, in historically under-sampled or remote regions (such as many mountain ranges), can help to provide evidence of regional variation in ecological responses to the wide variation in climate and climatic change across regions (Maclean et al. 2017). Future studies of this kind could therefore help to determine common or divergent responses not only among species but also among different populations of the same species, illuminating the factors driving responses to climate change, variation in vulnerability within or between species, and possible conservation responses.

### CRedit authorship contributions statement

RW and MG conceptualized the study. RW, GU and AB undertook field investigation. MG, GU and AB processed collections. MG and GU curated data, and conducted formal analysis and visualisation of results. RW acquired funding, administered and supervised the project. MG prepared the original draft. All authors contributed to writing review and editing.

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### Declarations

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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