RESEARCH ARTICLE



Factors shaping the abundance of two butterflies sharing resources and enemies across a biogeographic region

P. Colom¹ \bigcirc | A. Traveset¹ | M. R. Shaw² | C. Stefanescu³ \bigcirc

¹Mediterranean Institute of Advanced Studies (IMEDEA, CSIC-UIB), Esporles, Spain

²National Museums of Scotland, Edinburgh, UK

³Natural Sciences Museum of Granollers. Granollers, Spain

Correspondence

P. Colom, Miquel Marqués 21, 07190 Esporles, Balearic Islands, Spain. Email: pau.colom.montojo@gmail.com

C. Stefanescu, Francesc Macià 51, 08402 Granollers, Barcelona, Catalonia, Spain. Email: cstefanescu@mcng.cat

Funding information

Diputació de Barcelona; Govern d'Andorra: Govern de les Illes Balears: Ministerio de Ciencia, Innovación y Universidades

Abstract

Aim: Intraspecific variation in species relative abundance is shaped by a complex interplay of abiotic and biotic factors, making it both necessary and challenging to assess their combined relative importance in explaining variations across space and time. We used two congeneric butterfly species for which extensive count data and a deep understanding of their natural history is available to test three hypotheses explaining intraspecific variation in their abundance: (H1) seasonal dispersal behaviour driven by climate, (H2) resource availability and (H3) apparent competition mediated via shared parasitoids.

Taxon: Gonepteryx rhamni (Brimstone) and G. cleopatra (Cleopatra).

Location: NE Iberian Peninsula, where both species coexist, and a nearby archipelago (Balearic Islands), where only Cleopatra occurs.

Methods: We analysed spatial abundance variations for both species in the mainland and island-mainland differences in the abundance of Cleopatra. Abiotic and biotic factors, including temperature, host plant and overwintering habitat availability, larval parasitism and density dependence, were tested to explain the observed variations.

Results: H1 can explain variation in butterfly abundance between mainland regions since in warmer summers populations increased in cooler areas but decreased in warmer areas. H2 explains the variation within mainland climate regions with a strong positive relationship between resource availability and abundance but is unlikely to explain the island-mainland variation in the abundance of Cleopatra. H3 could neither explain biogeographical variation in abundance because although richer parasitoid communities were found on the mainland, larval mortality rates were similar or lower on the mainland than in the islands.

Main Conclusions: Climate and resource availability jointly account for variation in butterfly abundance across the mainland, but neither these factors nor parasitism can explain island-mainland differences. Both coexisting butterfly species and their larval parasitoids may have undergone evolutionary processes, resulting in spatial segregation that promotes the coexistence of the two butterfly species on the mainland.

KEYWORDS

apparent competition, Gonepteryx, larval parasitism, Lepidoptera, Mediterranean butterflies, overwintering habitat, resource availability, seasonal dispersal

1 | INTRODUCTION

WILEY-

Journal of Biogeogram

Insect diversity is critical for maintaining ecosystem functioning, as different species play distinct roles in essential ecological processes, such as herbivory, detrivory, nutrient recycling and pollination (Chapman, 1998). However, it is not only the presence of different species that matter but their relative abundance within a community also plays a crucial role. The relative abundance determines the strength of interactions among species and influences the impact that species may have on ecosystem processes. Species' relative abundance is shaped by a complex interplay of abiotic and biotic factors across space and time. Abiotic factors such as temperature can significantly affect abundance through direct (e.g. temperaturedependent metabolic processes) or indirect mechanisms (e.g. changes in resource availability). Biotic factors such as competition for resources, predation and parasitism also have an important impact on species abundance. Therefore, it is both necessary and challenging to assess the relative importance of some of these factors together to explain variations in species abundance across space and time. In this regard, it is advantageous to select study systems with extensive data on relative abundance to allow the analysis of long-term trends and spatial population dynamics across diverse environmental contexts. In particular, species sharing similar life histories (e.g. resource use) and co-occurring in some areas but not in others offer valuable opportunities to investigate the role of interspecific competition in explaining abundance variations across regions. Additionally, species characterized by high dispersal capacities serve as valuable subjects for assessing the impact of individual movements that can be motivated by abiotic and biotic factors on abundance fluctuations across spatial and temporal scales.

Here, we examined two butterfly species, *Gonepteryx rhamni* (Brimstone) and *G. cleopatra* (Cleopatra), for which hundreds of populations have been monitored in a Mediterranean region for more than two decades. Although both species coexist on the mainland (Northeast Iberian Peninsula), only one (Cleopatra) is present on nearby islands (Balearic Islands) (Figure 1). On the mainland, the two species occupy different climatic niches, although their distribution broadly overlaps in the warmer area of Brimstone's range, which corresponds to the colder area of Cleopatra distribution. Both species are highly dispersive, as pre-overwintering and post-overwintering adults can occur in different areas (Gutiérrez & Wilson, 2014; Pollard & Hall, 1980). They also share some fundamental aspects of their ecology, such as the use of the same host plants of the genus *Rhamnus* and the parasitism, in the larval stage, by specialist wasps (Shaw et al., 2009).

The purpose of this study is twofold. First, we evaluated different hypotheses to explain the spatial variation in the relative abundance of these two coexisting species on the mainland. We specifically tested whether the spatial distribution of the abundance of the species could be explained by the following hypotheses: (H1) Seasonal dispersive behaviour of butterfly adults, driven by climate, influences abundance fluctuations across climatic regions within years. (H2) Relative abundance is determined by resource availability, including host plant and overwintering habitat availability, at the sites they inhabit. (H3) Apparent competition, mediated by shared specialized larval parasitoids (Holt & Bonsall, 2017), increases larval mortality, consequently reducing population size. Second, we aimed to test hypotheses that could explain the differences in the abundance of Cleopatra between the mainland and the surrounding islands. In this case, we tested Hypotheses H2 and H3 to explain mainland-island differences in the population size of Cleopatra.

We calculated and compared the population densities of the two species in different biogeographic and climate regions (including two islands in the Balearic archipelago and multiple sites on the mainland) and tested the predictive ability of abiotic and biotic factors (including resource availability and temperature as a driver of dispersion) to explain spatial variation in species abundances, considering separately post-overwintering and pre-overwintering adults. We also analysed the importance of natural enemies (i.e. larval parasitoids) through indirect interactions. Testing apparent competition in natural systems requires long-term studies that track both hosts and parasitoid species over time and space, which is inherently difficult (Holt & Bonsall, 2017). However, we used two approaches to test for potential apparent competition. First, we collected 4 years of data on parasitoid complexes and their impact on butterfly mortality on both the mainland and islands. Second, we tested whether density dependence was higher when these two species coexisted as a possible sign of apparent competition. Finally, we discuss which hypotheses best account for the variation in relative abundance of both species in the mainland and Cleopatra across biogeographic regions.

2 | MATERIALS AND METHODS

2.1 | Study system

We analysed the coexistence of Brimstone and Cleopatra in a Mediterranean area of ca 36,900 km², in which butterfly populations have been systematically monitored for more than two decades within the framework of a citizen science project (www.catal anbms.org). The study area encompasses two biogeographic regions (islands: Mallorca and Menorca – Balearic archipelago; mainland: Catalonia and Andorra-NE Iberian Peninsula) and three distinct climate regions: Mediterranean xeric, Mediterranean mesic and alpine-subalpine (Figure 1). These climate regions were established using a threshold of 21GDD (number of hours per year in which a temperature of 21°C was exceeded): (1) alpine-subalpine (0–150 GDD), (2) mesic (150–400 GDD) and (3) xeric (≥400 GDD).

The Brimstone is widely distributed in North Africa and Europe and extends eastwards into Siberia and Mongolia. In its southern distribution (e.g. Maghreb and the Iberian Peninsula), their presence tends to be restricted to upland and/or humid areas. In our study area, it is found only sporadically in the xeric region and is completely absent from the Balearic Islands. In contrast, Cleopatra is mainly found in the Mediterranean Basin, where it is common in the mesic and xeric regions, including the Balearic Islands and, as



FIGURE 1 Mean annual relative abundance of the two study species, Brimstone (yellow circles) and Cleopatra (red circles), calculated using all available data from 1994 to 2021. Orange circles indicate the coexistence of the two species. The maps show the different climate regions represented by different colours.

a previous study has shown, flies in very high population densities on Menorca Island (Colom et al., 2019). Although the two species have different climatic niches (Settele et al., 2008), in our study area they often co-occur in the Mediterranean mesic zone, where they are among the commonest butterfly species. Both species occur in a wide range of habitats (Figure S1) but depend on woodland for overwintering.

The Brimstone and Cleopatra are very closely related phylogenetically (Dapporto et al., 2022) and have similar phenologies and hostplant use (Vila et al., 2018). They overwinter in the adult stage and behave as essentially univoltine species. Mating occurs soon after the adult butterflies come out of hibernation in early spring (henceforth overwintered adults or OW adults). Oviposition is concentrated in the spring, and eggs are laid individually on the underside of the most tender leaves of the host plants. In the NE Iberian Peninsula, they both use *Rhamnus alaternus* as their main larval resource, which does not seem to be a limiting factor for their populations, as it is frequent and abundant in Mediterranean habitats. In the alpine region, where *R. alaternus* does not occur, the main host plants of Brimstone are *R. frangula* and *R. alpina*. In general, the adults of the annual generation of both species emerge in June–July (henceforth, summer adults or SU adults), although their flight periods vary depending on the climate region (Figure 2a,b).

Cleopatra and Brimstone potentially share solitary hymenopteran larval parasitoids specific to their *Gonepteryx* genus: *Hyposoter rhodocerae* (Ichneumonidae: Campopleginae), *Cotesia gonopterygis* and *C. risilis* (Braconidae: Microgastrinae) (Jubany & Stefanescu, 2009; Shaw, 2009). They are also attacked by other more



FIGURE 2 Adult phenology and relative abundance across climate and biogeographic regions. (a) Cleopatra and (b) Brimstone flight curves estimated by GAM models using count data from 2019, 2020 and 2021 to illustrate the adult phenology in each climate region. The relative abundances of each flight curve are standardized to add up to 1. Pannels (c-f) show abundance comparisons between biogeographic and climate regions: overwintered adults of (c) Cleopatra and (d) Brimstone; summer adults of (e) Cleopatra and (f) Brimstone. Abundance estimates were standardized by transect length and log-transformed to reach normality.

generalist hymenopteran parasitoids, including egg (*Trichogramma cordubensis*: Trichogrammanidae; CS unpublished data) and pupal (*Pteromalus apum*: Pteromalidae; Shaw et al., 2009) parasitoids.

Both butterfly species are highly dispersive, and several studies have provided evidence of seasonal migration between habitats (Pollard & Hall, 1980), including altitudinal migration (Gutiérrez & Wilson, 2014; Jubany & Stefanescu, 2009).

2.2 | Abundance data

We used data from 205 sites obtained since 1994 through a citizen science recording scheme (Figure 1). Adult butterfly counts were obtained annually through 30 weekly samplings, from the 1st March to the 26th September. These samples were conducted along 5-m-wide fixed transects, following a standardized method (Pollard & Yates, 1993). To estimate annual abundances, only male counts were used because they are much more easily identified than females at the species level in the field. For each species-climate-region-year combination, we fitted flight curves using generalized additive models (GAMs) following the approach of Schmucki et al. (2016). The GAMs fit bimodal curves that represent the postoverwintering and pre-overwintering flight periods of each species in each year and climate region (Figure 2a,b). This allowed us to estimate, separately, the total abundance of overwintering and summer adults in each population for each year by running distinct models for winter-spring and summer abundance. Annual abundance estimates were standardized by dividing them by the transect length and then log-transformed to ensure normalization. For all statistical models, except for the density dependence models (see below), the response variable was the mean standardized abundance for 2019-2021, as this is the period that maximizes the number of available

island sites and for which resource availability and larval parasitism were measured.

2.3 | Resource availability variables

Field data on habitat structure and host plant availability were collected at 84 random sites of the butterfly monitoring network between 2019 and 2021 (Figure S2). At each of these sites, we then calculated the percentage cover of all types of forest communities as an estimate of habitat availability for overwintering adults (henceforth overwintering habitat availability or OHA). The coverage of host plants (i.e. m² of *Rhamnus* sp.) along the 5-m-wide butterfly transect was calculated for the whole transect and standardized to a common area of 1000 m² (henceforth host plant availability or HPA).

2.4 | Temperature data

We extracted daily maximum temperature data at 0.1 degree resolution (ca. 11km in latitude) from the Copernicus Climate Change Service (Cornes et al., 2018) from 2019 to 2021 for the 84 sites where resource availability was also measured. For each site and year, the average maximum temperatures in spring (March-May) and summer (June-August) were calculated, as they determine larval development and adult thermoregulation, and thus may influence the distribution of butterfly abundance over space (Gutiérrez & Wilson, 2014).

2.5 | Larval parasitism

We studied larval parasitism at several sites in Mallorca, Menorca and the mainland (Catalonia) to test the potential apparent competition between coexisting populations of Cleopatra and Brimstone on the mainland. From late March to early June over a period of 4 years (Menorca: 2019; Mallorca: 2019-2022; mainland: 2021-2022), we collected larvae from 14 sites (Mallorca: 6 sites; Menorca: 4 sites; mainland: 4 sites). Larvae were reared indoors using transparent plastic containers $(155 \times 105 \times 45 \text{ mm})$ in groups of up to five individuals from the same sample. We recorded the larval instar for each collected individual. When a caterpillar was killed by a Cotesia parasitoid, we waited for the cocoon of the parasitoid to be fully formed and hardened before isolating it in a corked glass tube (80 mL). When Hyposoter rhodocerae kills the host, it spins its cocoon within the host's larval skin, after which we isolated its structure in a corked glass tube. After emergence, the adult parasitoids were preserved in pure ethanol. All parasitoids were identified by MRS.

Species identification of butterfly larvae from the mainland killed by *Cotesia* parasitoids was carried out by means of DNA sequencing following standard protocols (deWaard et al., 2008; Hebert et al., 2013; Ivanova et al., 2006) at the Centre for Biodiversity Genomics, University of Guelph, Canada. All new sequences are deposited in BOLD, which are publicly available at dx.doi. org/10.5883/DS-GONCOLOM.

2.6 | Statistical analyses

2.6.1 | Abundance variation across biogeographic and climate regions

lournal of <u>Biogeogr</u>aphy

To investigate the variation in relative abundance between different climate and biogeographic regions, we analysed data from 185 sites (Mallorca: 10; Menorca: 9; mainland xeric: 15; mainland mesic: 123; and mainland alpine-subalpine: 28) with available data from 2019 to 2021. We used generalized linear models (GLMs) with a Gaussian distribution and zero-inflation parameter (Brooks, Kristensen, & Van Benthem, 2017). We performed four models in which the response variable was the mean annual abundance of each flight period (overwintering and summer adults) for each species (Brimstone and Cleopatra). The independent variable was a categorical factor of four levels (Mallorca, Menorca, mainland xeric and mainland mesic) for the models of Cleopatra and two levels (mainland mesic and mainland alpine-subalpine) for the models of Brimstone. We focused on differences in the relative abundance of (i) Brimstone between mainland climate regions, and (ii) the relative abundance of Cleopatra between the islands and the mainland (considering the different mainland climate regions).

2.6.2 | Environmental determinants of relative abundance

To test the climate-driven dispersive behaviour (H1) and resource availability (H2) hypotheses, we analysed the effects of spring and summer average maximum temperatures, overwintering habitat (i.e. forest cover) and host plant availability (i.e. Rhamnus sp. cover) on the abundance of each species-flight period-climate region combination. We expected that the differences in relative abundance between mainland climate regions would increase in summer when adults would disperse to cooler areas (H1). Summer adult abundance would be higher in the cooler than in the warmer region of their mainland distribution (i.e. Cleopatra: xeric < mesic; Brimstone: mesic < alpine-subalpine). We also expected that within mainland climate regions, abundance would be higher at sites with higher resource availability (H2). Similarly, differences in resource availability between biogeographic regions would explain differences in relative abundance between mainland and island Cleopatra populations. To test H1 and H2, we used data from the 84 random sites where resource availability was assessed. Predictor variables were rescaled to values ranging from 0 to 1 to ensure consistent scaling and prevent certain predictors from dominating the model. Because the data were extremely unbalanced to zero, GLMs were performed with a Tweedie distribution that best fitted the models (Brooks, Kristensen, van Bentham, et al., 2017). To compare resource

-WILEY-

-WILEY- Journal of Biogeography

availability between biogeographic (Mallorca, Menorca and mainland) and climate regions (xeric, mesic and alpine-subalpine), Tukey's multiple-comparison tests were used.

2.6.3 | Apparent competition analyses

To test the apparent competition hypothesis (H3), we used two approaches. First, to explain the variation in the abundance of both species across mainland climate regions, we tested for differences in density dependence among populations. A recent study has shown that density dependence in our study region plays an important role in the population dynamics of most butterfly species including the Brimstone and Cleopatra (Ubach et al., 2022). Density dependence is likely related to the impact of natural enemies, particularly parasitoids, which have been shown to be a major cause of mortality (e.g. Shaw et al., 2009; Stefanescu et al., 2022). Under apparent competition, we expected that the interannual population growth of one species would depend not only on its own abundance in the previous year but also on the abundance of the other species. To test this hypothesis, we used mainland sites with data from at least 10 consecutive years in which both species coexisted (i.e. the Mediterranean mesic region; Figure 1; n = 41). For each species *i*, the response variable of the models was the interannual population growth calculated as the difference between the log-transformed abundance in the current year (t) and in the previous year (t-1). The predictors of the models were (a) the abundance of the species i in t-1; (b) the abundance of the species *j* in *t*-1; and (c) the sum of the abundance of the species *i* and *j* in *t*-1. As predictor *c* was highly correlated with predictors a and b, it was included in a model as the only predictor. For each species, generalized linear mixed models (GLMMs) were carried out with all the combinations of the predictors and we then selected the best model based on AIC. For all the models, a Gaussian distribution including a zero-inflation parameter was used, with site controlled as a random effect.

The second approach was used to explain abundance variation between island and mainland Cleopatra's populations. Specifically, we performed unpaired t-tests to compare parasitism rates between Menorca and Mallorca in 2019 and Mallorca and Catalonia in 2021 and 2022. We expected larval parasitism rates to be higher on mainland populations than on the islands due to apparent competition between mainland populations of both coexisting species.

All analyses were carried out using R v. 4.2.1 (R Core Team, 2020) and the following packages: *climateExtract* to extract and manipulate ECAD climate data (Schmucki, 2022), *rbms* to fit the flight curves (Schmucki et al., 2022), *fitdistrplus* to find the statistical distribution that best fitted the data (Delignette-Muller & Dutang, 2015), *glmmTMB* to conduct GLMs and GLMMs (Brooks, Kristensen, van Bentham, et al., 2017), *DHARMa* to evaluate the goodness-of-fit of the models (Hartig, 2017), and *MuMIn* (Barton, 2020) for model comparison.

3 | RESULTS

3.1 | Abundance variation across biogeographic and climate regions

Overwintered adults of both species had similar relative abundance values throughout the study area regardless of biogeography or climate (Figure 2c,d). By contrast, we found significant differences between regions for summer adults (Cleopatra: F=5.4, p=0.002, $R^2=0.11$; Brimstone: t=3.59, p<0.001, $R^2=0.08$). In summer, Cleopatra was approximately 2.6 times more abundant in Menorca (0.52 ± 0.36) than in both Mallorca (0.2 ± 0.18) and the two mainland climate regions. Within the mainland, Cleopatra's summer adults were approximately 3.1 times more abundant in the mesic (0.28 ± 0.22) than in the xeric region (0.09 ± 0.08) (Figure 2e). Brimstone was approximately two times more abundant in the alpine-subalpine (0.18 ± 0.18) than in the mesic region (0.09 ± 0.1) (Figure 2f). All test statistic parameters and results are shown in Tables S1 and S2.

3.2 | Environmental determinants of relative abundance

The importance of each of the different environmental factors in predicting butterfly abundance depended on the climate region and the flight period (Table 1). Resource availability had a positive effect on the abundance of Cleopatra in the mesic region (OW adults: β HPA=0.14±0.06, β OHA=1.73±0.87; SU adults: β HPA=0.15±0.06, β OHA=1.74±0.76), while the maximum temperature constrained its abundance in the xeric region; nevertheless, this was only significant for the overwintered adults (OW adults: $\beta = -0.55 \pm 0.23$, Z = -2.41, p = 0.02; SU adults: $\beta = 0.08 \pm 0.35$, Z=0.22, p=0.82). Similarly, the abundance of Brimstone adults was constrained by the maximum temperature in the mesic region (OW adults: $\beta = -0.28 \pm 0.09$, Z = -3.15, p = 0.01; SU adults: -0.26 ± 0.12 , Z = -2.12, p = 0.03). For Brimstone, unlike Cleopatra, resource availability was found to be important only in relation to overwintering habitat, as host plant availability had no significant effect on abundance in any flight period-climate region combination. A higher abundance of Brimstone overwintered adults occurred at sites with greater forest cover in both regions (mesic: $\beta = 2.29 \pm 0.94$, Z=2.43, p=0.02; alpine-subalpine: $\beta=1.28\pm0.58$, Z=1.99, p=0.04). In the alpine-subalpine region, overwintering habitat availability also positively influenced the abundance of summer adult Brimstones $(\beta = 1.81 \pm 0.88, Z = 2.06, p = 0.03)$, while temperature had a slight but significant positive effect on summer adults ($\beta = 0.17 \pm 0.04$, Z = 3.97, p = 0.01).

The two biotic factors, host plant and overwintering habitat availability, were well represented throughout the biogeographic and climate regions (Figure 3a,b), with no significant differences TABLE 1 Results of the GLMs testing the effect of the environmental predictors on the relative abundances of each species in each flight period and climate region. Test statistics for the best-fit models based on the AIC are shown: Coefficient estimate, standard error, z-value (z), p-value (p), sample size (n), degrees of freedom (d.f.) and dispersion parameter (d.p.). Predictors that had statistical significance (p < 0.05) in the best-fit models are indicated in bold.

			Fixed effects								
Data subset			Max. temperature		НРА		ОНА				
Species	Flight	Region	Coef [SD]	Z (p)	Coef [SD]	Z (p)	Coef [SD]	Z (p)	n	df	dp
Cleopatra	WO	Xeric	-0.55 [0.23]	-2.41 (0.02)	_	_	_	_	21	17	1.28
		Mesic	-	-	0.14 [0.06]	2.27 (0.02)	1.73 [0.87]	1.98 (0.04)	43	38	0.91
	SU	Xeric	0.08 [0.35]	0.22 (0.82)	-	-	-	-	21	17	2.08
		Mesic	-	-	0.15 [0.06]	2.55 (0.01)	1.74 [0.76]	2.29 (0.02)	43	38	0.93
Brimstone	OW	Mesic	-0.28 [0.09]	-3.15 (0.01)	-	-	2.29 [0.94]	2.43 (0.02)	43	38	1.01
		Alpine	-	-	0.32 [0.2]	1.56 (0.12)	1.28 [0.58]	1.99 (0.04)	19	14	0.27
	SU	Mesic	-0.26 [0.12]	-2.12 (0.03)	-	-	1.66 [1.2]	1.36 (0.17)	43	38	0.89
		Alpine	0.17 [0.04]	3.97 (0.01)	-	-	1.81 [0.88]	2.06 (0.03)	19	14	0.35



FIGURE 3 Resource availability variables across climate and biogeographic regions. Comparison of the environmental variables between biogeographic and climate regions: (a) overwintering habitat availability. Total percentage (0–1) of cover of woodland habitats along the butterfly transects. (b) Host plant availability (*Rhamnus* sp. cover) standardized per 1000m of transect length. All test statistic results are shown in Tables S1 and S1.

between regions (OHA: F=0.74, p=0.57, $R^2=0.04$; HPA: F=2.05, p=0.1, $R^2=0.1$). However, host plants were scarce in the alpine–subalpine sites. See Table S3 for full information regarding GLM models and Table S4 for results of Tukey's multiple-comparison tests.

3.3 | Larval parasitism

Journal of Biogeogra<u>phy</u>

During the study, we collected 949 larvae from Menorca, Mallorca and Catalonia (including sites in the xeric and mesic climate regions): 103 larvae from Menorca in 2019, 412 from Mallorca (2019: 152; 2020: 122; 2021: 110; 2022: 28) and 434 from mainland Catalonia (2021: 144; 2022: 290). However, 35% of the larvae died during rearing for unknown reasons and were excluded from the calculations of parasitism rates. Parasitism was an important source of mortality in *Gonepteryx* larvae (Figure 4). On the islands, the percentage of larvae killed by parasitoids ranged from 15% to 45% in Mallorca, and was 28% in Menorca in 2019. In Catalonia, a total of 9% of larvae died from parasitism in both 2021 and 2022.

Interestingly, different parasitoid species occurred on the mainland and the islands (Figure 4a). At mainland sites, two species known to be specialist parasitoids of the genus Gonepteryx (Shaw et al., 2009), the braconid and the ichneumonid wasps Cotesia gonopterygis and Hyposoter rhodocerae, respectively, were recorded. All adults of C. gonopterygis emerged from G. rhamni larvae (n = 12), most of them from the sample taken from the coolest sampled site on the mainland, while only two individuals were recorded from the warmest site (Figure 4a). We could not identify the hosts of H. rhodocerae to species level (because it is formed within the host's larval skin) but they were found at all except the coolest site, including a site where no larvae of G. rhamni was found (Sant Quintí, Figure 4b). Surprisingly, Cotesia risilis, a fairly common specialist parasitoid of Gonepteryx species in the study area (Jubany & Stefanescu, 2009), did not appear at any site. On the islands, Cleopatra was only attacked by an endemic parasitoid, which we described as Cotesia balearica (Shaw & Colom, 2023).

Parasitism was concentrated in larvae collected in the first three larval instars (Figure S4) and all parasitoids generally killed the larvae in the third instar. Parasitism rates were greater in Mallorca than in Catalonia in 2022 (mean diff. = -0.132 ± 0.049 , t=2.72, p=0.035, df=6), but no statistical difference was found between Mallorca



FIGURE 4 Larval parasitism in *Gonepteryx* species. (a) Comparison of local parasitism rates (site level) between regions in the same year. *p*-values of unpaired *t*-tests comparing parasitism rates are provided. Statistic results are shown in Table S5. (b) Bipartite plot showing quantitative associations between *Gonepteryx* larvae and its parasitoids in different study sites. Gonepteryx larvae were collected for a given side (lower nodes) and associated parasitoids (upper nodes). The width of the bottom nodes is proportionate to the number that developed into adults (brown, purple and green for mainland, Menorca and Mellorca, respectively) and the number parasitized (red). The width of the upper nodes is proportional to the abundance of a given species in a sample (i.e. the number of larvae that were parasitized).

and Catalonia in 2021 (mean diff. = 0.003 ± 0.111 , t=0.03, p=0.977, df=4) and between Menorca and Mallorca in 2019 (mean diff. = -0.115 ± 0.094 , t=1.22, p=0.261, df=7) (Figure 4c; Table S5).

3.4 | Density dependence

Both the density of the same species and the sum of the densities of *Gonepteryx* sp. had significantly negative effects on the interannual population growth of Brimstone and Cleopatra (Table S6). Interannual population growth was best predicted by the density of the same species in t-1 than by the sum of the densities of the two species (Cleopatra: dAIC=41; Brimstone: dAIC=118.9). Models only including the interspecific density effect also had a significant effect but of lower magnitude (Cleopatra: -0.5 vs. -0.07; Brimstone: -0.62 vs. -0.06) and had the highest AIC values (Cleopatra: dAIC=88.7; Brimstone: dAIC=132.8).

4 | DISCUSSION

Observational and experimental studies have shown that insect populations fluctuate strongly over space according to differences in environmental conditions, resource availability and biotic interactions (Speight et al., 1999). In this study, we used a system of two cogeneric butterfly species sharing many ecological traits to test three different hypotheses explaining the influence of (H1) seasonal dispersal movements mediated by climate, (H2) resource availability and (H3) apparent competition mediated by shared specialized parasitoids on (i) regional variation in a mainland area and, for one of the species, (ii) island-mainland differences in abundance. Below, we discuss the observed patterns in our focal system with the aim of providing insight into the complex and interrelated factors that influence insect population dynamics in Mediterranean ecosystems.

4.1 | Climate-driven dispersal behaviour

Climate is a major factor that determines species distribution by shaping the physical environment, including temperature, precipitation and other environmental variables. These factors can directly or indirectly affect the physiology, behaviour and survival of organisms, causing significant spatiotemporal fluctuations in species abundance. In our study, we specifically examined the hypothesis (H1) that population abundance differences among climate regions change seasonally within a year due to the movement of individuals seeking more suitable climatic conditions. Our findings suggest that temperature plays a crucial role in driving such fluctuations at regional scales in the populations of two mobile insect species through seasonal dispersal movements.

While no differences were found in the abundance of overwintered populations between climate regions, summer populations of both species were more abundant in the cooler climate region of their mainland distribution (Figure 2e,f). This result seems to indicate that higher temperatures increase the rates of adult dispersal from warmer to cooler sites, as temperature had a negative effect on the abundance of overwintered populations in the warmer regions (xeric for Cleopatra and mesic for Brimstone) and a positive effect on the abundance of summer adults in the cooler regions (at least for Brimstone in the alpine-subalpine region) (Table 1). Moreover, the fact that host plant abundance was minimal at the alpine-subalpine study sites (Figure 3b) supports the idea that butterflies present at these sites in summer came from other areas. Our results also suggest that the differences between cold and warm sites are likely to increase with future global warming, potentially causing long-term shifts in the range margin of their distributions.

If we consider that temperature can explain the dispersal of individuals of our two study species, we could think that resource availability is interacting with climate. Temperature affects the distribution, quality, timing and duration of trophic resources, including host plants and flowers. In Mediterranean regions, temperature can negatively affect the availability and quality of these resources, leading to butterflies dispersing to cooler regions, where resources are more abundant and of higher quality. However, Gutiérrez and Wilson (2014) found no support for the resource availability hypothesis as an explanation for the summer altitudinal migration of Brimstone in central Spain. Therefore, temperature may play a direct role in driving the dispersal of butterflies by affecting their metabolism and physiology. Cooler temperatures can slow down metabolic processes of insects, reducing energy consumption and potentially extending their lifespans (Karl & Fischer, 2009; Karlsson & Wiklund, 2005). In the same way, lower temperatures can enhance the persistence of host plants in ideal conditions for larval development (Kuczyk et al., 2021; Stefanescu et al., 2022). Overall, these factors will increase reproductive success and, hence, population size, explaining the observed higher population abundance in the cooler regions of our studied species.

An alternative explanation for the seasonal differences in abundance between climatic regions could be an increase in aestivation propensity among adult butterflies in response to higher temperatures, as observed in other butterfly species (Birch & Gottschalk, 2021; Scali, 1971). Nevertheless, the substantial concentrations of both Brimstone and Cleopatra butterflies regularly observed at high altitudes during the summer (Gutiérrez & Wilson, 2014; Jubany & Stefanescu, 2009), even in open habitats where hibernation is not possible, strongly support the hypothesis of seasonal dispersal movements (including altitudinal migration).

Our results also suggest that in small, flat Mediterranean islands, such as Menorca (area: 695.7 km²; highest elevation: 385 m), Cleopatra may exhibit resilience to warm and dry climate conditions, even when adults cannot locate cooler habitats for summer dispersal (but see Colom et al., 2021). In contrast, Brimstone may not tolerate these conditions as effectively. Indeed, unlike Cleopatra, which is found in most of the islands of the Western Mediterranean where the host plant is present, Brimstone is limited to a few larger and mountainous Mediterranean islands.

4.2 | Resource availability

Our second evaluated hypothesis (H2) posits that resource availability explains spatial variation in relative abundance. The availability of nectar and host plants is known to play an important role in shaping the spatial heterogeneity of butterfly abundance (Yamamoto et al., 2007). Although both are important, host plant availability is generally considered to have a stronger effect than nectar plant availability on butterfly abundance (Curtis et al., 2015). This is particularly true for species with narrow diet breadths, such as Brimstone and Cleopatra. In addition to trophic resources, the availability of suitable overwintering habitats can also be a critical factor for species that undergo annual movements, such as those studied here. Loss of forest habitat in overwintering areas of *Danaus plexippus* in Mexico, for instance, has been identified as a major factor Journal of <u>Biog</u>eography

explaining population decline (Brower et al., 2012). Similarly, host plant and overwintering habitat availability significantly influenced the abundance of overwintered and summer Cleopatra adults, suggesting that both larval trophic resources and overwintering habitats are important. However, a positive effect of resource availability on abundance was found in the mesic region but not in the xeric region. This suggests that while temperature is the main factor explaining abundance in the warmer sites, resource availability may be the limiting factor in the cooler sites for Cleopatra. Therefore, the importance of resource availability in Cleopatra's abundance seems to be mediated by regional climate conditions.

Differences in overwintering habitat and host plant cover are unlikely to be large between the mainland and the islands and between the two islands, at least at the study sites (Figure 3a,b) and, therefore, the high densities of Cleopatra in Menorca do not appear to be due to increased resource abundance or overwintering habitat on this island. Nevertheless, our data set is restricted to the transect level and data on host plants and overwintering habitat over wider areas may be needed to establish whether or not differences in summer populations between Menorca and the other regions are attributable to differences in these environmental variables at larger scales. Menorca may have been less affected by land use changes, urbanization and the loss of habitat heterogeneity over the past two decades than either Mallorca or the mainland given that it has been a Biosphere Reserve since 1993. In spite of the high mobility of Cleopatra adults, capable of reaching suitable distant habitats and food resources, landscape structure may still play a role and enhance in Menorca the connectivity between resources and their exploitation and, consequently, maintain larger butterfly populations.

In contrast to Cleopatra, Brimstones at cooler sites were more limited by overwintering habitat than by host plant availability. Indeed, host plant availability in the alpine–subalpine sites was minimal, suggesting that although brimstone adults may benefit from the environmental conditions of this region in summer for reproduction (as discussed earlier), egg laying may concentrate in warmer areas with sunny exposed sites (McKay, 1991). It is possible, therefore, that Brimstones move from warmer to cooler sites in summer but then return to warmer areas in the autumn for breeding the following spring, as suggested to occur along an altitudinal gradient in Central Spain (Gutiérrez & Wilson, 2014).

4.3 | Variation in parasitism pressure and apparent competition

Our results do not support the hypothesis (H3) which posits that indirect interactions mediated by shared specialized parasitoids (i.e. apparent competition) between Brimstone and Cleopatra on the mainland lead to lower abundances than on the islands where only Cleopatra is present, ruling out the possibility of suffering apparent competition. This is because, firstly, compared to the mainland regions, Cleopatra populations were more abundant in Menorca but not in Mallorca. Secondly, because parasitism rates were not higher WILEY Journal of Biogeography

on the mainland than on the island sites. However, it should be noted that parasitism rates were underestimated because egg and pupal parasitoids, which could represent significant sources of mortality and population regulation, were not examined in this study. Focusing on larval parasitoids, only one parasitoid species was found on the islands, which caused mortality rates similar to or even greater than those induced by the two parasitoid species combined on the mainland (Figure 4a). The endemic Cotesia balearica was found at all island sites and was found to have a great capacity to parasitize Cleopatras in a wide range of habitats and environmental conditions (Figure 4b). On the other hand, our data suggest that the two parasitoids found on the mainland have a low niche overlap as they only co-occurred in one of the four sampled sites (Figure 4b). Specialist parasitoids tend to vary their use of temporal and spatial resources to facilitate coexistence (Hood et al., 2021); therefore, more natural enemies on the mainland do not necessarily imply higher levels of butterfly larval mortality. The low niche overlap between the two parasitoids on the mainland can be explained by climate, habitat and/or host preferences, differences that may have originated as a result of competitive exclusion. Our findings suggest that Cotesia gonopterygis occurs at colder sites and Hyposoter rhodocerae at warmer sites, although H. rhodocerae is known to be a common parasitoid of Brimstone in colder regions such as the United Kingdom (MRS pers. obs.). The fact that all C. gonopterygis individuals emerged from Brimstone larvae suggests that it specializes in this species; yet, *H. rhodocerae* was found at a site where there were no Brimstone larvae, which suggests that it can use both Brimstone and Cleopatra larvae as hosts. However, apparent competition between Brimstone and Cleopatra populations seems unlikely if we take into account the fact that larval coexistence was unexpectedly low despite the high adult overlap (Figure S3). While Brimstone adults were common at three of the four sampled mainland sites, larvae of this species were only well represented at the coolest sites. Therefore, our results indicate that there is great segregation in the breeding areas of both Brimstone and Cleopatra, which limits the possibility of indirect effects. This suggests that these two closely related species have differentiated their climatic niches more than might be expected from the spatial distribution of adults and that this could be the result of an evolutionary process promoting coexistence (Duyck et al., 2006). Moreover, an indirect approach using density dependence models also failed to support the apparent competition hypothesis (Table S6).

5 | CONCLUSIONS

Our findings show that both climate and resource availability shape regional and local spatiotemporal variations in the abundance of our studied butterflies. Temperature drives seasonal movements from hotter to cooler regions, which could help avoid the direct negative effects of high summer temperatures on the metabolism and physiology of adults. On the other hand, host plant and overwintering habitat availability are key to explaining differences between sites in the same climate region. However, differences in resource availability are unlikely to explain abundance differences between biogeographic regions. Interestingly, although larval parasitism was found to be a notable source of mortality, it does not seem to explain the island-mainland differences in abundance. Our results suggest that evolutionary processes have driven both segregation of the breeding areas of the two coexisting butterfly species and segregation of the niche of the different larval parasitoids on the mainland. These processes would prevent apparent competition between species sharing specialized natural enemies, such as Brimstone and Cleopatra, thereby promoting their partial coexistence at regional scales.

ACKNOWLEDGEMENTS

We express our sincere gratitude to all the CBMS volunteers for their valuable contributions in collecting butterfly data. We would also like to thank the Observatori Socioambiental de Menorca, S'Albufera des Grau Natural Park and the Agencia Reserva de la Biosfera de Menorca for their support with recording stations in Menorca. We extend our gratitude to Direcció General d'Espais Naturals i Biodiversitat of the Government of the Balearic Islands and the Direcció General de Polítiques Ambientals i Medi Natural for granting us the essential permissions required for our fieldwork (permission references: CAP082023; 62020MP). Special thanks to Andreu Ubach and Ferran Páramo for management of the CBMS data, Roger Vila for his help with the DNA analyses, Jordi Corbera for his help with the larval sampling and Clàudia Pla-Narbona for creating Figure 1. The CBMS is funded by the Departament d'Acció Climàtica, Alimentació i Agenda Rural de la Generalitat de Catalunya, the Diputació de Barcelona and the Andorran Government (via BMSAnd project). P.C. is funded by a PhD fellowship financed by the Govern de les Illes Balears (grant no. FPI-CAIB-2018) within the DEPICT research project (grant no. PID2020-114324GB-C2) funded by the Spanish MCIU Ministry to A.T.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the Catalan Butterfly Monitoring Scheme. Restrictions apply to the availability of these data, which were used under licence for this study. Data are available from the author(s) with the permission of the Catalan Butterfly Monitoring Scheme.

ORCID

P. Colom D https://orcid.org/0000-0003-0309-8886 C. Stefanescu D https://orcid.org/0000-0001-8952-7869

REFERENCES

Barton, K. (2020). MuMIn: multi-model inference. R package version 1.43.17.

- Birch, R. J., & Gottschalk, T. K. (2021). Aestivation as a response to climate change: The great banded Grayling Brintesia circe in Central Europe. *Ecological Entomology*, 46(6), 1342–1352.
- Brooks, M., Kristensen, K., van Bentham, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). Package 'glmmTMB' R topics documented: The R Journal (Vol. 9).
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). Modeling zero-inflated count data with glmmTMB. BioRxiv. https:// doi.org/10.1101/132753
- Brower, L. P., Taylor, O. R., Williams, E. H., Slayback, D. A., Zubieta, R. R., & Ramírez, M. I. (2012). Decline of monarch butterflies overwintering in Mexico: Is the migratory phenomenon at risk? *Insect Conservation and Diversity*, 5(2), 95–100. https://doi.org/10.1111/j. 1752-4598.2011.00142.x
- Chapman, R. F. (1998). The insects: structure and function. Cambridge University Press.
- 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. https://doi.org/10.1007/s1053 1-019-01764-1
- Colom, P., Traveset, A., Carreras, D., & Stefanescu, C. (2021). Spatiotemporal responses of butterflies to global warming on a Mediterranean Island over two decades. *Ecological Entomology*, 46(2), 262–272. https://doi.org/10.1111/een.12958
- Cornes, R. C., van der Schrier, G., van den Besselaar, E. J. M., & Jones, P. D. (2018). An ensemble version of the E-OBS temperature and precipitation data sets. *Journal of Geophysical Research: Atmospheres*, 123(17), 9391–9409. https://doi.org/10.1029/ 2017JD028200
- Curtis, R. J., Brereton, T. M., Dennis, R. L. H., Carbone, C., & Isaac, N. J. B. (2015). Butterfly abundance is determined by food availability and is mediated by species traits. *Journal of Applied Ecology*, 52(6), 1676–1684. https://doi.org/10.1111/1365-2664.12523
- Dapporto, L., Menchetti, M., Vodă, R., Corbella, C., Cuvelier, S., Djemadi, I., Gascoigne-Pees, M., Hinojosa, J. C., Lam, N. T., Serracanta, M., Talavera, G., & Vila, R. (2022). The atlas of mitochondrial genetic diversity for Western Palaearctic butterflies. *Global Ecology and Biogeography*, 31, 2184–2190. https://doi.org/10.1111/geb.13579
- Delignette-Muller, M. L., & Dutang, C. (2015). Fitdistrplus: An R package for fitting distributions. *Journal of Statistical Software*, 64(4), 1–34. https://doi.org/10.18637/jss.v064.i04
- deWaard, J. R., Ivanova, N. V., & Hebert, P. D. N. (2008). Assembling DNA barcodes: Analytical protocols. In M. Cristofre (Ed.), Methods in molecular biology: environmental genetics. Humana Press https://medium.com/@arifwicaksanaa/pengertian-use-case-a7e576e1b6bf
- Duyck, P. F., David, P., & Quilici, S. (2006). Climatic niche partitioning following successive invasions by fruit flies in La Réunion. *Journal* of Animal Ecology, 75(2), 518–526. https://doi.org/10.1111/j.1365-2656.2006.01072.x
- Gutiérrez, D., & Wilson, R. J. (2014). Climate conditions and resource availability drive return elevational migrations in a single-brooded insect. *Oecologia*, 175(3), 861–873. https://doi.org/10.1007/s0044 2-014-2952-4
- Hartig, F. (2017). Package 'DHARMa.' R package.
- Hebert, P. D., DeWaard, J. R., Zakharov, E. V., Prosser, S. W. J., Sones, J. E., McKeown, J. T. A., Mantle, B., & La Salle, J. (2013). A DNA "barcode blitz": Rapid digitization and sequencing of a natural history collection. *PLoS One*, 8(7), e68535. https://doi.org/10.1371/journ al.pone.0068535
- Holt, R. D., & Bonsall, M. B. (2017). Apparent competition. Annual Review of Ecology, Evolution, and Systematics, 48, 447–471. https://doi.org/ 10.1146/annurev-ecolsys-110316-022628
- Hood, G. R., Blankinship, D., Doellman, M. M., & Feder, J. L. (2021). Temporal resource partitioning mitigates interspecific competition

and promotes coexistence among insect parasites. *Biological Reviews*, 96(5), 1969–1988. https://doi.org/10.1111/brv.12735

Ivanova, N. V., Dewaard, J. R., & Hebert, P. D. N. (2006). An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes*, 6(4), 998–1002. https://doi.org/10.1111/j. 1471-8286.2006.01428.x

rnal of geography

- Jubany, J., & Stefanescu, C. (2009). Gonepteryx rhamni i G. cleopatra, un toc de groc que marca el final de l'hivern. *Cynthia, Butlletí Del Butterfly Monitoring Scheme a Catalunya, 8,* 18–22.
- Karl, I., & Fischer, K. (2009). Altitudinal and environmental variation in lifespan in the copper butterfly Lycaena tityrus. *Functional Ecology*, 23(6), 1132–1138. https://doi.org/10.1111/j.1365-2435.2009.01607.x
- Karlsson, B., & Wiklund, C. (2005). Butterfly life history and temperature adaptations; dry open habitats select for increased fecundity and longevity. *Journal of Animal Ecology*, 74(1), 99–104. https://doi.org/ 10.1111/j.1365-2656.2004.00902.x
- Kuczyk, J., Raharivololoniaina, A., & Fischer, K. (2021). Populationspecific responses of an insect herbivore to variation in host-plant quality. *Ecology and Evolution*, 11(24), 17963–17972. https://doi. org/10.1002/ece3.8392
- McKay, H. V. (1991). Egg-laying requirements of woodland butterflies; brimstones (Gonepteryx rhamni) and Alder buckthorn (Frangula alnus). Journal of Applied Ecology, 28(2), 731–743.
- Pollard, E., & Hall, M. L. (1980). Possible movement of *Gonepteryx rhamni* (L.) (Lepidoptera: Pieridae) between hibernating and breeding areas. *Entomologist's Gazette*, 31, 217–220.
- Pollard, E., & Yates, T. J. (1993). Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme. Springer Science & Business Media.
- R Core Team. (2020). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
- Scali, V. (1971). Imaginal diapause and gonadal maturation of Maniola jurtina (Lepidoptera: Satyridae) from Tuscany. *The Journal of Animal Ecology*, 40, 467–472.
- Schmucki, R., Harrower, C. A., & Dennis, E. B. (2022). rbms: Computing generalised abundance indices for butterfly monitoring count data. R package version 1.1.3. https://github.com/RetoSchmucki/rbms
- Schmucki, R. (2022). climateExtract: Extract and manipulate daily gridded observational dataset of European climate (E-OBS) provided by ECA&D. R package version 1.25. https://github.com/RetoSchmuc ki/climateExtract
- Schmucki, R., Pe'er, G., Roy, D. B., Stefanescu, C., van Swaay, C. A. M., Oliver, T. H., Kuussaari, M., van Strien, A. J., Ries, L., Settele, J., Musche, M., Carnicer, J., Schweiger, O., Brereton, T. M., Harpke, A., Heliölä, J., Kühn, E., & Julliard, R. (2016). A regionally informed abundance index for supporting integrative analyses across butterfly monitoring schemes. *Journal of Applied Ecology*, *53*(2), 501–510. https://doi.org/10.1111/1365-2664.12561
- Settele, J., Kudrna, O., Harpke, A., Kühn, I., & van Swaay, C. (2008). Climatic risk atlas of European butterflies. *Biodiversity and Ecosystem Risk Assessment*, 1. http://books.google.hu/books?id= emxFAQAAIAAJ, 1-712.
- Shaw, M. R. (2009). Cotesia Cameron (Hymenoptera: Braconidae: Microgastrinae) parasitoids of Heliconiinae (Lepidoptera: Nymphalidae) in Europe, with description of three new species. British Journal of Entomology and Natural History, 22, 133–146.
- Shaw, M. R., & Colom, P. (2023). Notes on the three species of Cotesia Cameron, 1891 (Hymenoptera: Braconidae, Microgastrinae) parasitizing Gonepteryx [leach, 1815] species (Lepidoptera: Pieridae) in Europe, with description of a new species from the Balearic Islands. Entomologist's Gazette, 73(8), 253–260. https://doi.org/10.31184/ G00138894.734.1872
- Shaw, M. R., Stefanescu, C., & van Nouhuys, S. (2009). Parasitoids of European butterflies. In T. Josef Settele, M. K. Shreeve, & H. van Dyck (Eds.), *Ecology of butterflies in Europe* (pp. 130–156). Cambridge University Press.

509

-WILEN

-WILEY-

510

Speight, M. R., Hunter, M. D., & Watt, A. D. (1999). Ecology of insects. Concepts and applications.

Journal of

- Stefanescu, C., Colom, P., Barea-Azcón, J. M., Horsfield, D., Komac, B., Miralles, A., Shaw, M. R., Ubach, A., & Gutiérrez, D. (2022). Larval parasitism in a specialist herbivore is explained by phenological synchrony and host plant availability. *Journal of Animal Ecology*, 91(5), 1010–1023. https://doi.org/10.1111/1365-2656.13689
- Ubach, A., Páramo, F., Prohom, M., & Stefanescu, C. (2022). Weather and butterfly responses: A framework for understanding population dynamics in terms of species' life-cycles and extreme climatic events. *Oecologia*, 199(2), 427–439. https://doi.org/10.1007/s0044 2-022-05188-7
- Vila, R., Stefanescu, C., & Sesma, J. M. (2018). Guia de les papallones diürnes de Catalunya (Lynx Edici). Barcelona.
- Yamamoto, N., Yokoyama, J., & Kawata, M. (2007). Relative resource abundance explains butterfly biodiversity in Island communities. Proceedings of the National Academy of Sciences of the United States of America, 104(25), 10524–10529. https://doi.org/10.1073/pnas. 0701583104

BIOSKETCHES

Pau Colom is a community and population ecologist interested in insect demography, phenology and trophic interactions. This paper is part of his PhD at the Mediterranean Institute of Advanced Studies (CSIC-UIB), focusing on butterfly ecology in the context of global change and with an island perspective.

Anna Traveset is a research Professor at the Mediterranean Institute of Advanced Studies (CSIC-UIB) where she leads the laboratory of Terrestrial Ecology. She is interested in the ecology and evolution of species interactions, and in the impact of global change on them. Mark R. Shaw is a Honorary Research Associate at the National Museums Scotland. He is a taxonomist working on a large group, Ichneumonoidea, of western Palaearctic parasitoid wasps with a particular interest in their biology and host associations.

Constanti Stefanescu is researcher at the Natural Sciences Museum of Granollers, where he coordinates the Catalan Butterfly Monitoring Scheme. He is interested in butterfly ecology, including population dynamics, parasitism and migration.

Author Contributions: Pau Colom and Constanti Stefanescu conceived the ideas and designed the methodology; Pau Colom and Constanti Stefanescu collected the data; Mark R. Shaw identified the parasitoids; Pau Colom analysed the data; Pau Colom and Constanti Stefanescu wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Colom, P., Traveset, A., Shaw, M. R., & Stefanescu, C. (2024). Factors shaping the abundance of two butterflies sharing resources and enemies across a biogeographic region. *Journal of Biogeography*, *51*, 499–510. https://doi.org/10.1111/jbi.14764