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Aridity could have driven the local extinction of a common and multivoltine butterfly

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Abstract

1. Identifying which species are being negatively impacted by climate change and the mechanisms driving their decline is essential to effectively protect biodiversity.
2. *Coenonympha pamphilus* is a common and generalist butterfly, widely distributed throughout the Western Palearctic, being multivoltine in southern Europe. Previous studies indicate that it will not be substantially affected by climate change; however, it has seemingly disappeared from the southeast of the Iberian Peninsula in the last decades.
3. Here, we aim to determine if it has effectively disappeared from this area, as well as identify the environmental conditions limiting its distribution and the potential causes behind this a priori local extinction.
4. We downloaded all the occurrence records of *C. pamphilus* and analysed their spatial and temporal trends. To identify the climatic variables driving the distribution of this butterfly in the Iberian Peninsula, we performed an ensemble species distribution model (SDM), combining 600 individual models produced with 6 algorithms.
5. We confirmed that *C. pamphilus* has not been observed in the southeast of the Iberian Peninsula since 2008. Aridity was the main factor limiting the distribution of *C. pamphilus* in our ensemble SDM, with areas with high aridity being unsuitable for this species.
6. We hypothesise that multivoltinism is the mechanism driving this local extirpation, as high aridity is causing host plants (*Poaceae*) to wither prematurely, precluding the development of the second and/or third generations of the butterfly. Even though generalist species are theoretically more resilient to climate change, other traits such as multivoltinism may increase their vulnerability and need to be further investigated.

Abstract

1. Para proteger eficazmente la biodiversidad es esencial identificar qué especies están siendo afectadas negativamente por el cambio climático y los mecanismos que impulsan su declive.

2. *Coenonympha pamphilus*, es una mariposa diurna común y generalista, ampliamente distribuida por el Paleártico occidental, siendo polivoltina en el sur de Europa. Estudios previos indican que no se verá sustancialmente afectada por el cambio climático. Sin embargo, parece haber desaparecido del sureste de la Península Ibérica.
3. Aquí, pretendemos determinar si efectivamente ha desaparecido de esta zona, así como identificar las condiciones ambientales que limitan su distribución y las posibles causas que están detrás de esta a priori extinción local.
4. Descargamos todos los registros de presencia de *C. pamphilus* y analizamos sus tendencias espaciales y temporales. Para identificar las variables climáticas que impulsan la distribución de esta mariposa en la Península Ibérica, realizamos un modelo de distribución de especies (SDM), combinando 600 modelos individuales producidos con 6 algoritmos.
5. Confirmamos que *C. pamphilus* no se ha observado en el sureste de la Península Ibérica desde 2008. La aridez fue el principal factor que limitó su distribución en nuestro SDM, siendo las zonas con alta aridez poco adecuadas para esta especie.
6. Nuestra hipótesis es que el polivoltinismo es el mecanismo que impulsa esta extinción local, ya que la elevada aridez está provocando el agostamiento prematuro de las plantas hospedadoras (*Poaceae*), impidiendo el desarrollo de la segunda y/o tercera generación de la mariposa. Aunque las especies generalistas son teóricamente más resistentes al cambio climático, otros rasgos como el polivoltinismo pueden aumentar su vulnerabilidad y deben ser investigados más a fondo.

KEYWORDS
bioindicator, citizen science, climatic change, *Coenonympha pamphilus*, species distribution model, Voltinism

INTRODUCTION

Biodiversity is currently undergoing a human-induced extinction crisis comparable to previous mass extinctions (Ceballos et al., 2015; Dirzo et al., 2014; Pievani, 2014). Among the main drivers of loss, climate change has already impacted biodiversity from individual genotypes to whole ecosystems (IPBES, 2019; Scheffers et al., 2016). This has resulted in species extinctions, local extirpations and changes in distribution, phenology and morphology (Bellard et al., 2012; Parmesan & Yohe, 2003; Thomas et al., 2004).

Arthropods constitute half of the current animal biomass (Bar-On et al., 2018), of which insects are the most diverse and cosmopolitan group, with more than 1 million species and an estimated 80% yet to be described (Chapman, 2009). Insects play an essential role in maintaining trophic networks and ecosystems (Losey & Vaughan, 2006; Vanbergen & Insect Pollinators Initiative, 2013), and are also considered good climate change bioindicators due to their ectothermy, short generation times and because some species show a narrow resource dependency (McGeoch, 1998; Markert et al., 2003; Markert, 2007). Among insect bioindicators, butterflies stand out as the best known and most studied group (McGeoch, 1998; Thomas, 2005; Hill et al., 2021), monitored in many places around the world following the BMS framework (Butterfly Monitoring System; Pollard & Yates, 1994), with multiple studies reporting insect responses to the effects of climate change (Hill et al., 2021; Parmesan et al., 1999; Rödder et al., 2021). The genus *Coenonympha* Hubner, 1819 (Nymphalidae, Satyrinae) constitutes a relatively diverse Holarctic group, with around 30 species in the Palearctic and 2 in the Nearctic (Bozano, 2002; García-Barros et al., 2013; but also see Wiemers et al., 2018, 2020 who propose a total of 20 Palearctic species with 18 in Europe). In the Iberian Peninsula, there are currently 4 species: *Coenonympha dorus* (Esper, 1782), *Coenonympha arcania* (Linnaeus, 1760), *Coenonympha glycerion* (Borkhaunsen, 1788), and *Coenonympha pamphilus* (Linnaeus, 1758) (Figure 1 and Figure S1). All four species are currently classified as of Least Concern by the International Union for Conservation of Nature (IUCN) in Europe, like most Mediterranean butterflies (Numa et al., 2016).

This study is focused on the species *C. pamphilus*, also known as Small Heath (Figure 1). This species is widely distributed in the Palearctic region (Boillat, 2003; García-Barros & Meneguz, 2012). Previously published distribution maps indicated that the species was widely distributed in the Iberian Peninsula and the Balearic Islands (García-Barros et al., 2004; Romo et al., 2003), and it is considered a common species (Cancela et al., 2020; Vila et al., 2018). Initially, it was proposed that areas with no *C. pamphilus* records were due to a lack of information (Romo et al., 2003). However, García-Barros et al., 2004 has suggested that the species has become spatially scarcer in areas of Mediterranean influence, and Montagud and García-Alamá

FIGURE 1 Photographs of specimens of *Coenonympha pamphilus* (Linnaeus, 1758). Author of the photographs: José Manuel Sesma Moranas. Photographs hosted in www.biodiversidadvirtual.org. Note the absence of conspicuous ocelli on the ventral side of the hindwing of the species, which distinguishes it from other Iberian *Coenonympha* species.

(2010) indicate that populations of the Valencian Community, in eastern Spain, are very dispersed and localised.

C. pamphilus is considered a generalist grassland species, with a multivoltine biology in Southern Europe, having two (bivoltine) or three (trivoltine) generations per year depending on the area and a wide variety of larval host plants of the *Poaceae* family. Bivoltine cycles are more common in mountainous areas, while trivoltine cycles are characteristic of warmer areas. The first annual generation occurs in April or May, the second in July or August, and the third in September or October (Vila et al., 2018). In Northern Europe, in areas of high latitude and altitude, *C. pamphilus* is univoltine. Its preferred habitat is pasture meadows (Vila et al., 2018), with grass species such as *Festuca rubra* L., *Poa annua* L., *Poa pratensis* L., *Anthoxanthum odoratum* L., *Brachypodium phoenicoides* (L.) Roem. & Schult., *Cynosurus cristatus* L. or *Dactylis glomerata* L. that serve as larval host plants (García-Barros et al., 2013; Vila et al., 2018). This nymphalid also exhibits very territorial behaviour, forming leks (García-Barros et al., 2013; Wickman & Rutowski, 1999).

Technological advances, such as digital photography, the Internet and social media have greatly facilitated the generation and dissemination of georeferenced species occurrence data (Newman et al., 2011; Nov et al., 2014). Data derived from the collaboration between citizen and academic science, hosted in free databases, such as GBIF (Global Biodiversity Information Facility; www.gbif.org), has helped advance our knowledge in key areas, such as species distributions (Goula et al., 2013; Jiménez-Valverde et al., 2019; Sardón-Gutiérrez et al., 2021; Shirey et al., 2019), or invasive species (Comont & Ashbrook, 2017; Sesma & Gil-Tapetado, 2020), and facilitated the identification of threatened species.

The main objective of this study is to analyse the distribution patterns of *C. pamphilus* in the Iberian Peninsula, using the available records to model the climatically suitable or potentially habitable areas and identify the climatic variables and processes that could be limiting its distribution. In addition, we evaluate the importance of *C. pamphilus* records obtained from citizen science globally and in the Iberian Peninsula and their relevance in monitoring this species in the

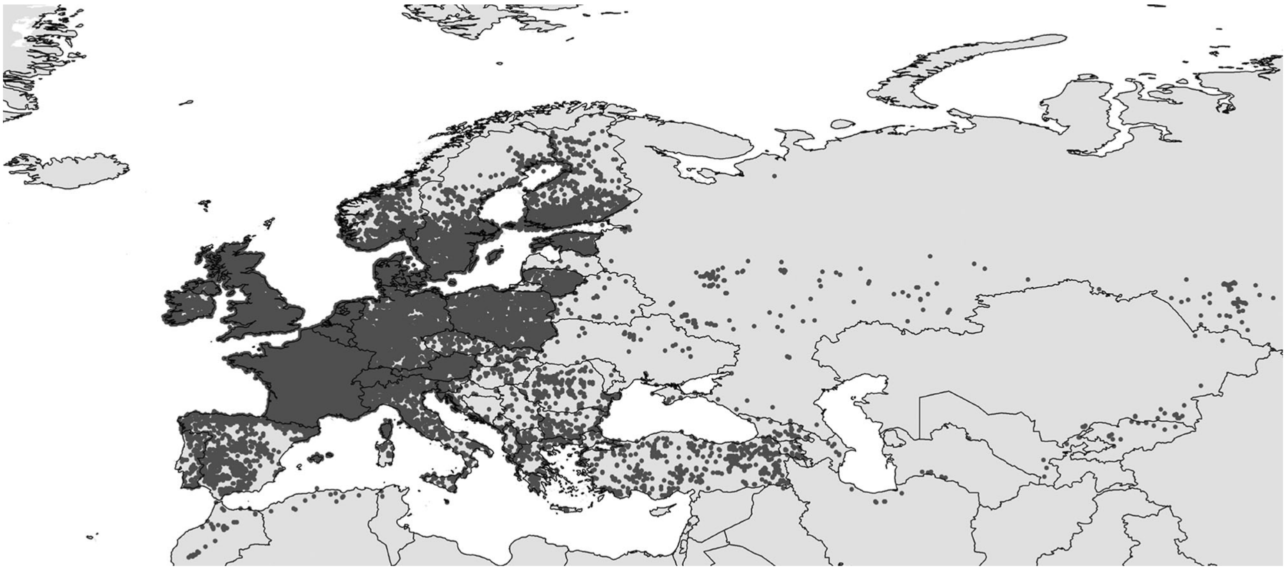

FIGURE 2 Total records of *Coenonympha pamphilus* (Linnaeus, 1758) in GBIF (Global Biodiversity Information Facility; www.gbif.org) from 1665 to 2020.

last decade (2010–2020) as an example of butterfly monitoring using citizen science.

MATERIALS AND METHODS

Selection of *C. pamphilus* records

We downloaded all the records of *C. pamphilus* stored in the Global Biodiversity Facility (GBIF) with complete coordinates, data type and origin (GBIF.org, GBIF, 2021a; 669,852 records). We further filtered these data, eliminating duplicates and records with georeferencing errors, retaining 88,557 global records. We considered two study areas: the global (restricted to the Western Palearctic) and the Iberian distributions of *C. pamphilus*; and three different periods: from 1665 to 2020 and from 2010 to 2020 for both areas, and from 1665 to 2009 for the Iberian Peninsula. We analysed the data source and the total number of records per year for the GBIF global records and the 4019 Iberian records between 1665 and 2020. All global records were homogenised to one presence per 10 × 10 km grid cell. All Iberian records were homogenised to one presence per 1 × 1 km grid cell (1963 records) and 10 × 10 km grid cell. Due to the special high redundancy of the occurrence coordinates, distribution data prior to 1970 have been subsequently re-observed (especially in the last decade, see Figure 2b).

We represented the historical (1665–2009) and current (2010–2020) distribution of *C. pamphilus* in the Iberian Peninsula at a 10 × 10 km resolution. Historical data came from the maps by García-Barros et al. (2004), Romo et al. (2003) and Montagud and García-Alamá (2010) (specific to the Valencian Community, east of the Iberian Peninsula), alongside GBIF records between 1665 and 2009. We considered the period between 2010 and 2020 as representative of the current distribution of *C. pamphilus* because citizen science platforms experienced a substantial activity increase in Spain during this period. We classified cells into those with the most records in the historical distribution and those with the most records in the current distribution.

To estimate sampling effort in each province in Spain, we downloaded and filtered all Papilionoidea records from the *Biodiversidad Virtual* platform—the biggest local biodiversity citizen science platform—between 2010 and 2018 (116,525 records), also stored in GBIF. We calculated the number of records, richness, inventory completeness, and species accumulation curve slopes in each province. We considered a rational curve and a cut-off value of 0.1 for the slope of the accumulation curve. These analyses were performed using the package KnowBr (Lobo et al., 2018) in the software RWizard 4.3 (Guisande et al., 2014) in the R v 3.5.0 (R Development Core Team, 2015) programming environment.

To further ensure that there were no sampling biases, we compared the distribution of *C. pamphilus* with that of *C. dorus*. *C. dorus* is similar in appearance to *C. pamphilus* (Figure S1), differentiated by a curved, proximally convex row of ocelli on the underside of the hindwing following the curve of the wing (García-Barros et al., 2013). Unlike *C. pamphilus*, *C. dorus* only has one generation per year, from May to July or August, depending on the altitude (Vila et al., 2018). Both species share genera of host plants (*Festuca*, *Cynosurus*, *Poa*, or *Brachypodium*; Montagud & García-Alamá, 2010), thus making *C. dorus* an ideal species to compare with *C. pamphilus*. We downloaded and filtered all GBIF records for *C. dorus* in the Iberian Peninsula between 2010 and 2020 (GBIF.org, 2021b; 1044 records) and homogenised them to one presence per 10 × 10 km grid cell (652 cells). We represented and analysed the distribution of both species between 2010 and 2020 on a 10 × 10 km grid map.

TABLE 1 Summary of all WorldClim bioclimatic variables, altitude and aridity index for all occurrences of *Coenonympha pamphilus* (Linnaeus, 1758) in the Western Palearctic hosted in GBIF (Global Biodiversity Information Facility; www.gbif.org) between 1665 and 2020.

Variable	Abbr.	Mean	SD	Maximum	Minimum
Altitude	Alt	321.28	437.77	3242.00	−10.00
Annual Mean Temperature	bio1	8.67	2.97	18.85	−6.29
Mean Diurnal Range	bio2	8.08	1.50	14.61	3.29
Isothermality	bio3	32.86	4.96	48.12	15.92
Temperature Seasonality	bio4	627.90	142.05	1413.89	233.47
Max Temperature of Warmest Month	bio5	22.50	3.50	39.05	6.15
Min Temperature of Coldest Month	bio6	−2.44	4.29	9.31	−23.89
Temperature Annual Range	bio7	24.94	4.77	51.25	9.79
Mean Temperature of Wettest Quarter	bio8	10.58	5.04	21.82	−7.55
Mean Temperature of Driest Quarter	bio9	7.03	7.80	28.92	−17.78
Mean Temperature of Warmest Quarter	bio10	16.56	2.75	29.37	2.28
Mean Temperature of Coldest Quarter	bio11	1.24	4.07	12.94	−18.64
Annual Precipitation	bio12	835.87	331.92	3344.00	102.00
Precipitation of Wettest Month	bio13	98.14	39.82	406.00	14.00
Precipitation of Driest Month	bio14	43.94	19.99	140.00	0.00
Precipitation Seasonality	bio15	25.90	11.23	101.92	4.85
Precipitation of Wettest Quarter	bio16	274.24	114.70	1158.00	39.00
Precipitation of Driest Quarter	bio17	147.42	62.52	474.00	4.00
Precipitation of Warmest Quarter	bio18	207.63	78.88	605.00	5.00
Precipitation of Coldest Quarter	bio19	208.84	114.63	1056.00	19.00
Aridity Index	aI	9994.95	5406.76	562.00	72462.00

Note: Abbreviation (Abbr.), mean, standard deviation (SD), maximum and minimum values are included. Data marked in red indicate values for areas where individuals of *C. pamphilus* have been observed but which may not be suitable for long-term establishment of the species. Note that low aridity index values indicate high aridity and vice versa.

To determine if host plant distribution is driving changes in the distribution of *C. pamphilus*, we obtained all host plant records in the Iberian Peninsula from the Anthos platform (http://www.anthos.es) and compared their distributions with the past and current distributions of *C. pamphilus*.

Variable selection and species distribution modelling

To identify suitable areas for *C. pamphilus* globally and in the Iberian Peninsula, we downloaded bioclimatic and environmental variables at a 10 × 10 km (10 arcminutes) and 1 × 1 km (30 arcseconds) resolution, respectively. Our variables consisted of the 19 WorldClim 2.1 bioclimatic layers (see Table 1), altitude (Fick & Hijmans, 2017), and aridity index (aI, Trabucco & Zomer, 2018; low values indicate high aridity/low humidity and vice versa). These variables are different from those previously used by Settele et al. (2008), which addressed the distribution modelling of European butterfly species, including *C. pamphilus*. However, in the case of bioclimatic variables, the usual correlation among them is very high, so the useful climatic information used for the models should not be very different. We summarised the mean, standard deviation, maximum and minimum values for each variable for both global and Iberian Peninsula records across the whole time series (1665–2020) and the last decade (2010–2020).

To obtain an estimate of the global distribution of *C. pamphilus*, we performed a simple environmental coverage model, using the maximum and minimum values of each bioclimatic variable and aI (Gil-Tapetado et al., 2018; Lobo et al., 2010). We considered areas that had all their variables within the maximum and minimum values as potentially suitable (i.e., habitable) for the species. Areas with at least one value outside the maximum and minimum range were considered unsuitable (i.e., uninhabitable), restricting the distribution of the species. This allowed the identification of the variables that most limit the distribution of the species.

To determine which climate variables influence *C. pamphilus* distribution in the Iberian Peninsula, we developed species distribution models (SDMs; Elith & Leathwick, 2009), using presences (1963 records) and the 19 WorldClim 2.1 bioclimatic layers and the aI at a 1 × 1 km resolution. To avoid variable correlation, we selected a subset of variables following the methodology employed by Polidori et al. (2021) and Sardón-Gutiérrez et al. (2021). We first performed a hierarchical cluster analysis, resulting in a dissimilarity dendrogram (Dormann et al., 2013). This analysis segregates the variables into clusters, considering the distance between them. We used Ward's clustering method, based on Pearson's correlation matrix (Harrell, 2015). We established 0.3 as the distance threshold for variable selection (i.e., less than 70% correlation). We selected one variable per cluster below the threshold, prioritising: (1) variables that restrict the distribution in the global simple environmental coverage model; (2) variables considered to be important for Papilionoidea (following Schweiger et al., 2014) and (3) derived variables (i.e., prioritising seasonal over annual variables). Variables with unrealistic patterns in the study area, such as mean temperature of the wettest quarter (bio8) and the mean temperature of the driest quarter (bio9) (Fajardo et al., 2014), were discarded. Finally, we calculated the variance inflation factor (VIF; Lin et al., 2011) of the selected variables, discarding those that overestimated the variance and contributed the most redundant information to the model (VIF >5; Miles, 2005).

We developed ensemble SDMs using the following six algorithms: generalised linear model (GLM; McCullagh & Nelder, 1989), generalised additive model (GAM; Hastie & Tibshirani, 1990), artificial neural network (ANN; Ripley, 1996), classification tree analysis (CTA; Breiman et al., 1984), maximum entropy (MaxEnt; Elith et al., 2006) and random forest (RF; Breiman, 2001).

Background and pseudo-absences were generated from a previously calculated simple environmental coverage model for the Iberian Peninsula. Background points were randomly selected in areas that had all variable values within the maximum and minimum range (suitable or habitable areas), while pseudo-absence points were randomly selected in areas with at least one variable value outside of that range (unsuitable or uninhabitable areas) (Gil-Tapetado et al., 2018; Polidori et al., 2021). External model evaluation was performed by dividing presence and pseudo-absences into a training dataset (75%) and a testing dataset (25%) and calculating the area under the curve (AUC) from a Receiver Operating Characteristic (ROC) curve (Jiménez-Valverde, 2012). Each individual model in the training dataset was evaluated following the same procedure, with a dataset subdivision of 85% (training) and 15% (testing). We ran a total of 600 individual models (100 replicates for each of the six algorithms) and kept those with an internal AUC >0.7, considered to be good to excellent performance (Thuiller, 2003). All models that fulfilled this condition were used to calculate the average consensus model and the upper and lower bounds models. To identify high suitability areas for *C. pamphilus*, we calculated and used a cut-off value (=0.70) of the average consensus model. Therefore, areas with a suitability value higher than 0.70 were considered as suitable, while areas with a value lower than 0.70 were considered unsuitable. We performed an ANOVA to test whether the values of the variables that contributed the most to the consensus model were significantly different in areas with high and low suitability.

Variable selection, VIF analysis, habitat suitability models and statistical analysis were performed in the programming environment R v 3.5.0 (R Development Core Team, 2015), using the software RStudio v 1.1.453 (RStudio Team, 2015) and the biomod2 package (Thuiller et al., 2019). Background and pseudo-absence point generation and all maps were done in ArcGIS v 10.4.1 (ESRI, 2015).

RESULTS

Occurrence record selection

Global occurrence records for *C. pamphilus* were distributed throughout Europe (Figure 2), with most of them clustered in central Europe, southern Scandinavia, Great Britain, northern Italy and the western Iberian Peninsula. There were sparse records throughout Eastern Europe, reaching Russia and Kyrgyzstan, central Scandinavia, south of Italy, north of Africa, and east of Spain (Valencian Community).

Most global GBIF records came from monitoring schemes belonging to the BMS (e.g., the United Kingdom BMS provided 44.57% of all records, 298,565, www.ukbms.org) and citizen science platforms, such as Observation (www.observation.org) (GBIF.org, 2021a). This pattern is the same when considering only filtered records, 92% (82,044) of them come from butterfly monitoring and citizen science platforms, while 3% (2675) come from scientific surveys or preserved specimens (Figure 3a). Regarding the number of records per year (Figure 3b), the oldest records date to 1665, increasing slowly during the 20th century and exponentially during the 21st century (dashed black line in Figure 3b). The periods of 1665 to 2014 and 2015 to 2020 roughly have the same number of records (44,278, marked in Figure 3b by a dashed green line). In the Iberian Peninsula, most records came from citizen science platforms (around 70% of all Iberian records, 2806), specifically *Biodiversidad Virtual* (35.38%, 1422 records) and Observation.org (26.5%, 1066 records) (Figure 3c). Iberian citizen science data started to exponentially increase in 2010 (Figure 3b, blue dotted line), following a similar trend to global data. The year 2020 showed a notable decrease in the number of records globally, probably due to the combined effects of the COVID-19 global pandemic and a lag in data upload to GBIF from the data sources.

Iberian occurrence records indicate that *C. pamphilus* has been absent from the Spanish south-eastern area, specifically from the Autonomous Community of Murcia and the province of Almeria throughout the whole time series and from the Valencian Community since at least 2010. The latest records in the latter region date from 2008, in the localities of Sinarcas (39.7322, −1.231) and El Regajo (38.8815, −0.9153) (see Figure 4a). The easternmost records date to 2002 in the locality of Elche (38.2692, −0.6961) (see Figure 4a). Many host plants, such as *P. annua*, *P. pratensis*, *B. phoenicoides* and *D. glomerata* can be found throughout the whole Iberian Peninsula and, specifically, in the Valencian Community. However, species such as *Cynosurus cristatus*, *F. rubra* and *A. odoratum* are missing in this area. None of the host plant species, aside from *D. glomerata*, are present in Murcia and Almeria.

The Papilionoidea sampling effort analysis in the Iberian Peninsula (Figure S2) showed high sampling effort in many Spanish territories. There were around 2000 and 3000 records in each of the following territories: Valencian Community, Almeria and Murcia (southeastern Spain). The observed richness was highest in the northern Iberian subplateau. The inventory completeness in the east and southeast of the Iberian Peninsula was high (>85%), while the slope of the species accumulation curve was low (<0.02), indicating an adequate or high

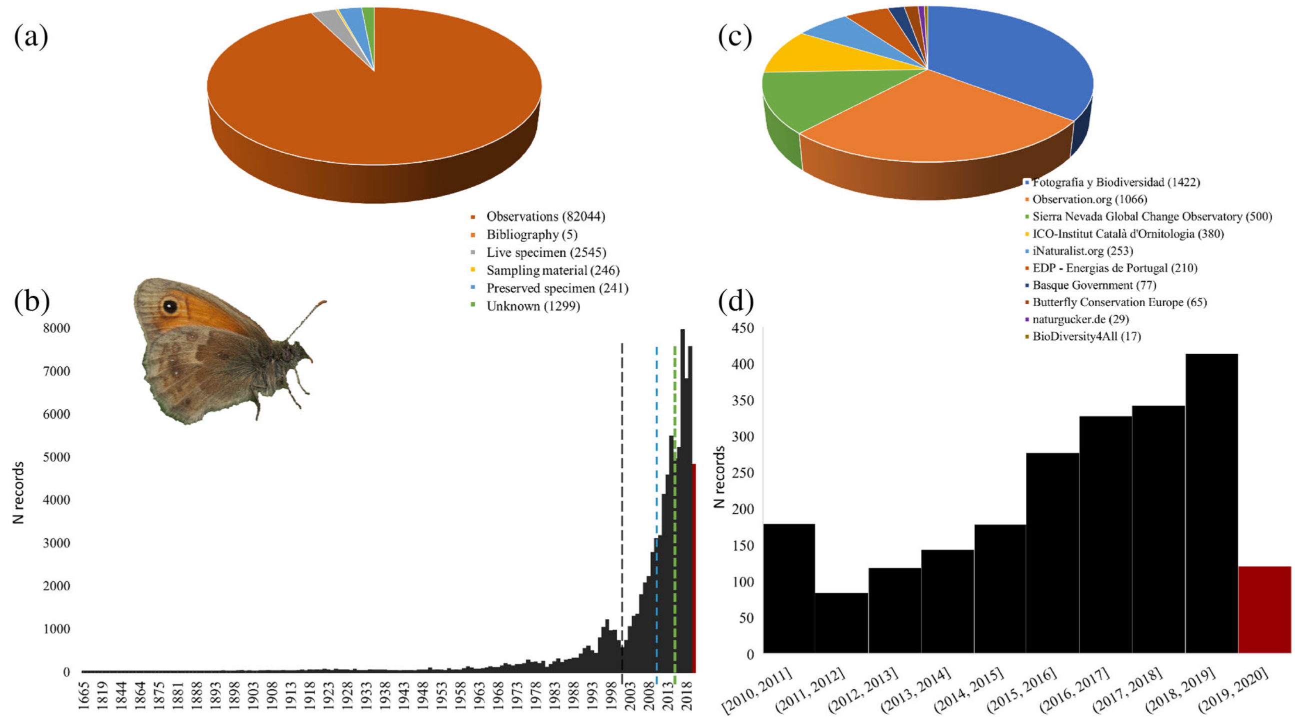

FIGURE 3 (a) Comparison of the records of *Coenonympha pamphilus* (Linnaeus, 1758) in GBIF (Global Biodiversity Information Facility; www.gbif.org) considering the different types of data sources (observation, literature, live specimen, sampling, preserved specimen or unknown). (b) Comparison by year of the number of *C. pamphilus* records in GBIF from 1665 to 2020. The red bar marks the year 2020, an anomalous year, due to the COVID-19 epidemic and possibly not yet updated in GBIF. The black dashed line marks the year 2000, when the rise of citizen science platforms in Europe began, the blue dashed line marks the year 2010, when the rise of citizen science platforms in Spain began, and the green dotted line indicates the year 2015, which marks the half of data accumulation (i.e.,: there are the same number of records in GBIF between 1665–2014 and 2015–2020). (c) Comparison of data sources of *C. pamphilus* records hosted in GBIF (Global Biodiversity Information Facility; www.gbif.org) in the Iberian Peninsula during the period 2010–2020. (d) Comparison by year of the number of *C. pamphilus* records in GBIF from 1665 to 2020. The red bar marks the year 2020 as an anomalous year, as mentioned above.

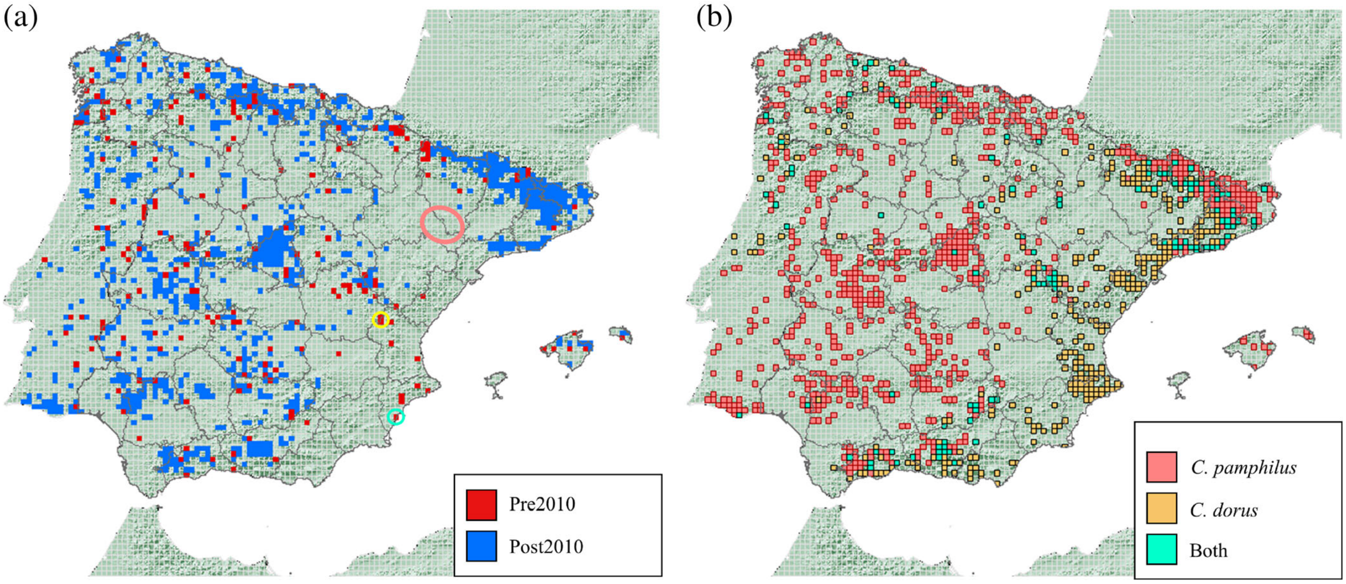

FIGURE 4 (a) Map with 10 × 10 km grid showing the occurrences of *Coenonympha pamphilus* (Linnaeus, 1758) hosted in GBIF (Global Biodiversity Information Facility; www.gbif.org). The red cells are those with most records obtained during the 1665 to 2009 period and the blue ones those with most records obtained during the 2010 to 2020 period. The yellow circle shows the localities of Sinarcas and El Regajo, and the blue circle the locality of Elche. The pink circle shows the approximate area of Los Monegros. (b) Map with 10 × 10 km grid with *C. pamphilus* (red grids) and *Coenonympha dorus* Esper, 1782 (orange grids) occurrences at GBIF from the period 2010 to 2020. Grids with presence of both species are marked in green.

TABLE 2 Summary of all WorldClim bioclimatic variables, altitude and aridity index for all occurrences of *Coenonympha pamphilus* (Linnaeus, 1758) in the Iberian Peninsula hosted in GBIF (Global Biodiversity Information Facility; www.gbif.org) between 1665–2020 and 2010–2020.

	1665–2020				2010–2020			
Variable	**Mean**	**SD**	**Maximum**	**Minimum**	**Mean**	**SD**	**Maximum**	**Minimum**
Altitude	754.22	542.14	2926.00	0.00	768.91	530.25	2926.00	0.00
Annual mean temperature	12.56	3.51	18.42	−0.46	12.37	3.43	18.36	−0.46
Mean diurnal range	10.13	1.89	13.82	3.52	10.12	1.82	13.38	3.52
Isothermality	38.84	3.29	46.38	19.98	38.78	3.23	46.38	19.98
Temperature seasonality	580.29	86.83	750.46	316.75	581.56	83.84	750.07	321.94
Max temperature of warmest month	25.52	4.61	32.70	8.90	25.35	4.45	32.70	8.90
Min temperature of coldest month	−0.50	3.07	7.50	−8.70	−0.68	3.05	7.30	−8.70
Temperature annual range	26.02	4.12	33.70	14.10	26.04	3.97	33.70	15.20
Mean temperature of wettest quarter	9.29	3.74	21.03	−3.15	9.39	3.93	21.08	−3.15
Mean temperature of driest quarter	18.01	6.66	26.05	1.02	17.29	6.97	25.85	1.02
Mean temperature of warmest quarter	20.16	3.87	26.20	6.38	19.98	3.75	26.03	6.38
Mean temperature of coldest quarter	6.13	3.23	12.53	−5.28	5.92	3.19	12.53	−5.28
Annual precipitation	773.98	312.95	1813.00	296.00	778.30	305.71	1834.00	325.00
Precipitation of wettest month	101.03	38.59	271.00	40.00	100.76	37.90	267.00	40.00
Precipitation of driest month	25.61	21.43	81.00	1.00	26.82	21.42	81.00	1.00
Precipitation seasonality	40.42	16.67	77.63	12.93	39.29	16.74	77.07	12.93
Precipitation of wettest quarter	277.17	111.07	742.00	109.00	275.81	108.90	742.00	109.00
Precipitation of driest quarter	99.75	68.98	281.00	14.00	103.29	68.76	281.00	14.00
Precipitation of warmest quarter	110.47	74.56	281.00	21.00	116.07	75.55	281.00	21.00
Precipitation of coldest quarter	241.01	116.06	723.00	72.00	237.52	114.95	742.00	73.00
Aridity index	6100.59	3456.31	1738.00	19002.00	6151.61	3376.13	2110.00	19002.00

Note: Variable names are the same as in Table 1 but only for the Iberian Peninsula (IP). Mean, standard deviation (SD), maximum and minimum values are included. Data marked in red indicate values for areas where individuals of *C. pamphilus* have been observed but which may not be suitable for long-term establishment of the species.. Note that low aridity index values indicate high aridity and vice versa.

sampling effort in this area. *C. pamphilus* and *C. dorus* showed a complementary distribution in the Iberian Peninsula at a 10 × 10 km resolution, sharing territories uniquely in the limits of their distributions (Figure 4b). This also indicates an adequate sampling effort, with records of similar species such as *C. dorus* in cells where *C. pamphilus* is absent.

Variable selection and habitat suitability modelling

The summary of the global (Table 1) and Iberian (Table 2) bioclimatic and environmental variables indicates that *C. pamphilus* is a generalist species, with a priori wide distribution and little bioclimatic restrictions. However, both the aridity index (al) and mean diurnal range (bio2) limit its area of distribution by 7.57% and 6.45% in the Western Palearctic, respectively. *C. pamphilus* is absent in the driest areas of the Western Palearctic (see Figure 2, the southernmost areas), with potentially unsuitable areas in the east of the Iberian Peninsula, especially during the 2010 to 2020 period. Figure S3 shows that Europe is suitable for *C. pamphilus* (including the United Kingdom, Iceland, and Mediterranean islands), except for the previously mentioned areas. Nevertheless, we must acknowledge that some of our data seem unreliable, such as those indicating that the species is present in areas with annual mean temperatures around or below 0°C.

The final set of selected bioclimatic variables for the SDMs in the Iberian Peninsula included isothermality (bio3), temperature annual range (bio7), mean temperature of the coldest quarter (bio11), precipitation of the driest quarter (bio17), and aridity index (al). The variables mean diurnal range (bio2) and precipitation of the wettest quarter (bio16) were not selected as they were collinear with the rest of the variables (Figure S4). However, its effects are represented by the rest of the variables, especially the aridity index, both indicating temperature fluctuations due to the absence of humidity in the atmosphere.

The final consensus SDM showed a high internal validation with a mean AUC of 0.957 (Thuiller, 2003), a mean sensitivity of 88.8% and a mean specificity of 90.57%. The external validation, performed with the remaining 25% of presence and pseudo-absence data, had an AUC of 1, resulting in an optimal species distribution model of *C. pamphilus* in the Iberian Peninsula (Figure S5). The whole peninsula was considered highly suitable (>0.70 cut-off value), except the

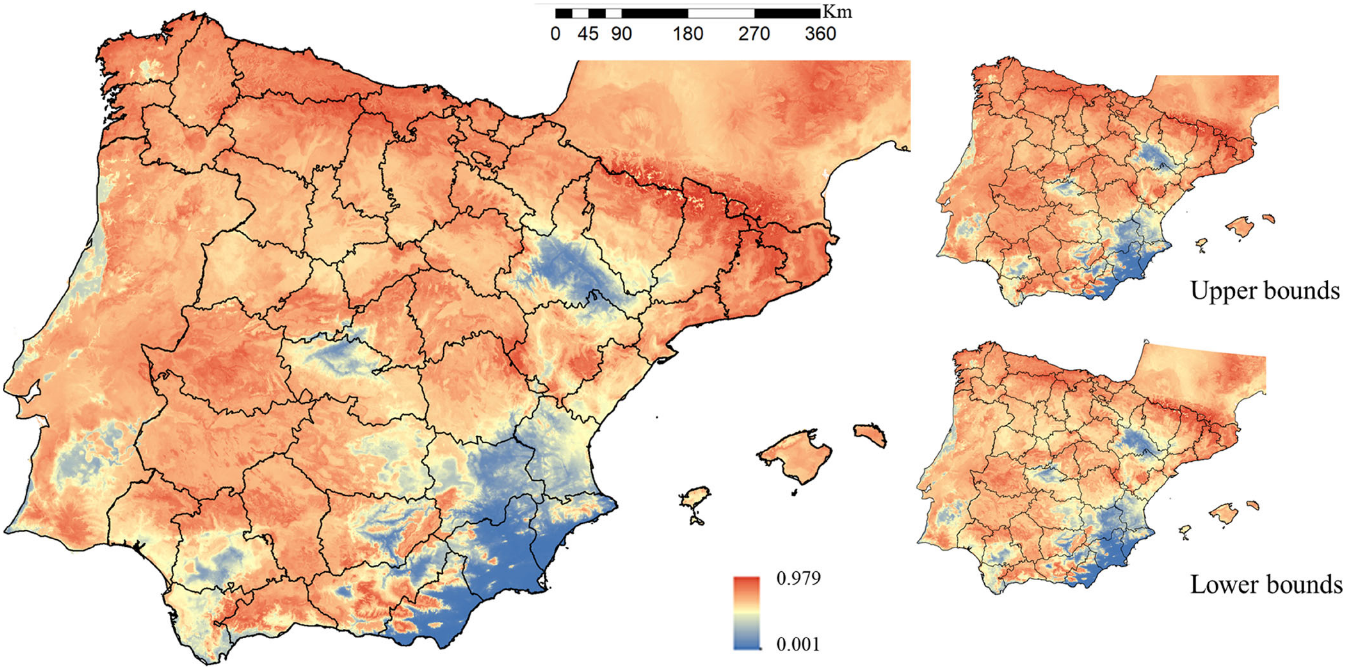

FIGURE 5 Map of the consensus model of habitat suitability for *Coenonympha pamphilus* (Linnaeus, 1758) in the Iberian Peninsula (left). The upper bounds and lower bounds (right), are also included.

TABLE 3 Contribution percentages of the variables used in the distribution models of *Coenonympha pamphilus* (Linnaeus, 1758) in the Iberian Peninsula for each of the six algorithms used (GLM, generalised linear model; GAM, generalised additive model; ANN, artificial neural networks; CTA, classification tree analysis; RF, random Forest; and MaxEnt, maximum entropy).

	Isothermality	Temperature annual range	Mean temperature of coldest quarter	Precipitation of driest quarter	Aridity index
GLM	2.6	0.6	2.6	0.1	95.6
GAM	5.6	26.1	8.2	10.9	48.1
ANN	8.7	7.5	11.2	25.9	82.9
CTA	4.7	18.8	2.1	17.3	54.3
RF	22.2	20.4	28.6	37.2	38.3
MaxEnt	8.3	27.8	20.5	18.2	39.8

Note: Variable names are listed in Table 1.

southeastern and some inland areas (Figure 5). The aridity index was the variable that contributed the most in all 6 algorithms (Table 3). We performed the ANOVA comparing aridity index values of areas with high and low suitability, obtaining significant differences between both areas ($p < 0.00001$), indicating that areas with low suitability have high aridity/low humidity and vice versa (Figure 6).

DISCUSSION

Distribution of *C. pamphilus* in the Iberian Peninsula

Our results indicate that the species *C. pamphilus* is rare, scarce, or absent in the east and southeast of the Iberian Peninsula (Figures 4a and 5), as previously suggested by Montagud and García-Alamá (2010). This local absence contrasts with the previous categorization of this species as common in the Iberian Peninsula (Cancela et al., 2020; *C. pamphilus* was the third most abundant species in Spanish BMS transects in 2019), widely distributed, without threats (García-Barros et al., 2013), and found across most of the Western Palearctic region (Figure 2 and Figure S3). Previous studies affirm that this species does not seem to be negatively affected by anthropic stressors in the east of the Iberian Peninsula (Montagud & García-Alamá, 2010), and that climate change will not substantially change its distribution (Settele et al., 2008). However, we did not find any species records in the area between 2010 and 2020 (Figure 4a). Even if unpublished or inaccessible records existed, *C. pamphilus* would still be rare in these areas, as publicly available data in the rest of the Iberian Peninsula has been exponentially increasing (Figure 3d).

Our results of the sampling effort of Iberian butterflies in the last decade using records from *Biodiversidad Virtual* showed high completeness values in areas with no records of *C. pamphilus*, such as Murcia, Almeria, or Valencian Community (Figure S2). Therefore, absences in the east and southeast of the Iberian Peninsula between 2010 and 2020 seem to be true absences and not a lack of sampling efforts as indicated by Romo et al. (2003). It is possible that the lack of sampling might have had an impact in the province of Toledo (central Iberian Peninsula), an area in which there is not only a low sampling effort (Figure S2) but also high aridity (Figures 5 and 6b).

Therefore, considering the 'previous' distribution of *C. pamphilus* before 2010, with the easternmost records dating to 2002, more than 20 years have passed without a record of *C. pamphilus* in the east and southeast of the Iberian Peninsula. Although we still need 30 more years to confirm that this species has gone locally extinct, our study highlights the need to study this possibility in depth (Mackenzie et al., 2003). We could not obtain confirmation from the BMS of our findings, however, there was only one transect in the east and southeast of the Iberian Peninsula (Alicante, Valencian Community) before 2019 (Cancela et al., 2020), so BMS information on the situation of *C. pamphilus* in this area may be scarce. The Zerynthia Association (www.asociacion-zerynthia.org) has butterfly transects in the Valencian Community, but only the reports of País Vasco were available. The Catalan BMS (https://www.catalanbms.org/), the biggest Iberian butterfly monitoring organisation, does not have data from this area either. We assumed that the data hosted in GBIF (contributed by many users of citizen science platforms) and those from the different BMS schemes in the Iberian Peninsula would not differ notably, and we still consider *C. pamphilus* as a rare or absent species in the Eastern and Southeastern Iberian Peninsula.

Implications of citizen science on species monitoring

Most of our data came from citizen science platforms devoted to the study of nature and biodiversity (Figure 3a, c). These data undoubtedly provides the scientific community with an immense number of records that can be used to study biological and ecological processes, such as changes in species distributions (Abolafya et al., 2013; Champion et al., 2018; Sesma & Gil-Tapetado, 2020). Although the use of Big Data is not risk-free and can accumulate biases and errors (Beck et al., 2014)—as indicated by insect records in areas with a mean temperature under 0°C (Tables 1 and 2)—platforms, such as GBIF are excellent tools within biogeography (Robertson et al., 2014).

Regarding the use of georeferenced photographs from citizen science platforms, even though not all species can be identified visually, many of them can be. For example, if we assume that only 10% of all insect species can be identified visually or in photographs, this percentage would amount to 10,000 visually identifiable species. If this percentage were 1%, it would still be 10,000 species. Applying this 1% to Iberian and Balearic Hexapoda species, roughly 360 of ~36,000 species (Ortuño & Martínez-Pérez, 2011) would be identifiable. Considering that this percentage is, in fact, higher and that most biodiversity records come from easily accessible citizen science platforms, we can affirm that they are a useful tool for the study of biodiversity. In addition, species recorded on these platforms tend to share traits with

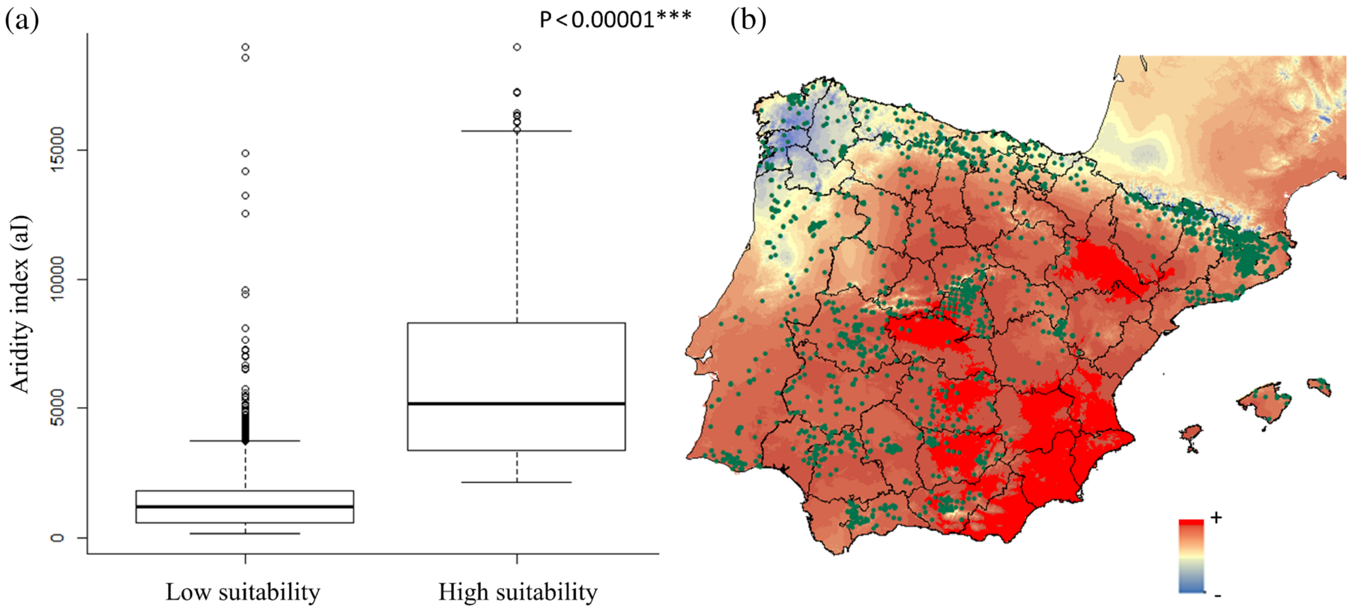

FIGURE 6 Boxplots considering the low and high suitability areas of the model in Figure 5 and the aridity index (aI). There are more areas of low suitability in areas with high aridity (low aI values) and areas of high suitability in areas with low aridity (high aI values). The ANOVA analysis shows significant differences between groups ($F = 1621$, df = 1, $p < 0.00001$***). B) Map showing the occurrence of *Coenonympha pamphilus* (Linnaeus, 1758) in the Iberian Peninsula (green dots) on the aridity index map. The areas with the highest aridity (low aI values) have been marked in red.

bioindicator species, as they are conspicuous, easily recognisable, and abundant (Ribera & Foster, 1997). These records have increased exponentially throughout the years (e.g., 3B and 3D) and may be representative of the species richness of each sampling area (e.g., Figure S2). By combining data from citizen science platforms and standardised monitoring programmes, such as the BMS (Cancela et al., 2020; Pollard & Yates, 1994), we can obtain current species distributions, facilitating the identification of species that are or will become endangered. Here, we have applied this study scheme to *C. pamphilus*, showing that this butterfly is disappearing locally due to the severe effects of climate change.

Implications of aridity on *C. pamphilus*

The habitat suitability model (Figure 5) indicated that the absence of *C. pamphilus* in the east and southeast of the Iberian Peninsula is related to aridity (Table 3 and Figure 6). Climate change has caused an increase in aridity in the east and southeast of the peninsula in the last decades (Andrade & Corte-Real, 2016; Paniagua et al., 2019) and could have driven the disappearance of *C. pamphilus* in this area, contrary to the modelling of Settele et al., 2008. Many different causes or processes could explain the absence of *C. pamphilus* in areas where aridity has increased. Extreme aridity could have made the territory unsuitable for the development of the host plants (Brook et al., 2008; Koh et al., 2004). For example, this could be the case in the Los Monegros desert (centroid: 41.7752, −0.3458) in Zaragoza (Figure 5), one of the most arid areas in the Iberian Peninsula. Another related potential cause is the direct negative effect of low humidity on the larvae, the most vulnerable stage of the species. In the Mediterranean basin and meridional Europe, long-term climatic series and multiproxy studies have demonstrated an unprecedented and significant increase in heat waves and drought impacts over the last several decades (Briffa et al., 2009; Della-Marta et al., 2007; Luterbacher et al., 2004), that would have affected mainly the larvae. However, these hypotheses are not supported because other species, including most host plants of *C. pamphilus* (Figure S6) or *C. dorus*, are present and established in the area (Figure 4b). It could also be that *C. dorus* has displaced *C. pamphilus* in the area, although both species share distribution areas in Catalonia or other western parts of the peninsula, so the disappearance of *C. pamphilus* would not have been caused only by increased aridity or climate change.

Montagud and García-Alamá (2010) suggested that *C. pamphilus* could have a narrower diet breadth in the east of the peninsula (Valencian Community), the absence of certain grass species limiting the distribution of *C. pamphilus* in this area. It could be hypothesised that the Mediterranean subspecies *C. pamphilus lyllus* (García-Barros et al., 2013) has a different or narrower host plant preference compared to *C. pamphilus pamphilus* (distributed in the north of the Iberian Peninsula and Europe), however, the distribution of host plants does not support this suggestion. Most of these plants have a wide distribution throughout the entire Iberian Peninsula (Figure S6), including the east and southeast. As there are no geographic barriers that isolate the east and southeast from the interior of the Iberian Peninsula, it is unlikely that individuals of *C. pamphilus lyllus* in the east and southeast have different biological and dietary preferences than those located in the interior or west. Even if some host species such as *Cynosurus cristatus* and *A. odoratum* are absent in the east and southeast of the peninsula, these plants are present in the interior, where *C. pamphilus lyllus* is highly abundant (Cancela et al., 2020).

A potential cause for the disappearance of *C. pamphilus* in the east and southeast of the peninsula lies in the species' bivoltinism, leading it to an evolutionary trap (Schlaepfer et al., 2002; Van Dyck et al., 2014). In southern Europe, as in the Iberian Peninsula, *C. pamphilus* is bivoltine in warmer areas (e.g., Catalonia, Catalan BMS, 2022 and also southeastern Iberian Peninsula), due to the influence of high temperatures, increasing the number of generations (see Forrest, 2016 on insect phenologies in general and, for example, Kingsolver, 2000 or Van Dyck et al., 2014, for closer and more specific cases, such as the butterfly species *Pieris rapae* (Linnaeus, 1758) or *Lasiommata megera* (Linnaeus, 1767), respectively). Apparently, in the warmer areas of this territory, this butterfly has a faster life cycle and enters into an 'obligate' or 'forced' bivoltinism. Together with rising temperatures, an increase in aridity could be causing host plants to wither in summer, before the development of the second generation of this nymphalid. Consequently, the species would develop its first generation in April or May but would not have available resources for the following generations in July or August and, facultatively, September or October (Vila et al., 2018). *C. pamphilus* has a territorial and sedentary behaviour (Öckinger et al., 2006), hindering the recolonization of areas with high aridity and displacing its populations towards the interior and west of the peninsula, although some studies suggest that climate change could be favouring its dispersal (Cormont et al., 2011). Ultimately, this generalist and multivoltine species likely optimised the speed of its life cycle in areas with high temperatures (Roy et al., 2001) and abundant resources. However, increased aridity in the east and southeast of the peninsula could break the synchronicity between larvae and plants in the following generations, as plants wither prematurely. Probably, populations of *C. dorus* have not been impacted as this species is univoltine, with an adult stage between May and August and larvae that hibernate until the next year, avoiding the effects of host plants withering at the end of the season (Montagud & García-Alamá, 2010). This would corroborate the findings of Melero et al. (2016), who linked multivoltinism to steeper declines in Mediterranean and Spanish populations of butterflies. Warmer temperatures have caused several univoltine or bivoltine European butterfly species to add an extra generation since 1980 (Altermatt, 2010). While an increment in the number of generations can aid population growth, it may not always have a positive effect, as multivoltine species could experience extreme droughts or other adverse conditions during their last generation (Hill et al., 2021; MacGregor et al., 2019; Melero et al., 2016). For this species to escape this evolutionary trap in the southeast of the Iberian Peninsula, *C. pamphilus* would have to be univoltine (as in northern Europe) and that the effect of high temperatures would not accelerate its life cycle, taking advantage only of the favourable spring season with food availability for its caterpillars, like *C. dorus*.

These and other processes must be explored and analysed to determine the direct and indirect effects of aridity on *C. pamphilus*. Increasing aridity and severe drought events are associated with long-term disruptive effects on food webs (Carnicer et al., 2011). Whether large-scale food web disruptions produced by aridity or drought can influence the extinction risk of vulnerable insect species is an open question that warrants further research. In this sense, we recommend conducting multiple samplings or establishing BMS itineraries in the southeast of the Iberian Peninsula, which will also confirm this potential local extirpation. Aridity and the frequency and severity of drought events are increasing throughout the Iberian Peninsula as an effect of climate change (Andrade & Corte-Real, 2016; Carnicer et al., 2011; Paniagua et al., 2019), so the distribution of *C. pamphilus* will contract towards the centre and west of the peninsula, making this butterfly a potential bioindicator of aridity changes. Considering our results, the threat category of this species in the Iberian Peninsula should be revised and potentially considered as vulnerable locally or in Spain. This species could be one more example of what is happening with other currently endangered populations and food webs in the Mediterranean basin and of the complex conservation problems that we will face in the future regarding climatic change.

AUTHOR CONTRIBUTIONS

Diego G. T. and José Manuel S. M. conceived and designed the work; Diego G. T. identified materials, performed the experiments, and analysed the data; Diego G. T., Carmen D. S., Jose F. G., Francisco J. C. S. contributed materials/analysis tools; and Diego G. T., Carmen D. S., Jose F. G., Francisco J. C. S. wrote the paper.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in FigShare at https://doi.org/10.6084/m9.figshare.17290052.v1, reference number 17290052.v1.

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SUPPORTING INFORMATION

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

Figure S1. Photographs of *Coenonympha pamphilus* (Linnaeus, 1758) (left) and *Coenonympha dorus* (Esper, 1782) (right). Photographs authors Jose Manuel Sesma Moranas and Fernando Camuñas.

Figure S2. Number of records, observed richness, completeness, and slope of the estimation of sampling effort (Slope) of the data of butterflies (Lepidoptera, Papilionoidea) in Spain from the *Biodiversidad Virtual* platform (www.biodiversidadvirtual.org).

Figure S3. Areas potentially habitable by *Coenonympha pamphilus* (Linnaeus, 1758) in the Western Palearctic considering (a) all records hosted in GBIF (Global Biodiversity Information Facility; www.gbif.org) from 1665 to 2020 and (b) all records from 2010 to 2020.

Figure S4. Dissimilarity dendrogram used for the selection of variables for the species distribution model for *Coenonympha pamphilus* (Linnaeus, 1758) in the Iberian Peninsula. The red line marks the dissimilarity selection threshold (0.3). The variables selected a priori are those boxed in blue. Variables selected after the VIF analysis (variance inflation factor; VIF <5), are in green and those discarded by correlation, in red. The names of the variables are the same as in Tables 1 and 2.

Figure S5. External evaluation of the suitability model for *Coenonympha pamphilus* (Linnaeus, 1758) in the Iberian Peninsula in Figure 5.

Figure S6. Occurrence points of nutrient plants of *Coenonympha pamphilus* (Linnaeus, 1758) in the Iberian Peninsula. Data and maps from Anthos (http://www.anthos.es).

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