SPECIES ACTION PLAN FOR THE NEVADA GRAYLING

Pseudochazara williamsi

Junta de Andalucía | Consejería de Sostenibilidad y Medio Ambiente

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Butterfly Conservation Europe

European Butterflies Group

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Pseudochazara williamsi

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Consejería de Sostenibilidad y Medio Ambiente (Junta de Andalucía)

Plan de Recuperación y Conservación de Especies de Altas Cumbres de Andalucía

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Preferred citation:

Barea-Azcón, J.M., Olivares, J. Ellis, S., Davies, M., Clarke, H.E. & del Río, J. (2025). Species Action Plan for the Nevada Grayling *Pseudochazara williamsi*. Ministry of Sustainability and the Environment (Junta de Andalucía), European Butterflies Group and Butterfly Conservation Europe. 60 pp.

Design and layout: Manuel Jaime Carretero - manuelcarretero.com
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CONTENTS

PROLOGUE

More than 40 years ago, the first steps were taken toward the conservation of Spanish butterflies. The paradigm of those early studies was similar to today's: to gather as much information as possible about each species in order to design actions as precisely as possible for the efficient conservation of butterflies. We need detailed knowledge of the distribution, biology, and ecology (with special emphasis on population dynamics) of the threatened species for these actions to succeed. To this end, the first distribution maps were created, and knowledge deepened on habitats, immature stages, trophic relationships, and threats to each species. Since those early days, we have made great progress and now have powerful tools to protect our fauna, among which the extraordinary network of Spanish protected areas stands out.

At the beginning of the 21st century, thanks to the sponsorship of the Ministry of the Environment, the Atlases and Red Books of various groups of Spanish fauna were published. These works compiled relevant information on a selection of invertebrate species, marking another milestone in the conservation of our animals.

Years later, the Species Recovery Plans emerged as essential documents to address the conservation of taxa in the most critical situations. Thanks to the efforts of Butterfly Conservation Europe, the Regional Ministry of Andalusia and the MAVA Foundation, in 2015 the first recovery plans for endemic and threatened butterflies were developed. Similarly, in 2019, basic information was gathered, and conservation proposals were drawn up for Spanish lepidopteran species protected under the Habitats Directive. At the same time, during this decade, the first concrete conservation measures were implemented, arising from these initial recovery plans and other initiatives aimed, for example, at the conservation of ant-associated butterflies.

This current study, published ten years after the first recovery plans, also focuses on an endemic and seriously threatened species. As with other mountain species, climate change is particularly affecting this butterfly, which has already disappeared from many localities where it once lived. We hope that the actions proposed in this plan can be carried out soon, and that we can still prevent the extinction of this valuable species of our fauna in time.

Miguel López Munguira
Former Professor of Zoology, Autonomous University of Madrid

PRESENTATION

Europe's butterflies are under ever increasing threat. The recently published European butterfly Red List (Van Swaay *et al*. 2025b) shows that the number of species threatened with extinction has increased by 73% from 37 to 65 since the last assessment (Van Swaay *et al*. 2010). This study also found that over one quarter (28%, 125 species) are now threatened or Near Threatened. The situation is even worse when it comes to endemic species for which Europe has a unique responsibility with over 40% of Europe's endemic butterflies now threatened or close to being so.

The biggest threats to butterflies in Europe now and in the past are habitat loss and degradation. These have been caused by agricultural intensification, wetland drainage, land abandonment and overgrazing from livestock. As a result of these changes, many species are now suffering from the consequences of habitat fragmentation, which greatly increases the chances of local extinction.

However, climate change is a major new threat that has severely affected European butterflies in the last decade. The new Red List found that 52% (34 species) of all threatened species in Europe are threatened by climate change. Although the warming climate has allowed some widespread species to spread north, it is having a devastating effect on certain species in both the far north and far south of Europe as well as in the high mountains.

Pseudochazara williamsi is one of those butterflies at the greatest risk of extinction and is listed as one of just six Critically Endangered species in Europe. This butterfly appears to be suffering from the devasting effects of both habitat degradation and climate change. The new Red List identifies urgent actions required to halt and reverse of those species most at risk. For the most threatened, the development of species recovery plans is the highest priority in order to ensure appropriate actions are formulated and then implemented over the plan's timescale. Urgent research on this species began as soon as it became apparent that it was likely to be amongst the continent's most threatened butterflies. It is very welcome indeed, that this species action plan has been published so soon after the new Red List and demonstrates the commitment of Europe's conservationists and of the Ministry of Sustainability and Environment of Andalusia to save this butterfly from extinction.

Chris van Swaay and Martin Warren
Butterfly Conservation Europe

Photo 1. *Pseudochazara williamsi* is a species endemic to some mountainous areas of the south-eastern Iberian Peninsula (Author: José Miguel Barea).

1. INTRODUCTION

This document summarises all the information available for the Nevada Grayling *Pseudochazara williamsi* (Romei, 1927) butterfly, and describes and analyses the results of field surveys undertaken in 2023-25.

Species Action Plans (SAPs) are documents which bring together relevant information about a given threatened species, present an analysis of the threats that the species faces, and list actions needed to reverse these threats. If successful, these actions will help protect the species from extinction and greatly improve its conservation status. SAPs are vital tools for the conservation of highly threatened animal and plant species.

This Species Action Plan is an output of a partnership project between the Andalusian Government (Ministry of Sustainability and the Environment) and the European Butterflies Group (EBG) of Butterfly Conservation and Butterfly Conservation Europe.

The production of this SAP involved three steps (see methods section for further details). First, we gathered all the information available for the species in the form of scientific papers, reports and distribution records. Second, fieldwork was undertaken during June-July (the adult flight period) 2023, 2024 and 2025 to survey all known and potential sites within south-east Spain recording the distribution and abundance of the adult butterflies using a standardised methodology. Casual observations were also made of the species' ecology (e.g. nectar sources, larval hostplants), as well as any threats to the butterfly at each survey site. Finally, we liaised with local stakeholders and conservation experts to develop appropriate measures and discussed possible conservation actions during 2024-2025.

The document is divided into three main sections. The first section summarizes the available information for the species and shows new data gathered during the project. A second section deals with information that is relevant for the conservation of the species, particularly an analysis of the threats that have been mentioned for the species and those that were detected during fieldwork. The final section explains in detail the specific actions that are proposed for an improvement of the species' conservation status. At the end of the document there is a comprehensive list of references and an acknowledgement section.

Photo 2. The extensive slopes of some of the large river valleys on the southern slopes of the Sierra Nevada still support some populations of *Pseudochazara williamsi* (Author: José Miguel Barea).

2. IDENTIFICATION

The life cycle of *P. williamsi* has been described in detail by Olivares *et al.* (2011) and by García-Barros *et al.* (2013) and constitutes the main sources of the descriptions provided below.

Wing morphology

The male wingspan ranges from 41-48 mm. The upperside of the male forewing is light brown, with a broad orange-yellowish postdiscal band; two large black ocelli are visible in spaces S2 and S5. The upperside hindwings present a similar pattern, with the yellow postdiscal band distally tinged light orange and bearing a small ocellus in S2; the outer margin is dentate.

The underside of the male forewing is pale yellow extending from the base, bearing two black ocelli with pupils; the outer margin fringes are chequered brown and white. The hindwing underside is beige, speckled with brown, and crossed by sinuous concentric lines, much less contrasted in one specific population.

The female is larger, with a wingspan of 42-51 mm, and is lighter in colour with less contrast. On the underside of the female forewing, a brown indentation at V4 extends into the postdiscal yellow band and provides the most reliable diagnostic feature for distinguishing females from males (Olivares *et al.*, 2011; Leraut, 2016).

Photo 3. Male *Pseudochazara williamsi* from Sierra Nevada (Author: Javier Olivares).

Photo 4. Female *Pseudochazara williamsi* from Sierra Nevada (Author: Javier Olivares).

Immature stages

The egg is elliptical in outline, with 21-26 longitudinal ridges, and is satin white in colour.

There are five larval instars. The young caterpillar is very pale, gradually becoming grey with wavy dark lateral lines and a broken dorsal line. The final instar larva bears short setae and a discontinuous dark dorsal band, darker at the beginning of each segment; the dorso-lateral band is similar but less pronounced. The head capsules display broad, dark bands that almost merge, masking the lighter background colour. The pupa is similar to that of closely related genus.

Photo 5. Mating pair of *Pseudochazara williamsi* from Sierra Nevada (Author: Javier Olivares).

Photo 6. *Pseudochazara williamsi* is well camouflaged in its habitat thanks to its cryptic colors (Author: José Miguel Barea).

Photos 7 to 14. Eggs (A and B), larvae L1 (C), larvae L2 (D), larvae L3 (E), larvae L4 (F), larvae L5 (G) and pupae (H) of *Pseudochazara williamsi* (Author: David Jutzeler).

3. TAXONOMY

Common name: Nevada Grayling (English) or Cuatro Ocelos Bética (Spanish).

Scientific name: *Pseudochazara williamsi* (Romei, 1927)

Original reference: Romei, E. (1927) Notes of collecting in Spain in 1925-1926. *The Entomologist's Record and Journal of Variation*, 39(10): 136-138. (Described as *Hipparchia hippolyte williamsi* and lectotipus and paralectotipus deposited at the Barcelona Natural Sciences Museum; Macià *et al*., 2017).

Phyllum: Arthropoda

Class: Insecta

Order: Lepidoptera

Family: Nymphalidae

The taxon is often considered as a subspecies of the Asian *Pseudochazara hippolyte* Esper, 1783. However, the type species of *P. hippolyte* was described from the Ural Mountains and showed clear morphological differences from Iberian specimens described by Romei in 1927 (Olivares *et al*., 2011). Subsequently, Kudrna *et al*. (2011, 2015), Gil (2017), Wiemers *et al*. (2018) and Wiemers *et al*. (2020) accepted full species status of *P. williamsi*.

Four subspecies have been described from the mountains of south-east Spain and all of them show obvious morphological differences (Fig. 1). The species has given rise to phenotypes adapted to the heterogeneous geological substrates of different habitats. These ecotypes would have been further promoted by the geographic isolation of populations within each of these mountain systems since the last glaciation (Olivares, 2002). Particularly noteworthy are the adaptations exhibited by populations from the Sierra de María, Sierra de Gádor, and Sierra Nevada.

Sierra de María constitutes an isolated mountainous massif dominated by very light gray limestone substrates, which has resulted in a distinctive ecoform of generally paler appearance, especially on the ventral surface of the hindwings: *P. williamsi aislada* Eitschberger & Steiniger, 1973. This subspecies is believed to have been probably lost.

Sierra de Gádor is another mountain range, geographically close to Sierra Nevada, but with a markedly different substrate. This is a mining area where limestones and dolomites are conspicuously stained with a reddish-brown hue. The corresponding population exhibits a more ochraceous general coloration, particularly evident on the ventral surface of the hindwings: *P. williamsi augustini* Weiss, 1980.

Specimens from Sierra Nevada are characterized by a somewhat darker overall colouration compared with other populations, associated with substrates of schists and quartz-schists of generally gray to dark-gray appearance: *P. williamsi williamsi* (Romei, 1927). No significant differences are observed between the specimens of Sierra Nevada and those of the nearby Sierra de Baza, despite differences in lithology, as the latter is dominated by limestones and dolomites. This suggests the occurrence of relatively recent genetic contact between these two mountain systems, likely facilitated through the Sierra de Filabres, which is geologically very similar to Sierra Nevada.

Finally, from the north-eastern sierras, specifically the type locality Sierra de Guillimona, the subspecies *P. williamsi reverchoni* Tarrier, 1993 was described. This is a remarkable population in which individuals generally display an unusually small body size for the species, a trait likely associated with the clima-

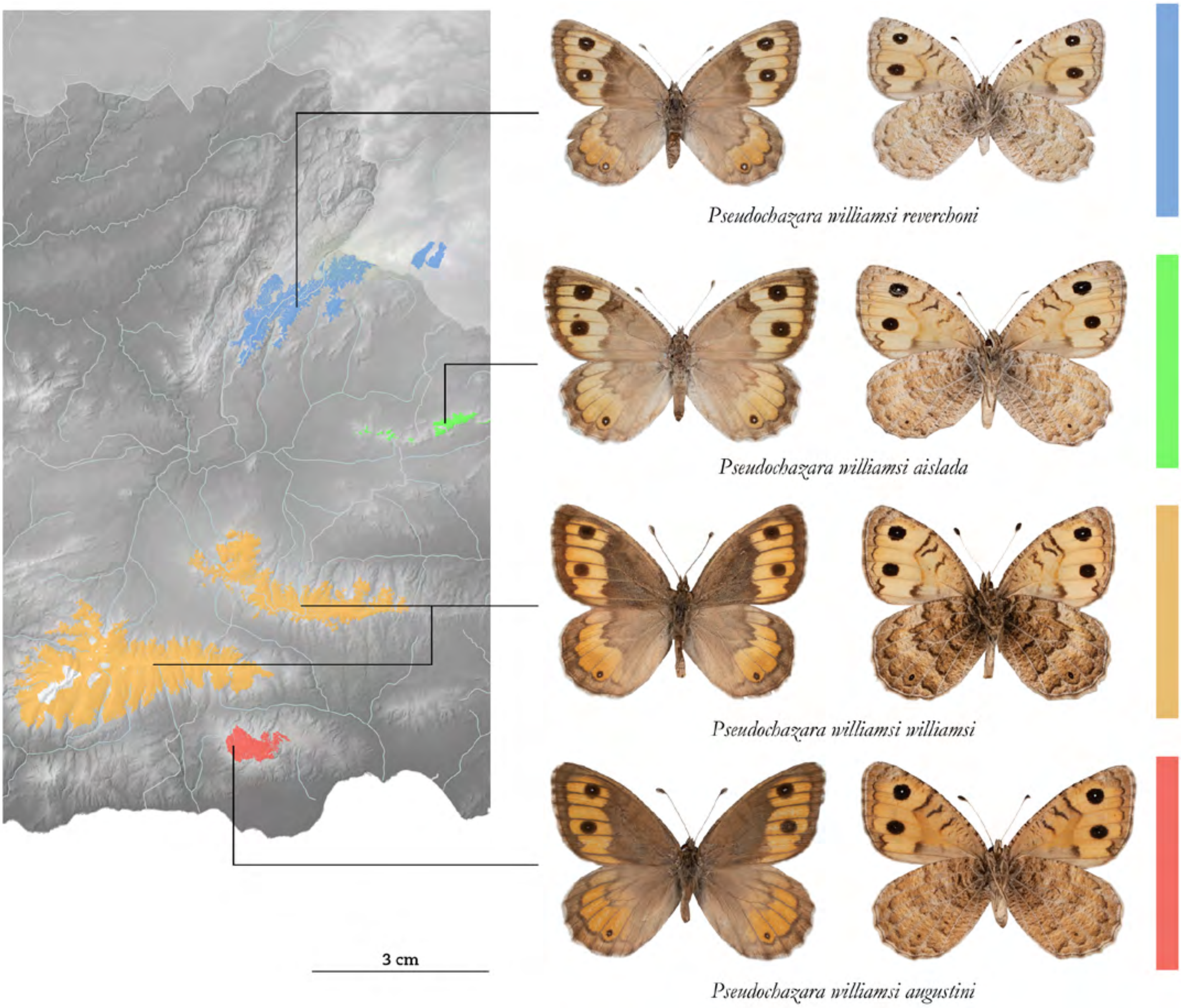


Figure 1. Subspecies (ecotypes) of *Pseudochazara williamsi* described and approximate historical distribution of each during the 20th century.

tic conditions of these sierras, which are considerably colder and less insolated than the others.

The genus *Pseudochazara* comprises 27–32 species with a wide distribution in the Palaearctic region from North Africa to the Himalayas and Mongolia (Verovnik & Wiemers, 2016). In Europe there are eleven species (Wiemers *et al.*, 2018). Seven of these are endemic to Europe, three of which are endemic to the European Union, including *P. williamsi*.

Of the endemic *Pseudochazara* species, only *P. williamsi* occurs in western Europe, with the other seven being restricted to south-east Europe: Grecian Grayling *Pseudochazara graeca* (Staudinger, 1870) (mainland Greece), Brown's Grayling *Pseudochazara amymone* (Brown, 1976) (Albania, mainland Greece), *Pseudochazara euxina* (Kuznetzov, 1909) (Ukraine), Macedonian Grayling *Pseudochazara cingovskii* (Brown, 1980) (North Macedonia), Dark Grayling *Pseudochazara tisiphone* (Brown, 1981) (Albania, mainland Greece), Dils' Grayling *Pseudochazara orestes* de (Prins & van der Poorten, 1981) (Bulgaria, mainland Greece).

Of the non-European endemic *Pseudochazara*, the Grey Asian Grayling *Pseudochazara geyeri* Herrich-Schäffer, 1846 occurs in Albania, mainland Greece, North Macedonia, Turkey and the Caucasus; the White-banded Grayling *Pseudochazara anthelia* (Hübner, 1824) occurs in Cyprus, Eastern Aegean Islands and Turkey; *Pseudochazara amalthea* (Frivaldszky, 1845) occurs in the Balkans, Turkey and northern Iraq; *Pseudochazara mercurius* (Staudinger, 1887) occurs in the Southern Urals in Russia and further east across Kazakhstan and the northern Tian-Shan to Mongolia and the north of Tibet.

4. METHODS

DISTRIBUTION INFORMATION

Different sources of historical and current information on *P. williamsi* were consulted. As a result, we have gathered 353 presence records (Fig. 2). In the case of records recorded on the same day, those that occur at a distance greater than 100 meters are considered independent records and, therefore, were incorporated as such into the database. The most important source in terms of data volume, with 173 records were those collected during the present study. This dataset comprises our own field data, own data registered in periods prior to the present study, the data from consultations and interviews with numerous amateur and professional entomologists affiliated with various research institutions (public Universities and from the Spanish Research Council, CSIC) and information from public or private scientific collections. References present in the scientific literature also provided highly valuable information. The second most important data set, with 157 records, were the GBIF portal (Global Biodiversity Information Facility), from which a bulk data download was carried out [GBIF.org (24 November 2024) GBIF Occurrence Download https://doi.org/10.15468/dl.f8f2q4]. Finally, information was retrieved from the Natusfera portal (www.spain.inaturalist.org), and direct contact was established with the authors of the records to confirm coordinates and dates.

Some of the records obtained (mainly from the GBIF dataset) were not precisely georeferenced; in such instances, the record was retained but without the associated coordinates. In numerous other cases, the date was either missing or deemed unreliable. In those cases, the record was retained but without a date. The examination of complementary sources generated some duplicate records, which were subsequently removed from the database to retain only a single entry per record. The final database is therefore the result of a process of compilation, detailed examination of each record and exhaustive filtering. It consists of a total of 353 records spanning the period 1925-2025 (one century) (Fig. 2). Of these, 259 records (73.4%) contain precise and reliable information on location, 277 records (78.5%) include precise and reliable information on date, and 210 records (59.5%) provide precise and reliable information on both location and date. On the other hand, 306 records (86.7%) contained accurate and reliable information on elevation, although only 275 of them also contained information on the year in which the record was made. Records below 1,400 m a.s.l. were dismissed as outside the expected range for this species.

FIELD SURVEYS (PRESENT STUDY)

The line transect method designed by Pollard & Yates (1994) (Pollard walks) was chosen for monitoring the densities of *P. williamsi* in the present study. This method involves walking along a transect line while recording all adults detected within a band of 2.5 meters on each side of the observer, 5 meters ahead, and 5 meters above. In essence, this corresponds to an imaginary box with 5-meter sides in which every individual appearing within its limits is recorded. Densities have been expressed in terms of individuals per hectare. A total of 89 surveys were conducted between 2023 and 2025: 36 in 2023, 28 in 2024, and 25 in 2025. One important bias in our study is the fact that we can make only one visit per year to each locality. During 2023, 2024 and 2025, all existing and historical populations of the species were surveyed at the most suitable times (July, primarily the central weeks). This effort was preceded by a bibliographic and records review, as well as based on expert knowledge. Additionally, numerous punctual surveys were carried out each year to complement existing knowledge about the distribution of the species.

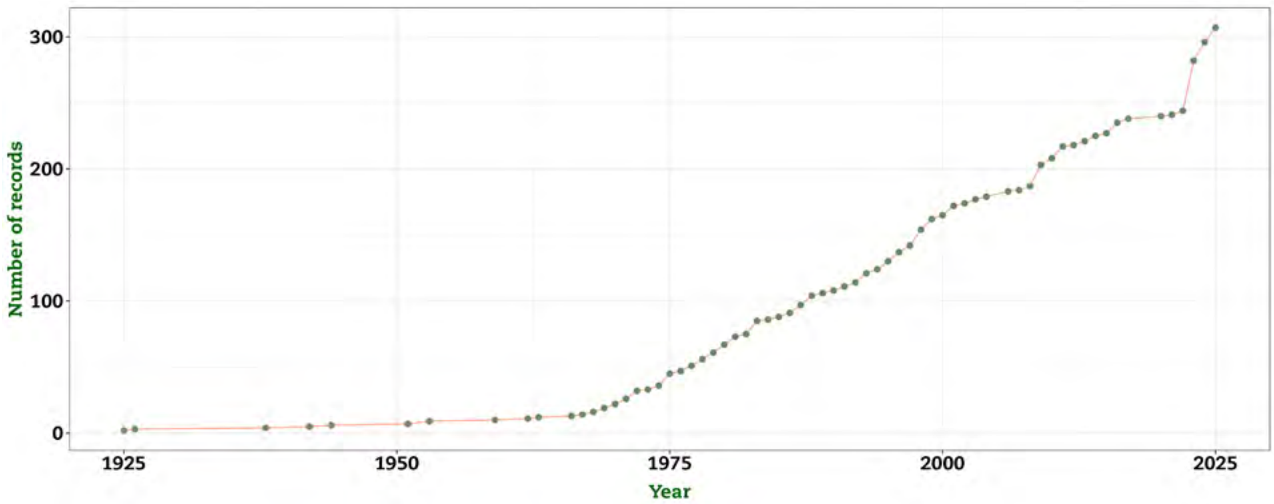


Figure 2. Accumulative number of records of *Pseudochazara williamsi* (only records with reliable information about date).

Finally, in some localities, 15-minute counts were conducted. These comprise calculations based on a unit of time (butterflies/15 minutes) rather than space, following the same method established by Pollard and Yates (1994) regarding the 2.5-meter band on each side of the observer as the recording zone. The 15-minute counts were uploaded to the European Butterfly Monitoring Scheme platform using the mobile application *Butterfly Count App* but these data have not yet been analysed.

These surveys involved volunteers and researchers from the European Butterfly Group, Butterfly Conservation Europe, technicians from the 'High Mountain Species Recovery and Conservation Plan' of the Regional Ministry of Sustainability and Environment (Junta de Andalucía) and students and researchers from the University of Granada and from the Autonomous University of Madrid. In total, 17 people were involved in the field work.

POTENTIAL DISTRIBUTION

The potential distribution of *Pseudochazara williamsi* was modeled using MaxEnt software (Phillips *et al.*, 2006). MaxEnt is a niche-based modelling algorithm that utilizes presence-only data and serves as a general-purpose method for making predictions or inferences from incomplete information. This software estimates a target probability distribution by identifying the maximum entropy distribution subject to a set of constraints that represent the available, but incomplete, knowledge about the target distribution. In this context, MaxEnt generates species distribution models (SDMs) based solely on presence records and exhibits strong predictive performance, particularly when the number of presence records is limited compared to other modelling algorithms.

To minimize spatial autocorrelation among presence records (Kühn, 2007), a minimum distance threshold of 100 m between sampling locations was applied (based on expert criteria). Consequently, only spatially independent localities were included in the modelling process. Two different models were computed:

1. **Historical distribution**: All presence records used were obtained during the 20th century (1925-1999), comprising a total of 47 independent records.
2. **Current distribution**: Only presence records collected during the last decade (2016-2025) were included, totalling 51 independent records.

Once the models were generated, each grid cell was classified as either "present" (indicating potential butterfly habitat) or "absent," based on the suitability threshold associated with the 10th percentile training presence logistic threshold value reported by MaxEnt. These thresholds were used to convert the continuous suitability maps into binary presence-absence maps, resulting in threshold values of 0.18 for the historical model and 0.44 for the recent model.

To model the distribution of the *Pseudochazara williamsi* within the study area, 15 environmental descriptors were incorporated, grouped into three conceptual categories: topography, vegetation, and water availability. These variables were selected to represent key ecological resources, and all were obtained at a spatial resolution of 40 meters. Topographic and hydrological variables were derived from a 40-m resolution digital elevation model provided by the Environmental Information Network of Andalusia (REDIAM, Andalusian Government). The elevation model was processed using GRASS GIS software (GRASS Development Team, 2009) with the following modules: *r.param.scale*, *r.slope.aspect*, *r.terraflow*, *r.sun*, and *r.recode*. Land cover and land use data were obtained from the Andalusian Land Cover and Land Use Map (SIOSE Andalusia, 2003, scale 1:25,000). These vector maps were converted into raster format, and distances to target entities were calculated using the *v.extract*, *v.to.rast*, and *r.grow*.distance modules. Frequency analyses were conducted on the resulting raster's using the *r.neighbors* module, which quantified the number of pixels containing a given feature within a 1,000 m radius.

Subsequently, potential habitat patches smaller than 50 hectares were excluded, corresponding to the minimum area that we estimate is required for the long-term maintenance of a viable *Pseudochazara williamsi* population, based on expert criteria.

Model performance was evaluated using the receiver operating characteristic (ROC) curve, with the area under the curve (AUC) serving as a widely accepted metric of SDM accuracy. Both models demonstrated high predictive performance, with AUC values of 0.99 for the historical model and 0.97 for the recent distribution model.

The modelling process was applied exclusively to Andalusian populations, which retain nearly all known current and historical occurrences. Moreover, Andalusia was selected for practical reasons, as it provides highly detailed and precise environmental information necessary for developing high-resolution (40 m) models such as those presented here.

SOFTWARE EMPLOYED

All cartographic work and geographic information management presented in this Action Plan were conducted using QGIS software (version 3.28.7-Firenze), except for the processing of environmental data described in the methodological section on potential distribution. Graphs and analyses were performed using RStudio 2022.07.2 (R Core Team, 2022), employing the following packages: *tidyverse*, *readxl*, *writexl*, *data.table*, *ggplot2*, *lme4*, and *sysfonts*.

5. DISTRIBUTION

Pseudochazara williamsi is a species endemic to some mountainous areas of the south-eastern Iberian Peninsula. The first record of this species dates from just one century ago (1 July 1925), and corresponds to a specimen collected in Sierra Nevada by the Italian entomologist Enzo Romei (Romei, 1927). The original reference explicitly mentions the locality of Puerto del Lobo and reports an altitude of 5,000 feet (slightly over 1,500 m a.s.l.), which must be an error, since the cited site is located at around 2,500 m a.s.l. Subsequently, this species has been historically recorded in 29 10-kilometer UTM grid squares (Fig. 3). The butterfly has been recorded on eleven different sites: from the provinces of Almería, Granada and Murcia: Sierra de Gádor, Sierra Nevada, Sierra de Baza, Sierra de los Filabres, Sierra de María, Sierra de Orce, Sierra de La Sagra, Sierra Seca, Sierra de Guillimona, the Revolcadores Massif and Sierra Espuña (see Figs. 3, 4 and 5 and Table 1 for further details).

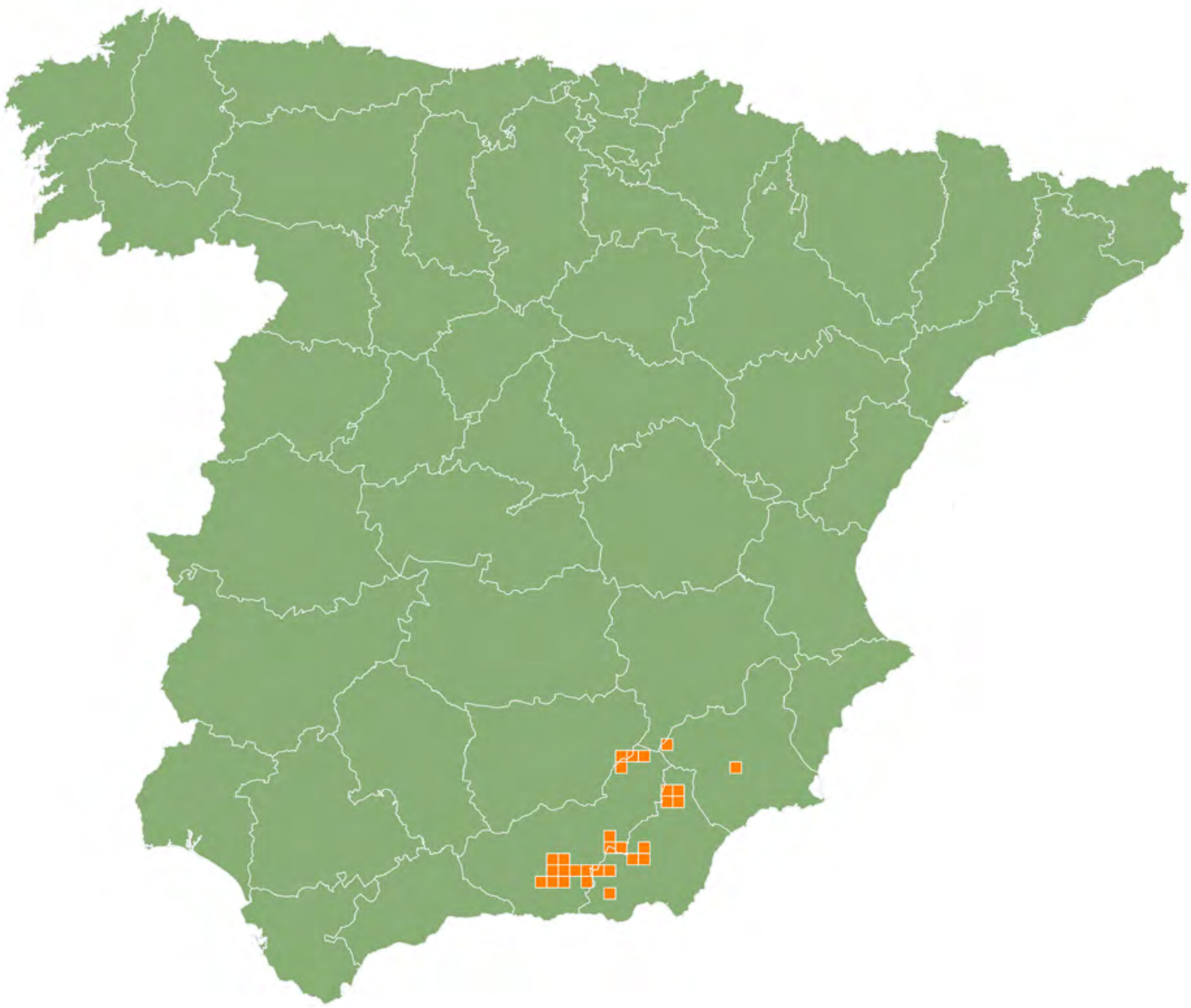


Figure 3. Distribution of *Pseudochazara williamsi* in 10-kilometer UTM grid cells in mainland Spain (administrative boundaries of the provinces are also shown).

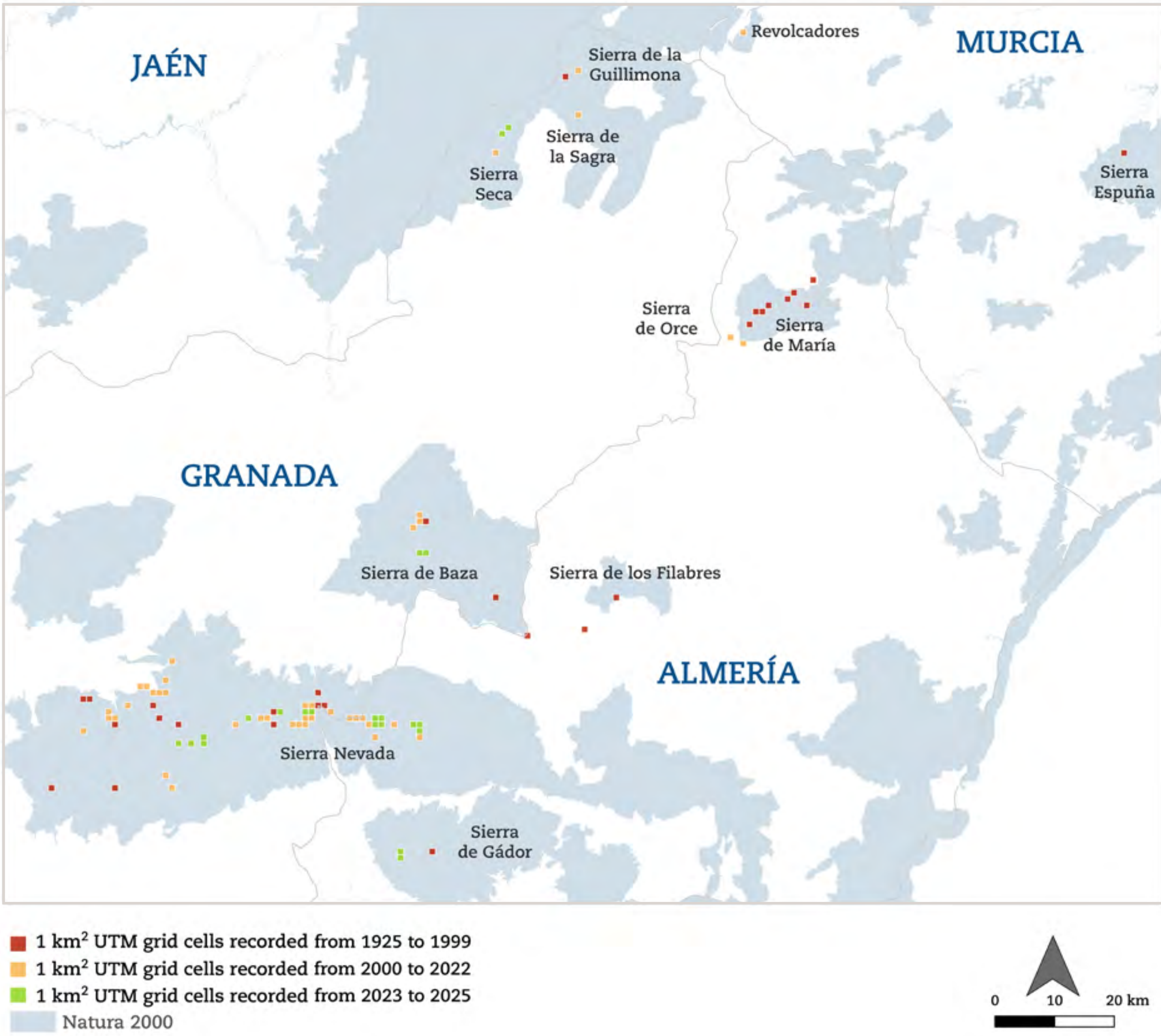


Figure 4. Distribution of *Pseudochazara williamsi* in 1-kilometer UTM grid squares.

The status of *P. williamsi* on each of the aforementioned eleven sites is described below (Figs. 4 and 5 and Table 1):

1. Sierra de Gádor

These populations are on the wing earlier, since there are numerous records from June, which is not typical for other localities. The first record of this species in Gádor dates from 1975 and the most recent is from this year (2025). Except for the first record, the rest of the sightings are concentrated in a relatively small area of just over 100 hectares at most. Here, population densities are relatively low, which contrasts with data from the 1990s that reflect a local abundance, with several dozen individuals present in each colony.

2. Sierra Nevada

Pseudochazara williamsi has always been more abundant in the central and eastern parts of the Sierra Nevada massif. In the westernmost third, although some records exist, we believe the species was never abundant or well distributed.

In recent years there has been a gradual loss of localities on the northern slope of the central part of the massif, to the point that it has disappeared from Loma del Veleta, a classic site cited by numerous entomologists visiting Sierra Nevada. Many of them describe considerable densities of this species in areas where we now know it is no longer present (see e.g. Worms, 1976). In the headwaters of the Genil River there has also been a notable absence of records in

Photo 15. The surroundings of Pico del Buitre (Sierra Nevada, Almería) are home to one of the most representative populations of *Pseudochazara williamsi* in the Sierra Nevada (Author: José Miguel Barea).

recent years, with the last sightings from 2022. These headwaters can generally be considered well surveyed, but it is possible the butterfly may still persist here. However, given the losses of other well-known colonies in more accessible localities we could expect at least a drastic population reduction.

At present, Sierra Nevada still harbors some of the best populations of this species, especially on the slopes and peaks between Pico del Almirez and Pico del Buitre (province of Almería). It also remains present on some peaks and ridges located between Puerto de la Ragua and Picón de Jeres, as well as at certain points in the wide valley comprising the headwaters of the Trevélez River.

At this eastern edge of the massif, the definite extinction of the species at Puerto de la Ragua (2,000 m a.s.l., with no records this century) is noteworthy, as is its more recent disappearance from places where it was once regularly observed, such as Pico del Chullo (2,600 m a.s.l.) and Lagunilla Seca (2,300 m a.s.l.). In the latter locality nearly 30 individuals were counted in 2007 (Olivares pers. comm.).

These results suggest a local loss of colonies over the past decades and a reduction in population densities. It is noteworthy that there are localities where dozens of individuals were once reported and where the species was considered locally abundant, although restricted to very specific areas.

3. Sierra de Baza

This is one of the populations that still persists today, although records are concentrated in small areas. These areas coincide with elevated points locally known as '*calares*', that comprise limestone massifs that usually reach elevations above 2,000 m a.s.l. The area in this mountain range above 2,000 m a.s.l. covers more than 2,400 hectares, which might be interpreted as good news if not for the fact that these elevations are isolated, leading to a fragmented distribution of butterfly populations.

The most recent visits have focused on three '*calares*'. In 2024 and 2025, the species was confirmed only at one of them (Calar de Rapa). In recent visits to Calar de Santa Bárbara no individuals were found, and the last visit (2025) to Calar de Casa Heredia also yielded negative results. In any case, we consider it likely that some isolated populations persist in places like Cerro del Calar, Cerro de Quintana or even Calar de Santa Barbara itself, which should be surveyed more intensively.

4. Sierra de los Filabres

This mountain range is part of the same unit as Sierra de Baza, being its continuation into the province of Almería. Here, the species is currently considered extinct. The first record dates as far back as 1942, and the last from 1994. It has been visited on several occasions since, the most recent being in 2023 during this study.

5. Sierra de María

Pseudochazara williamsi was first recorded in Sierra de María in 1951. During the 1990s, the species could be observed relatively easily in different areas of the upper part of this mountain range, including some information about more than 10, or even 20, individuals in one day. Although we have records from 1996-2001, there have been none since. Surveys in 2023-25 also failed to find the butterfly and we believe it is now probably extinct.

6. Sierra de Orce

Like Baza and Filabres, Sierra de Orce forms part of the same mountain range, being the continuation of Sierra de María into the province of Granada. However, the Sierra de Orce includes a small sector in the province of Almería. In our dataset, we have only two records of *P. williamsi* in Sierra de Orce, one from 1996 (4-5 specimens) and the other from 2001 (11 specimens). Both were in the same place, at an elevation of 1,600 m a.s.l. As in Sierra de María, we consider the species probably extinct in Sierra de Orce. The likelihood that the species is extinct in the Sierra de Orce is even greater than in the Sierra de María.

7. Sierra de La Sagra

We have found only two completely reliable records of *P. williamsi* in Sierra de La Sagra. One is from 1993 and the second and last from 2002. We have reliable information that '*several specimens were seen with a noticeable small size*' in 1993. These records were from near the summit of the mountain. During the current study the summit of La Sagra was surveyed annually but none were recorded, and we can now consider the species probably extinct here.

8. Sierra Seca

The only population persisting north of Sierra de Baza is that of Sierra Seca. First recorded at the end of the first decade of this century (Gil & Ibáñez, 2009), our results confirm that the species has survived until present. After detailed surveys of much of the mountain, we found only a tiny, highly localized population in the central section of the ridge.

9. Sierra de la Guillimona

First recorded in 1988 (Aistleitner, 2016), we have no records later than the year 2001. The species had been observed in various locations within this area; however, only in a specific site could 4-6 specimens be seen with some regularity during each visit. Tarrier (1993) indicates that the species was frequent in the Sierra de la Guillimona at the end of the 1980s or even at the beginning of 1990s and wrote: '*the discovery of a large colony distributed by the Sierra de Guillimona was a satisfaction...*'. We consider it very likely that the species became extinct on this mountain several decades ago. Only a single visit was conducted as part of the 2023-25 survey and failed to locate any individuals.

10. Revolcadores Massif

The first record from the Revolcadores Massif in Murcia dates from 1982. Whilst there are records from 2001, the last specimen was observed on July 27, 2002 (Garre *et al.*, 2025). Everything currently suggests that this population is probably extinct. The most recent visit (July 20, 2023) conducted as part of this survey failed to locate any individuals

11. Sierra Espuña

The information about this species in Sierra Espuña is old and confusing, partly because the records come from elevations very unusual for the species (two of them below 1,390 m a.s.l.). These records date from 1971 and 1972, and no one has found *P. williamsi* in this mountain range since, despite considerable survey efforts (A. Ortiz pers. comm.).

Figure 5. Years in which *P. williamsi* has been recorded in each of the previously described populations (green dots) and years in which the species was last recorded at each location (red dots).

Table 1. Locality [province: Granada (GR), Almería (AL) and Murcia (MU)], highest general elevation in that locality, area above 2,000 m a.s.l. (in hectares), first and last record of *Pseudochazara williamsi* and elevational distribution (mean). Populations where the species currently persist are highlighted in green; light pink where it is probably extinct and pink, where extinction has been confirmed.

Locality (province)	**Max. elevation in the mountain range (m a.s.l.)**	**Surface area above 2,000 m a.s.l. (ha) in the mountain range**	**N of *P. williamsi* records**	**Date of first record**	**Date of last record**	**Mean of elevational distribution of *P. williamsi*** (from 1925 to 2022/from 2023 to 2025)
Sierra de Gádor (AL)	2,249	1,790.7	27	1975	2025	1,945/1,926
Sierra Nevada (GR/AL)	3,479	55,963.6	214	1925	2025	2,328/2,402
Sierra de Baza (GR)	2,269	2,441.3	23	1983	2025	2,162/2,269
Sierra de los Filabres (AL)	2,168	849.9	20	1942	1994	1,810
Sierra de María (AL)	2,045	34.3	36	1951	2001	1,583
Sierra de Orce (GR)	1,677	0	2	1996	2000	1,600
Sierra de La Sagra (GR)	2,383	271.1	2	1993	2002	2,339
Sierra Seca (GR)	2,136	252.4	5	2008	2025	1,998/2,014
Sierra de la Guillimona (GR)	2,065	48.4	13	1988	2001	1,867
Revolcadores Massif (MU)	1,974	0	9	1982	2002	1,900
Sierra Espuña (MU)	1,583	0	3	1971	1972	1,417

Photo 16. *Pseudochazara williamsi* exhibits an extraordinarily cryptic coloration that blends with its surroundings and usually remains with its wings closed while at rest (Author: José Miguel Barea).

Elevational distribution

The altitudinal distribution of the records shows a trend toward upward elevation over time (Fig. 6). This trend is statistically significant (p-value= 0.0026) and it involves an elevation increase of approximately 18 meters per decade. Furthermore, our findings indicate a marked contraction of the altitudinal distribution range of *Pseudochazara williamsi* over time (Fig. 7). This contraction is particularly pronounced at the lower elevational limits when comparing records from the 20th century with those from the present century. As a consequence, the elevation of occupied sites (measured as the median of the values) has shifted upward from 2,103 m a.s.l. to 2,317 m a.s.l., representing an altitudinal increase of 214 meters. The lower elevational limits appear to have remained stable during the last 25 years (21st century). These paterns can be attributed in part to the extinction of populations in regions where the species formerly occurred at lower elevations (i.e. Sierra de María and, to a lesser extent, Sierra de los Filabres), but nevertheless this elevational shift is still evident in the Sierra Nevada. Notably, records below 2,000 m a.s.l. have almost entirely disappeared, with only 13 occurrences documented below this elevation in the last 25 years. The upper elevational limits have also contracted, particularly when contrasted with 20th century data, but also when comparing the most recent three-year period with earlier records from the present century. It remains possible, however, that higher-elevation areas have been undersampled in recent years, and that increased survey effort above 2,700 m a.s.l. could reveal the persistence of remnant colonies at these uppermost elevations.

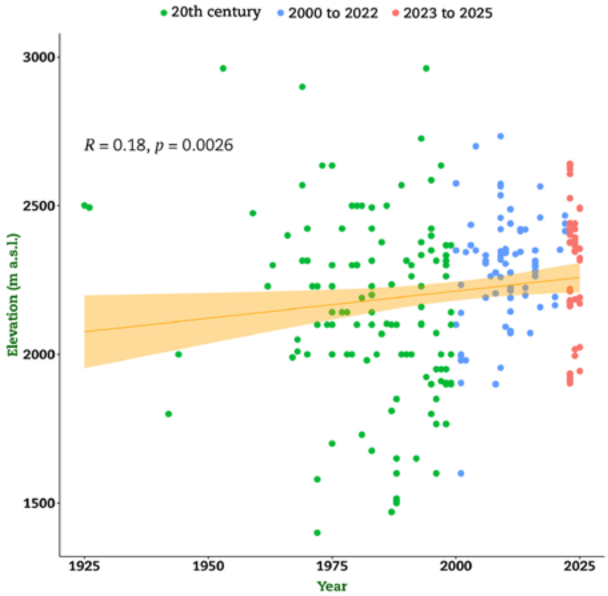


Figure 6. Temporal trend in the altitudinal distribution of *Pseudochazara williamsi* records (yellow line) and standard deviation of the data (yellow area). Records are shown separated by period, along with the R value and the p-value of the bivariate correlation (Spearman).

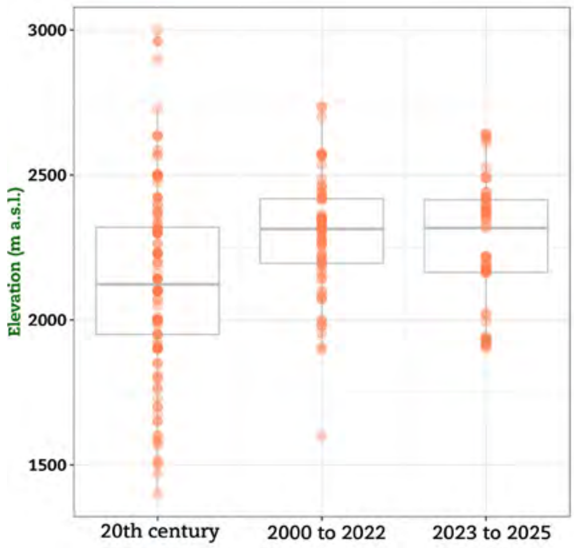


Figure 7. Distribution of *Pseudochazara williamsi* records by elevation across three time periods. The orange dots represent the records for each period. The box plot shows the 25th and 75th percentiles, respectively, at the lower and upper limits of the box, and the 50th percentile (median) at the center line.

As a consequence of the aforementioned patterns, the altitudinal distribution of the species has clearly contracted, with the majority of records now concentrated within a much narrower elevational range (Fig. 8). In this figure we can also comprobe as the proportion of records occurring below 2,000 m a.s.l. has declined markedly during the last 25 years.

Currently (2023 to 2025 records), existing populations of *P. willamsi* persist in an elevational distribution range of 738 meters, which is the range between the population established at the lowest altitude (Gádor: 1,903 m a.s.l.) and the one known at the highest altitude (Sierra Nevada: 2,634 m a.s.l.) (Table 2).

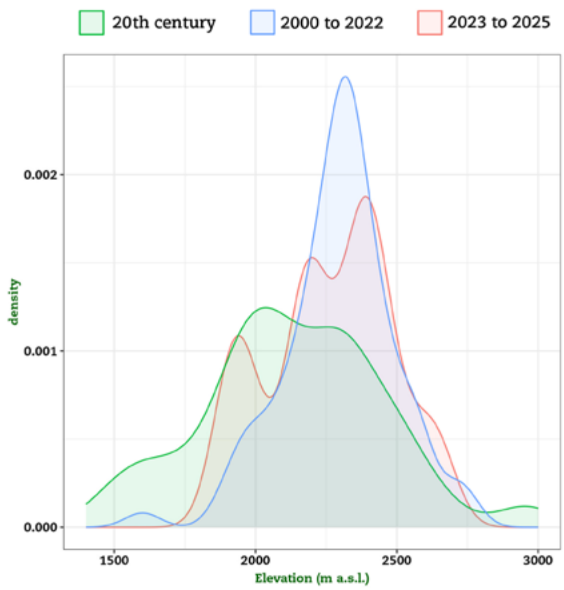


Figure 8. Density of *Pseudochazara williamsi* records by elevation in three time periods. Density represents a smoothed version of a histogram and describes the probability that the variable 'elevation' takes a certain value.

Table 2. Elevational parameters (in m a.s.l.) of the existing *Pseudochazara williamsi* populations (data from 2023 to 2025).

Site name	**Elevation** (mean)	**Elevation** (median)	**Min. Elevation**	**Max. Elevation**
Sierra Nevada	2,402	2,391	2,173	2,634
Sierra de Gádor	1,926	1.933	1,903	1,944
Sierra de Baza	2,269	2,175	2,162	2,220
Sierra Seca	2,014	2,019	1,995	2,024

Photo 17. The Sierra de La Sagra (in the background), rising to an elevation of 2,383 m a.s.l. and encompassing 271.1 hectares above 2,000 m a.s.l., constitutes a relatively isolated landform of considerable biogeographical significance. The most recent record of *P. williamsi* documented for this mountain dates from 2002 (Author: Javier Olivares).

6. HABITAT

HABITAT DESCRIPTION

Pseudochazara williamsi occurs in open, dry montane/sub-alpine and alpine habitats where grassy vegetation alternates with bare, sandy or pebbly ground, sometimes with scattered, tufted shrubs. Flight areas usually occur on the scree-covered higher slopes of mountain ridges which are sunny and exposed to the wind and the soils are thin. At higher altitudes, flight areas seem to be restricted to south-facing slopes (Olivares *et al*., 2011).

Sierra Nevada
Here the species occupies rocky slopes exposed to the wind, with acidic substrate of schists and poor vegetation dominated by high-altitude grasses (e.g. oromediterranean grasslands of *Festuca indigesta* Boiss. and local broom communities). The grass *Koeleria* spp. always appears together with *Festuca* spp.

Sierra de Gádor
Here the population is concentrated on a slope and the upper parts of an old mining area with limestone and dolomites rich in iron oxides, and small amounts of other elements such as fluorine, sulphur, zinc, silver and lead. It is an area with relatively abundant flowering species, especially *Arenaria tetraqueta* L., *Carduncellus monspelliensium* All., *Carduus platypus* Lange, *Helianthemum apenninum* (L.), *Pterocephalus spatulathus* (Lag.) Coult. (very abundant) and *Thymus serpylloides* Bory, Mill. The habitat structure is similar to that of other populations of the species, with scattered scrub and fairly open ground covered with small rock fragments, predominantly 5 to 10 cm in size.

Sierra de Baza
The habitat occupies high slopes or summit areas of some of the main elevations of the massif. Once again it comprises scattered cushion-like scrub on skeletal soils, poor in vegetation and with a calcareous, sometimes dolomitic substrate, where rock fragments do not usually exceed 10–15 cm. *P. williamsi* is found in areas where *Koeleria* spp. occurs together with *Festuca* spp. The plants are scattered across the upper part of the habitat, in zones where *Juniperus* spp. shrubs are absent, although these are often present in this biotope.

Sierra de Filabres
Here the habitat is found in the summit areas of this range above 1,900 m a.s.l. up to 2,100 m a.s.l. The dominant scrub is cushion-like, on acidic soils of mica-schists and quartz schists. In the areas with poor vegetation, alpine grasses grow: *Festuca* spp. and *Koeleria* spp. Nectar sources are scarce, with *Thymus serpylloides* and *Carduus platypus* predominating.

Sierra de María and Sierra de Orce
The species used to occupy habitat that is at its altitudinal limit, appearing very close to the highest zones and always in areas almost devoid of vegetation, where *Festuca* spp. and *Koeleria* spp. grow relatively abundantly, once more, in zones where *Juniperus* spp. shrubs are absent. The soil structure is calcareous substrate with scattered and abundant small-sized scree (2-5 cm). In addition to the scattered alpine grasses, there is a herbaceous layer with annual grasses, *Carduus* ssp. and *Erodium cheilanthifolium* Boiss.

Sierras de La Sagra and Guillimona
Pseudochazara williamsi occupies high slopes in an area with abundant cushion-like scrub and nectar sources, where in addition to *Carduus* spp., *Thymus* spp., *Erodium cheilanthifolium*, *Anthyllis vulneraria* L. and other Fabaceae occur. Areas of poor soils with little vegetation, scattered small-sized rock fragments and isolated grasses are infrequent here, which is probably a limiting factor for the species. In addition, overgrazing is critical in the occupied habitat.

Sierra Seca
The only area where the species has been observed is a high slope near the summit of the mountain, where

there are small areas of very poor soils with *Koeleria* spp. and *Festuca* spp. Here vegetation is very scarce and nectar sources are few. The substrate is calcareous, with dolomite areas and scree of small to medium size. It is an area frequently grazed by sheep and especially goats, which even use certain parts as overnight summer shelters.

Revolcadores:

Very similar to Sierra de Guillimona, with areas heavily trampled by livestock. The summit habitat has very poor, somewhat nitrified soils with scattered small-sized calcareous scree. Nectar sources are scarce during the species' flight period.

Photos 18 to 25. *Pseudochazara williamsi* habitat in Sierra Nevada (A), Sierra de Baza (B), Sierra de los Filabres (C), Sierra de Gádor (D), Sierra de María (E), Sierra de la Sagra (F), Sierra de la Guillimona (G) and Sierra Seca (H) (Authors: José Miguel Barea, Javier Olivares and Emilio González).

Photo 26. Hábitat of *Pseudochazara williamsi* at Sierra de Baza (Author: Javier Olivares).

NATURAL HABITAT TYPES OF COMMUNITY INTEREST (92/43/EEC)

Most records of the species during the last decade in Sierra Nevada are located in natural habitats of community interest (CIH) with codes 6160 (Oro-Iberian *Festuca indigesta* grasslands), 5120 habitat (Mountain *Cytisus purgans* formations) and 8220 (Siliceous rocky slopes with chasmophytic vegetation). In Sierra de Baza the records from the last decade were mainly from 4060 (Alpine and Boreal heaths), 6170 (Alpine and subalpine calcareous grasslands) and 9530 ((Sub-)Mediterranean pine forests with endemic black pines). The latter (9530) is a priority habitat in danger of disappearance and whose range mainly falls within the territory of the European Union. The main CIH where the butterfly occurs on Sierra de Gádor are 6220 (Pseudo-steppe with grasses and annuals of the Thero-Brachypodietea), also a priority habitat, and to a lesser extend 9240 (*Quercus faginea* and *Quercus canariensis* Iberian woods). All the records from the last decade from Sierra Seca occur within CIH 4090 (Endemic oro-Mediterranean heaths with gorse). In summary, all recent (2015-2025) records of *P. williamsi* have occurred within a CIH, confirming the conservation importance of the localities where this species still persists.

7. SPECIES DISTRIBUTION MODEL

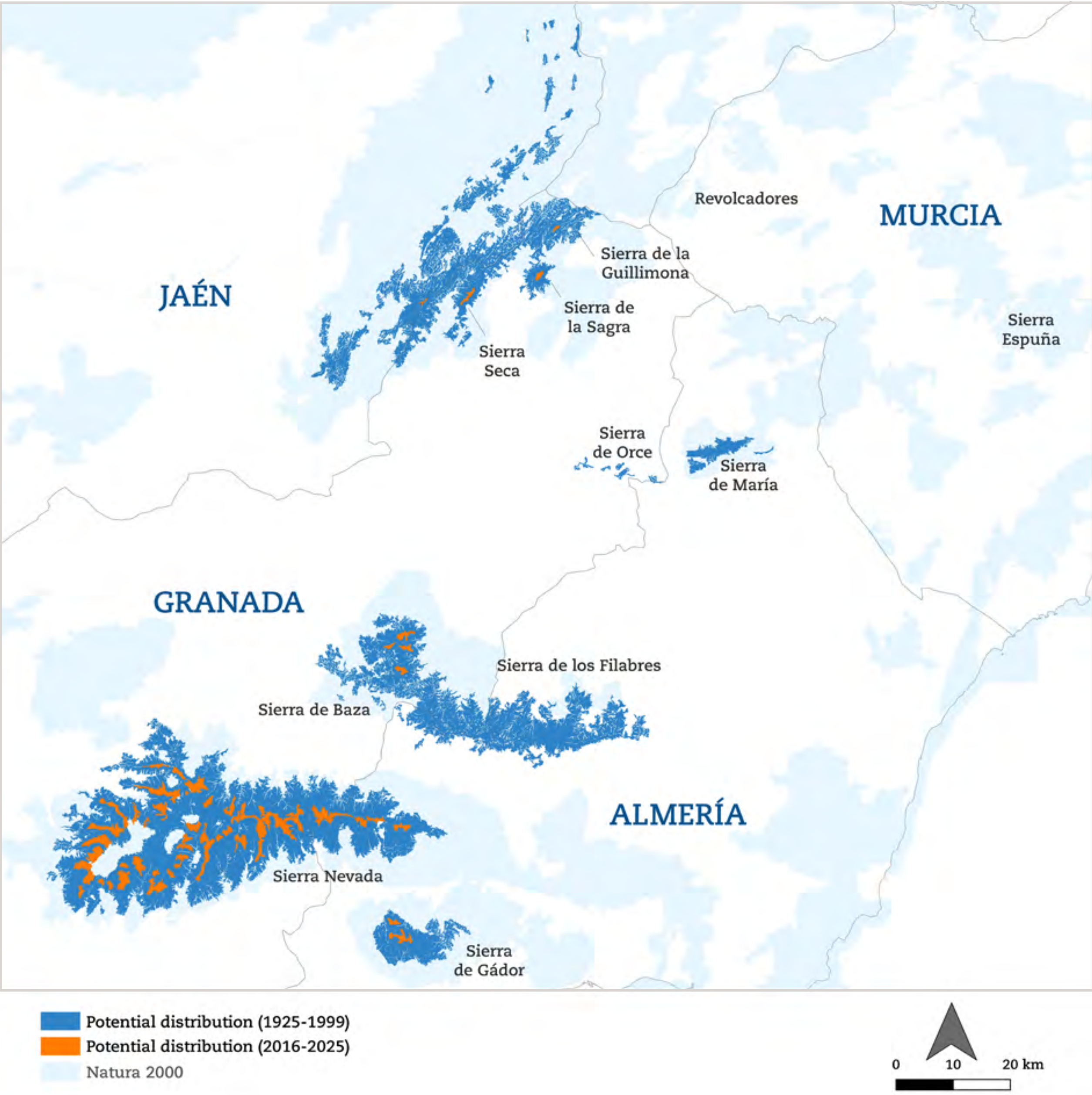


Figure 9. Species distribution model for *Pseudochazara williamsi* showing potential habitat during the 20th century and during the last decade.

Two potential distribution models were developed and compared (see methodology, page. 16): one constructed using occurrence data from the 20th century (1925–1999) and another based on records from the last decade (ca. 2016–2025).

According to our model results, *Pseudochazara williamsi* has currently lost approximately 91.6% of its potential habitat relative to that available during the previous century (Fig. 9 and table 3). This corresponds to a reduction from 191,570 hectares of suitable habitat in the 20th century to only 16,180.9 hectares at present.

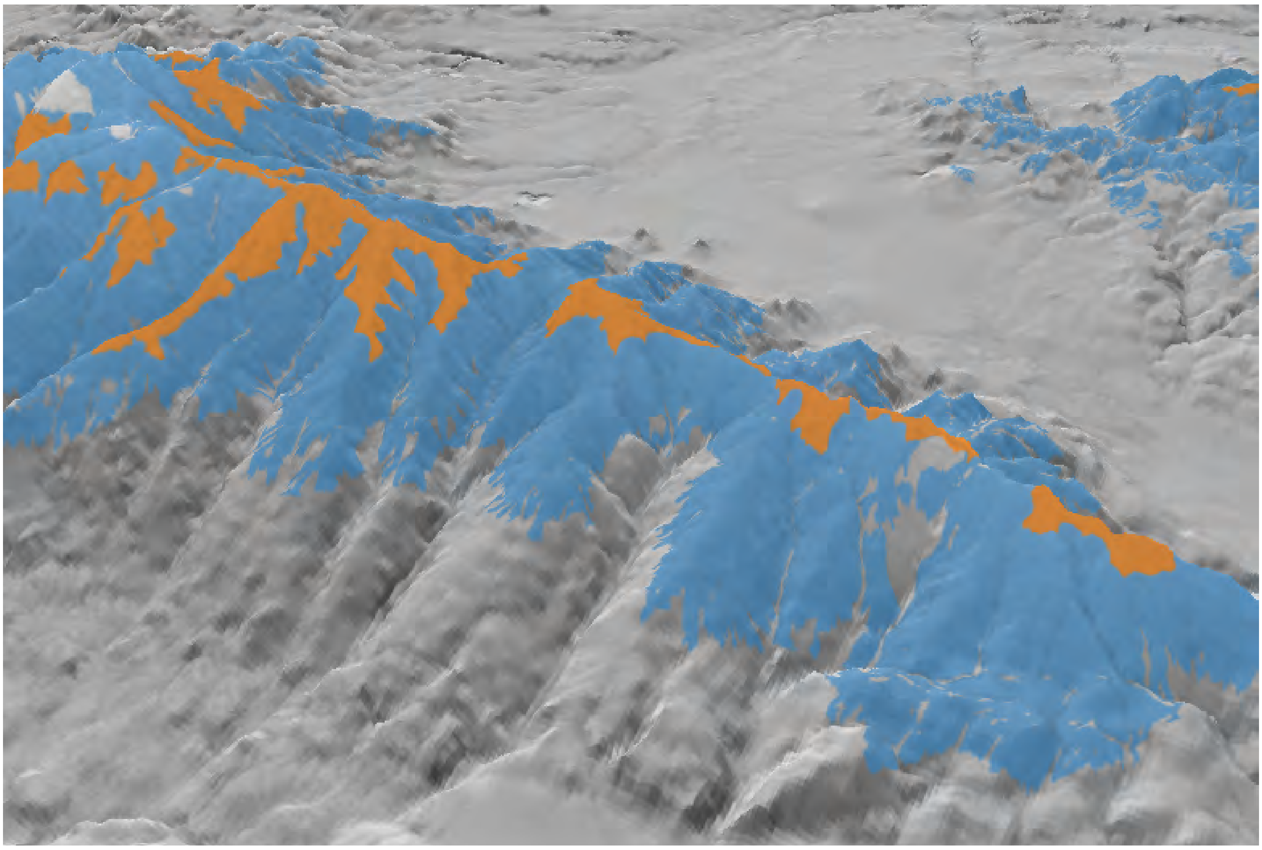


Figure 10. 3D view of the eastern end of the Sierra Nevada where it is possible to see the drastic reduction in the extension of the potential habitat of *Pseudochazara williamsi* from the 20th century (blue) to the present day (orange).

As shown in Table 3, this substantial loss of potential habitat is widespread across the species' range, although it is less severe in the Sierra Nevada (84.9% loss) and, to a lesser extent, in the Sierra de Gádor (93.6% loss). In contrast, in the Sierras of Baza and the group of populations located in the north-eastern part of Granada Province - extending into parts of Jaén - the loss of potential habitat exceeds 99%. In this area, we have checked that some small patches remain in the summit's areas of Sierra Seca, Sierra de La Sagra and Guillimona, despite the fact that we have only been able to confirm the survival of the species in Sierra Seca. It is very important to note that our model based on 20th century data show as favorable extensive areas in the Sierras of Cazorla and Segura, which likely extend into the provinces of Granada, Albacete and Murcia, where adjacent mountain systems include the massifs of La Sagra, Guillimona, Sierra Seca and Revolcadores. This suggests that the species may have had populations in these areas in the past, even though we lack specific records. In fact, the model using data from the last decade still identifies a 60-hectare patch in the vicinity of Pico Empanadas (2,106 m a.s.l., Sierra de la Cabrilla, Cazorla), and we cannot rule out the discovery of new populations in these regions, which are generally difficult to access and rarely visited. Currently, it is possible that the only patch large enough to retain populations to the present is found exclusively in Sierra Seca. In the Sierras of María and Orce, potential habitat has disappeared entirely. Within the Sierra de Baza, habitat loss has also been extreme, with only 703 hectares (1.7%) remaining. The largest concentration of suitable habitat is now restricted to the Sierra Nevada, where approximately 14,483.4 hectares persist. In this mountain, a clear upward shift of potential habitats can be observed when comparing the two study periods (Fig. 10).

Table 3. Extent of potential *Pseudochazara williamsi* habitat in the 20th century (1925-1999) and the last decade (2016-2025). *Northeast Granada and Jaen populations (Sagra, Guillimona, Sierra Seca, Cazorla and Segura).

	20th century (1925-1999) (ha)	**2016-2025** (ha)	**Lost potential habitat** (ha)	**Remaining potential habitat** (%)	**Lost potential habitat** (%)
Sierra de Gádor	8,624.6	555.8	8,068.8	6.4	93.6
Sierra Nevada	95,820.6	14,483.4	81,337.2	15.1	84.9
Sierras de Baza/Filabres	41,090.0	703.0	40,387.0	1.7	98.3
Sierras de María/Orce	3,427.2	0.0	3,427.2	0.0	100.0
Sierras del Nordeste*	42,706.7	438.7	42,268.0	1.0	99.0
Total	191,570.0	16,180.9	175,389.1	8.4	91.6

Regarding the environmental variables defining these potential distributions, elevation was the most influential factor in both temporal models, contributing 90.5% in the historical model and 85.9% in the recent model (Table 4). In this regard, the models for the 20th century show probabilities of presence beginning at elevations around 1,500 meters above sea level, whereas the model for the last decade indicates that the likelihood of presence below 2,000 m a.s.l. is very low. Likewise, the range of potential elevations is much narrower under current scenarios, which is entirely consistent with the available records. In the 20th century model, the frequency of both sparse and dense shrublands, along with the presence of soils with high water-retention capacity, also contributed substantially. The potential habitats for *P. williamsi* during the past century are therefore characterized by a high frequency of sparse shrubland and a low frequency of dense shrubland, as well as by the presence of soils with a high capacity to retain sediments and moisture. The frequency of pastureland or grassland further influenced habitat suitability. The contribution of this last variable becomes negative when grassland cover exceeds one quarter of the area within a one-kilometer radius from a given pixel. Additionally, two variables associated with proximity to the treeline - distance to forests and frequency of pine forest - were highlighted as important predictors. This implies that during the past century, the areas adjacent to the tree line (1,500–1,900 m a.s.l., depending on the mountain) constituted suitable habitats for *P. williamsi*.

Just like in the model based on data from the 20th century, besides elevation, the proximity to coniferous forest stands, represented here by distance to the treeline, also played significant roles in the last decade model. This means that, within the geographical context in which the models were developed, the presence of forested areas (mainly pine forests) remains an important variable. However, in the last decade model there is also a certain shift of the potential areas away from the previously mentioned tree line, according to the individual responses of these variables in relation to habitat suitability. The presence of both dense and sparse scrublands appears to remain important for *P. williamsi* (again with a positive relationship with sparse scrublands and negative with dense ones), along with a secondary set of variables with comparatively minor influence. These include areas relatively distant from water sources, with high topographic exposure indices, and subject to intense solar radiation. Suitable habitats for *P. williamsi* are generally now found in relatively flat sites lacking steep slopes, within a broader mountain landscape. This latter set of variables clearly represents the environments found on the ridges and peaks where this species currently occurs. In other words, in areas where the slope is typically less steep than on the lower-altitude hillsides, and where the rate of solar radiation is usually very high.

The results of both models are, in general terms, highly consistent with the findings derived from the analysis of records from different periods, as well as with our understanding of the environment and the changes that have occurred in it over recent decades. The geographical projection of the models and the drastic reduction in potential habitats further reinforce the evidence of a continuous regression in the distribution range of *P. williamsi*, along with a progressive decline in the number of populations.

Table 4. Relative contributions of environmental variables to the MaxEnt model (%) of *Psesudochazara williamsi* distributions in the 20th century (1925-1999) and the last decade (2016-2025).

Variable	Percent contribution 20th century (1925-1999) model	Percent contribution last decade (2016-2025) model
Elevation	90.5	85.9
Disperse shrubland frequency	2.5	1.3
Water accumulation index	1.7	-
Dense shrubland frequency	1.4	0.8
Pastureland frequency	1.2	-
Distance to forests	1	4.3
Pine forests frequency	0.9	5.2
Topographic convergence index	0.3	-
Distance to water	0.2	0.1
Topographic exposition	0.2	1.5
Slope	0.1	0.2
Solar radiation	-	0.6

The predominance of elevation as a surrogate for multiple climatic variables is unsurprising and delineates an ecological profile for *P. williamsi* that is closely associated with the cold conditions' characteristic of high-mountain environments. Changes in these climatic conditions have led to an upward shift in the species' optimal isotherm, resulting in a retraction of its lower elevational limits across all occupied mountain ranges. However, because mountains are conical in shape, the available surface area decreases with altitude. Consequently, this upward shift has reduced habitat availability and increased isolation among populations, processes that likely preceded the local extinctions documented in the current Species Action Plan.

In lower mountain ranges, this altitudinal displacement has led to the near-complete disappearance of suitable habitat for *P. williamsi*. This pattern is evident across all the studied ranges except the Sierra de Gádor. This locality is particularly noteworthy, as it represents the southernmost limit of the species' distribution. Although habitat loss in this range has also been considerable, it remains significantly lower than in other areas, with up to 32.7% of the total potential habitat outside the Sierra Nevada still suitable. The reasons for this remain unclear, and it is likely that factors not captured by the distribution model are involved. The fact that populations in the Sierra de Gádor occupied particularly favorable conditions during the 1990s (Olivares, pers. comm.) likely explains their comparatively better current status. Additionally, the range's proximity to the Mediterranean Sea may provide extra, though not readily apparent, humidity that enhances flowering rates - an observation confirmed during our field surveys.

8. BIOLOGY

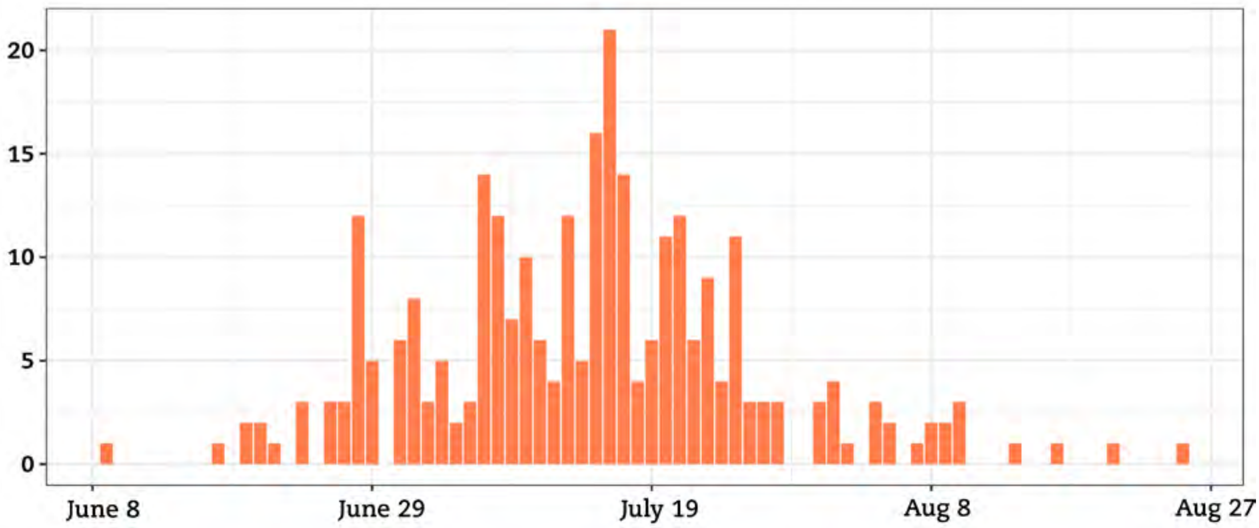


Figure 11. Phenology chart for *Pseudochazara williamsi* records (277 records between 1925 and 2025).

PHENOLOGY

Pseudochazara williamsi has one generation per year. We have compiled 277 records of *P. williamsi* that include the date of capture (Fig. 11). The earliest record is from June 9 (Faluke pers. comm.), while the latest is from August 26. Only 11.2% (n = 31) are June records (with only one record prior to June 18), and only 7.6% (n = 25) are from August. The remaining records are all from July (81.2%; n= 221). The mean date across all records falls around July 15. More than half of the records are concentrated between July 10 and July 20.

When sightings are allocated to three-time frames [(previous century, current century (2000-2022), present study (2023-2025)], we find no temporal shifts in mean dates (Fig. 12). In two first periods, July 15 consistently emerges as the mean date, and an advance of only three days is detected for the last three years. However, differences were detected in the timing of the first and, especially, the last records of the year. Indeed, in the previous century, up to 23 records were documented in August, compared to only 2 so far in the current century (year 2010), and none in the present study.

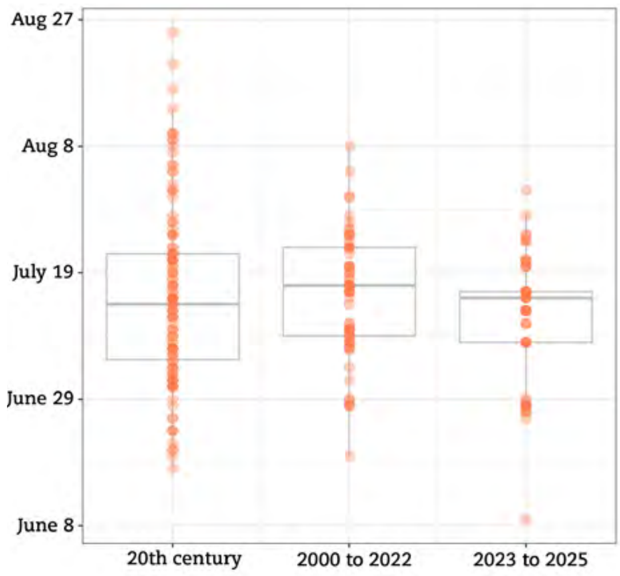


Figure 12. Phenology chart for *Pseudochazara williamsi* records across three time periods. The orange dots represent the records for each period. The box plot shows the 25th and 75th percentiles, respectively, at the lower and upper limits of the box, and the 50th percentile (median) at the center line.

These results indicate a narrowing of the flight period (Fig. 13), with a marked contraction at the end of the season and a slightly later onset. This reduction in the flight period of adults may have consequences for the biological performance of populations and is most likely linked to the abrupt onset of summer conditions in the Mediterranean high mountains. Anecdotal evidence suggests a reduction in flower abundance during the flight season, which could explain the contraction in flight period.

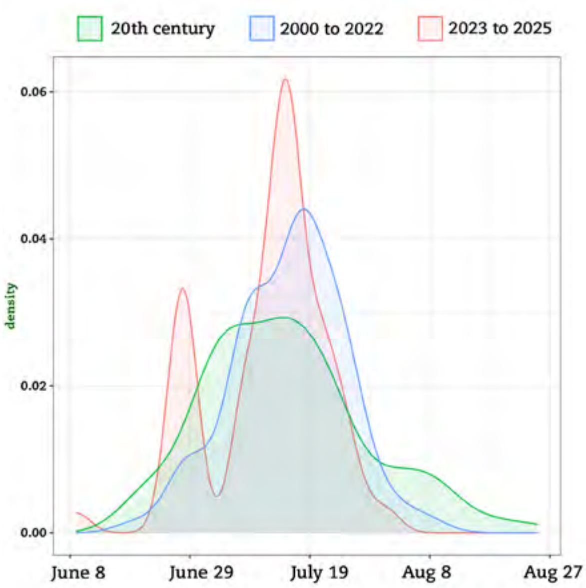


Figure 13. Density of *Pseudochazara williamsi* records by date in three time periods. Density represents a smoothed version of a histogram and describes the probability that the variable 'date' takes a certain value.

ADULTS' BEHAVIOUR

Males are territorial and make short, fast flights at ground level. They generally perch on stones with closed wings at an oblique angle and are very well camouflaged. If disturbed, the two ocelli on the underside of the upper wings are displayed. The females perch for much longer periods and only fly when no threats are apparent (Olivares *et al.*, 2011).

LARVAL HOSTPLANTS

The larvae feed on grasses, though the exact species remain uncertain. Olivares *et al.* (2011) and Clarke (2024) suggested *Festuca indigesta*, the most abundant grass in the habitat, as the primary hostplant. However, recent field surveys have revealed the significant presence of *Koeleria dasyphylla* Willk. subsp. *nevadensis* (Hack.) Quintanar & A.T. Romero García (in silicious soils) and *Koeleria vallesiana* (Honck.) Gaudin subsp. *vallesiana* (in calcareous soils) alongside *Festuca indigesta* in areas where the species occurs. *Festuca nevadensis* (Hack.) Markgr. Dann. cannot be excluded as a possible host, as it is found on limestone soils in other parts of the massif (Olivares *et al.*, 2011).

EGGS

Eggs are laid in June or July (Olivares *et al.*, 2011), usually on the stems of hostplants, and hatch within a few days.

LARVA

Larvae hatch in July. Newly hatched larvae feed slowly and irregularly at any time of the day during August, being sensitive to high temperatures. From the second or third instar in September, they shift to nocturnal feeding. Feeding suspends during the cold periods of December and January, and resumes during warmer periods in early spring, they enter hibernation positioning themselves head downwards at the base of plant stems. Larvae reach the L5 stage within a few days and they are negatively phototactic, preferring to feed in darkness before midnight, even at temperatures near 0 °C (Jutzeler & De Bros, 1995). This information originates from observations of outdoor rearing in Switzerland, under cold conditions that were likely not as extreme as those in the Sierra Nevada.

Photo 27. *Koeleria vallesiana* at the Sierra de Baza (Author: Javier Olivares).

PUPATION

In May or June, fully grown larvae burrow a few centimetres underground to pupate (Olivares *et al*., 2011).

NECTAR SOURCES

Nectar sources are generally scarce in the habitat of this species, which may be a critical factor explaining the small size of its populations. Important sources include *Pterocephalus spatulathus* (Sierra de Gádor), *Arenaria tetraqueta*, *Anthyllis vulneraria* (Sierra de la Guillimona and La Sagra), *Carduncellus monspelliensium*, *Carduus platypus*, *Erodium cheilanthifolium*, *Helianthemum apenninum* and *Thymus serpylloides*. Most adult feeding observations in Sierra Nevada have been recorded on *Jurinea humilis* (Desf.) DC., *Scabiosa turolensis* Pau, *Thymus serpylloides* subsp. *serpylloides*, and some *Carduus* species occurring in the area.

NATURAL ENEMIES

No parasitoids are currently known for this species. *P. williamsi* has few natural predators because its aposematic wing patterns provide an effective defence with the butterfly displaying its ocelli in response to disturbance. The most frequent natural predators are high mountain insectivorous birds [e.g. *Oenanthe oenanthe* (Linnaeus, 1758) or *Phoenicurus ochruros* (Gmelin, 1774)].

Photo 28. *Pseudochazara williamsi* feeding on *Scabiosa turolensis* (Author: José Miguel Barea).

9. POPULATION

In summary, *P. williamsi* is a local species, restricted to (semi-) natural habitats. The butterfly has always been rare but is now declining in abundance across most of its range (Figs. 14 to 16). Several local extinctions have occurred, and remaining populations are now severely fragmented and persist at low densities. Higher density and more abundant populations persist in the Sierra Nevada and in Sierra de Baza. We describe below the current population sizes at the four sites where the butterfly still persists:

1. Sierra de Gádor

Nine individuals were recorded during the 2023-25 fieldwork. The mean density in localities with confirmed presence was 5.14 individuals/ha, ranging from a minimum of 2.86 to a maximum of 5.71. Of the four surveyed localities, adults were detected in only two. Consequently, the population in this mountain range is extremely low.

2. Sierra Nevada

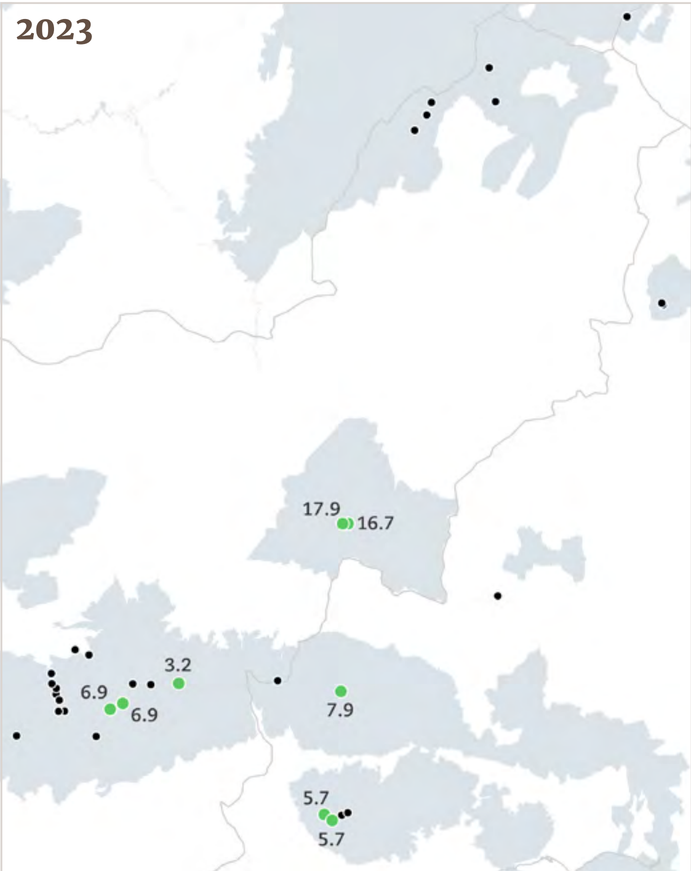
Over the three years of fieldwork, 91 individuals of *P. williamsi* were documented: 34 in 2023, 42 in 2024, and 15 in 2025. The mean population density across these years (considering only localities with confirmed presence) was 2.92 butterflies/ha, with values ranging from 0.4 individuals/ha in 2023 at Puerto de Aldeire (approximately 2,600 m a.s.l.) to 7.86 individuals/ha in 2023 at Pico del Buitre (approximately 2,400 m a.s.l.). Independent of transect counts, up to 25 individuals of *P. williamsi* have been recorded in a single morning at certain localities within Sierra Nevada. Nonetheless, it is common to encounter isolated sub-populations only after covering long distances in mountainous terrain, where often only one individual, or at most two or three, are detected.

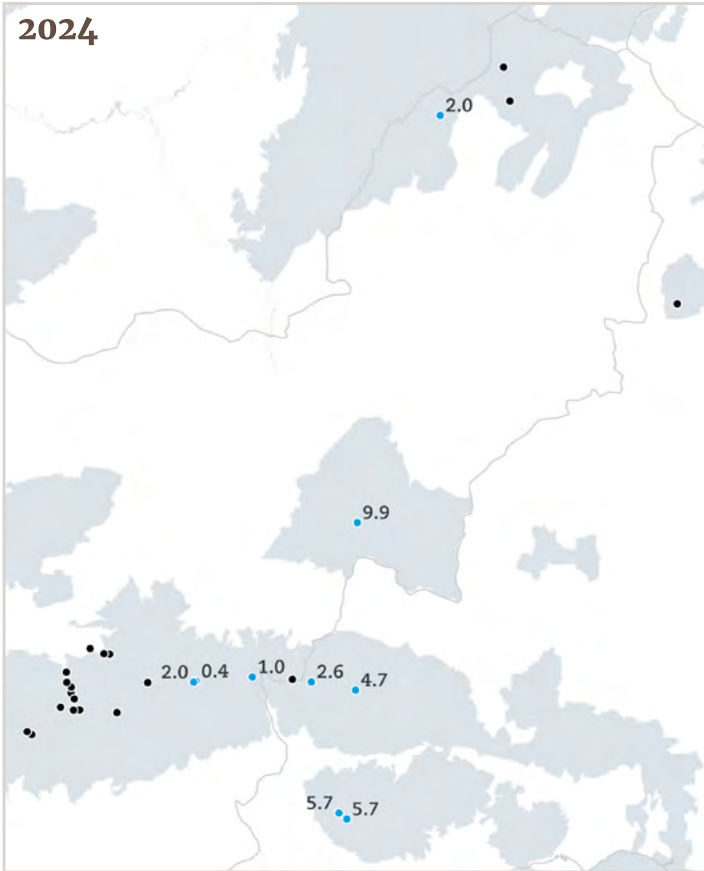
3. Sierra de Baza

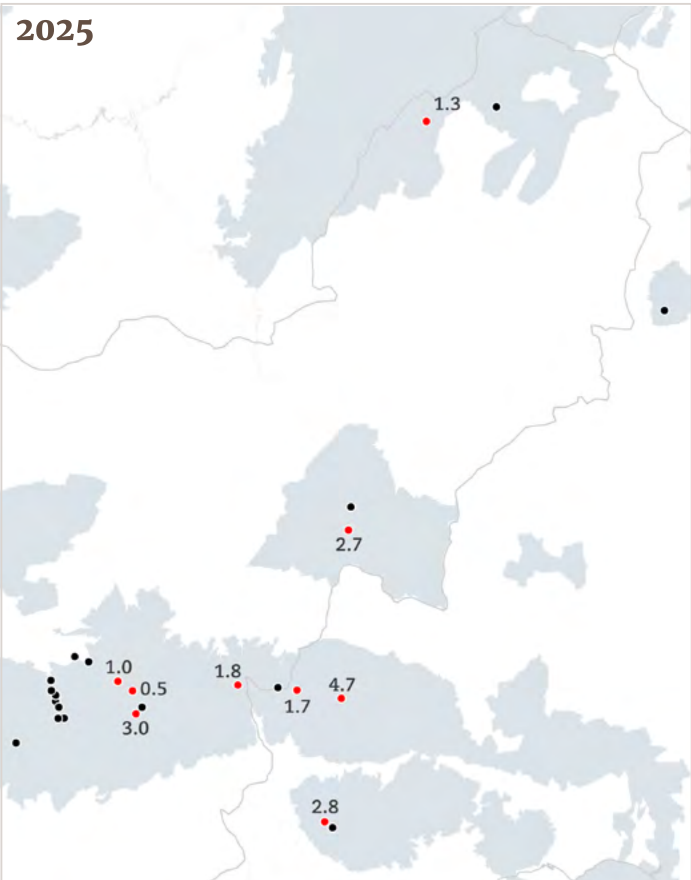
Populations are isolated. Localities with confirmed presence appear to maintain relatively dense populations. Across the three years of fieldwork, 47 individuals were recorded. The average density was 11.8 butterflies/ha, with some values reaching nearly 18 individuals/ha in 2023.

4. Sierra Seca

The population is highly restricted to an area that, under an optimistic estimate, probably does not exceed 15 hectares, where rarely more than three individuals are detected. Accordingly, population density is low, with values of 2 individuals/ha in 2024 and 1.3 in 2025. Given the small area of occupied habitat, the total population size is likely to be very small.







Figures 14 to 16. Density of *Pseudochazara williamsi* butterflies recorded on standard Pollard transect counts in 2023, 2024, and 2025 (individuals/ha). Black dots represent monitoring sites, but with negative results.The distribution of the Natura 2000 network is also shown.

Photo 29. Adult of *Pseudochazara williamsi* from Sierra de Gádor (Author: José Miguel Barea).

Photo 30. Adult of *Pseudochazara williamsi* from Sierra Nevada (Author: José Miguel Barea).

Photo 31. Adult of *Pseudochazara williamsi* from Sierra Seca (Author: José Miguel Barea).

10. CONSERVATION

LEGAL PROTECTION

Currently, *P. williamsi* is included (as *Pseudochazara hippolyte*) in the Andalusian List of Wild Species under Special Protection Regime (LAESPE) (approved by Royal Decree 139/2011, of February 4, with subsequent amendments included in Annex X of Decree 23/2012). This list comprises species, subspecies, and populations that merit particular attention and protection due to their scientific, ecological, or cultural value, as well as their uniqueness, rarity, or degree of threat, in addition to those that are listed as protected under the Annexes of international directives and conventions ratified by Spain. The current category afforded to this species represents a lower level of protection than that granted to species directly included in the Catalogue of Protected Species, which currently encompasses other endemic and endangered Lepidoptera such as *Polyommatus golgus* (Hübner, 1913), *Agriades zullichi* Hemming, 1933, and *Agrodiaetus violetae* Gómez Bustillo, Expósito y Martínez, 1979.

The entire distribution range of this species falls within the Natura 2000 network (92/43/EEC). Furthermore, all Sierra Nevada localities are encompassed within the boundaries of the National Park, the highest protection category a territory can hold within the Spanish state. The Baza populations are included within the Sierra de Baza Natural Park, while the Sierra Seca population is located on the boundary of the Sierra de Castril Natural Park, with some areas lying outside the park and therefore not covered by this protection status. Lastly, the Sierra de Gádor populations occur in areas that are protected solely under the Habitats Directive via the Natura 2000 network, but not by the Natural Park designation.

Regarding the historical distribution of the species, the populations of Filabres, Orce, Guillimona, Sagra, and Revolcadores also lie within the Natura 2000 network but do not benefit from any form of regional territorial protection. In the case of Sierra de María, most populations were located within the Sierra de María-Los Vélez Natural Park, designated in 1989. Finally, the Sierra Espuña population falls within a Regional Park, the Murcian equivalent of Andalusian Natural Parks, which was declared in 1992, twenty years after the last recorded observation of *P. williamsi* in this area.

CONSERVATION STATUS

As *P. williamsi* was not considered a full species at the time, it was not included in the previous European butterfly Red List assessments by Van Swaay & Warren (1999) and Van Swaay *et al*. (2010). However, the species was included in the Global, Europe & Mediterranean butterfly Red List (Van Swaay *et al*., 2015) when it was assessed as Least Concern, since it had not declined by more than 25% in the previous ten years and its population size was probably larger than 10,000 adult individuals. However, this assessment was based solely on the expert opinions of the authors.

The latest update of the IUCN Red List consider this species as Critically Endangered (Van Swaay *et al*., 2025a) The assessment criteria met were A3c; B1ab (i,ii,iii,iv): which indicate that the range is <100km², populations are severely fragmented and the extent, distribution, habitat quality and number of location or sub-populations have all declined during the previous decade. Moreover, during the next ten years, the range, distribution and/or habitat quality are expected to decline further by over 80%. *P. williamsi* is therefore one of the most threatened butterfly species in Europe [only six species listed as Critically Endangered in Europe (Van Swaay *et al*., 2025b)] and even in the world.

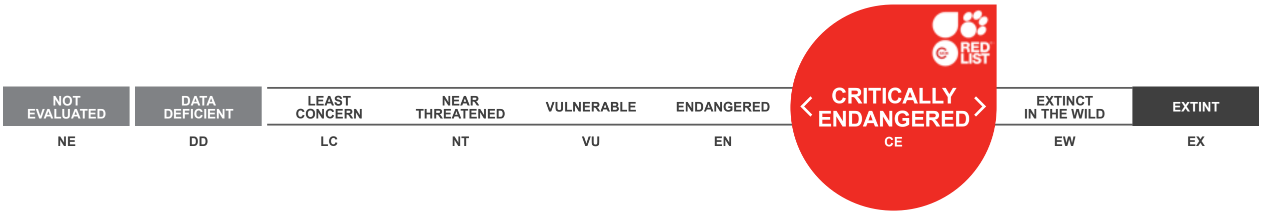


Photo 32. *Pseudochazara williamsi* is the most threatened butterfly species in Spain, and is among the six most endangered species in Europe, following the last IUCN Red List update (Author: Harry Clarke).

11. THREATS

CLIMATE CHANGE

High temperatures appear to be lethal to young caterpillars and very humid conditions increase pupal mortality. This suggests ideal localities for *P. williamsi* are cold and dry. Dry conditions must be moderate, because the presence of flowers seems to be very important, and the abundance of flowers is linked to the presence of rain during the late spring and during the summer. Olivares *et al*. (2011) consider these climatic requirements to effectively explain the butterfly's existing distribution. Climate change leading to warmer and wetter conditions are likely to have a very negative impact on *P. williamsi* populations, particularly those located on mountain peaks where there is no possibility of the butterfly utilising suitable habitat at higher altitudes. For example, the medium-term climate scenario (1971-2022) in Sierra Nevada shows an increase in minimum temperatures of 0.53ºC/decade, maximum temperatures of 0.37ºC/decade, and average temperatures of 0.36ºC/decade (Barea-Azcón, 2024). The average temperature has increased by 1.85ºC since 1971. Regarding precipitation in Sierra Nevada, the pattern since 1950 is not as clear, indicating an annual average reduction of 25.3 mm/decade, with 131.7 mm less rainfall than in the mid-20th century (Barea-Azcón, 2024). In addition to this trend, which clearly shows warming and aridification, it is also necessary to mention the impact of extreme climatic events on biodiversity. Extreme weather events in the Mediterranean, such as heatwaves and droughts, are intensifying due to climate change and they involve, for example, the occurrence of very early heatwaves that coincide with the development of *P. williamsi* final larval stages.

Following Pérez-Luque *et al*. (2016), climate simulations forecast higher annual maximum and minimum temperatures for the end of the century in Sierra Nevada, which will increase by 2 to 6ºC for the maximum temperatures and by 1 to 4ºC for minimums. For precipitation, the models predict a reduction although the high uncertainty of the simulations for this variable should be taken into consideration.

Consequently, warming and changes in precipitation patterns are likely to be the main factors explaining the decline of this species throughout its range. These factors have favored an elevational shift, which in all the mountains occupied by the species except the Sierra Nevada, has led populations to occupy residual areas on the summits where there are no higher-altitude territories to which they can move in search of optimal climatic conditions. Additionally, a shift in the optimal climatic conditions has also led to an isolation of remaining populations. Isolation and habitat fragmentation is one of the main drivers of species extinction.

The effects of climate change have been exacerbated by other drivers that have acted with greater or lesser intensity, depending on the location and the specific factor concerned. Climate change is a global crisis which cannot be directly addressed in this Species Action Plan, but these other additional drivers can be tackled to mitigate its negative effects. Mitigation of climate change impacts on *P. williamsi* is in fact the main tool available to halt and reverse the ongoing decline of this species.

These additional drivers of *P. williamsi* decline are:

SCRUBLAND EXPANSION

The abandonment of livestock farming is leading to excessive mountain scrub development. This is especially evident in the mid-mountain range, although scrub growth is also being detected in some areas above the tree line. Sheep and goat herds have suffered the greatest decline in recent decades. Scrub-clearing and traditional activities have practically disappeared in many of the locations where this butterfly traditionally flew. Scrubland expansion in the high mountains leads to loss of open *P. williamsi* breeding habitat. Typically, brooms (mainly *Genista versicolor* Boiss. and *Cytisus galianoi* Talavera & P.E. Gibbs) and species such as *Astragalus nevadensis* Boiss. subsp. *nevadensis* are the main shrub colonisers. Additionally, scrub also impacts the abundance of those plant species which are the main nectar sources for the butterfly. Some of these plant species depend on a certain degree of nitrification of the environment, which was largely provided by livestock faeces. A clear example of this is the loss of large *Cardus* spp., which as far as we know, are essential sources of nectar for this and other species of butterflies in the high mountains [e.g. *Parnassius apollo* (Linnaeus, 1758)]. However, this problem is complex in that it does not have a uniform impact throughout the species' distribution area.

Photo 33. One of the last remaining herds of sheep at the headwaters of the Trevelez river basin (Author: José Miguel Barea).

OVERGRAZING

The impact of intensive livestock grazing is particularly evident in Sierra Seca, and it has probably also had a considerable impact in the Sierras de Guillimona and La Sagra, as well as in the Revolcadores Massif. In Sierra Seca, moreover, the species occupies a very small area where overstocking, especially by sheep, is evident. However, whilst livestock pressure is undoubtedly excessive, it appears that the herds do not exert as much pressure on the occupied habitat as elsewhere in the Sierra Seca. Whilst we cannot be certain, this could well be the reason why the small remaining Sierra Seca population persists. In the case of Sierra Espuña, various testimonies point to the pressure exerted by the Barbary sheep (*Ammotragus lervia* Pallas, 1777), an exotic ungulate species, as the cause of local extinction (Gil, 2016 and A. Ortiz, pers. comm).

Photo 34. The effects of overgrazing on vegetation are very evident on either side of a fence in the Sierra de Guillimona (Author: José Miguel Barea).

NECTAR SOURCES SCARCITY

Nectar source availability appears to be one of the main problems facing this species and is closely linked to the effects of climate change. The longevity, fecundity and survival of butterfly populations is dependent on there being suitable nectar sources (King & Schultz, 2024 and Lebeau *et al.*, 2018). The decline in butterfly abundance has been linked to the decline in flowers (Wallisdevries *et al.*, 2012). During our fieldwork, we detected a striking shortage of floral resources available to the butterfly. Furthermore, numerous studies link the effects of climate change with

Photo 35. A herd of sheep resting under a pine tree in Sierra Seca. Densities here exceed the ecosystem's carrying capacity (Author: José Miguel Barea).

a shortening of the flowering period (see, e.g., Bock *et al*., 2014). The lack of moisture in the mountains as summer progresses makes it difficult for many plant species to flower into August, which could be related to the decrease in *P. williamsi* records during this month. Records of *P. williamsi* in August in the current century have decreased by 91,3% compared to those from the 20th century. The most recent *P. williamsi* August record dates from 2010. This narrowing of the flowering period is accompanied by a reduction in the available floral resources, which is especially striking in the case of Sierra de Gádor and Sierra Nevada, but could apply to all populations.

UNFAVORABLE HOST PLANT CONDITION

During our field work, we observed that the likely *P. williamsi* larval host plant, *Koeleria* spp., was apparently in a very unfavorable physiological state in many locations. This pattern, once again, is closely linked to the effects of climate change. The appearance of the grass' shoots is particularly unfavorable in the Sierra de Baza, in more specific areas of the Sierra Nevada, and especially in the Sierra de María. In the latter location, all or virtually all of the shoots appeared to be completely withered almost at the beginning of July.

ENVIRONMENTAL POLLUTANTS

Several studies suggest severe effects of ivermectin (a drug widely used in veterinary medicine to combat nematodiasis, ticks, and mange) on plants (Navrátilová *et al*., 2020) and, more notably, on arthropods (de Souza & Guimarães, 2022). Ivermectin exerts neurotoxic effects on insects, additionally impacting oviposition, fertility, and longevity. This drug continues to be administered to livestock in many of the areas where *P. williamsi* occurs and, although its effects have not been specifically studied, it can be inferred that it could be related to the decline in abundance of this species.

Furthermore, the use of *Bacillus thuringiensis* in the control of the pine processionary moth [*Thaumetopoea pityocampa* Denis &. Schiffermüller, 1775)] across many pine forests in the mountain ranges where *P. williamsi* occurs is likely to have had a detrimental effect on some of its populations, particularly those inhabiting areas near the tree line. Indeed, Olivares (2002) and Gil (2016) identified this factor as the main cause of the species' disappearance from the Sierra de los Filabres, in combination with other factors related to the management of extensive pine plantations in the mountain range. *Bacillus thuringiensis* is an entomopathogenic bacterium employed as a bioinsecticide due to its ability to produce crystalline toxins. When larvae ingest spores and crystals, these dissolve in the alkaline midgut and protoxins are activated by digestive proteases. The active toxins then bind to specific receptors on midgut epithelial cells, forming pores that disrupt the cell membrane. This results in ion leakage, osmotic imbalance, cell lysis, and severe tissue damage. Consequently, the insect suffers intestinal paralysis, feeding cessation, septicemia from secondary bacterial invasion, and ultimately death.

Photo 36. Withered appearance of a *Koeleria vallesiana* plant in the Sierra de Baza (Author: José Miguel Barea).

OTHER FACTORS OF HABITAT DEGRADATION

Currently, the impact of changing land use (e.g. pine plantations, urban infrastructure) on the habitats of *P. williamsi* must currently be regarded as a relatively minor threat, given that all extant populations inhabit territories legally protected against major land-use changes in natural environments. However, this has not always been the case, as the Andalusian Law on Protected Areas was only enacted in 1989 and the Natura 2000 network came into effect in 1992 (92/43/EEC). Prior to these dates, several impacts can be identified, including the accelerated expansion of pine plantations, which at higher elevations usurped thousands of hectares of prime habitat for this and other mountain butterfly species. This was particularly severe in the Sierra de Baza and Sierra de los Filabres, though also in Sierra Nevada. Across these and other Andalusian mountains, large expanses of pine stands were planted between the 1930s and 1980s, many of them at elevations once formed part of the habitat of *P. williamsi*.

In addition, since the mid-1960s, the Sol y Nieve ski resort (Sierra Nevada) has been under development. Today, this has resulted in the construction of an urban complex comparable in size to a small town (Prado Llano, between 2,100 and 2,300 m a.s.l.), along with extensive works for slope preparation and ski lift installations. At the time, this had a considerable impact on *P. williamsi* populations that are now extinct. That said, while the impact of the ski resort has been very significant, it must nonetheless be considered highly localized in the broader context of the historical distribution of this species in Sierra Nevada.

ISOLATION AND FRAGMENTATION

Pseudochazara williamsi is a stenothermal species and, consequently, is closely associated with environmental conditions that are naturally distributed in a fragmented way. This, combined with the environmental pressures outlined in previous sections, results in populations of this butterfly naturally occurring in an isolated and fragmented pattern as described in section 5. Such isolation has led to differentiation among populations (Leraut, 2016) and disruption of gene flow. In the absence of more detailed molecular studies, it is reasonable to expect that most populations of this species exhibit reduced genetic variability. Many organisms associated with mountain environments experience range contractions and expansions depending on climatic cycles, while others can increase their fitness under more favorable conditions (See Zamora *et al.*, 2022 for the specific case of *Juniperus communis* L. in the Sierra Nevada). In the case of *P. williamsi*, however, the current degree of fragmentation makes connectivity between populations highly unlikely and consequently prevents the genetic exchange that is essential for their long-term persistence.

Photo 37. Impact of the development of the Sol y Nieve Ski resort on the Veleta north slope (Author: José Miguel Barea).

12. SPECIES ACTION PLAN

This chapter discusses the possible actions, which, if implemented over the five-year period 2026-2031, could significantly improve the conservation status of the species. In each section we discuss the actions that are necessary and where appropriate, describe them for the different parts of the species' geographic range. The actions have been discussed and agreed with representatives of list conservation institutions.

It is essential to monitor the populations of the species because the effectiveness of the proposed measures would only be evident if the butterfly population trends are positive. The main goal is to propose positive interventions, avoiding negative interventions wherever possible. Public awareness actions are also important to inform civic society of the importance of the species and the main goals of conservation measures.

The measures outlined here are for experimental purposes only and must be monitored to enable us to determine whether any of these possible solutions can be redefined and applied elsewhere or more extensively in the mountain ranges. It is necessary to highlight the complexity involved in managing Mediterranean high-mountain environments, where ecosystem evolution is slow due to extreme conditions and the physiological limitations of the organisms involved. Consequently, the most favorable outcomes are expected in the medium and long term.

Photo 38. Example of an livestock exclusion fence installed in the Sierra Nevada high mountain to protect *Agriades zullichi* and *Polyommatus golgus* (Author: José Miguel Barea).

LEGAL PROTECTION

It is necessary to include this species in the Andalusian Catalogue of Protected Species with the category 'En Peligro' (in danger of extinction).

PROTECTED AREAS

Currently, most populations are located in areas that enjoy an adequate level of protection. In the case of the Sierra Seca population, the unprotected portion of the territory will be covered by a new Natural Park in the northern part of the province of Granada (Sierra de La Sagra Natural Park), which will also cover the Sierras de La Sagra and de la Guillimona and is currently in the approval process. In the case of the known localities in the Sierra de Gádor, it is recommended that some type of ecological reserve be established to help buffer potential impacts on the area.

CONSERVATION MEASURES

The main habitat actions for the conservation of the species can be summarized as follows:

Installation of livestock exclusion fences

The installation of temporary enclosures measuring at least 20 × 20 meters (400 square meters) must be planned for the populations at Pico del Almirez (Sierra Nevada), Pico del Buitre (Sierra Nevada), and Calar de Rapa (Sierra de Baza). This measure aims to prevent the impacts of livestock on the trophic resources of the larvae, as well as to promote the growth of plant species with potential as nectar sources. These fences will need to be monitored to ensure they are opened if early shrub encroachment occurs within their boundaries. They should also be installed with the option to remove the enclosures during periods of maximum snowfall, as the weight of snow can cause significant structural damage.

In the case of Sierra Seca, the installation of a larger fence is urgently needed, encompassing most of the area occupied by the species. This task is challenging due to difficult access caused by the current poor condition of the access track.

Creating butterfly oases

This measure complements the installation of livestock exclusion fences and involves the active planting of *Koeleria* spp., *Scabiosa turolensis*, *Thymus serpylloides* subsp. *serpylloides*, *Jurinea humilis*, *Carduus* spp., and *Eryngium* spp. The recommended propagation technique should be direct sowing, which would reduce production costs. In specific cases when plantations are the recommended technique, the plants will be produced within the network of Botanical Gardens of the Junta de Andalucía under conditions similar to those they will encounter at the planting sites. The provision of water is essential, at least during the establishment phase and especially in mid-summer. These butterfly oases should be protected with livestock exclusion fences to prevent high rates of predation by both wild and domestic ungulates. This task should be led by professionals, although the involvement of local volunteer groups is recommended.

Nature-based Solutions

Nature-based Solutions (NbS) are strategies that utilize ecosystems and natural processes to address social, environmental, and economic challenges in a sustainable way. Their goal is to protect, sustainably manage, or restore ecosystems to provide benefits both for biodiversity and for people. These solutions aim to be multifunctional, resilient, and adaptable to climate change, providing ecosystem services while enhancing communities' capacity to cope with environmental risks.

In the case of *P. williamsi*, the priority is to implement solutions that help mitigate the effects of climate change, promote flowering processes in the mountains, and enhance the redistribution of water resources. In this regard, Sierra Nevada holds an extensive network of traditional irrigation channels (*acequias*) that collect water from high-mountain springs during snowmelt and redistribute it across its dry slopes. This network of canals reached its peak development during the Arab period, primarily as support for mountain agriculture and livestock farming, and has been maintained to our days. Even when the '*acequia*' carries no water, it retains moisture, fostering a significantly higher abundance of flowers along its course compared to non-irrigated areas. This network represents a true nature-based solution, although it has gradually fallen into disuse. However, in recent decades, the regional government and the National Park managers have been making considerable efforts toward its restoration and maintenance. Notably, in 2025, one of the main known populations of *P. williamsi* was discovered associated with one of the most important traditional irrigation channels (irrigation channel of Bérchules-Trevelez). In this regard, we believe it is highly advisable to ensure the proper functioning of this specific traditional irrigation channel, which would translate into support for the irrigation community and collaboration in cleaning tasks, especially in the catchment areas, which are the ones that best guarantee adequate water flow.

Captive Breeding

Captive breeding could represent a useful tool for improving the conservation status of threatened species (New, 1997). In the case of *Pseudochazara williamsi*, it is proposed to collect eggs from gravid females (originating from an area where the population size allows for the extraction of individuals) and to rear them under environmental conditions as similar as possible to those the species experiences in the wild. To this end, the facilities of the Hoya de Pedraza Botanical Garden (Sierra Nevada), which is part of the Network of Botanical Gardens of the Regional Government of Andalusia, are proposed for use. The facilities of this garden, located at 1,900 m a.s.l., provide suitable conditions to optimize the likelihood of success of the initiative. The release of individuals should be carried out during the final larval stages or even as adults. This action should also be undertaken with an explicitly experimental approach.

Photo 39. Ancient irrigation channel at 2,500 m. a.s.l. in the south slope of Sierra Nevada, very close to one of the most important populations of *P. williamsi* (Author: José Miguel Barea).

SURVEY AND MONITORING

Establish long-term monitoring areas

It is important to continue the work initiated in 2023 and maintain the network of sites subject to long-term ecological monitoring. This activity will allow for an early warning signal in the event of population declines in those areas, which are precisely those that host the best-known populations. The linear transect method is ideal for this purpose, although it can also be complemented with 15-minute count surveys. A limitation of our work that should be addressed in future monitoring is that we only conducted one visit per year. In the future, we consider that each of these sites should be visited at least three times during each flight season.

Photo 40. Typical habitat of *P. williamsi* in one of the sites proposed for a long-term survey (Author: Harry Clarke).

Additionally, we consider it important to carry out capture-mark-recapture studies in certain key areas, such as Pico del Buitre (Sierra Nevada) and Cerro del Almirez (Sierra Nevada). These areas are accessible, which facilitates this type of study, usually too intensive to plan in hard-to-reach locations. Such studies would enable accurate population size estimates to be made and the degree of mobility between sub-populations to be determined. If transect or 15-minute counts are undertaken on the same sites at the same time, these can be calibrated against capture-mark-recapture population estimates. Such a calibration means that population estimates on other less accessible sites can then be made from transect or 15-minute counts.

The search for larvae in their final developmental stage has not yet been explored as a monitoring tool. Nighttime surveys are needed to investigate the possibility of developing a census methodology based on this critical life stage. This task is also going to confirm definitively which grass species is the host plant.

Conduct intensive surveys

The intensive search for new populations must continue. This requires increased survey effort in specific areas of Sierra Nevada currently considered under-sampled, including the headwaters of the Trevélez and Poqueira rivers, as well as the ridges connecting Picón de Jeres with Puerto de la Ragua. In the Sierra de Baza, all high plateaus (*calares*) should be surveyed, as any area above 2,000 m a.s.l. may host populations. Similarly, new populations must be sought in Sierra Seca to provide hope in a region where only a single population is currently known. Regarding sites where the species is probably extinct, our proposal focuses on conducting new surveys in Sierra de María, Guillimona, Revolcadores, and La Sagra, as the likelihood of a positive result in other locations is virtually nil.

Promote citizen science campaigns

It is proposed to launch a campaign to disseminate images and information about *P. williamsi* among hikers and naturalists, providing a contact point for submitting photos, locations, and additional information. Furthermore, volunteer teams should be trained to contribute to conducting censuses, intensively searching for new populations, and even assisting in the installation and maintenance of plant species beneficial for *P. williamsi*.

Research

In addition to the long-term ecological monitoring of populations, it is important to address the following research priorities:

- **Study of thermal survival thresholds**: understanding the thermal thresholds of different species is essential to assess their degree of exposure to stressors associated with climate change (Pallares *et al.*, 2025). In the case of *P. williamsi*, laboratory studies are required to advance this area of knowledge through experimentation with larvae. Whilst such research is very desirable it is also particularly complex due to the intrinsic scarcity of the species and, consequently, the inherent difficulty of obtaining a sufficient number of larvae to conduct the experiments under the required conditions. The capture of a gravid female in one of the few localities with an adequate number of individuals could be considered as an alternative.
- **Identification of climatic refugia**: in line with the above, it is important to determine in detail the specific areas of the mountain that maintain distinct and cooler microclimatic conditions compared to the surrounding environment. The identification of climatic refugia is a key activity within the framework of a conservation strategy for biological resources in mountain regions (Ursul *et al.*, 2024).
- **Study of larval host plants**: it is necessary to search for late-instar larvae in order to confirm with absolute certainty the host plant species of *P. williamsi*.
- **Study of pollen sources**: as previously noted, nectar sources are likely to play a decisive role in explaining the population dynamics and size of *P. williamsi*. Detailed research is needed to determine which species are selected by *P. williamsi* and whether their use depends on their availability in the environment. In other words, a comprehensive study of the floristic community is required to establish use-versus-availability analyses.
- **Impact of livestock on host plants and nectar sources**: the presence or absence of livestock influences the habitat properties of *P. williamsi*. A detailed study is needed on grazing pressure as well as on the consumption rates of *Koeleria* spp. and of the species' main nectar sources.
- **Genetic analysis of populations**: aimed at determining levels of genetic variability and their relationship with potential conservation issues.
- **Monitoring of management actions**: the monitoring of proposed actions is essential to assess their effects, to identify which measures are effective and which are not, and to evaluate the relationship between costs and benefits.
- **Installation of devices for monitoring climatic conditions at a detailed scale**: given the scarcity of multiparametric stations in high mountain areas, the installation of sensors (e.g. dataloggers) is considered essential to record climatic conditions in specific control zones where *Pseudochazara williamsi* inhabits. This will allow for a comprehensive understanding of these parameters, with significant implications for conservation and as a complement to other proposed monitoring initiatives.

PUBLIC AWARENESS

The process of dissemination and communication is a key tool in the development of an effective strategy for the conservation of the natural environment and threatened species, and must therefore be integrated from the initial design stages of conservation plans. In this case, the following set of activities is proposed:

- **Outreach conferences for the general public**: these will be directed at people living within the area of influence of the habitats where this species occurs. They will be designed with a clear outreach perspective and will aim to convey the importance of conserving this and other species of the Mediterranean high mountains.
- **Training sessions for administrative staff with environmental competences and protected area managers**: these will target technicians and environmental managers. It is necessary to articulate, through these professionals, the enforcement policy actions required to ensure the conservation of the species and the habitats it occupies. Participation of rangers in delivery of the proposed actions will also be essential in order to ensure the success of this action plan.
- **Participation in scientific-technical forums**: this will include the publication of scientific articles and participation in conferences, symposia, and workshops on related topics.
- **Development of outreach materials**: the preparation of a leaflet is proposed, which will also request information on occasional records that mountain users may provide. In addition, the development of interpretation panels to be installed in the field is suggested. Two panels should be installed in Sierra Nevada, one in Sierra de Baza, and another in Sierra Seca. These panels will explain the presence of the species, its ecological importance, and the critical situation it faces, while also providing measures that visitors may adopt during their stay (e.g., reporting new records, avoiding trampling, or preventing environmental degradation along their route). The publication of a dissemination article in a national Spanish magazine is also planned for 2026.

PLAN IMPLEMENTATION

Implementation of this action plan can only be overseen and delivered by organisations based in Spain but other organisations from outside the target area (e.g. European Butterfly Group and Butterfly Conservation Europe) can also make a significant contribution.

Regional Ministry of Sustainability and Environment (Junta de Andalucía) are best placed for the coordinating role, as they are either the lead or the partner in all the actions in the table below. The essential framework for the development of the proposed action should be the 'High Mountain Species Recovery and Conservation Plan of Andalusia'. This plan was approved by the Agreement of March 13, 2012, of the Andalusian Governing Council. It establishes protection measures for 56 plant species and five invertebrate fauna species, most of which are endemic to the Baetic Mountain ranges of Andalusia. The 'High Mountain Species Recovery and Conservation Plan of Andalusia' serves as the guiding framework for efforts aimed at achieving or maintaining a favourable conservation status of the target species. To this end, it defines the purpose and general objectives, the scope of application, and the conservation measures.

The Regional Ministry of Sustainability and Environment (Junta de Andalucía) proposes to gather together a panel of representatives of stakeholder groups and government agencies with a biennial frequency. The purpose of the group will be to review actions undertaken to conserve *P. williamsi*.

Suggested panel participants are:

Name	Role
Regional Ministry of Sustainability and Environment (Junta de Andalucía)	Coordination of actions and main responsibility for monitoring them and for the ecological monitoring of the species itself.
Research institutions	Support for the scientific validation of the proposed work and promotion of research initiatives related to the species.
SOCEME (Society for the Conservation and Study of Butterflies in Spain)	Support for dissemination and communication actions.
European Butterfly Group	Provide technical advice, contribute to research, survey and monitoring as required.
Butterfly Conservation Europe	Provide technical advice, contribute to research, survey and monitoring as required.
Local communities and stakeholders	Support for the actions proposed here in relation to the processes of governance and custody of the territory.

SPECIES ACTION PLAN SUMMARY

ACTION	PRIORITY (High, medium, low)	PARTNERS	TIMESCALE
Legal protection			
Include this species in the Andalusian Catalogue of Protected Species with the category 'En Peligro' (in danger of extinction).	High	RMSE (JA)	2026-2027
Protected areas			
Declaration of a Natural Park in La Sagra and Guillimona mountain ranges, and the currently unprotected portion of the Sierra Seca.	High	RMSE (JA)	2026 to 2030
Establishment of an ecological reserve in the area where the *P. williamsi* populations are located in the Sierra de Gádor.	High		
Conservation measures			
Installation of livestock exclusion fences	High	RMSE (JA), EBG, BCE and LC/S.	2026 to 2030
Creating butterfly oases	High		
Nature-based Solutions	Medium		
Captive breeding	Medium	RMSE (JA)	2026 to 2028
Survey and monitoring			
Establish long-term monitoring areas	High	RMSE (JA), EBG and BCE	2026 to 2030
Conduct intensive surveys	High		
Promote citizen science campaigns	High		
Research			
Study of thermal survival thresholds	Medium	RMSE (JA), RI, EBG and BCE	2026 to 2031
Monitoring of management actions	High		
Study of larval host plants	High		
Study of pollen sources	High		
Impact of livestock on host plants and nectar sources	High		
Genetic analysis of populations	Medium		
Identification of climatic refugia	Medium		
Installation of devices for monitoring climatic conditions at a detailed scale	Medium		
Public awareness			
Outreach conferences for the general public	High	RMSE (JA), RI, SOCEME, EBG and BCE	2026 to 2031
Training sessions for administrative staff with environmental competences and protected area managers			
Participation in scientific-technical forums Development of outreach materials	Medium		

RMSE (JA): Regional Ministry of Sustainability and Environment (Junta de Andalucía)
EBG: European Butterflies Group
BCE: Butterfly Conservation Europe
LC/S: local communities/stakeholders
RI: research institutions.
SOCEME: Society for the Conservation and Study of Butterflies in Spain

SPECIES ACTION PLAN FOR THE NEVADA GRAYLING

Pseudochazara williamsi

Current Situation

Species Action Plan Objectives

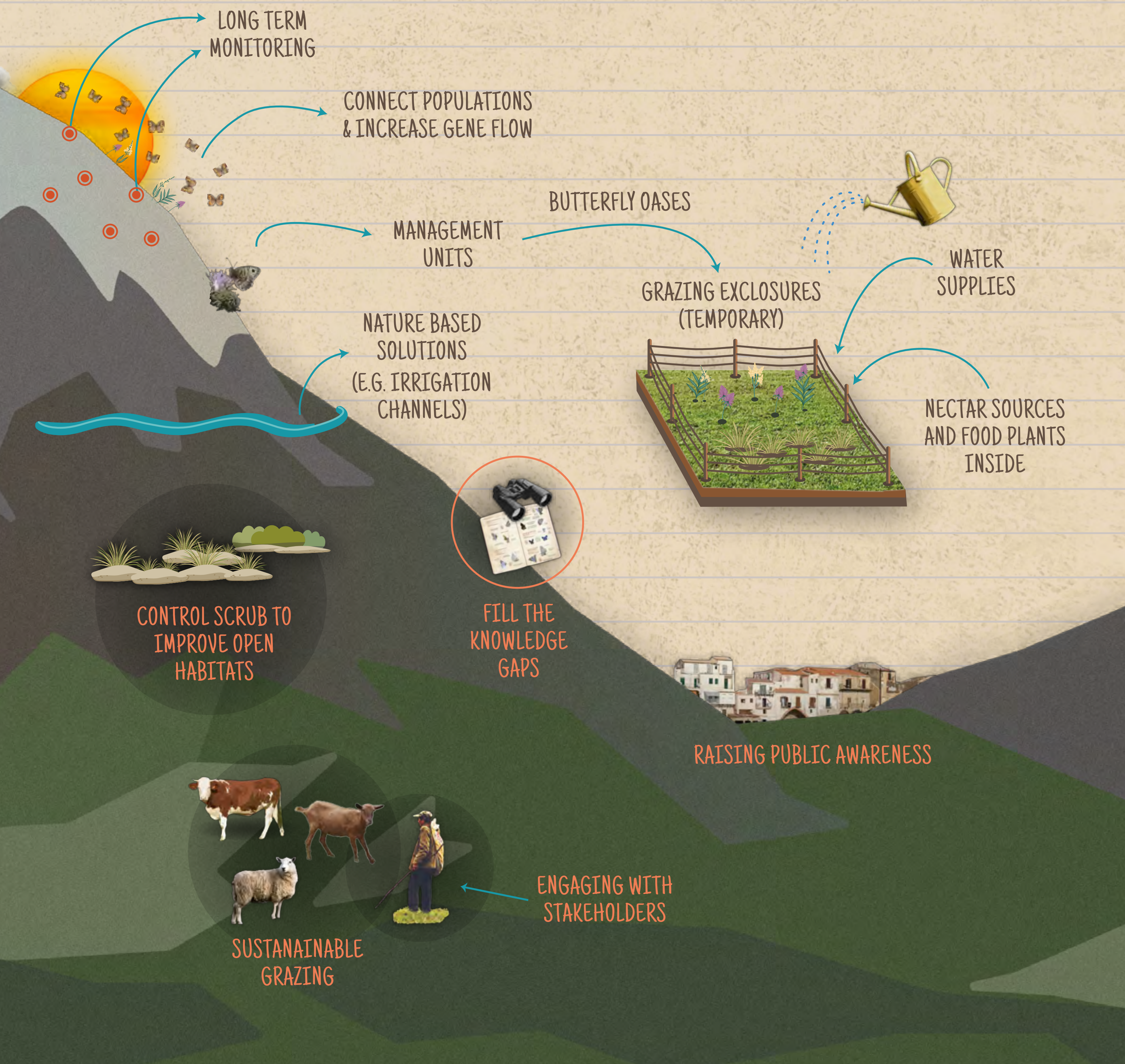
CROSS-FUNCTIONAL ASPECTS OF THE WORK FRAMEWORK

ADAPTIVE MANAGEMENT

GOVERNANCE

MULTIDISCIPLINARY WORK

COLLABORATION BETWEEN SECTORS INVOLVED



OTHER BUTTERFLY SPECIES THAT MAY BENEFIT FROM THIS ACTION PLAN

The measures proposed in this action plan have been designed to also benefit other threatened endemic butterfly species of conservation interest that share the same habitats as *P. williamsi*:

Polyommatus golgus: an endemic species of southeastern Iberia whose distribution overlaps with that of *P. williamsi* in Sierra Nevada and Sierra Seca. In recent history, *P. golgus* shared habitats with *P. williamsi* in the Sierras de la Guillimona and La Sagra. In Guillimona, as has occurred with *P. williamsi*, *P. golgus* populations appear to have disappeared, whereas in Sierra de La Sagra, *P. golgus* still maintains large populations at higher altitudes on this mountain. *P. golgus* would benefit from limiting overgrazing in Sierra Seca, while in Sierra Nevada, the promotion of nectar sources and protection from localized livestock pressure also constitute suitable habitat improvement measures (Munguira *et al*., 2015). *Polyommatus golgus* is listed in Annexes II and IV of the Habitats Directive (92/43/EEC).

Agriades zullichi: a strict endemic species of Sierra Nevada, for which approximately 39 populations have been described (Barea-Azcón *et al*., 2014). In at least two of these populations - the two easternmost ones - it overlaps with localities currently inhabited by *P. williamsi*. Particularly important for this species could be the promotion of nectar sources and the limitation of shrub encroachment on Pico del Buitre (Munguira *et al*., 2015).

Parnassius apollo: populations of this butterfly in Andalusia are experiencing a marked decline (Barea-Azcón *et al*., 2025), and currently, its distribution only overlaps with that of *P. williamsi* in Sierra Nevada. Historically, both species shared flight areas in Sierra de Gádor (where *P. apollo* is now extinct), Sierra de Baza (where *P. apollo* has also disappeared from localities where *P. williamsi* occurs), Sierra de los Filabres (where both taxa are considered extinct), and Sierra de María (where *P. williamsi* may also be regarded as probably extinct). The measures proposed in this Action Plan for controlling scrub expansion and promoting nectar sources are presumed to be beneficial for both species. *Parnassius apollo* is listed in Annex IV of the Habitats Directive (92/43/EEC).

***Erebia hispania* Butler, 1862**: a strict endemic species of Sierra Nevada that historically shared numerous flight areas in this mountain range with *P. williamsi*. Currently, the reduction in *P. williamsi* populations has limited the areas of overlap. The main areas where this overlap still occurs are found at the head of the Trevelez River valley and on some slopes, ridges and peaks located between Picón de Jeres and Puerto de la Ragua. As in the case of *P. apollo*, this species will benefit from the habitat improvement measures proposed for *P. williamsi*, particularly those related to the enhancement of nectar resources, as well as from nature-based solutions such as the restoration of traditional mountain irrigation systems.

***Aricia morronensis* (Ribbe, 1910)**: an Iberian endemic species that occurs within the same area as *P. williamsi* in Sierra Nevada and Sierra Seca. This lycaenid species will undoubtedly also benefit from actions aimed at increasing the availability of floral resources. In the case of Pico del Buitre, actions aimed at limiting scrub expansion would also prove favorable for *A. morronensis*.

Photo 41. *Polyommatus golgus* in Sierra Nevada, a protected species by the Habitat Directive and the Spanish and Andalusian Endangered Species Act (Author: José Miguel Barea).

13. ACKNOWLEDGEMENTS AND REFERENCES

ACKNOWLEDGMENTS

The Species Action Plan for *Pseudochazara williamsi* is an output of a partnership project between the Andalusian Government (Ministry of Sustainability and the Environment), the European Butterflies Group (EBG) of Butterfly Conservation and Butterfly Conservation Europe. The Society for the Conservation and Study of the Butterflies in Spain (SOCEME) has also brought their support.

Together with the authors the following persons helped with the field work, and their contribution is gratefully acknowledged:

Dave Plowman, John Austin, Mike Bailey, Robert Bleay, Andrew Lipczynski, Kevin Tolhurst, Keith Woonton, Walter Woonton, Dave Wright, Maria Luisa Campón Amado, Elsa Sendra Felipe, Alberto Tinaut, Enrique Ledesma Ruiz and Sara Castro Cobo.

We also express our gratitude to the following for their generosity in sharing their information: Miguel Munguira, Enrique García-Barros, Roger Vila, Antonio Ortiz, Ángel Romero, F. Javier Pérez López, Juan Francisco Martínez, Manuel López, Paco Rodríguez 'Faluke', Yeray Monasterio, Andrew Teed and Alberto Tinaut.

David Jutzeler kindly provided us with the photographs of the preimaginal stages that appear in this document and Emilio González provided us with a picture of the habitat in Sierra de Gádor. We are also grateful to Alexey Prozorov and Günter C. Müller for providing us with photographs of specimens from his collection.

Francisco Bruno Navarro shared his knowledge of the plant species on which *Pseudochazara williamsi* depends as nectar sources.

To Mike Prentice and the European Butterflies Group, for their unconditional support in promoting field campaigns and the publication of this Action Plan.

REFERENCES

Aistleitner, E. (2016). Zur Kenntnis der Schmetterlingsfauna der Iberischen Halbinsel I. Topografie, Geologie, Klima und Vegetation. Daten der Tagfalter aus den Geländeprotokollen zwischen den Jahren 1970 bis 2013 (Insecta, Lepidoptera, Papilionoidea). *Linzer Biologische Beiträge*, 48(2): 907-978.

Barea Azcón, J.M. (2024). *Conservación de las mariposas diurnas en Sierra Nevada (SE España) bajo un escenario de cambio global*. Tesis Doctoral. Granada: Universidad de Granada. [https://hdl.handle.net/10481/90686]

Barea-Azcón, J.M., Benito, B.M., Olivares, F.J., Ruiz, H., Martín, J., García, A.L. & López, R. (2014). Distribution and conservation of the relict interaction between the butterfly *Agriades zullichi* and its larval foodplant (*Androsace vitaliana nevadensis). Biodiversity and Conservation*, 26(4): 927-944.

Barea-Azcón, J.M., Tinaut, A. Olivares, F.J., del Río, J., González, E. & Galiana, M. (2025). El declive de la mariposa apolo en Andalucía. *Quercus*, 474: 34-40.

Bock, A., Sparks, T.H., Estrella, N., Jee, N., Casebow, A., Schunk, C., Leuchner, M. & Menzel, A. (2014). Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. *Global Change Biology*, 20: 3508-3519.

Clarke, H. E. (2024). A checklist of European butterfly larval foodplants. *Ecology and Evolution*, 14(1), e10834.

de Souza, R. B. & Guimarães, J. R. (2022). Effects of avermectins on the environment based on its toxicity to plants and soil invertebrates-a review. *Water, Air, & Soil Pollution*, 233(7): 259.

Eitschberger, U. & Steiniger, H. (1973). Eine neue Rasse von *Pseudochazara hippolyte* (Esper, 1783) aus Andalusien (Lep. Satyridae). *Atalanta*, 4: 211–217.

García-Barros, E., Munguira, M.L., Stefanescu, C. & Vives-Moreno, A. (2013). *Lepidoptera: Papilionoidea*. Fauna Iberica (vol. 37). Museo Nacional de Ciencias Naturales (CSIC). 1.213 pp.

Garre, M., Lencina, F., Rubio, R. M., Guerrero, J. J., Albaladejo, A., Abad, C., & Ortiz, A.S. (2025). An annotated checklist of the Papilionoidea of the Murcia region (Spain) with new records, distribution and biological data (Lepidoptera: Papilionoidea). *Ecologica Montenegrina*, 89: 111-139.

Gil-T, F. (2016). *Pseudochazara williamsi* (Romei, 1927): distribución actualizada, corregida, y ampliada con nuevas localidades (Lepidoptera, Nymphalidae, Satyrinae). *Revista gaditana de Entomología*, 7(1), 429-439.

Gil-T, F. (2017). Compared morphology and distribution of the taxa described of *Pseudochazara williamsi* (Romei, 1927) [= "*Pseudochazara hippolyte*" Esper from Spain]. Are they valid subspecies or only the result of phenotypic plasticity (ecological forms)? *Atalanta*, 48(1-4): 188–196

Gil-T, F. & Ibañez, S. (2009). New localities for *Polyommatus sagratrox* (Aistleitner, 1986) and *Pseudochazara hippolyte* (Esper, 1783) in Granada province (S. Spain), with considerations on the taxonomic status of the first taxon. *Atalanta*, 40(1/2): 185-190.

Jutzeler, D. & Bros, E. D. (1995). Observations on *Pseudochazara hippolyte williamsi* (Romei, 1927) and *Erebia hispania hispania* (Butler, 1868) from Sierra Nevada (Andalousia, Southern Spain)(Lepidoptera: Nymphalidae, Satyrinae) in the natural habitat and in rearing. *Linneana Belgica*, 15(4).

King, K.C. & Schultz, C.B. (2024). Fecundity without nectar is insufficient for the persistence of a blue butterfly. *Oecologia*. https://doi.org/10.1007/s00442-024-05609-9

Kudrna, O., Harpke, A., Lux, K., Pennerstorfer, J., Schweiger, O., Settele, J. & M. Wiemers (2011). *Distribution atlas of butterflies in Europe*. Halle a.d. Saale (Society for Butterfly Conservation e.V.). 576 pp.

Kudrna, O., Pennerstorfer, J. & Lux, K. (2015). *Distribution atlas of European butterflies and Skippers*. Schwanfeld (Wissenschaftlicher Verlag PEKS). 632 pp.

Kühn, I. (2007). Incorporating spatial autocorrelation may invert observed patterns. *Diversity and Distributions*, 13: 66-69.

Lebeau J., Wesselingh, R.A. & Van Dyck, H. (2018). Impact of floral nectar limitation on life-history traits in a grassland butterfly relative to nectar supply in different agricultural landscapes. *Agriculture, Ecosystems and Environment,* 251: 99–106.

Leraut, P. (2016). *Butterflies of Europe and Neighbouring Regions*. N. A. P. Editions. 1,100 pp.

Macià, R., Caballero-López, B. & Masó, G. (2017). Designació dels lectotipus de *Pseudochazara williamsi* (Romei, 1927)(Lepidoptera: Nymphalidae: Satyrinae) i *Carcharodus tripolinus* (Verity, 1925)(Lepidoptera: Hesperiidae: Pyrginae) de la collecció d'Ignasi de Sagarra dipositada al Museu de Ciències Naturals de Barcelona. *Butlletí de la Institució Catalana d'Història Natural*, 81: 19-21.

Munguira, M.L., Barea-Azcón, J.M., Castro, S., Olivares, J. & Miteva, S. (2015). *Species Recovery Plan for the Zullichi's blue* (Agriades zullichi). Butterfly Conservation Europe. 33 pp.

Munguira, M.L., Castro, S., Barea-Azcón, J.M., Olivares, J. & Miteva, S. (2015). *Species Recovery Plan for the Sierra Nevada Blue* (Polyommatus (Plebicula) golgus). Butterfly Conservation Europe. 32 pp.

Navrátilová, M., Raisová Stuchlíková, L., Skálová, L., Szotáková, B., Langhansová, L. & Podlipná, R. (2020). Pharmaceuticals in environment: the effect of ivermectin on ribwort plantain (*Plantago lanceolata* L.). *Environmental Science and Pollution Research.*, 27, 31202-31210.

New, T.R. (1997). *Butterfly conservation* 2nd Edition. Oxford University Press. 248 pp.

Olivares, J. (2002). Analyse des populations connues de *Pseudochazara hippolyte* (Esper, 1784) dans le Sud-Est ibérique (Lepidoptera: Nymphalidae, Satyrinae). *Linneana Belgica*, 7 (XVIII): 361-369.

Olivares, J., Barea-Azcón, J.M., Pérez-López, F.J., Tinaut, A. & Henares, I. (2011). *Las mariposas diurnas de Sierra Nevada*. Consejería de Medio Ambiente, Junta de Andalucía. 512 pp.

Pallarés, S., Mammola, S. & Sánchez-Fernández, D. (2025). Adapted yet at risk: the paradox of thermotolerant species in a warming world. *Global Change Biology*, 31, no. 9: e70500.

Pérez-Luque, A.J., Pérez-Pérez, R., Aspizua, R., Muñoz, J.M. & Bonet, F.J. (2016). Climate in Sierra Nevada: present and future. Pp.: 27-31. In: Zamora, R., Pérez-Luque, A.J., Bonet, F.J., Barea-Azcón, J.M. & Aspizua, R. (editors). (2016). *Global Change Impacts in Sierra Nevada: Challenges for Conservation*. Consejería de Medio Ambiente y Ordenación del Territorio. Junta de Andalucía.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190: 231-259.

Pollard, E. & Yates, T.J. (1994). *Monitoring butterflies for ecology and conservation*. Chapman & Hall, London. 292 pp.

R Core Team (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Romei, E. (1927). Notes of collecting in Spain in 1925-1926. *The Entomologist's Record and Journal of Variation*, 39(10): 136-138.

Tarrier, M. (1993). La Sierra de La Sagra: un écosystème-modèle du refuge méditerranéen (Lepidoptera: Rhopalocera, Zygaenidae). *Alexanor*, 18(1): 13-42.

Ursul, G., Mingarro, M., Romo, H., Cancela, J.P. & Wilson, R.J. (2024). Refugia from climate change, and their influence on the diversity and conservation of insects. Pp.: 329-352. In: González-Tokman, F. & Dátilo, W. (2024). Effects of Climate Change on Insects: *Physiological, Evolutionary, and Ecological Responses*: 329.

Van Swaay C.A.M. & Warren M. S. (1999). *Red Data book of European butterflies (Rhopalocera)*. Nature and Environment, No. 99, Council of Europe Publishing. Strasbourg. 260 pp.

Van Swaay C.A.M., Cuttelod A., Collins S., Maes D., Lopez Munguira, M., Šašić M., Settele J., Verovnik R., Verstrael T., Warren M., Wiemers M. & Wynhoff I. (2010). *European Red List of Butterflies*. Luxembourg: Publications Office of the European Union. 47 pp.

Van Swaay, C.A.M., Ellis, S. & Warren, M. (2025)a. *Pseudochazara williamsi*. *The IUCN Red List of Threatened Species 2025*. Accessed on 27 September 2025.

Van Swaay, C., Warren, M., Ellis, S., Clay, J., Bellotto, V., Allen, D.J. & Trottet, A. (2025)b. *Measuring the pulse of European biodiversity using the Red List. European Red List of Butterflies*. Brussels, Belgium: European Commission. 80 pp. doi.or/10.2779/935927

Verovnik, R. & Wiemers, M. (2016). Species delimitation in the Grayling genus *Pseudochazara* (Lepidoptera, Nymphalidae, Satyrinae) supported by DNA barcodes. *ZooKeys*, (600): 131.

Wallisdevries, M.F., Van Swaay, C.A.M. & Plate, C.L. (2012). Changes in nectar supply: a possible cause of widespread butterfly decline. *Current Zoology,* 58(3): 384–391.

Weiss, J.C. (1980) Le genre *Pseudochazara* de Lesse en Europe et un Afrique du Nord, description d'une sous espèce nouvelle de *P. hippolyte* Esper. *Linneana Belgica*, 8(3): 98–108.

Wiemers, M., Balletto, E., Dincă, V., Fric, Z. F., Lamas, G., Lukhtanov, V., Munguira, M.L., Van Swaay, C. A. M., Vila, R., Vliegenthart, A., Wahlberg, N. & Verovnik, R. (2018). An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea). *ZooKeys,* 81: 9–45.

Wiemers, M., Chazot, N., Wheat, C. W., Schweiger, O. & Wahlberg, N. (2020). A complete time-calibrated multi-gene phylogeny of the European butterflies. *Zookeys*, 938: 97-124.

Worms, C.G.M. (1976). *Plebicula golgus* Hübner and other butterflies in the Sierra Nevada, July, 1975. *Entomologist's Record and Journal of Variation*, 88: 59-63.

Zamora, R., Barea-Azcón, J.M., Pérez-Luque, A.J., García, D., Aspízua, R. & Cano-Manuel, F.J. (2022). *Los enebrales de la alta montaña de Sierra Nevada: conservación y restauración*. Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible (Junta de Andalucía)-Universidad de Granada. 89 pp.

Photo 42. *Pseudochazara williamsi* nectaring on *Jurinea humilis* in the Sierra Nevada (Author: José Miguel Barea).

SPECIES ACTION PLAN FOR THE NEVADA GRAYLING

Pseudochazara williamsi

Junta de Andalucía | Consejería de Sostenibilidad y Medio Ambiente

SOCEME

Butterfly Conservation Europe

European Butterflies Group