Rural abandonment and its impact on biodiversity: Ecology and dynamics of butterfly populations at Picos de Europa National Park, Spain

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This thesis is submitted for the degree of Doctor in Philosophy in Environmental Science

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Abstract

Mountains occupy around 25% of Earth's land but they hold disproportionate amounts of biodiversity. Southwestern European mountain ranges harbour one of the highest butterfly biodiversity of the continent, but they have not been extensively long-term monitored due to the difficult terrain and weather conditions. Nowadays, the abandonment of traditional land uses is giving rise to a succession towards forest habitats in these mountains. Coupled to these land use changes, climate change is predicted to severely affect mountain ecosystems.

The general aim of this thesis was to investigate the conservation status of butterflies at Picos de Europa National Park (NW Spain). Overall, we found a rapid decline both on total butterfly numbers and for individual species populations: 45% of butterfly abundance lost and species richness and Shannon diversity declining in the last 14 years. Moreover, 26% of species with sufficient data to assess population trends, showed a significant negative population trend. Using multispecies abundance indicators allowed us to identify the drivers of those declines, with the advance of forests over grasslands due to rural abandonment and warming most likely to be responsible for the decline and re-organisation of butterfly communities. We found an annual increase of mean temperature in the study area of 0.021 ºC in the period 1979-2019, representing an increase of 0.21ºC per decade in the last 40 years. We also explored the patterns of butterfly diversity along elevation, which peaked twice, at lower (150 m) and intermediate elevations (1500 m), and identified the environmental drivers of those patterns. Butterfly diversity was positively affected by near-surface relative humidity and continentality. Butterfly communities composition was affected by abandonment, with a species turnover of 48% after 18 years. Species with higher preference for closed habitats increased their densities as time since abandonment proceeded.

Land abandonment and amplified effects of climate change are acting upon other mountain ranges in Europe (Pyrenees, Carpathian mountains, Balkan mountains and the Alps, among many others). More focus is needed on mountain ecosystems, biodiversity and cultural hotspots, that are undergoing accelerated major changes.

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List of acronyms used

ANOVA – Analysis of Variance
BC – Before Christ
BMS – Butterfly Monitoring Scheme
CAP – Common Agricultural Policy (of the European Union)
CatalanBMS – Catalan Butterfly Monitoring Scheme
CHELSA – Climatologies at high resolution for the Earth's land and surface areas
CTAO – Community preference for open/closed habitats
DEFRA – Department of Environment, Food and Rural Affairs
EUNIS – European Nature Information System
GLMM – Generalized Linear Mixed-effects Models
HPI – Hostplant Specificity Index
IPCC – Intergovernmental Panel on Climate Change
IUCN – International Union for the Conservation of Nature
LIDAR – Light Detection and Ranging
N – North
NE – North East
NMDS – Non-metric multidiomensional scaling
PCA – Principal component analysis
PENP – Picos de Europa National Park
SPI – Species temperature index
SPIc – Community temperature index
STI – Species temperature index
STIc – Community temperature index
TAO – Tancat/Obert in catalan which means Closed/Open.
TRIM – Trends and Indices for Monitoring
UK – United Kingdom
UKBMS – United Kingdom Butterfly Monitoring Scheme
UV – Ultraviolet
W – West
WWF – World Wildlife Fund

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Declaration and funding statement

I declare that this thesis is my own work and has not been submitted in substantially the same form for the award of a higher degree elsewhere.

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Author's contribution in both cases as follow:

Amparo Mora: conceptualisation, experimental design, data collection, analysis and interpretation, writing of the original draft.

Rosa Menéndez: conceptualisation, experimental design review & editing of drafts, supervision.

Andrew Wilby: conceptualisation, experimental design, review & editing of drafts, supervision.

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FOREWORD

Understanding the pressures affecting species population dynamics is central in management, especially when the aim is to conserve biodiversity. Rural abandonment, together with global climate change, are the two main conservation problems faced at Picos de Europa National Park (Northern Spain), a South European mountain range, affecting all the ecosystems and species inside. Very quick changes are reshaping a system that had been traditionally managed for centuries. After working as a conservation biologist in this territory for 22 years, and being part of its rural society, I am deeply concerned about the silent and incredibly fast lost of traditional ecological knowledge with the pass of the elder generation, the last one that has sustained the traditional management of this territory. I could suspect a parallel loss of biodiversity and could witness the long lasting crisis of this rural economy decaying with no other sustainable model proposed instead. I sustain we are losing culture, biodiversity and economic resources altogether. The central aim of this thesis is to investigate the consequences of rural abandonment on biodiversity.

Chapter 1: Introduction and Literature Review

Sooty copper (*Lycaena tytirus*) mating at Güembres (Picos de Europa). Photo: Amparo Mora.

1.1 GLOBAL CHANGE AND BIODIVERSITY DECLINE

Biodiversity loss caused by human actions has reached a critical threshold. Up to 75% of the terrestrial environment has been severely altered and 66% of the ocean area has been also affected (Brondizio *et al.*, 2019). In the last 50 years, human population has doubled, global trade has grown tenfold and there has been a spatial decoupling of production from consumption, and this has had a great influence on landscapes and economies across the globe. The direct drivers of change in nature have been: changes in land and sea use; direct exploitation of organisms; climate change; pollution; and invasion of alien species (Brondizio *et al.*, 2019). Although there is no complete consensus in the scientific community on this catastrophic view of biodiversity decline (Thomas, 2017; Blowes *et al.,* 2024), it is clear that rapid changes are happening, altering biological communities, driving biotic homogenization and population declines, and ultimately species extinctions (Dornelas *et al.,* 2023).

The Living Planet Index, which tracks trends in the abundance of mammals, fish, reptiles, amphibians and birds, showed a 69% decrease between 1970 and 2018 (WWF, 2022). Regarding invertebrates, globally, long-term monitoring data on a sample of 452 invertebrate species indicated an overall decline in abundance of individuals since 1970 (Dirzo *et al.*, 2014). In their cornerstone paper, Hallmann *et al.*, (2017) showed more than 75% decline over 27 years in total flying insect biomass in protected areas in Germany, which has been related to landscape-level drivers (Seibold *et al.*, 2019). Experts like Joseph H. Reichholf or Dave Goulson have documented insect declines for the general public, trying to raise awareness on biodiversity loss (Reichholf, 2020; Goulson, 2021).

Focusing just on Lepidoptera (butterflies and moths), for which the best data are available, there is strong evidence of declines in abundance globally (35% over 40 years) (Dirzo *et al.*, 2014). In Europe, data from existing monitoring schemes, point to a global crisis of butterflies (Fox *et al.*, 2023; Van Strien *et al.*, 2019; Van Swaay *et al.*, 2020). The main drivers, in line with global changes elsewhere, are reported to be habitat loss or degradation, climate change and chemical pollution (Warren *et al.*, 2021).

In Southern Europe, assessments of butterfly population trends have, to date, only been made in Catalonia (NE Spain; Stefanescu *et al.*, 2011a; Stefanescu *et al.*, 2011b), reporting a worrying decline of a substantial component of the butterfly fauna. Stefanescu *et al.*, (2011b) suggest serious population declines in specialist species restricted to mountain areas, likely resulting from a combination of climate warming and habitat loss caused by the abandonment of traditional grazing and mowing. They also found negative trends for generalist species due to an increase in aridity in combination with an increase in the intensification of human land use in lowland areas.

In mountains, drivers of global change take particular forms. Instead of agricultural intensification, which is commonly seen in low lying areas, we tend to see rural abandonment, principally because the difficult topography means that mountainous areas tend not to be amenable to mechanisation. Climate change, also, has particular features on mountains. There is growing evidence that the rate of warming is amplified with elevation (Inouye, 2020; IPCC, 2022; Pepin *et al*., 2015). As a result, the spatial distributions of many species, including plants and butterflies, have shifted to higher elevations in recent decades (Gottfried *et al*., 2012, Wilson *et al*., 2007). Mountains occupy around 25% of Earth's land, but they hold disproportionate amounts of biodiversity: 87% of the world's species of amphibians, birds and mammals (Rahbek *et al*., 2019; Myers *et al*., 2000). Although mountains are predicted to be severely affected by environmental change, observations in these areas are typically sparse; we may not be monitoring areas at a high risk (Pepin *et al*., 2015).

1.2 DRIVERS OF BIODIVERSITY IN MOUNTAINS

Determining the main drivers of mountain diversity is particularly relevant in a context of global change (Brondizio *et al*., 2019) and global insect decline (Wagner, 2020). Disentangling which factors contribute in maintaining mountain biodiversity may give us important clues to help conservation management. Elevational and latitudinal gradients, climate, topography, landscape composition and configuration, as well as historical factors, contribute to mountain biodiversity.

1.2.1 Elevational and latitudinal gradients

Elevation of a territory over sea level can be considered an indirect driver of diversity as it encompasses a wide arrange of environmental factors which vary with elevation, such as changing temperature, air pressure, humidity and UV exposure.

Atmospheric pressure declines with elevation and this is associated with decreasing temperatures (vertical temperature gradient, approximately -0.65°C each 100 metres). This air cooling is constant for 11 kilometres above sea level, where the troposphere (part of the atmosphere directly in contact with the earth) ends (Díaz, 1996).

Humidity also varies with elevation. Although absolute humidity in the air declines with elevation, relative humidity increases because air temperature falls in parallel. Rainfall is also larger in mountains compared to nearby lowlands. This can be explained because winds cool as they rise up along mountain sides. When air rises on the windward side of an orographic barrier, it cools at a rate of 1°C each 100 metres of elevation (dry adiabatic lapse rate). If the air is moist, water condenses at a certain point forming cloud and air cools at a lower rate of 0.6°C /100 metres (wet adiabatic lapse rate), and sinks on the leeward side of the mountain, usually warming with a higher, dry-adiabatic lapse rate (1°C/100 m). Mountain Foehn winds are a kind of dry, relatively warm, downslope wind that occurs in the lee of a mountain range. It is a rainshadow wind that results from the subsequent adiabatic warming of air that has dropped most of its moisture on windward slopes. Foehn winds can raise temperatures by as much as 14°C in just a matter of hours. These effects of elevation on humidity are particularly relevant on mountain barriers near the coast (Cortesi *et al.*, 2014).

The gradients in these abiotic factors (air pressure, air temperature, humidity) strongly influence the distribution of floral and faunal species, and therefore the changes in habitats and communities that is observed as we climb in elevation. The most documented patterns of species richness with elevation are decreasing species richness with increasing elevation and mid-elevation peak of species richness (McCain & Grytnes, 2010). Some of the variation in elevational diversity patterns may be artefactual, due to differences in sampling, scale of study or data analysis. Two common sampling problems tend to occur: sampling effort is not spread evenly over the entire elevational gradient (for example, less sampling at higher locations because of its more challenging sampling logistics), which can be resolved by using rarefaction (Grytnes & Romdal, 2008); a second common sampling problem is sampling only a portion of the mountain elevation gradient, producing a misleading pattern (for example, a mid-elevational peak trend for the whole mountain will appear to be a decreasing if only the upper half of the gradient is sampled) (Nogués-Bravo *et al.*, 2008).

In European mountains, butterfly species richness tends to peak at mid-altitude, with an array of factors proposed to explain the pattern. This may represent the product of temperature and moisture gradients, with peaks occurring in favourable conditions; they may represent the area where low and high elevation species coincide or the elevational pattern of richness might be influenced by a loss of species at low elevations due to human pressures (Gutiérrez, 2009). Diversity peaks at intermediate altitudes have been found for mountain butterflies in several studies in the Iberian Peninsula: Gutiérrez (2009) found that pattern at Sierra de Javalambre, Sierra de Gredos, Sistema Ibérico and Picos de Europa; Wilson *et al.*, (2007) and Álvarez *et al.*, (2024) at Sierra de Guadarrama and Barea-Azcón *et al.*, (2023) at Sierra Nevada.

Elevation richness patterns can also be influenced by the latitudinal location of the sampled mountain. At the global scale, biodiversity declines from the Equator to the Poles (Rohde, 1999; Rosenzweig, 1995; Hillebrand, 2004). The underlying mechanisms leading to this spatial variation are still under debate. Several factors co-vary with latitude: decreasing gradients of energy and water supply (Allen *et al.*, 2002) and biome area (Rosenzweig, 1995) have been proposed as ultimate causes for the latitudinal diversity decline.

Gutiérrez (2009) showed a humped pattern for the relationship between species richness of European butterflies and latitude, increasing from 36° to 42°N, and then decreasing up to the northernmost latitudes in Scandinavia. This pattern can be explained by two potentially complementary mechanisms. Southern peninsulas (Iberian Peninsula, Italian Peninsula and the Balkans) would have acted as refugia for butterfly species during the glacial-interglacial cycles (Dennis *et al.*, 1991). Whereas, in northern areas, where there is lower genetic diversity in butterfly populations (Schmitt & Hewitt, 2004) would have lost all the species during the glacial periods and been subsequently recolonised during the interglacial periods (Dennis, 1993). Alternatively, Hawkins & Porter (2003b) explained the latitudinal gradient of butterfly species in Europe using a measure of water-energy balance, actual evapotranspiration, which accounted for 75% of variance in species richness. Evapotranspiration can act in two ways, directly via the physiological effects of heat/cold stress and water availability and indirectly via its influence on plant productivity (Hawkins & Porter, 2003b). This result suggests that the latitudinal richness gradient in Europe is in equilibrium with the current climate. More accurate distribution data, alternative statistical methods and molecular phylogenies with estimated dates for diversification events, could provide new insights into the role of these two mechanisms, which may not be mutually exclusive.

Picos de Europa, located 43°N, is just in the middle of the humped pattern of species richness versus increasing latitude found by Gutiérrez (2009). It is also bordering the line highlighted by Hawkins *et al.*, (2003), dividing the southern peninsulas (Iberian, Italic and Balcanic) from northern Europe (Fig. 1.1). Across all latitudes, animal richness is constrained by the interaction of energy and water, but north of these lines energy is hypothesized to represent the limiting component of the interaction, whereas south of these lines water is assumed to be the key limiting component (Hawkins *et al.*, 2003). This particular latitudinal location, interacting with a wide altitudinal gradient, is expected to be related with particularly high species richness and diversity in Picos de Europa.

Fig.1.1 Hypothesis for the geographic distribution of the limits to the species richness of butterflies in Europe. The red line represents the breakpoint above which energy is the limiting component of the interaction, whereas south of this line water is assumed to be the key limiting component. Based on: Hawkins *et al*., (2003).

1.2.2 Climate

It is now well established that species diversity is often strongly correlated with climatic conditions, namely temperature, water availability and resulting ecosystem productivity (Hillebrand, 2004; Rohde, 1999; Bohdalková *et al*., 2021). At the global scale, Coehlo *et al*. (2023) have recently shown that climate and its geographical configuration and extension can explain as much as 90% of the variation in global species richness (terrestrial tetrapods: reptiles, amphibians, mammals and birds). Coehlo *et al*., (2023) used the first two axes of a principal components analysis of 12 global-scale climate variables to define a two-dimensional orthogonal climate space that represents thermal and water availability limits to species distribution. The first axis was defined by temperature variables and the second axis by a balance of energy and water availability. They used a grid to define geographical cells covering the surface of the Earth and then they calculated the geographic area associated with a specific climate and the physical isolation of the geographic cells linked to that climate. The authors report that the geography of climate (area and isolation) nearly doubles the effect of climate itself on species diversity.

An aspect of climate used by Coehlo *et al*., (2023) in their multidimensional analysis, water-energy dynamics (solar energy and water availability) (Hawkins & Porter, 2003b) has been shown to be a good explanatory factor of the diversity of European dung beetles (Hortal *et al*., 2011), angiosperm families (Hawkins *et al*., 2011), Neotropical birds (Ruggiero & Hawkins, 2008), European and North African dragonflies (Keil, Simova & Hawkins, 2008), European reptiles and amphibians (Rodríguez *et al.*, 2005) and Western Palearctic butterflies (Hawkins & Porter, 2003b). Hawkins& Porter (2003b) further suggest that plant productivity is the driving force of butterfly richness patterns in Western Palearctic, given its strong link with evapotranspiration. However, an integrative approach which takes into account the interaction of topography with climate is lacking at the regional scale. Particularly, temperature and humidity gradients caused by air moving along slopes in mountains (Brun *et al.*, 2022; Díaz, 1996), which result in horizontal precipitation (small droplets intercepted directly by plants and soil surfaces on mountain slopes), mist, strong warm wind leeward, thermal inversions, cool air pools and other remarkable effects (Iglesias *et al.*, 2017), are not usually considered in their relation to the distribution of biodiversity (but see Chan *et al.*, 2024).

1.2.3 Landscape composition and configuration

Landscape structure has been shown to exert a strong influence on butterfly community dynamics (Perovic *et al.*, 2015; Seibold *et al.*, 2019; Gámez-Virués *et al.*, 2015; Dainese *et al.*, 2017; Öckinger *et al.*, 2012). Heterogeneous landscapes support large species pools, providing a diversity of patches with different disturbance dynamics and encouraging organisms to use different habitat patches with complementary resources (van Halder *et al.*, 2011; Tscharnke *et al.*, 2012; Janisová *et al.*, 2014). Movements of species between landscape elements may ensure community resilience, through the capacity to reorganise after disturbance in changing environments (Tscharnke *et al.*, 2007).

Therefore, understanding how landscape structure moderates the response of species and communities is critical to comprehending their dynamics (Tscharnke *et al.*, 2012). Landscape scale simplification—both reduced diversity of land cover types (reduced compositional landscape heterogeneity) and an increase in patch sizes within the landscape (reduced configurational landscape heterogeneity)—has been shown to act as an ecological filter, selecting against specialized butterfly species (Perovic *et al.*, 2015). These two distinct components of landscape structure: compositional heterogeneity (diversity of land cover types) and configurational heterogeneity (size and arrangement of patches) have been included in studies of agricultural intensification (Farig *et al.*, 2011; Gámez-Virués *et al.*, 2015) but their effects on abandoned landscapes are still unexplored.

Human influence on European landscapes dates back for millenia. In Southern Europe, the components and dynamics of current biodiversity cannot be understood without taking into account the history of human-induced changes, resulting in a large diversity of cultural landscapes (Blondel, 2006; Pedroli *et al.*, 2006). In the domain of temperate forests, human action by cattle grazing, mowing and coppicing have resulted in diverse and heterogeneous cultural landscapes: mosaics of forest patches intersected with seminatural grasslands (hay meadows and pastures). Recently, Pearce *et al.* (2023) have shown that temperate forest biomes, in the last interglacial period (129,000-116,000 years ago, before *Homo sapiens*-linked megafauna declines), was heterogeneous, with more than 50% cover of light woodland and open vegetation. The degree of openness was highly variable and only partially linked to climatic factors, indicating the importance of natural disturbance regimes (large wild herbivores and fire). Human populations would have substituted large wild herbivores in exploiting these landscapes. In recent decades, the abandonment of traditional low intensity land-use has led to a loss of habitats dominated by sparse vegetation, thereby giving rise to a succession towards forest habitats (Poschlod *et al.*, 2005). The effect of this disappearance of human disturbances on biodiversity is still unknown. Furthermore, species responses may not be immediate, delayed extinctions could happen (extinction debt) resulting from demographic and stochastic processes: a population in which mortality is slightly larger than natality will eventually go extinct, but it might require many generations to get to extinction (Jackson & Sax, 2010). Considering time as another variable in the building of biodiversity is necessary to appreciate long-term effects like extinction debt processes or further in time, historical drivers of biodiversity.

Although extensively related to butterfly community dynamics at the local scale, landscape composition and configuration have not been used widely to explain diversity patterns at a regional scale (but see Bergman *et al.*, 2004). Links between landscape ecology and broad scale biodiversity patterns (macroecology) are still underexplored (Teng *et al.*, 2020).

1.2.4 Historical drivers of biodiversity in Iberia

In line with most biodiversity research, Coehlo *et al.* (2023) found that mountain regions emerge as exceptionally diverse, occupying 25% of terrestrial land but being home to almost 90% of tetrapod species (Rahbek *et al.*, 2019). However, it is also recognised that climate and its components are not enough to explain the disproportionately higher biodiversity found on mountains, as mountainous regions have had a crucial role as biodiversity refugia under climatic oscillations in the past (Rahbek *et al.*, 2019; Coelho *et al.*, 2023; Dennis & Schmitt, 2009). In Europe, the Southern Peninsulas (Iberian, Italic and Balcanic) have acted as refugia during the Pleistocene glaciations in the Quaternary period (1.8M years ago) and contributed to the postglacial colonization of northern Europe (Hewitt 1996, 1999, 2000). Implicit in this historical model is that southern refugia harbour higher levels of biodiversity. The southern peninsulas are highly fragmented by mountain ranges and bordered by seas, creating highly heterogeneous landscapes that foster species diversification (Weiss & Ferrand, 2007). They are centres of biodiversity, containing high rates of endemism as well as threatened taxa and populations. In fact, the Mediterranean region as a whole is one of the twenty-five biodiversity hotspots on Earth (Myers *et al*., 2000).

In the Iberian Peninsula, in particular, a model of multiple glacial refugia was proposed by Gómez & Lunt (2007) in light of the evidence shed by patterns of phylogeographic concordance of diverse taxons. They suggested terrestrial glacial refugia coincide with current areas of endemism (Gómez-Campo *et al*., 1984; García-Barros *et al*., 2002; Rosso *et al*., 2018; Buira *et al*., 2017) and tend to occur in the mountain ranges (Fig. 1.2). Despite its geographically isolated position on the westernmost point of Europe, several characteristics favoured species survival in the Iberian Peninsula throughout the Pleistocene. Its high topographic complexity, with several large mountain ranges, allowed persistence of populations by altitudinal shifts, tracking suitable microclimates up or down mountains as the general climate cooled or warmed (Hewitt 1996). As a result, south European mountain ranges like those present in the Iberian Peninsula hold a remarkable diversity of species with different biogeographical origins: boreo-alpine fauna and flora can be found, persisting as relictic populations at higher summits and northern exposures (e.g. *Saxifraga oppositifolia*); Mediterranean and tropical species are present at low altitudes and in gorges free from the effects of frosts (e.g. *Culcita macrocarpa*, golden-striped salamander); along with endemic, Atlantic and Eurosiberian species.

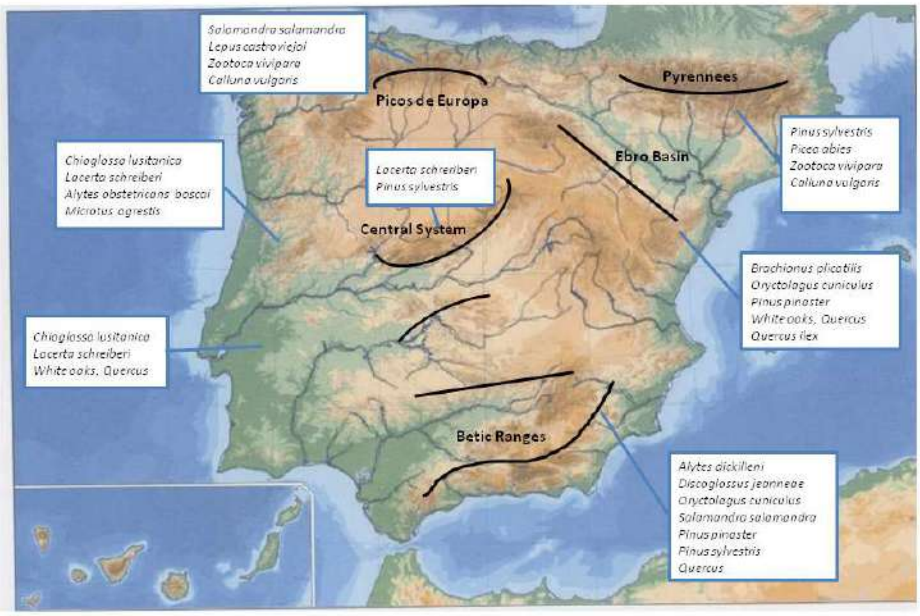

Fig. 1.2 Map of the Iberian Peninsula showing the approximate location of presumed Quaternary refugia for terrestrial fauna and the species that supports them. Based on: Gómez & Lunt (2007).

1.3 BUTTERFLIES AS INDICATORS OF HABITAT CHANGE

As butterflies have short life cycles and react rapidly to environmental change, they are good ecological indicators. Their limited dispersal capacity, their specialisation in certain host plants and their dependence on ambient conditions, such as temperature and humidity, make them sensitive to slight environmental changes. Moreover, butterflies occur in a wide range of habitat types, their taxonomy is well established, and they are easy to identify and survey (Thomas, 2005; van Swaay *et al.*, 2020).

Butterflies are also attractive to the general public making extensive citizen science programmes possible (Dennis *et al.*, 2017). Long-term monitoring programmes have been running in the United Kingdom (UKBMS, United Kingdom Butterfly Monitoring Scheme) since 1976 (Middlebrook *et al.*, 2023), in Catalonia, Spain (CatalanBMS) since 1994 (https://www.catalanbms.org) and recently this type of scheme has been adopted in many other European countries in a coordinated program called the European Butterfly Monitoring Scheme, the largest invertebrate monitoring network across the world (Sevilleja *et al.*, 2020). Data from such monitoring schemes can be used to study different aspects of butterfly ecology: species abundance, species diversity (richness and diversity indexes), community composition and their changes over time.

Butterfly diversity metrics give us an idea of the species pool in an area and the relative abundance of rare and common species. Three metrics of species diversity – species richness, the Shannon index and the Simpson index – are widely used in ecology. Over the past decade, ecologists have begun to incorporate two important tools for estimating diversity: coverage and Hill numbers (Roswell *et al.*, 2021). Coverage is a method for equalising samples and it can be estimated from the number of singletons (species represented by one individual), doubletons (species represented by two individuals) and the total number of individuals in the sample (Chao & Jost, 2012). Hill numbers comprises a spectrum of diversity metrics: species richness and variants of the Shannon and Simpson indices based on common estimate procedure and they can be expressed on the same scale and in units of species (Chao *et al.*, 2014; Roswell *et al.*, 2021). Hill-species richness emphasises rare species while Hill-Shannon diversity emphasises neither rare nor common species and Hill-Simpson diversity emphasizes the common species (Roswell *et al.*, 2021).

Long-term data series on species abundance gathered by monitoring schemes are also useful to investigate butterfly population trends. The existing European butterfly monitoring schemes calculate the abundance of each species in each year using the generalised abundance index approach (Dennis *et al.*, 2016), which provides an efficient method for modelling seasonal count data. The method uses all counts from all the sites in which a species occurs to describe the species phenology for each year, which is then used to estimate the abundance for any gaps in sampling. From the real and estimated counts, annual measures of relative abundance are produced for each monitoring site. An overall abundance trend over time for each species is then calculated by applying a Poisson generalised linear model to the site-level annual abundance values. A bootstrapping procedure is used to determine the statistical significance of the abundance trends. Multispecies abundance indicators can be compiled for all butterfly species in an area combined, or for certain groups of species, for example, grassland species (Van Swaay *et al.*, 2020).

Other aspects of butterfly ecology can be investigated by focusing on community composition. When analysing short periods of time, in particular, changes in species composition and abundances of individual species or types can remain undetected if we only measure species richness or species diversity indexes (Eriksson & Hillebrand, 2019). This aspect of diversity becomes especially important as human-induced rapid changes are provoking a rapid reorganisation of local species assemblages over time globally, with nearly a third of all species being replaced by new species every decade (Blowes *et al.*, 2019). Different drivers (e.g. agricultural intensification or land abandonment) act as ecological filters on butterfly communities affecting both their functional and taxonomic composition (Gámez-Virués *et al.*, 2015; Herrando *et al.*, 2016). Recent research has shown that focusing on traits at the community level provides ecologically meaningful insights into the landscape-level processes affecting community assembly, which would not be detectable by focusing on single species or taxonomic diversity alone (Öckinger *et al*., 2010; Ubach *et al*., 2020; Hodapp *et al*., 2018). Community trait indices weighted by species abundances have proved to be very powerful tools in detecting community responses to environmental change (Julliard *et al*., 2006; Devictor *et al*., 2012; Moretti *et al*., 2017). For example, species with limited dispersal ability, diet specialisation and low fecundity are selected against in intensively managed ecosystems (Mckenney and Lockwood, 1999; Perovic *et al*., 2015), being at higher risk of extinction as a result.

In butterflies, the number of generations per year (voltinism), trophic range (in terms of numbers of larval host plants) and mobility (dispersal capacity) seem to determine their vulnerability to global changes (Carnicer *et al*., 2013; Slancarova *et al*., 2016). Low number of generations, low mobility and narrow trophic range collectively define specialism (Slancarova *et al*., 2016), and several studies have shown greater declines for habitat specialists than for habitat generalists (DEFRA, 2021; Stefanescu *et al*., 2011 a,b). In mountain areas, species' thermal tolerance range has been shown to be an important trait determining response to climate change. Species with wider thermal tolerances are more likely to persist, moving both up or downhill (Rödder *et al*., 2021).

Environmental change (i.e. global warming and land use change) require species to either adapt, disperse or go extinct. Changes in the relative abundances of species reflect internal shifts in dominance, while immigration and replacement of species (species turnover) require the presence of additional species in the regional species pool (Hodapp *et al*., 2018). Large species pools may be the result of heterogeneous environmental conditions in space and time, providing different habitats that allow a higher number of species to coexist (Holyoak *et al*., 2005). The initial spatial heterogeneity of species composition strongly affects community responses to environmental change (Hodapp *et al*., 2018).

1.4 BUTTERFLY CONSERVATION

Protected areas are considered an essential tool to halt the collapse of biodiversity (Convention on Biological Diversity, 2020). Even if they are meant to preserve ecosystem functions and biodiversity, threats to organisms have been shown to permeate their boundaries. Hallmann *et al*. (2017) showed a worrying decline of more than 75% of flying insect biomass in 27 years (1989-2016) in 63 nature protected areas in Germany, the majority of them of limited size and enclosed by agricultural fields. In Great Britain, Cunningham *et al*. (2021b) showed that the distributional trends of declining and priority species in the period 1974-2014, were similar in landscapes containing protected areas and in the wider countryside, implying that protected areas were not resilient to landscape-scale pressures. Regardless of protected area coverage, topographically heterogeneous landscapes were more likely to retain priority species. In contrast, Rada *et al*. (2019) found higher butterfly species richness inside protected areas in Germany and Thomas *et al*. (2012) showed that butterflies and some other invertebrates undergoing climate-driven range expansion, disproportionately colonised protected areas in the UK. As the evidence that protected areas conserve butterfly communities is equivocal, further research on protected areas management that could best mitigate global threats is needed, as is the development of conservation approaches that integrate both protected areas and the broader landscape (Chowdhury *et al*., 2023).

Landscape-scale conservation has been proved an effective management approach (Ellis *et al*., 2012). It is defined as the coordinated conservation and management of habitats for a range of species across a large natural area, often made up of a network of sites (Bourn and Bulman, 2005; Ellis *et al*., 2012). The area and isolation of habitat patches are essential variables governing whether species thrive across a landscape (Hanski, 1999). Maintaining high quality habitat within individual sites is also very important as rare species are often found in very specific habitats (Thomas *et al*., 2001). Landscape-scale projects must be based on sound ecological research (Pullin & Knight, 2001), designed upon good quality spatial data and their effectiveness must be monitored by an adequate sampling system (Ellis *et al*., 2012). In a context of climate change, a landscape-scale approach seems the best option to create habitat heterogeneity, which is likely to give species more opportunities in times of changing ecological requirements (Ellis *et al*., 2012).

Another promising approach to face these rapid environmental changes is to recognise the value of indigenous knowledge or ecological traditional knowledge, which has great potential to provide solutions to conserve both lands and cultures (Kimmerer & Artelle, 2024). Ecological traditional knowledge is a collective term that represents the many local knowledges gathered through generations in different cultural contexts (Jessen *et al*., 2022). Indigenous people have applied this traditional knowledge through millenia to solve environmental management problems (Atleo, 2011; Berkes, 2018). Mixed research integrating traditional knowledge with data collected through the scientific method have aid to the understanding of population trends (Lee *et al*., 2018), ecosystem function (Savo *et al*., 2016), habitat use (Polfus *et al*., 2014), or wildlife conservation (Hill *et al*., 2019).

Finally, we must mention wilding or rewilding, described by Soulé and Noss (1998) as a science-based methodology for conservation based on the restoration and protection of large reserves (cores), well connected (corridors), with wide-ranging keystone species (carnivores), which would have a disproportionate enriching influence on ecosystem function and diversity. In the European context, Vera *et al*. (2006) gave that keystone importance to large herbivores, which had disappeared due to human intervention in the late Holocene. In a context of land abandonment in mountains and wetlands, where agriculture is not competitive, rewilding may be considered as a tool to maintain the heterogeneity needed for species to adapt to their changing ecological requirements due to rapid global change (Tree, 2018; Knepp, 2024).

1.5 STUDY SYSTEM

Picos de Europa National Park (PNPE) is a mountain range, approximately 30 km x 20 km in area, running east to west 20 km inland from the northern coast of Spain (centred on 43º15’ N, 5º00’W). Due to its geographic location, it receives Atlantic influences from the ocean on its northern slopes and Mediterranean influences at its eastern and southern slopes. PNPE presents a temperate bioclimate and its mediterranean variant (in less than 5% of the territory). All the territory has an oceanic character, but southern slopes have less humidity as they are farther from the coast and the mountain barrier prevents the wet air coming from the sea to reach those southern slopes. In the northern slopes, more oceanic, there is a substantial increase in rainfall, which combined with lower temperatures results in an altitudinal decrease of the treeline (Jiménez-Alfaro *et al*., 2010). Average annual temperatures range from 2.5 °C at highest elevations to 15 °C in the gorges which divide the mountain massifs (Ninyerola *et al*., 2005). Average rainfall is between 1100 and 1300 mm/year (Ninyerola *et al*., 2005).

Based on the climatic stratification of the environment in Europe proposed by Metzger *et al*. (2005), Picos de Europa National Park covers three different climatic strata: Lusitanian climate at its northern slopes; alpine south climate at its highest elevations; and Mediterranean mountain climate at its southern slopes. Due to the wide altitudinal range (70-2648 m), a high diversity of habitats is present in the study region. As we climb up the mountains, we find extensive patches of temperate deciduous forests (mixed, beech and oak forests), natural and seminatural grasslands, hazel thickets, bramble thickets, *Genista* and *Cytisus* scrub, Atlantic heaths, *Genista* cushion type scrub, rocky and high mountain vegetation, as well as riverine, bog and lake vegetation (Alonso *et al*., 2011).

The Iberian Peninsula, within the Mediterranean Basin global hotspot (Mittermeier *et al*., 2011; Hewitt, 2011; Myers *et al*., 2000; Cuttelod *et al*., 2008), harbours more than 50% of European plant and vertebrate species (Médail & Quézel, 1997; Williams *et al*., 2000, Araujo, Lobo & Moreno, 2007; IUCN, 2013) and 47% of European butterflies (Maes *et al*., 2019). This is due to a distribution pattern reflecting major environmental changes associated with glacial-interglacial cycles and European landform distribution (Dennis & Schmitt, 2009). The study system of this thesis, the Picos de Europa National Park (PENP), within the Cantabrian Mountain Range (northwest Spain), is an endemism hotspot (Rosso *et al*., 2017; Buira *et al*., 2017) and might have acted as a refugia during the last glaciations (Gómez & Lunt, 2007). Picos de Europa harbours 1753 species of vascular plants (22% of Iberian floristic diversity, Alonso *et al*., 2011), 52 species of mammals (55% of Iberian species, García-Perea *et al*., 1997) and 137 species of butterflies (Mora, 2017), representing 60% of the Iberian species (García-Barros *et al*., 2013) and 28% of the European butterfly species (van Swaay *et al*., 2010). Several legally protected butterfly species at the European level are present in the regions (*Parnassius apollo, Euphydryas aurinia, Lopinga achine* and *Phengaris nausithous*) as well as several Iberian endemics (*Erebia palarica, Aricia morronensis* and *Agriades pyrenaicus*). Picos de Europa is a hotspot of butterfly diversity in the Iberian and in the broader European context (van Swaay & Warren, 2006; Romo *et al*., 2007). This highlights the importance of this region for conservation and the need to identify those factors generating and maintaining the characteristic high species richness of this area. Furthermore, determining to which extent climate and land-use drive species richness patterns will facilitate prediction of the likely consequences of global change for both species richness and species composition (Stefanescu *et al*., 2004; Illán *et al*., 2010).

A traditional land use system has operated in this territory for centuries, with pasturing (mainly sheep and goats in the past, substituted by cattle and horses at present), hay-making and woodland coppicing as the main human activities. Since the 1940's, sequential waves of rural depopulation have taken place with emigration to urban areas in the 1960's due to industrial development and poor living conditions in rural areas, resulting in a progressive abandonment of traditional land management. Currently, around 80% of the population in rural areas in the region works in tourism and services, 10% in agriculture and 10% in building and industrial activities (Rescia *et al*., 2008; Sadei, 2024).

Picos de Europa altitudinal range (70-2648 m) is modest compared to the other main mountain ranges in Western Europe (Pyrenees or the Alps), but its proximity to the sea results in very steep slopes and a rough topography, which limit human exploitation of much of the area. Despite this, humans have inhabited Picos de Europa since Prehistoric times (20,000-18,000 BC) (Menéndez, 2020). Remains of fire activity in sediments together with the analysis of fossil pollen have led researchers to date the first evidence of pasturing in the region between 4,900-4,500 BC (Niewendam *et al.*, 2015; Moreno *et al.*, 2011). Large mechanisation, agricultural development or intensification did not arrive to Picos de Europa, because of its mountainous character and difficult access. The persistence of an almost unchanged shepherding culture through millenia is a consequence of environmental constraints as well as the lack of capacity or interest of different cultures that approached these mountains to change the productive system (Izquierdo & Barrena, 2006). Traditional management of this territory is part of a local culture of immense value, which has been able to live together with, and respecting biodiversity.

1.6 SCOPE OF THE THESIS

The general aim of this thesis was to investigate the conservation status of butterflies at Picos de Europa National Park, a southern European mountain range which is a priority area for butterfly conservation in Europe, and which is experiencing dramatic change driven by land abandonment. The specific research objectives were to assess:

- The influence of land abandonment on butterfly communities.
- Species population trends during the last decade, and the key environmental factors explaining them.
- Which factors may govern or limit current butterfly species diversity spatial patterns in the area.

With the overarching final aim of informing future conservation efforts in South European Mountain Ranges and particularly at Picos de Europa National Park.

This thesis is structured in three primary data chapters each contributing to different aspects of the general aims, a general introduction and a general discussion.

Chapter one is a literature review synthesising existing knowledge to provide background and context on the topics covered by the thesis research and identifying important knowledge gaps which need to be addressed.

Chapter two details a study carried out on hay meadows at different stages of abandonment, to assess how traditional hay meadow abandonment is affecting butterfly communities and how local meadow characteristics and landscape context modulate these responses.

Chapter three focus on understanding species population changes over time. Monitoring data from 2013-2021 were used to assess their current status across an altitudinal gradient (80-2000 m) with different land use and climate change pressures.

Chapter four explore the patterns of butterfly diversity along the elevation gradient in Picos de Europa, taking into account the influence of temperature and humidity gradients in mountains and landscape configuration. Furthermore, butterfly diversity trend is investigated in the last 14 years (2009-2023).

A general discussion is presented in chapter five to highlight the implications of the research for conservation, providing advice for site managers and directions for future study.

Chapter 2: Abandonment of cultural landscapes: Butterfly communities track the advance of forest over grasslands

Santiago making hay at Güembres (Picos de Europa). Photo: Amparo Mora.

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2.1 ABSTRACT

Rural landscapes in Europe have suffered considerable land-use change in the last 50 years, with agricultural intensification in western regions and land abandonment in eastern and southern regions. The negative impacts of agricultural intensification on butterflies and other insects in western Europe have been well studied. However, less is known about the impacts of abandonment on mountain and humid areas of eastern and southern Europe, where landscapes have remained more natural.

We sampled butterfly communities in the Picos de Europa National Park (Spain), a region which is undergoing a process of rural abandonment. 19 hay meadows with different periods of abandonment were studied (long-term 18 years or mid-term abandoned, 3-7 years) and compared to meadows continuously managed in a traditional way. We examined how local meadow characteristics and landscape variables affected butterfly community response to abandonment.

Butterfly communities were affected by abandonment, with an overall increase in the density of individuals in the long term. Community composition appears to undergo major change over time, with a species turnover of around 48% after 18 years of abandonment. There was a tendency for species with higher preference for closed habitats to increase their densities as time since abandonment proceeded. Landscape variables had a major impact on butterfly communities, stronger than the effect of meadow management. Community preference for closed habitats was associated with higher forest cover in the surroundings of the meadows, but heterogeneous landscapes (in their composition or configuration) mitigated this effect.

Keywords: abandonment, biodiversity indicators, butterflies, meadow management, open /closed habitat, species traits.

2.2 INTRODUCTION

Biodiversity loss caused by human actions has overcome a critical threshold. Up to 75% of the terrestrial environment has been “severely altered”, with land use change among the most important direct drivers of habitat loss and degradation (Brondizio *et al*., 2019).Rural landscapes in Europe have suffered considerable land-use change in the last 50 years, with agricultural intensification in western regions and land abandonment in eastern and southern regions (van Swaay *et al*., 2016). The negative impacts of agricultural intensification on butterflies in western Europe have been well studied and landscape matrix composition around cultivated land has been shown to be crucial on butterfly community dynamics (Perović *et al*., 2015, Seibold *et al*., 2019, Gámez-Virués *et al*., 2015, Dainese *et al*., 2017, Öckinger *et al*., 2012). However, less is known about the impacts on grassland butterflies in mountain and humid areas of eastern and southern Europe, where landscapes have remained more natural and agricultural abandonment rather than intensification has taken place (but see Marini *et al*., 2009; Slancarova *et al*., 2016; Ubach *et al*., 2020; Colom *et al*., 2021).

The butterfly community in any given grassland will be the result of both local and landscape-level filters (Perović *et al*., 2015). Among the various negative local impacts of grasslands abandonment, decreases in plant diversity are particularly critical as several studies have shown that declines in producers reduces diversity at higher trophic levels (Pöyry *et al*., 2009, Uchida & Ushimaru, 2014, Dainese *et al*., 2017). A reduction in plant diversity within the grassland could affect nectar resources (Krauss *et al*., 2003) and potentially hostplant availability, which have been shown to negatively affect butterfly diversity (Skórka *et al*., 2007, Marini *et al*., 2009).

On the other hand, landscape heterogeneity can moderate the effects of local grassland management and influence species persistence, by supporting a larger species pool, providing a diversity of patches with different disturbance dynamics and encouraging spillover of organisms between complementary resources (van Halder *et al*., 2011, Tscharntke *et al*., 2012, Janisová *et al*., 2014, Dantas de Miranda *et al*., 2019). Therefore, understanding how landscape structure (i.e. composition:diversity of habitat types;- and configuration: number, size and arrangement of habitat patches) moderates the response of species and communities to changes in habitat management, is critical to comprehending their dynamics (Tscharnke *et al*., 2012). Movements of species between landscape elements may ensure community resilience, the capacity to reorganise after disturbance in changing environments (Tscharntke *et al*., 2007).

Agricultural intensification and land abandonment are changes that act as ecological filters on butterfly communities affecting both the functional and taxonomic composition of communities (Gámez-Virués *et al*., 2015; Herrando *et al*., 2016). Recent research has shown that focusing on traits at the community level provides ecologically meaningful insights into the landscape-level processes affecting community assembly, which would not be detectable by focusing on single species or taxonomic diversity alone (Öckinger *et al*., 2010, Ubach *et al*., 2020). Community trait indices weighted by species abundances have proved very powerful tools in detecting community responses to environmental change (Julliard *et al*., 2006, Devictor *et al*., 2012, Gagic *et al*., 2015, Moretti *et al*., 2017). For example, species with limited dispersal ability, diet specialisation and low fecundity are selected against in intensively managed agroecosystems (McKenney & Lockwood, 1999, Perović *et al*., 2015), being at higher risk of extinction as a result.

In the European context, responses to intensification are relatively well documented, but the impacts of abandonment are less clear, particularly in landscapes harbouring higher diversity of both habitats and species. The abandonment of traditional land is leading to a loss of habitats dominated by sparse vegetation, thereby giving rise to a successional progression towards forest habitats (Poschlod *et al*., 2005) and consequent changes in butterfly species composition. Balmer & Erhardt (2000) detected a peak on butterfly species richness 10 years after abandonment of extensively grazed grasslands in the Jura Mountains (Switzerland), with a subsequent decline at around 20-30 years of abandonment, when the grassland became young forest. In the southern Balkans, vegetation encroachment of formerly open habitats has been shown to decrease the representation of Mediterranean endemic butterfly species relative to northern European species (Slancarova *et al*., 2016).

In Spain, between 1962 and 2019, 4 million hectares of cultivated land were abandoned (around 8% of total national surface), increasing forest cover, which now accounts for 55% of total national surface, of which around 80% is not managed (Greenpeace Spain, 2020). The consequences of these huge land use changes on butterflies have been explored only in the northeast Mediterranean región (Stefanescu *et al*., 2009, Herrando *et al*., 2016, Ubach *et al*., 2020). These studies showed that grassland abandonment had immediate strong effects on butterflies, including the substitution of grassland specialist by habitat-generalist butterflies (Stefanescu *et al*., 2009). They also demonstrated that for both birds and butterflies, open-habitat species showed the most marked declines, whilst forest species increased moderately, a pattern in line with the changes occurring in forest cover in the surrounding landscape (Herrando *et al*., 2016; Ubach *et al*., 2020).

In the more humid Atlantic parts of Spain, the Cantabrian Mountains, recent studies have shown an increase of 16% of forest cover between 1990 and 2000 (García-Llamas *et al*., 2019).

Parallel to this regional pattern, the area of traditional hay meadows decreased by 70% between 1956 and 2017 in the Picos de Europa National Park, doubling the rate in the last decade (García *et al.*, 2018). The consequences of this land transformation on biodiversity are still largely unexplored. This is particularly worrying as Picos de Europa is a hotspot of butterfly diversity not only in the Iberian Peninsula, but in the broader European context (van Swaay & Warren, 2006, Romo *et al.*, 2007). There are 137 butterfly species in the National Park, representing 60.6% of the Iberian species (García-Barros *et al.*, 2013), including several legally protected species at European level (*Parnassius apollo, Euphydryas aurinia, Lopinga achine* and *Phengaris nausithous*) and some Iberian endemisms (*Erebia palarica, Aricia morronensis* and *Agriades pyrenaicus*).

Here, our aim was to assess how traditional hay meadow abandonment is affecting butterfly communities in the Picos de Europa National Park and how local meadow characteristics and landscape context modulate these responses.

We hypothesize that:

(1) Traditionally managed meadows harbour higher species richness, diversity and abundance of butterflies than abandoned grasslands.

(2) Abandonment affects butterfly communities through effects on vegetation characteristics within the meadow, such as increase in sward height and vegetation cover and reduction in plant richness and diversity.

(3) Landscape heterogeneity and the extent of open versus closed habitats in the landscape (grassland versus woodland), influences the response of butterfly communities to abandonment.

2.3 METHODS

2.3.1 Study area

The study was carried out in Soto de Sajambre (Oseja de Sajambre municipality), on the southern side of Picos de Europa National Park (43º09’49.53’’N 5º02’07.11’’W), in the north of Spain (Fig. 2.1). The study area comprised approximately 3 x 2 km^2, with an elevation range from 884 to 1137 m (average 1023.64 ± 89.14). Soto de Sajambre has a hyperhumid climate, with an average annual temperature of 9.3ºC and an annual rainfall of 1783 mm (Rivas Martínez *et al.*, 1984). Nevertheless, it receives Mediterranean influences from the south (Leon-Castilla plateau) and from the east (Ebro Depression), which is reflected in the flora of the region, containing 13.18% of Mediterranean plant species (Alonso Felpete *et al.*, 2011).

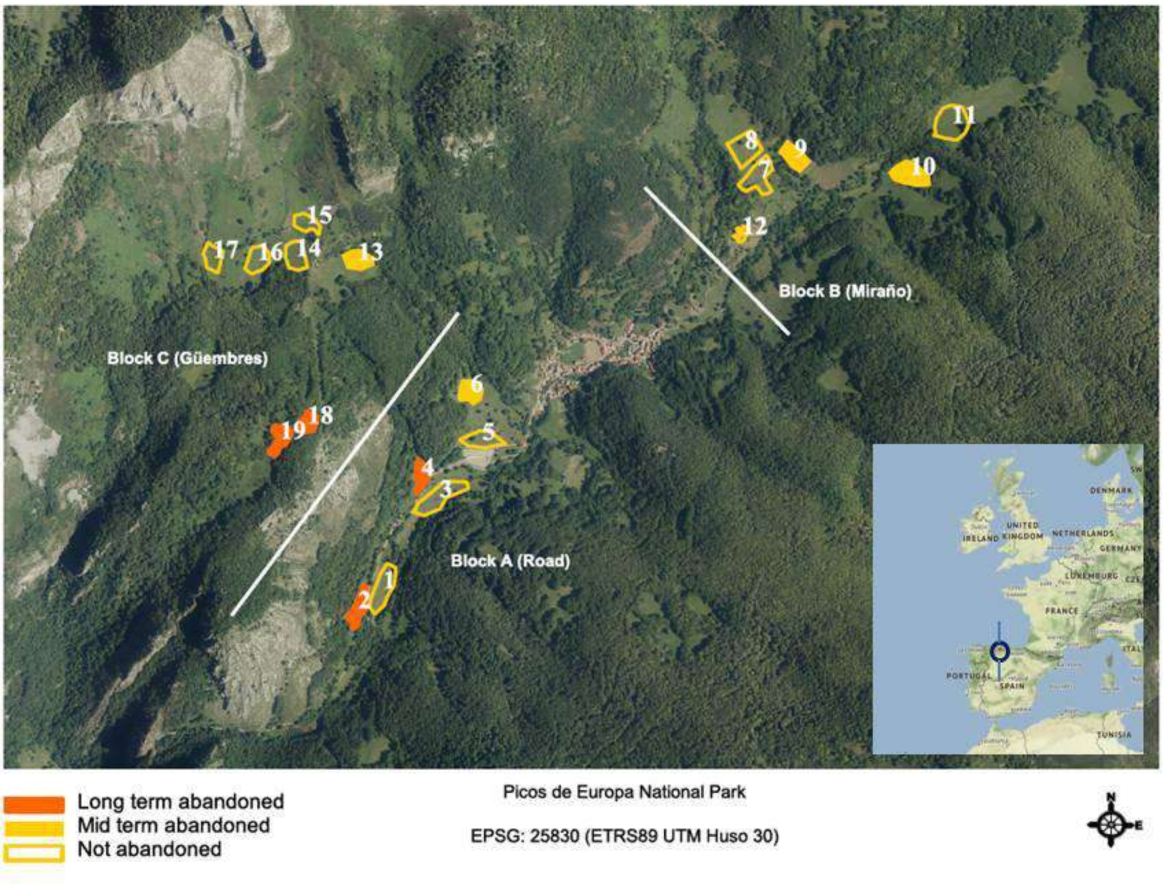

Fig. 2.1 Study site and sampled meadows at Picos de Europa National Park (northern Spain).

Nineteen hay meadows were selected, with size ranging between 0.29 and 0.81 ha (average 0.47 ha ± 0.15). The meadows were located in three areas/blocks (see Fig.2.1), each one containing continuously managed (for more than 50 years) and abandoned meadows (time since management varied between 3 and 18 years). Abandoned meadows were classified into two categories: mid-term abandoned (3-7 years) and long-term abandoned (18 years) (see Table S2.1 for details on each meadow). All meadows in blocks A and B were grazed from September to April by approximately 110 cows and 25 mares that moved freely around the village, with an approximate density of 0.18 cows/ha and 0.041 mares/ha. Meadows in block C were not grazed by domestic animals, being the uppermost and furthest location from the village. Wild herbivores (red and roe deer and wild boar) also foraged occasionally in small numbers on the meadows. Managed meadows are mown once a year, in July or August depending on their altitude. While the meadows were originally fertilised with manure, this practice has ceased to prevent wild boar damage. Other traditional management practices, such as pruning of trees in the hedgerows to prevent shadowing of the meadow and maintenance of water drainage channels, are also no longer used. Information about abandonment time (i.e. years without mowing) and use for grazing by cattle and wild herbivores was obtained from Park rangers and farmers.

2.3.2 Butterfly surveys and butterfly traits

In each selected meadow, a zig-zag transect was walked identifying and counting any butterfly seen 2.5 m either side and 5 m ahead following the standardized methods proposed by Pollard and Yates (1993). Minimum conditions for sampling were temperature above 17 ºC, wind below 3 (Beaufort scale) and no rain. Transect length was 500 m, transect duration around 20 minutes and they were walked between 11:00 and 16:00. Transects were repeated three times during the season: mid-May, mid-June and mid-July in 2019, in order to register the maximum diversity and abundance of butterflies in the area before meadows were mown. Some *Pyrgus spp* and *Melitaea spp* were not possible to identify to species level, as most species require dissecting their genitalia for correct identification, and were not included in the analysis.

Species traits related to habitat and trophic specialisation and dispersal ability were compiled from the scientific literature for each butterfly species recorded (Table S2.2). We used the TAO index of species preferences for open/closed habitats developed by Ubach *et al*., (2020), which is based on the Catalan Butterfly Monitoring Scheme data (1994-2017, 93 sites) (see details in www.catalanbms.org). Species showed great consistency in their preferences for open or closed habitats regardless of the climatic conditions in the different biogeographic regions analysed by Ubach *et al*., (2020), so we believe that this index is valid for our study area, and more appropriate than other indices used to describe butterfly habitat selection in western Europe. The TAO index takes a "+1" value when the butterfly species prefers completely open habitats and takes a "-1" value when the butterfly species prefers completely closed habitats.

We developed community indices based on species traits (preference for open/closed habitats, habitat specialisation, trophic specialisation and dispersal ability). These indices were calculated for each meadow, as the average of species individual indices weighted by species abundances. Therefore, changes in these indices mostly result from variations in the dominant species occurring locally.

We followed Julliard *et al*. (2006) and Devictor *et al*. (2012) to develop a community index of preference for open/closed habitats (CTAO) for each meadow (Table S2.3), by multiplying each species index by the square root of its abundance and then averaging across all species. Habitat specialisation, trophic specialisation and dispersal ability information for each species were taken from Stefanescu *et al*. (2011a) and the same procedure as described above was used to build the community indices (Table S2.3).

2.3.3 Vegetation surveys

Within each meadow, three 1m^2 quadrats were placed along the butterfly transect route. In every quadrat percentage cover of flowering plants, vegetation height and soil humidity were recorded. Soil humidity was measured with a ThetaProbe sensor (Delta-T Devices Ltd.), which measures volumetric soil moisture content by responding to changes in the dielectric constant of the soil. Soil samples were taken from several of the meadows for calibration of soil humidity measures in the laboratory. Surveys were repeated three times during the season: mid-May, mid-June and mid-July in 2019, paired to butterfly sampling periods.

2.3.4 Landscape metrics

A map of the Picos de Europa National Park at 1:10.000 scale containing vegetation cover features was used to extract landscape variables (Alonso *et al*., 2013). Vegetation cover was classified on 16 specific categories and in four general categories (grasslands, forest, scrub and other). For each meadow, we drew a circular landscape of 200 m radius and extracted vegetation data from the vegetation map (Fig. S2.1). We did not examine larger radii because study sites were close in proximity to each other (area was ca. 3 x 2 km^2).

The Shannon diversity index of vegetation types (those defined as specific categories) was used to represent compositional landscape heterogeneity. The average patch size inside the circular landscapes of 200 m radius was used to represent configurational landscape heterogeneity (Perovic *et al*., 2015; Gámez-Virués, 2015). For each landscape, the proportion of the three general vegetation categories (grassland, forest and scrub) was calculated. Landscape metrics were calculated using gvSIG2.5.1 (http://www.gvsig.com).

2.3.5 Data analysis

The response of butterfly community attributes to time since abandonment and to both meadow characteristics (plant species richness and diversity, vegetation height and cover, soil humidity, distance to water, elevation and slope) and landscape variables (compositional and configurational landscape heterogeneity; and forest, grasslands and scrub cover) were analysed using generalized linear mixed-effect models (GLMM). The response variables were: species richness (rarefied), Shannon diversity index (H'), butterfly density (as number of individuals recorded per 100 m transect), and functional community attributes, represented by the community index of each trait. All response variables followed a Gaussian error structure. The block was assigned as a random effect. The statistical significance of the fixed factors in each GLMM was tested with analysis of variance (ANOVA), comparing the fitted model containing the fixed factor with the null model containing only the random term. GLMMs were also used to test the effect of time since abandonment on plant richness, plant diversity (Shannon index) and plant cover (as average proportion in a 1 m^2 quadrat). Plant richness followed a Poisson distribution, plant diversity a Gaussian distribution and plant cover a negative binomial error structure. The fixed effect was time since abandonment (3 levels) and block was included as a random effect. The statistical significance of the fixed factor was assessed as described above for the butterfly analysis. GLMMs analyses were performed with "lme4" package in R (Bates *et al*., 2015).

To assess whether the community composition of butterflies differed among time since abandonment categories, we used non-metric multidimensional scaling (NMDS) ordinance analysis based on Bray-Curtis pairwise distance. We tested which meadow characteristics (plant richness, diversity and cover, vegetation height, distance to water, soil humidity, altitude and slope) were having an influence on butterfly communities. For these, we used functions "metaMDS" and "envfit" from "vegan" package (Oksanen *et al*., 2019).

Turnover in species identities among different "Time since abandonment" categories was calculated as ([number of species gained]+[number of species lost]/total number of species). This calculation is based on the original formulation by MacArthur and Wilson (1963) for evaluating species turnover in islands, as modified by Diamond (1969) to express proportional turnover in order to compare sites that differ in starting richness. For each period, turnover was calculated by combining all plots in a "Time since abandonment" category to minimise potential bias introduced by variation in sampling area across sites. We used function turnover from package "codyn" in R (Hallet *et al.*, 2020), to calculate species turnover.

We performed Indicator Species Analysis to test if there were butterfly species which were indicators of different abandonment categories (long-term or mid-term abandoned or unabandoned meadows). We used the "multipatt" function from "indicspecies" package in R (De Cáceres & Legendre, 2009). Function "multipatt" allows determination of lists of species that are associated to particular group of sites. It uses the approach by Dufrêne & Legendre (1997), who defined an Indicator Value (IndVal) index to measure the association between a species and a site group. The method calculates the index and then looks for the group corresponding to the highest association value. Finally, the statistical significance of this relationship was tested using a permutation test. Multipatt uses the IndVal index as test statistic (De Cáceres, 2020).

All statistical analyses were performed using the software RStudio for Statistical Computing (version 1.2.5019; RStudio Development Team, 2019).

2.4 RESULTS

In total, 741 individuals belonging to 56 butterfly species were recorded across the 19 surveyed meadows (Table S2.5). This represents 41% of species present in the Picos de Europa Nation Park and 25% of Iberian Peninsula and Balearic Islands butterfly fauna. The most abundant species were *Maniola jurtina*, *Melanargia galathea* and *Colias croceus* representing 58% of all recorded individuals. Several rare species were recorded at low density, including *Argynnis adippe, Boloria euphrosyne, Carterocephalus palaemon, Hamearis lucina* and *Lycaena hippothoe*.

2.4.1 Effects of time since abandonment on butterfly communities

There was no significant effect of time since abandonment on butterfly species richness or diversity (χ^2=1.736, p=0.419 and χ^2=1.978, p=0.371 respectively; Fig. 2.2a, 2.2b). However, density of butterflies was significantly higher in long term abandoned meadows than in mid-term abandoned or unabandoned meadows (χ^2=8.92, p=0.011; Fig. 2.2c).

Butterfly community preference for open/closed habitats (CTAO index) tended to increase with time since abandonment (Fig. 2.2d) but the differences were only marginally significant (χ^2=4.792, p=0.091). Butterfly communities did not differ in trophic specialisation index (χ^2=0.513, p=0.773), habitat specialisation index (χ^2=0.953, p=0.620) or dispersal ability index (χ^2=0.855, p=0.651) among long-term, mid-term or unabandoned meadows. Long-term abandoned meadows held butterfly communities that differed in composition from mid-term abandoned or unabandoned meadows (Fig. 2.3). These last two categories were not completely segregated. Six butterfly species (*Coenonympha arcania, Thymelicus sylvestris, Leptidea sinapis, Melanargia galathea, Aphantopus hyperanthus* and

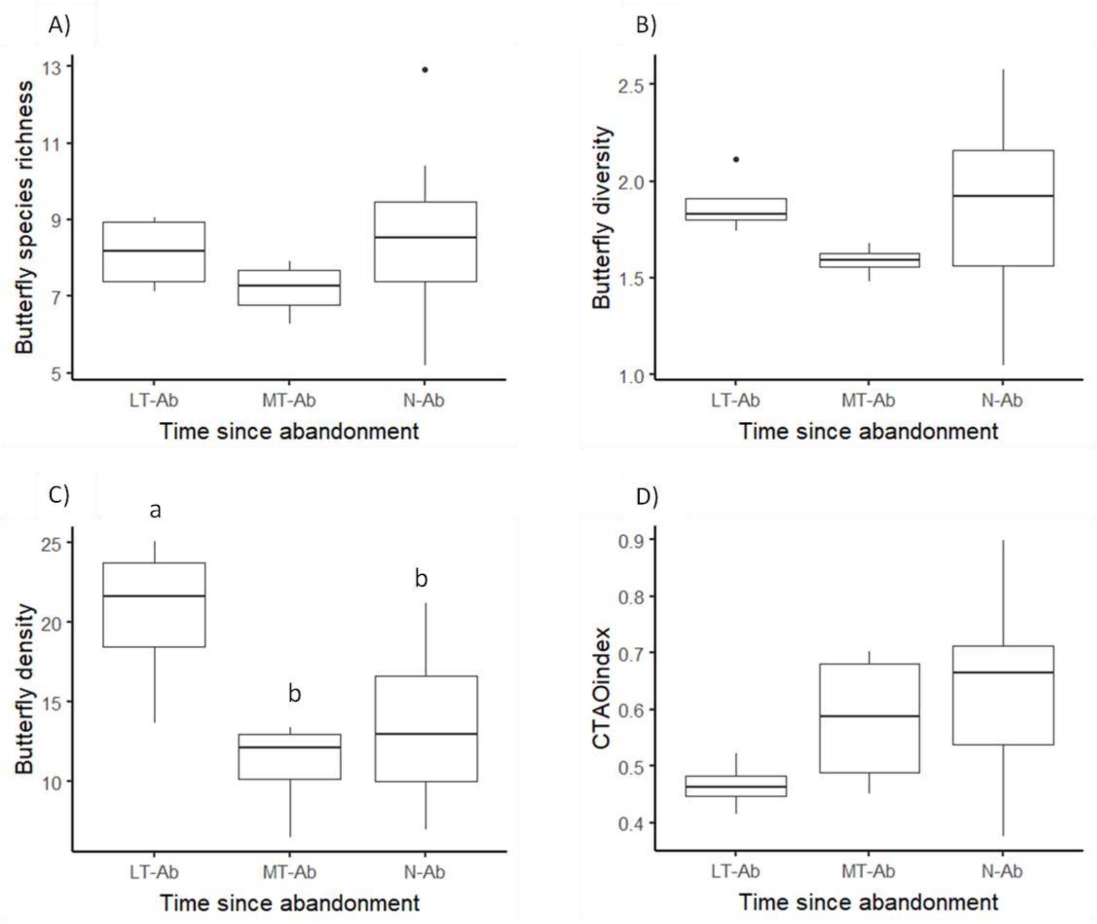

Fig. 2.2 Butterfly species richness (measured as rarefied species richness) (A), diversity (measured as Shannon index) (B), density (C) and community index of preference for open/closed habitats (CTAO index, -1=closed habitats, +1=open habitats) (D) in meadows of different years of abandonment, categorized as unabandoned (N-Ab), mid-term abandoned (MT-Ab) and long-term abandoned (LT-Ab). Different letters above the boxplots indicate significant differences between abandonment categories at $p<0.05$ (Post-Hoc Tukey test).

Lycaena virgaureae) came out as significant indicators of long-term abandoned meadows and two species (*Lysandra bellargus* and *Polyommatus icarus*) as indicators of unabandoned meadows (Table S2.4).

Species turnover in butterfly communities as time of abandonment proceeded was high, with a 52% of species change (6% appearances, 46% disappearances) in the first 3-7 years of abandonment; a 49% of change in the next 11-15 years (31% appereances, 18% disappereances) over the previous period and a global 48% of species change (10% appereances, 38.5% disappearances) after 18 years of abandonment (see Table S2.5 for the list of species present in each abandonment category).

2.4.2 Local context influence on butterfly community response to abandonment

Vascular plant species richness peaked at 3-7 years after abandonment and then declined below the initial values in unabandoned meadows (χ2=10.74, p=0.001; Fig. 2.4a). Vascular plant diversity was also higher after 3-7 years of abandonment and then decreased in the long term, remaining at higher values 18 years after abandonment than in unabandoned meadows (χ2=8.150, p=0.016; Fig. 2.4b). Vascular plant cover (χ2=0.874, p=0.645; Fig. 2.4c) and vegetation height (χ2=2.872, p=0.237; Fig. 2.4d) did not change with time since abandonment.

However, of the local environmental variables analysed (plant species richness, diversity and cover, vegetation height, distance to running water, soil humidity, altitude and orientation, see Table S2.6), only vegetation height had a marginally significant positive effect on butterfly species richness (χ2=2.825, p=0.092) and diversity (χ2=2.945, p=0.086). Butterfly community composition was also not significantly explained by any of the local variables measured within the meadow, except for time since abandonment (R2=0.274, p=0.034, see Table S2.7 for other variables).

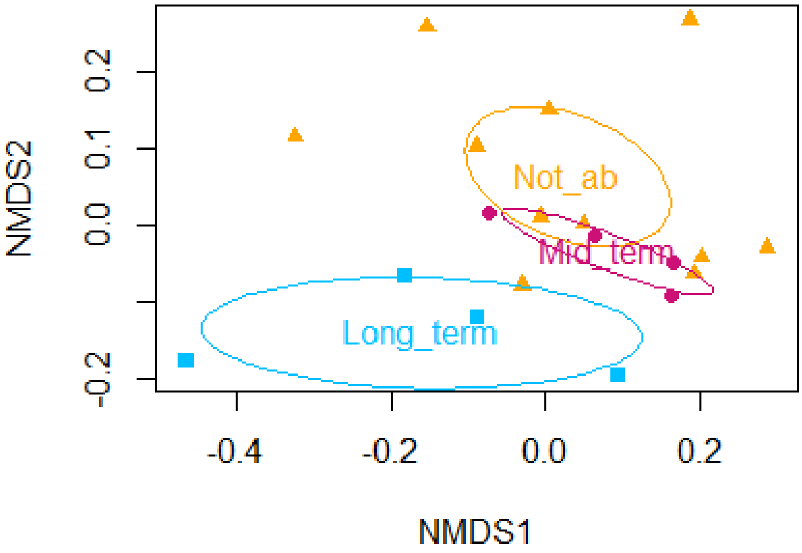

Fig. 2.3 NMDS analysis for butterfly communities (stress=0.09) grouped by time since abandonment categories: unabandoned (N-Ab), mid-term abandoned (MT-Ab) and long term abandoned (LT-Ab). Ellipses show the 95% confidence intervals for the group centroids.

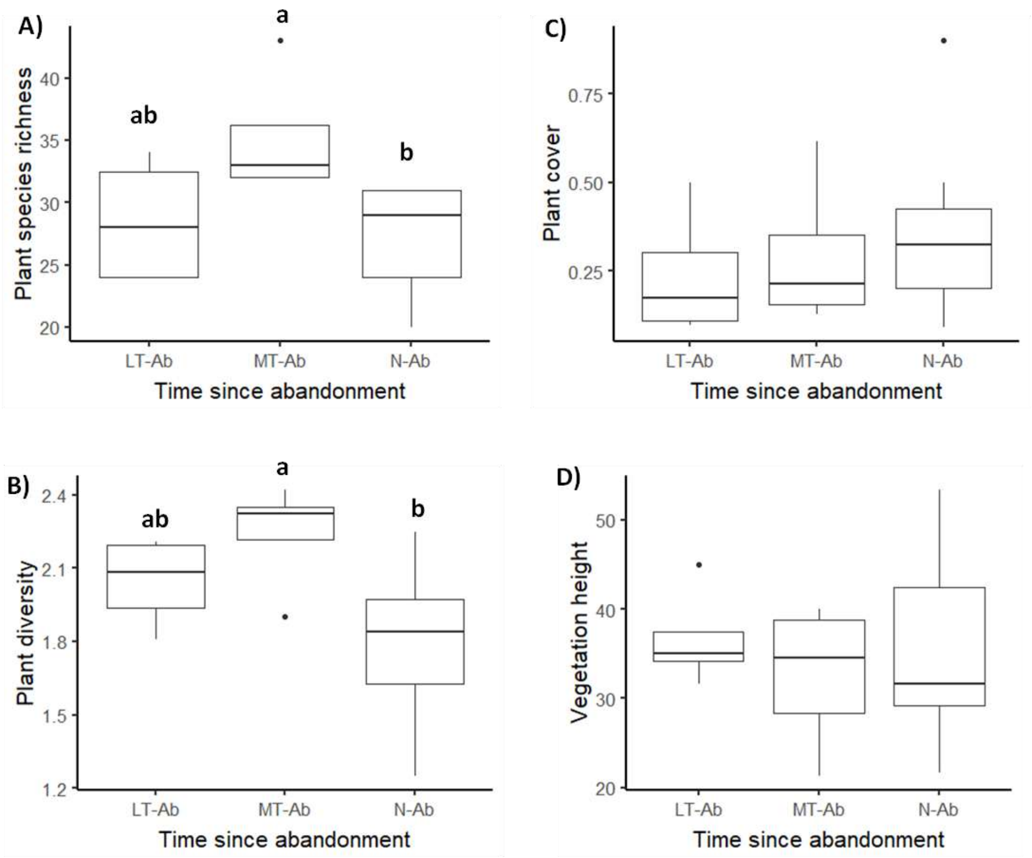

Fig. 2.4 Species richness (measured as observed species richness) (A), diversity (measured as Shannon index) (B) and cover (C) of vascular plants, and vegetation height (D) in meadows of different years of abandonment, categorized as unabandoned (N-Ab), mid-term abandoned (MT-Ab) and long-term abandoned (LT-Ab). Different letters above the boxplots indicate significant differences between abandonment categories at p<0.05 (Post-Hoc Tukey test).

2.4.3 Landscape context influence on butterfly community response to abandonment

Grassland and forest cover were strongly negatively correlated (R= -0.82, p<0.001) (see Table S2.8). Similarly, scrub and forest cover were negatively correlated, but not so strongly (R= -0.58, p<0.05). The advance of forests over grasslands because of abandonment was associated with a loss of landscape configurational heterogeneity (correlation between average patch size and grassland cover, R=0.54, p<0.05). Landscape habitat diversity increased parallel to scrub cover (R=0.50, p<0.05).

No landscape effects were detected on butterfly species richness, diversity or density, on community index for trophic specialisation, habitat specialisation or dispersal ability (see Table S2.9). The butterfly community preference index for open/closed habitats (CTAO index) increased when the landscape around the meadow was more heterogeneous (Fig. 2.5a, 2.5b), because of a higher habitat diversity (compositional heterogeneity, χ^2=5.872, p=0.015) or because of a smaller average habitat patch size (which means a higher configurational heterogeneity, χ^2=9.047, p=0.002). The result remained significant for configurational heterogeneity (χ^2=6.823, p=0.009, Fig. S2.2) after removing two outliers (meadows 23 and 24) but not for compositional heterogeneity (χ^2=0.051 p=0.819, Fig. S2.2).

The CTAO index also increased when there was a higher proportion of grassland and scrub in the landscape around the meadows (χ^2=7.443, p=0.006 and χ^2=6.083, p=0.013, respectively) but decreased when the proportion of forest cover was higher around the meadows (χ^2=10.74, p=0.001) (Fig. 2.5c, 2.5d, 2.5e).

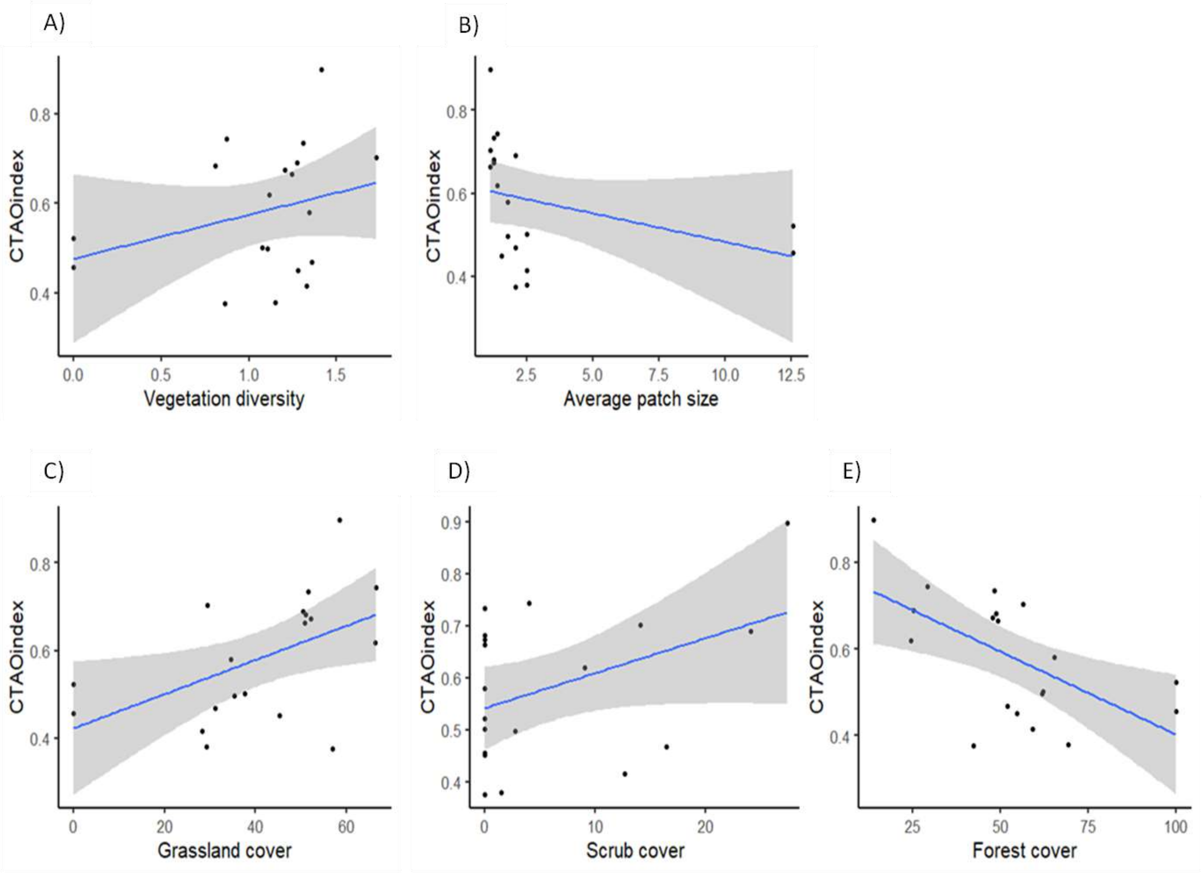

Fig. 2.5 Effects of landscape variables on butterfly community index of preferences for open/closed habitats (CTAO index). Landscape variables considered were: vegetation diversity (compositional heterogeneity) (A), average patch size (configurational heterogeneity) (B), and cover of grassland (C), scrub (D) and forest (E)- Grey shaded area shows the 95% confidence interval for the fitted line.

2.5 DISCUSSION

The aim of this study was to identify how abandonment of traditional hay meadows is affecting butterfly communities and how landscape context modulates these responses. The result shown that butterfly communities were affected by abandonment, with an overall increase in density of individuals after 18 years of abandonment. Community composition went through major changes with a species turnover of around 48% after 18 years of abandonment. There was a tendency of species with preference for closed habitats to increase in density as time since abandonment proceeded. Landscape variables had a larger impact on butterfly communities than local management, with butterfly community preference index for open habitats being lower in meadows surrounded by high forest cover. However, heterogeneous landscapes (in their composition or configuration) mitigated this effect, resulting in communities having a higher value for the index independent of the habitat cover surrounding the meadow.

We found that vascular plant communities changed quickly, with significant differences in both species richness and diversity with time since abandonment, peaking at 3-7 years after abandonment but decreasing in the long term to below the initial values. However, these changes in the plant community within the meadow did not have a significant effect on the butterfly communities. Some studies have demonstrated that declines in producers reduce diversity at higher trophic levels (Pöyry *et al.*, 2009; Uchida & Ushimaru, 2016; Dainese *et al.*, 2017). Moreover, higher plant diversity has been shown to correlate well with nectar resource availability (Krauss *et al.*, 2003), with potential effects on butterfly diversity (Skórka *et al.*, 2007; Marini *et al.*, 2009). However, we did not observe this pattern at the temporal and spatial scales studied.

We argue that previous studies were conducted in landscape matrices where remaining grasslands were a small percentage of the total land cover (2-3% as maximum). Such landscapes were very likely below extinction thresholds for species that exhibited long-term negative population trends (Pöyry *et al.*, 2009). In our study, with a remaining mean grassland cover of around 40%, mobility of butterflies across the landscape, among different successional patches of different age, could be buffering the negative effect of plant diversity loss in abandoned meadows. Our results suggest that a matrix with enough suitable habitat remaining, embedded in a more heterogeneous landscape, can slow down the negative effects of plant diversity loss on butterfly communities (Marini *et al.*, 2009).

Total butterfly density in the meadows increased with abandonment in the long term, this may be due to the absence of mortality caused by annual mowing. Mowing can be detrimental in the long term on butterfly populations, particularly for species with adults flying in late summer, low dispersal ability or very strict resource requirements (Johst *et al.*, 2006; Konvicka *et al.*, 2008). It has been shown that mowing leads to high insect mortality, with percentages ranging from 20% to 69% depending on the mowing technique (Humbert *et al.*, 2010; Humbert *et al.*, 2012). Dover *et al.* (2010a) found a significant decline in the abundance of typical grassland butterflies, such as the satyrids, in fields harvested for hay but no significant declines for other butterfly groups; which suggests that mortality rather local migration (due to decline in nectar resource) was likely responsible for the rapid decline in satyrids. Bruppacher *et al.* (2016) showed that simple modifications of mowing regime e.g. delayed cuts and maintaining uncut refuges, yielded higher butterfly densities (+70%) and could prevent the negative impact of mowing on butterflies. As in these previous studies, it is likely that mowing contributed to reduced butterfly density in managed meadows in our study.

We found that butterfly community composition also showed major changes with time since abandonment, with a species turnover of 52% in the first years after abandonment and of 48% in the long term. Other studies have detected important community composition changes immediately after abandonment (Stefanescu *et al.*, 2009) as well as an increasing tendency of community preference for closed habitats as time since abandonment proceeded (Herrando *et al.*, 2016; Stefanescu *et al.*, 2009).

We did not detect changes in butterfly species richness or diversity with time since abandonment, contrary to our expectations. In our study area, species richness response to environmental change seems to operate on a longer temporal scale than the 18 year period considered. Other studies on the effects of abandonment and grassland restoration with similar time spans (10 years) have been also unable to detect differences in species richness or diversity (Öckinger *et al.*, 2006). Several authors remark that other aspects of biodiversity than species richness, particularly those based on species traits, could be more strongly affected by land-use pressures (Rotchés-Ribalta *et al.*, 2018; Dainese *et al.*, 2017; Valiente-Banuet *et al.*, 2015).

Gagic *et al.* (2015) and Moretti *et al.* (2017) mention abundance-based traits composition of communities as a promising approach to advance current research on biodiversity and ecosystem functioning. Here we assessed the effects of abandonment on butterfly species traits, based on community indices for both habitat and trophic specialisation. We detected a tendency for communities to lose grassland specialists in the short term but reorganising in the long term by gaining woodland specialist species. This resulted in a difference in community composition despite species richness remaining relatively stable. Although marginally non-significant (p = 0.091), likely due to the limited number of meadows in our study, we found that community preference for closed habitats increased as time of abandonment proceeded. This makes sense as long-term abandoned meadows are generally located in parts of the landscape that have been abandoned first (not only meadows, but the whole mosaic) because they are located far from the village, or they have slopes over 30% that prevent mechanisation.

Landscape composition around the meadows strongly affected average community preference for open or closed habitats. The CTAO index for open/closed habitats decreased with forest cover (versus grassland or scrub cover) around the meadows but heterogeneous landscapes (in their composition - vegetation diversity, or in their configuration - average patch size) mitigated this effect. Our results show that landscape characteristics act as a strong filter of functional trait-diversity for butterfly communities within seminatural grasslands and dominate over local effects (Perović *et al*., 2015; Gámez-Virués *et al*., 2015; Seibold *et al*., 2019). This emphasises the importance of landscape scale management in conserving biodiversity (Gámez-Virués *et al*., 2015).

Our results support the idea that a highly heterogeneous cultural landscape mosaic around the meadows, produced by the combination of traditional farming practices, livestock grazing and forest management (Farina, 2000), is moderating the negative effects of local land-use abandonment and influencing grassland species persistence, at both the local and landscape level. Those landscapes are also supporting a larger species pool, providing a diversity of patches with different disturbance dynamics and encouraging organisms to use different habitat patches with complementary resources (Tscharntke *et al*., 2012; Oliver *et al*., 2010).

A large species pool has allowed butterfly communities to reorganise, in a relatively short period of time (18 years) after perturbations ceased, into diverse and specialised assemblages. Contrary to our initial hypothesis, we did not find a higher number of species in managed grasslands. Rather than the substitution of specialists by generalists found in studies on agriculture intensified landscapes (Dainese *et al*., 2017), we found a negative trend of grassland specialists (eg. *Colias crocea, Polyommatus icarus, Boloria dia, Plebejus argus, Melitaea phoebe*) versus a positive trend of woodland specialists (eg. *Vanessa atalanta, Ochlodes sylvanus, Carterocephalus palaemon, Lycaena tityrus, Aphantopus hyperanthus*), in line with other studies focusing on land abandonment (Stefanescu *et al*., 2011a; Herrando *et al*., 2016, Ubach *et al*., 2020), suggesting species responses to environmental changes are context dependent (Melero *et al*., 2016).

Although we observed increases in woodland specialists, these species may also be at risk in the longer term because of a lack of woodland management. European woodland butterflies utilise sunny habitats within woodlands, such as sparse stands, bogs, stream sides, clearings, rides or edges. Managing woodlands for many threatened species consists of maintaining relatively low tree density and/or permanent or dynamically managed clearings (Settele *et al*., 2009). Abandoned hay meadows, embedded in forest patches, may be acting as forest clearings for woodland species. For example, *Lopinga achine*, a rare and endangered woodland species, in Picos de Europa area has taken advantage of hay meadow edges with forests, using them as a suitable habitat for breeding (Bergman, 1999; Jubete *et al*., 2019). Population density of this species in Sweden peaked when canopy cover was around 70-85% and decreased at higher and lower canopy covers, with no populations being observed with canopy cover under 60% (Bergman, 2001). Therefore, more research is needed to determine if woodland butterfly species are also being affected by rural abandonment and vegetation encroachment.

In conclusion, butterfly communities associated with seminatural grassland in the Picos de Europa National Park are going through massive changes because of rural abandonment. The advance of forests over grasslands and the onward vegetation encroachment will homogenize landscapes, which may lead to a decline of open habitat specialist butterflies. Woodland specialist butterflies may also be at risk as they rely on woodland clearings, which are also disappearing because of vegetation encroachment and lack of woodland management. The Spanish Butterfly Monitoring Scheme, put in place in 2014, which includes the Picos de Europa National Park, will soon produce relevant data to analyse the wider impact of rural abandonment on the butterflies of Picos de Europa and Spain as a whole. In the meantime, we should ensure that communities have time to react to the diverse stressors imposed by global change. Facilitating survival to all kind of functional and taxonomic groups, implies promoting landscape heterogeneity and connectivity.

2.6. Supporting information

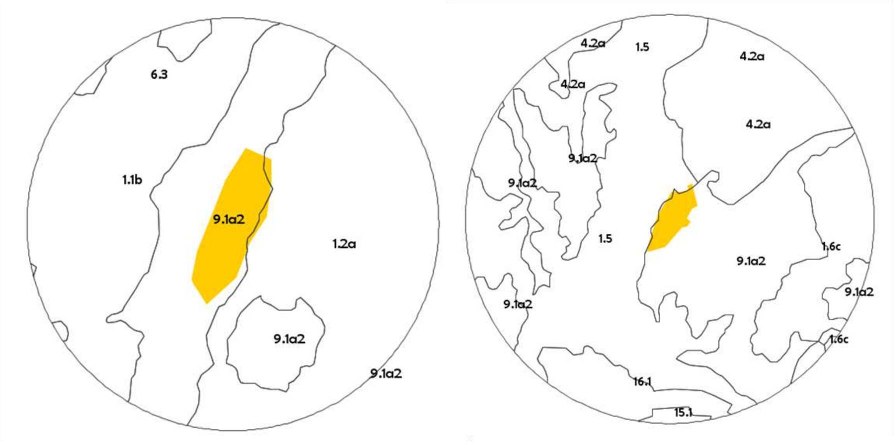

Figure S2.1 Compositional and configurational heterogeneity in 200 m radius buffers around meadows. Vegetation map of the 200 m radius buffer around Meadow 1 (on the left) and Meadow 14 (on the right) (surveyed meadows in yellow). Meadow 1 has five different vegetation patches and larger average patch size (less configurational landscape heterogeneity) while Meadow 14 has twelve different vegetation patches and smaller average patch size (more configurational landscape heterogeneity).

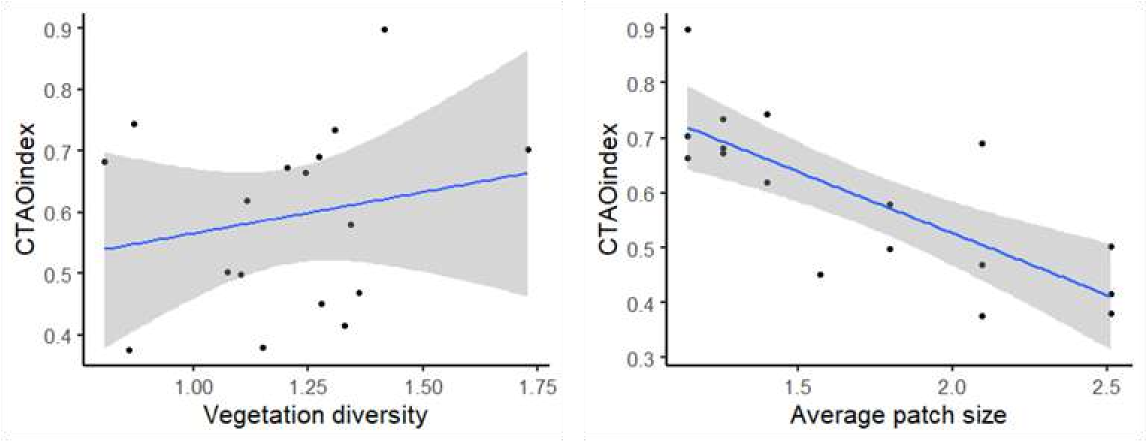

Figure S2.3. Effects of configurational and compositional heterogeneity on butterfly CTAO index without outliers. Effects of average patch size (configurational heterogeneity) (on the right) and effects of vegetation diversity (compositional heterogeneity) (on the left) on butterfly community index of preferences for open/closed habitats (CTAOindex), without meadows 23 and 24. Grey portions show the 95% confidence interval for the linear fit.

Table S2.1. Sampled meadows classified by time since abandonment.

Meadow Nº	Block	Abandonment category	Years since last management	Area (ha)
1	A (Road)	Unabandoned (N-Ab)	0	6143.77
2	A (Road)	Long-term abandoned (LT-Ab)	18	3670.42
3	A (Road)	Unabandoned (N-Ab)	0	7260.74
4	A (Road)	Long-term abandoned (LT-Ab)	18	2869.95
5	A (Road)	Unabandoned (N-Ab)	0	4370.24
6	A (Road)	Mid-term abandoned (MT-Ab)	4	4613.93
7	B (Miraño)	Unabandoned (N-Ab)	0	6004.58
8	B (Miraño)	Unabandoned (N-Ab)	0	6265.41
9	B (Miraño)	Mid-term abandoned (MT-Ab)	4	4959.56
10	B (Miraño)	Unabandoned (N-Ab)	0	5229.81
11	B (Miraño)	Mid-term abandoned (MT-Ab)	3	7095.00
12	B (Miraño)	Unabandoned (N-Ab)	0	8142.16
13	C (Güembres)	Mid-term abandoned (MT-Ab)	7	4722.11
14	C (Güembres)	Unabandoned (N-Ab)	0	4401.27
15	C (Güembres)	Unabandoned (N-Ab)	0	2992.13
16	C (Güembres)	Unabandoned (N-Ab)	0	4220.00
17	C (Güembres)	Unabandoned (N-Ab)	0	3372.84
18	C (Güembres)	Long-term abandoned (LT-Ab)	18	4239.96
19	C (Güembres)	Long-term abandoned (LT-Ab)	18	2893.44

Table S2.2 Plant species traits.

ID	Species	Ecological group	Nutrient index	Light index
1	Achillea millefolium	G	3	4
2	Agrimonia eupatoria	S	3	4
3	Anthemis arvensis	R	2	4
4	Anthyllis vulneraria	S	2	4
5	Astrantia major	M	3	3
6	Bellis perennis	G	4	4
7	Campanula patula	S	3	4
8	Campanula rapunculus	S	3	3
9	Centaurea nigra	S	3	4
10	Centaurium pulchellum	H	3	4
11	Cerastium fontanum	R	3	3
12	Chaerophyllum aureum	G	4	3
13	Cirsium monspessulanum	NA	NA	NA
14	Clinopodium vulgare	S	2	3
15	Conopodium pyrenaeum	NA	NA	NA
16	Convolvulus arvensis	R	4	4
17	Crepis capillaris	G	3	4
18	Crepis paludosa	H	3	3
19	Crepis pyrenaica	NA	NA	NA
20	Cruciata laevipes	G	4	3
21	Dianthus armeria	R	2	4
22	Dianthus deltoides	S	2	4
23	Echium vulgare	S	4	4
24	Erodium cicutarium	R	3	4
25	Eryngium bourgatii	NA	NA	NA
26	Euphrasia alpina	M	2	5
27	Galium estebanii	NA	NA	NA
28	Geranium columbinum	R	3	4
29	Geranium dissectum	R	3	4
30	Geranium pyrenaicum	R	4	3
31	Geranium sanguineum	F	2	3
32	Helianthemum nummularium	S	2	5
33	Hypochoeris radicata	G	3	4
34	Knautia arvensis	G	3	4
35	Knautia arvernensis	NA	NA	NA
36	Lathyrus pratensis	G	3	3
37	Leontodon hispidus	G	3	4
38	Leucanthemum vulgare	G	3	4
39	Linum bienne	S	2	4
40	Linum catharticum	H	1	3
41	Lotus corniculatus	G	3	4

ID	Species	Ecological group	Nutrient index	Light index
42	Malva moschata	R	3	4
43	Medicago lupulina	G	3	3
44	Myosotis discolor	R	2	4
45	Petrorhagia nanteuilii	NA	NA	NA
46	Plantago lanceolata	G	3	4
47	Plantago media	S	2	4
48	Polygala serpyllifolia	H	2	4
49	Polygala vulgaris	S	2	4
50	Polygonum bistorta	M	4	3
51	Potentilla erecta	H	2	4
52	Potentilla reptans	R	4	4
53	Prunella grandiflora	S	2	4
54	Prunella laciniata	S	2	4
55	Prunella vulgaris	G	3	4
56	Ranunculus acris subsp despectus	M	3	3
57	Ranunculus bulbosus	S	2	4
58	Ranunculus repens	R	4	3
59	Ranunculus tuberosus	F	2	3
60	Rhinanthus angustifolius	H	3	4
61	Rhinanthus minor	H	2	4
62	Sanguisorba minor	S	2	4
63	Sherardia arvensis	R	3	4
64	Silene vulgaris	S	2	3
65	Stachys recta	S	2	4
66	Stellaria graminea	G	3	3
67	Thymus praecox	S	2	5
68	Thymus pulegioides	S	2	4
69	Trifolium campestre	R	2	4
70	Trifolium dubium	G	3	4
71	Trifolium ochroleucon	F	2	4
72	Trifolium pratense	G	3	3
73	Trifolium repens	G	4	4
74	Trifolium striatum	S	2	4
75	Trollius europaeus	H	3	4
76	Valerianella dentata	R	4	4
77	Valerianella locusta	R	4	4
78	Valerianella rimosa	R	4	4
79	Veronica arvensis	R	4	3
80	Veronica chamaedrys	G	4	3
81	Vicia cracca	G	3	4
82	Vicia orobus	F	2	3
83	Viola cornuta	NA	NA	NA

After Lauber & Wagner (1998). F = forest plant; M=mountain plant; P=pioneer plant; E= aquatic plant; H= wetland plant; S=poor grassland plant; R=ruderal plant; G=rich grassland plant; C=cultivated plant; N=neophyte; NA= Not available.

Our 83 plant species belong to these ecological groups: forest plants (n=4), mountain plants (n=4), wetland plants (n=8), poor grassland plants (n=21), ruderal plants (n=18), rich grassland plants (n=20) and not available values (n=8).

No values were available for *Cirsium monspessulanum*, *Conopodium pyrenaeum* (Iberian endemism), *Crepis pirenaica*, *Eryngium bourgatii* (Pyrenean-Cantabrian endemism), *Galium estebanii* (Iberian endemism), *Knautia arvernensis*, *Petrorhagia nanteuilii* and *Viola cornuta* (Pyrenean-Cantabrian endemism), so they were not included in the community index.

Nutrient index (nitrates + salinity) indicates which nutrients plants need or can cope with, mainly nitrogen. 1=Plants of soils very poor on nutrients; 2= Plants of poor soils; 3= Plants growing on soils not poor, not rich; 4= Plants of rich nutrient soils; and 5=Plants of over enriched soils.

Light index indicates the average light intensity needed for adequate growing. 1=Plants of very shadowed places; 2=Plants of shadowed places; 3=Plants of half-shadowed places; 4=Plants growing in plain light conditions, but coping temporarily with shadow; and 5=Plants only growing on plain light.

Reference: Lauber, K. and Wagner, G. (1998) *Flora Helvetica. Flore illustrée de Suisse.* Editions Paul Haupt.

Table S2.3 Distribution of plant species sampled in ecological groups after Lauber & Wagner (1998).

Ecological group	Nº. species
Poor grasslands plants	21
Rich grasslands plants	20
Ruderal plants	18
Wetland plants	8
Mountain plants	4
Forest plants	4
Not available values	8
Total species number	83

Table S2.4 Plant community indices for traits analysed.

Meadow	Nutrients community index	Light community index	Rich grasslands plants cover	Ruderal plants cover	Poor grasslands plants cover
1	0.4181	0.3999	0.7409	0.3345	0.0024
2	0.5452	0.4674	0.5823	0.0001	0.3334
3	0.9205	0.8898	0.5576	0.6302	0
4	0.4551	0.3736	0.2922	0.0742	0.1483
5	0.4619	0.4652	0.3164	0.6543	0.1304
6	0.5472	0.6268	0.2730	0.8517	1.0000
8	1.0000	1.0000	1.0000	1.0000	0.4072
9	0.3136	0.3669	0.1214	0.1612	0.1491
10	0.3723	0.3908	0.1521	0.4695	0.1334
11	0.4667	0.4880	0.0667	0.5190	0.1854
12	0.3854	0.3542	0.1285	0.0125	0.4073
13	0.3902	0.3679	0.1516	0.0001	0.9273
17	0.3046	0.4104	0.0158	0.1173	0.1852
18	0.3826	0.4628	0.0915	0.0555	0.1953
19	0.2471	0.2555	0.0155	0.0185	0.0385
21	0.3732	0.3473	0.1311	0.3829	0.1027
22	0.2869	0.3280	0.0555	0.1055	0.1223
23	0.3310	0.3549	0.0759	0	0.2682
24	0.2494	0.3380	0.0081	0	0.3907

Table S2.5 Butterfly species traits

Species	Index of preferences for open/closed habitats	Trophic specialisation index	Habitat specialisation index	Dispersal ability index
Aglais_urticae	0.448	1	1	3
Anthocharis_cardamines	-0.027	2	4	2
Aphantopus_hyperanthus	0.216	2	2	1
Aporia_crataegi	0.454	2	3	2
Argynnis_adippe	0.317	1	3	2
Argynnis_aglaja	0.340	1	2	2
Argynnis_paphia	0.044	1	3	2
Aricia_cramera	0.503	1	4	2
Aricia_montensis	NA	NA	NA	NA
Boloria_dia	0.535	1	4	2
Boloria_euphrosyne	0.357	1	1	1
Boloria_selene	0.766	1	NA	1
Brenthis_ino	0.974	NA	NA	NA
Carcharodus_alceae	0.626	2	3	3
Carterocephalus_palaemon	NA	NA	NA	NA
Celastrina_argiolus	0.058	3	4	3
Coenonympha_arcania	0.047	2	3	1
Coenonympha_pamphilus	0.654	2	4	2
Colias_alfacariensis	0.545	1	2	2
Colias_croceus	0.598	2	4	4
Cupido_argiades	0.573	2	2	2
Cupido_minimus	0.274	1	3	1
Erynnis_tages	0.631	2	2	1
Gonepteryx_rhamni	0.070	1	4	3
Hamearis_lucina	0.406	1	2	1
Inachis_io	0.259	1	4	3
Iphiclides_feishtamelii	0.441	2	4	3
Issoria_lathonia	0.475	1	3	3
Lampides_boeticus	0.499	3	3	4
Lasiommata_maera	0.225	2	4	1
Lasiommata_megera	0.116	2	4	3
Leptidea_sinapis	-0.099	2	4	2
Leptotes_pirithous	0.496	3	2	4
Lycaena_hippothoe	NA	1	1	1
Lycaena_tityrus	0.852	1	1	1
Lycaena_virgaureae	0.669	1	1	2
Maniola_jurtina	0.257	2	4	2
Melanargia_galathea	NA	NA	NA	NA
Melitaea_cinxia	0.540	2	3	1
Melitaea_phoebe	NA	2	4	2
Nymphalis_polychloros	0.049	3	3	3
Ochlodes_sylvanus	0.255	2	4	2
Pararge_aegeria	-0.419	2	3	3
Pieris_brassicae	0.244	3	4	4
Pieris_napi	0.050	2	3	3
Pieris_rapae	0.284	3	4	4
Plebejus_argus	0.639	NA	NA	NA
Plebejus_idas	0.829	NA	NA	NA
Lysandra_bellargus	0.613	2	3	1

Species	**Index of preferences for open/closed habitats**	**Trophic specialisation index**	**Habitat specialisation index**	**Dispersal ability index**
Lysandra_coridon	0.460	1	2	1
Polyommatus_icarus	0.600	2	4	3
Pyronia_tithonus	0.206	2	3	2
Spialia_sertorius	0.540	1	4	1
Thymelicus_sylvestris	0.416	2	2	1
Vanessa_atalanta	0.134	2	4	4
Vanessa cardui	0.537	3	4	4

Index of preferences for open/closed habitats after Ubach *et al*. (2020). Not avalaible TAO index species for *Aricia montensis, Carterocephalus palaemon, Lycaena hippothoe, Melanargia galathea* or *Melitaea phoebe* (5 out of 56 species), so they were not included in the community index.

Trophic specialisation, habitat specialisation and dispersal ability species indexes after Stefanescu *et al*. (2011a). Trophic specialisation categories: 1=monophagous; 2=oligophagous; 3=polyphagous. Habitat specialisation categories, ranging from 1=Most specialised to 4=Least specialised. Dispersal ability categories, ranging from 1=minimal to 4=maximal. Not available trophic, habitat or dispersal information for *Aricia montensis, Brenthis ino, Carterocephalus palaemon, Melanargia galathea, Plebejus argus* or *Plebejus idas* (6 out of 56 species), so they were not included in the correspondent community indexes.

Table S2.6 Butterfly community indices.

Meadow	Community index for preferences for open/closed habitats	Community trophic specialisation index	Community habitat specialisation index	Community dispersal ability index
1	0.379	2.973	5.363	3.685
2	0.417	2.935	5.348	3.260
3	0.497	2.343	4.163	2.906
4	0.468	3.384	5.479	3.493
5	0.376	2.561	4.837	3.262
6	0.501	3.272	5.661	4.192
8	0.663	3.109	5.454	3.736
9	0.734	4.175	8.109	4.822
10	0.450	2.753	3.345	2.918
11	0.682	2.379	3.211	2.313
12	0.673	2.272	3.356	2.413
13	0.579	3.004	3.788	3.106
17	0.702	2.400	4.415	2.231
18	0.618	2.400	4.077	2.867
19	0.897	3.247	4.689	3.378
21	0.743	2.635	4.272	3.045
22	0.690	2.703	3.936	2.625
23	0.456	2.435	4.217	3.095
24	0.522	2.577	4.545	3.245

Table S2.7 Vegetation cover categories

Vegetation map code	Vegetation Unit (specific category)	General category
1.1a	Beech forest with *Carex sylvatica*	Forest
1.1b	Beech forest with *Carex caudata*	Forest
1.2a	Beech forest with *Blechnum spicant*	Forest
1.5	Oligotrophic *Quercus pyrenaica* oak forest	Forest
1.6c	Eutrophic mixed forest with *Quercus petraea* and *Fraxinus excelsior*	Forest
1.8a	*Quercus petraea* oak forest with *Luzula henriquesii* and *Fagus sylvatica*	Forest
2.1	Young forests with *Acer* and *Fraxinus*	Forest
4.2a	*Genista polygaliphylla* and *Cytisus cantabricus* scrub	Scrub
5.2a1	*Ulex gallii* and *Erica vagans* scrub	Scrub
6.2	*Genista occidentalis* scrub without *Ulex europaeus*	Scrub
6.3	*Genista legionensis* scrub	Scrub
6.3a	*Genista legionensis* scrub with *Helictotrichon cantabricum* and *Oreochloa confusa*	Scrub
8.1b	Ferns growing on basic substrates	Scrub
9.1a2	Hay meadows	Grassland
9.1b2	Hygrophilous hay meadows with *Juncus conglomeratus*	Grassland
13.1c	Casmophyte communities with *Centranthus lecoquii* and *Saxifraga canaliculata*	Other
15.1	Cultivated land and greenhouses	Other
16.1	Villages and towns	Other

Table S2.8 Model results for time since abandonment effects on butterfly and plant attributes.

Time since abandonment /Response variable	Estimate		Sd error	Stat	p	Post-Hoc Tukey test
Butterfly species richness	Intercept	8.140	0.889	χ^2= 1.736	0.419	
	Mid Term	-0.955	1.257			
	Not ab	0.330	1.038			
Butterfly Shannon diversity index	Intercept	1.929	0.198	χ^2= 1.978	0.371	
	Mid Term	-0.260	0.252			
	Not ab	-0.010	0.207			
Butterfly density	Intercept	20.609	2.558	**χ^2= 8.92**	**0.011**	**Mid term-Long term: 0.007** **Not ab – Long term: 0.018**
	Mid Term	-9.620	3.207			
	Not ab	-7.131	2.629			
CTAO index	Intercept	0.478	0.080	χ^2= 4.792	0.091	Not ab – Long term: 0.07
	Mid Term	0.097	0.077			
	Not ab	0.136	0.063			

Time since abandonment /Response variable	**Estimate**		**Sd error**	**Stat**	**p**	**Post-Hoc Tukey test**
Trophic specialisation index	Intercept	2.835	0.250	χ^2= 0.513	0.773	
	Mid Term	-0.162	0.352			
	Not ab	0.031	0.291			
Habitat specialisation index	Intercept	4.897	0.584	χ^2= 0.953	0.620	
	Mid Term	-0.703	0.827			
	Not ab	-0.179	0.682			
Dispersal ability index	Intercept	3.281	0.337	χ^2= 0.855	0.651	
	Mid Term	-0.346	0.463			
	Not ab	-0.026	0.382			
Plant species richness	Intercept	3.349	0.093	**χ^2= 6.337**	**0.042**	MT-LT, z= 1.688 p=0.207 Nab-LT, z=-0.430 p= 0.902 **Nab-MT, z=-2.544 p=0.029**
	Mid Term	0.212	0.125			
	Not ab	-0.047	0.110			
Plant Shannon diversity index	Intercept	2.044	0.148	**χ^2= 8.150**	**0.016**	MT-LT, z=1.037 p=0.549 Nab-LT, z=-1.626 p=0.231 **Nab-MT, z=-2.950 p=0.008**
	Mid Term	0.199	0.192			
	Not ab	-0.256	0.158			
Plant cover	Intercept	-1.098	1.154	χ^2= 0.874	0.645	
	Mid Term	$-0.007\cdot10^{-2}$	1.632			
	Not ab	-1.204	1.559			
Plant community nutrient index	Intercept	-0.425	1.022	z=-0.416	0.677	
	Mid Term	0.030	1.444	z=0.021	0.983	
	Not ab	0.338	1.187	z=0.285	0.776	
Plant community light index	Intercept	-0.475	1.028	z=-0.462	0.644	
	Mid Term	0.256	1.438	z=0.178	0.859	
	Not ab	0.428	1.192	z=0.359	0.720	
Rich grassland species cover	Intercept	-1.154	1.171	z=-0.986	0.324	
	Mid Term	-0.641	1.849	z=-0.347	0.729	
	Not ab	0.284	1.345	z=0.212	0.832	
Ruderal species cover	Intercept	-3.968	3.703	z=-1.071	0.284	
	Mid Term	3.404	3.847	z=0.885	0.376	
	Not ab	3.353	3.757	z=0.893	0.372	
Poor grassland species cover	Intercept	-0.919	1.107	z=-0.830	0.407	
	Mid Term	0.643	1.498	z=0.429	0.668	
	Not ab	-0.433	1.335	z=-0.324	0.746	

Table S2.9 Correlation analysis among landscape variables.

	Average patch size		Vegetation diversity		Grassland cover		Scrub cover		Forest cover	
	r	p	r	p	r	p	r	p	R	p
Average patch size			-0.15	0.572	-0.54	0.025	0.00	0.994	0.44	0.081
Vegetation diversity	-0.15	0.572			-0.48	0.050	0.50	0.042	0.11	0.681
Grassland cover	-0.54	0.025	-0.48	0.050			0.00	0.995	-0.82	<0.001
Scrub cover	0.00	0.994	0.50	0.042	0.00	0.995			-0.58	0.015
Forest cover	0.44	0.082	0.11	0.681	-0.82	<0.001	-0.58	0.015		

n=17 . Meadows 23 and 24 removed because they were outliers.

Table S2.10 Plant species indicating time since abandonment categories.

Plant species	Group	Stat	P
Clinopodium vulgare	Long term abandoned	0.644	0.006
Stellaria graminea	Long term abandoned	0.619	0.015
Potentilla erecta	Long term abandoned	0.617	0.053
Prunella grandiflora	Long term abandoned	0.553	0.067
Cruciata laevipes	Long term abandoned	0.470	0.058
Veronica chamaedrys	Long term abandoned	0.458	<0.001
Vicia cracca	Mid term abandoned	0.530	0.067
Linum bienne	Mid term abandoned	0.519	0.071
Sherardia arvensis	Mid term abandoned	0.478	0.094
Valerianella dentata	Mid term abandoned	0.430	0.099

Table S11. Model results for landscape variables on plant attributes.

Id Model	Response variable	Landscape variable	Estimate	Sd. Error	Stat	p
M1	Plant species richness	Average patch size	$-1.519e^{-06}$	$1.346e^{-06}$	z=-1.129	0.259
M2		Vegetation diversity	0.155	0.105	z=1.474	0.141
M3		Grassland cover	$0.007 \cdot 10^{-1}$	0.002	z=0.335	0.738
M4		Scrub cover	$-0.007 \cdot 10^{-1}$	0.004	z=-0.154	0.878
M5		Forest cover	$-0.004 \cdot 10^{-1}$	0.001	z=-0.231	0.817
M6	Plant diversity	Average patch size	0.012	0.022	χ^2=0.348	0.554
M7		Vegetation diversity	0.042	0.179	χ^2=0.035	0.850
M8		Grassland cover	-0.001	0.004	χ^2=0.043	0.834
M9		Scrub cover	0.008	0.008	χ^2=1.100	0.294
M10		Forest cover	-0.001	0.003	χ^2=0.058	0.809
M11	Plant cover	Average patch size	-0.107	0.192	z=-0.568	0.575
M12		Vegetation diversity	0.479	1.255	z=0.382	0.703
M13		Grassland cover	0.008	0.027	z=0.293	0.770
M14		Scrub cover	-0.037	0.064	z=-0.587	0.557
M15		Forest cover	$-0.002 \cdot 10^{-1}$	0.022	z=-0.013	0.990
M16	Nutrient community index	Average patch size	-0.064	0.147	z=-0.436	0.663
M17		Vegetation diversity	0.252	1.105	z=0.228	0.819
M18		Grassland cover	0.003	0.025	z=0.145	0.885
M19		Scrub cover	-0.027	0.055	z=-0.498	0.619
M20	Nutrient community index	Forest cover	0.001	0.021	z=0.076	0.939
M21	Light community index	Average patch size	-0.046	0.142	z=-0.327	0.744
M22		Vegetation diversity	0.156	1.093	z=0.143	0.886
M23		Grassland cover	0.002	0.025	z=0.113	0.910
M24		Scrub cover	-0.029	0.055	z=-0.522	0.601
M25		Forest cover	0.002	0.021	z=0.114	0.909
M26	Rich grasslands species cover	Average patch size	-0.128	0.234	z=-0.550	0.582
M27		Vegetation diversity	0.719	1.448	z=0.497	0.619
M28		Grassland cover	-0.001	0.028	z=-0.043	0.966
M29		Scrub cover	-0.044	0.073	z=-0.602	0.547
M30		Forest cover	0.006	0.024	z=0.280	0.780
M31	Ruderal species cover	Average patch size	-0.283	0.421	z=-0.671	0.502
M32		Vegetation diversity	0.154	1.227	z=0.126	0.9
M33		Grassland cover	0.026	0.032	z=0.826	0.409
M34		Scrub cover	-0.117	0.104	z=-1.128	0.259
M35		Forest cover	-0.005	0.023	z=-0.215	0.830
M36	Poor grasslands species cover	Average patch size	0.04	0.144	z=0.278	0.781
M37		Vegetation diversity	-0.137	1.196	z=-0.115	0.909
M38		Grassland cover	-0.014	0.027	z=-0.532	0.595
M39		Scrub cover	-0.067	0.080	z=-0.845	0.398
M40		Forest cover	0.019	0.024	z=0.792	0.428

Table S12. Environmental variables effect on butterfly community composition.

Environmental variable	**r^2**	**Pr(>r)**
Plant observed species	0.044	0.703
Plant diversity	0.079	0.553
Plant cover	0.030	0.763
Altitude	0.174	0.219
Distance to water	0.242	0.112
Vegetation height	0.015	0.881
Soil humidity	0.202	0.160
Orientation	0.373	0.183

Table S13. Butterfly species indicating time since abandonment categories.

Butterfly species	**Group**	**Stat**	**P**
Coenonympha arcania	Long term abandoned	0.797	<0.001
Thymelicus sylvestris	Long term abandoned	0.737	0.005
Leptidea sinapis	Long term abandoned	0.642	0.015
Melanargia galathea	Long term abandoned	0.569	0.054
Aphantopus hyperanthus	Long term abandoned	0.563	0.065
Lycaena virgaureae	Long term abandoned	0.557	0.055
Lysandra bellargus	Not abandoned	0.571	0.060
Polyommatus icarus	Not abandoned	0.524	0.100

Table S14. Butterfly species present and their density (individuals per 100m) in unabandoned, mid-term abandoned and long-term abandoned meadows.

Unabandoned		**Mid-term abandoned**		**Long-term abandoned**	
Species	**Density**	**Species**	**Density**	**Species**	**Density**
Maniola_jurtina	6,487	Maniola_jurtina	5,639	Maniola_jurtina	7,256
Melanargia_galathea	1,850	Melanargia_galathea	1,952	Melanargia_galathea	4,465
Colias_croceus	0,832	Colias_croceus	0,710	Coenonympha_arcania	1,798
Leptidea_sinapis	0,582	Boloria_dia	0,300	Leptidea_sinapis	1,294
Polyommatus_icarus	0,446	Cupido_argiades	0,300	Thymelicus_sylvestris	0,802
Boloria_dia	0,436	Pieris_napi	0,207	Ochlodes_sylvanus	0,383
Lysandra_bellargus	0,327	Polyommatus_icarus	0,200	Argynnis_aglaja	0,321
Cupido_argiades	0,219	Aglais_urticae	0,152	Lycaena_tityrus	0,281
Brenthis_ino	0,164	Leptidea_sinapis	0,152	Boloria_selene	0,261
Aglais_urticae	0,150	Ochlodes_sylvanus	0,150	Aphantopus_hyperanthus	0,247
Celastrina_argiolus	0,137	Anthocharis_cardamines	0,105	Colias_croceus	0,213
Argynnis_aglaja	0,127	Lycaena_tityrus	0,102	Lycaena_virgaureae	0,195
Issoria_lathonia	0,127	Issoria_lathonia	0,100	Pieris_rapae	0,139
Aporia_crataegi	0,091	Coenonympha_arcania	0,100	Lampides_boeticus	0,136
Coenonympha_pamphilus	0,091	Boloria_selene	0,100	Argynnis_paphia	0,132
Lycaena_tityrus	0,082	Vanessa_atalanta	0,052	Aricia_montensis	0,125
Thymelicus_sylvestris	0,077	Celastrina_argiolus	0,050	Polyommatus_icarus	0,123
Coenonympha_arcania	0,073	Argynnis_aglaja	0,050	Pieris_napi	0,121
Ochlodes_sylvanus	0,073	Thymelicus_sylvestris	0,050	Carterocephalus_palaemon	0,076
Pieris_napi	0,073	Lampides_boeticus	0,050	Iphiclides_podalirius	0,076
Lampides_boeticus	0,059	Aricia_montensis	0,050	Pararge_aegeria	0,066
Aricia_montensis	0,055	Lycaena_hippothoe	0,050	Celastrina_argiolus	0,066
Lycaena_hippothoe	0,055	Pieris_rapae	0,050	Aporia_crataegi	0,066
Melitaea_cinxia	0,055	Pyronia_tithonus	0,050	Inachis_io	0,066
Pieris_rapae	0,055	Iphiclides_podalirius	0,050	Anthocharis_cardamines	0,063
Anthocharis_cardamines	0,036	Leptotes_pirithous	0,050	Aricia_cramera	0,063
Aricia_cramera	0,036	Nymphalis_polychloros	0,050	Erynnis_tages	0,063
Boloria_selene	0,036	Lysandra_bellargus	0,000	Lasiommata_maera	0,063
Cupido_minimus	0,036	Brenthis_ino	0,000	Boloria_dia	0,060
Erynnis_tages	0,036	Aporia_crataegi	0,000	Argynnis_adippe	0,060
Melitaea_phoebe	0,036	Coenonympha_pamphilus	0,000	Vanessa_atalanta	0,060
Spialia_sertorius	0,036	Melitaea_cinxia	0,000	Hamearis_lucina	0,060
Boloria_euphrosyne	0,023	Aricia_cramera	0,000	Lysandra_bellargus	0,000
Argynnis_adippe	0,018	Cupido_minimus	0,000	Cupido_argiades	0,000
Argynnis_paphia	0,018	Erynnis_tages	0,000	Brenthis_ino	0,000
Colias_alfacariensis	0,018	Melitaea_phoebe	0,000	Aglais_urticae	0,000
Gonepteryx_rhamni	0,018	Spialia_sertorius	0,000	Issoria_lathonia	0,000
Inachis_io	0,018	Boloria_euphrosyne	0,000	Coenonympha_pamphilus	0,000
Lasiommata_megera	0,018	Argynnis_adippe	0,000	Lycaena_hippothoe	0,000
Lycaena_virgaureae	0,018	Argynnis_paphia	0,000	Melitaea_cinxia	0,000
Pararge_aegeria	0,018	Colias_alfacariensis	0,000	Cupido_minimus	0,000
Pieris_brassicae	0,018	Gonepteryx_rhamni	0,000	Melitaea_phoebe	0,000
Plebejus_argus	0,018	Inachis_io	0,000	Spialia_sertorius	0,000
Plebejus_idas	0,018	Lasiommata_megera	0,000	Boloria_euphrosyne	0,000
Lysandra_coridon	0,018	Lycaena_virgaureae	0,000	Colias_alfacariensis	0,000
Pyronia_tithonus	0,018	Pararge_aegeria	0,000	Gonepteryx_rhamni	0,000
Vanessa_atalanta	0,018	Pieris_brassicae	0,000	Lasiommata_megera	0,000
Aphantopus_hyperanthus	0,000	Plebejus_argus	0,000	Pieris_brassicae	0,000
Carcharodus_alceae	0,000	Plebejus_idas	0,000	Plebejus_argus	0,000
Carterocephalus_palaemon	0,000	Lysandra_coridon	0,000	Plebejus_idas	0,000
Hamearis_lucina	0,000	Aphantopus_hyperanthus	0,000	Lysandra_coridon	0,000
Iphiclides_podalirius	0,000	Carcharodus_alceae	0,000	Pyronia_tithonus	0,000
Lasiommata_maera	0,000	Carterocephalus_palaemon	0,000	Carcharodus_alceae	0,000
Leptotes_pirithous	0,000	Hamearis_lucina	0,000	Leptotes_pirithous	0,000
Nymphalis_polychloros	0,000	Lasiommata_maera	0,000	Nymphalis_polychloros	0,000
Average density	13,254	Average density	10,873	Average density	19,199

Table S15. Model results for landscape variables on butterfly attributes.

Landscape variable /Response variable	**Average patch size (Configurational heterogeneity)**	**Vegetation Shannon diversity index (Compositional heterogeneity)**	**% Grassland**	**% Scrub**	**% Forest**
Butterfly species richness	$\chi^2 = 0.027$ $p = 0.868$	$\chi^2 = 0.158$ $p = 0.690$	$\chi^2 = 0.035$ $p = 0.850$	$\chi^2 = 0.390$ $p = 0.531$	$\chi^2 = 0.009$ $p = 0.924$
Butterfly Shannon diversity index	$\chi^2 = 0.002$ $p = 0.962$	$\chi^2 = 0.012$ $p = 0.911$	$\chi^2 = 0.008$ $p = 0.948$	**$\chi^2 = 2.709$** **$p = 0.099$**	$\chi^2 = 0.272$ $p = 0.601$
Butterfly density	**$\chi^2 = 3.785$** **$p = 0.051$**	$\chi^2 = 1.945$ $p = 0.163$	$\chi^2 = 1.398$ $p = 0.237$	$\chi^2 = 1.430$ $p = 0.231$	$\chi^2 = 0.346$ $p = 0.556$
CTAO index	**$\chi^2 = 9.047$** **$p = 0.002$**	**$\chi^2 = 5.872$** **$p = 0.015$**	**$\chi^2 = 7.443$** **$p = 0.006$**	**$\chi^2 = 6.083$** **$p = 0.013$**	**$\chi^2 = 10.74$** **$p = 0.001$**
Trophic specialisation index	$\chi^2 = 0.875$ $p = 0.349$	$\chi^2 = 2.182$ $p = 0.139$	$\chi^2 = 0.165$ $p = 0.683$	$\chi^2 = 0.224$ $p = 0.635$	$\chi^2 = 0.290$ $p = 0.589$
Habitat specialisation index	$\chi^2 = 0.061$ $p = 0.804$	$\chi^2 = 0.494$ $p = 0.481$	$\chi^2 = 0.021$ $p = 0.882$	$\chi^2 = 0.007$ $p = 0.933$	$\chi^2 = 0.023$ $p = 0.879$
Dispersal ability index	$\chi^2 = 0.013$ $p = 0.906$	$\chi^2 = 6e-4$ $p = 0.979$	$\chi^2 = 0.019$ $p = 0.887$	$\chi^2 = 0.721$ $p = 0.395$	$\chi^2 = 0.201$ $p = 0.653$

Chapter 3: South European mountain butterflies at a high risk from land abandonment and amplified effects of climate change

Common blue (*Polyommatus icarus*) at Güembres (Picos de Europa). Photo: Amparo Mora.

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3.1 ABSTRACT

Data from existing monitoring schemes point to a global crisis of butterflies across Europe, with habitat loss/degradation, climate change and chemical pollution as the main drivers of decline. The existing butterfly time series from Western Europe come from densely populated, relatively flat areas. However, population trends from less populated areas such as mountain ranges in the south of Europe have been less studied, despite these areas harbouring one of the highest butterfly biodiversity of the continent. Here we analyse trends for butterfly populations in a Southwestern Europe mountain range (Picos de Europa, Northwest Spain), for the last 9 years (2013-2021), across an altitudinal gradient (80-2000 m). We show that this region, protected as National Park more than 100 years ago, is nonetheless under a great threat, with a declining in butterfly abundance of, on average, 5.7% per year (45.7% cumulative decline in the last 9 years). Species at higher elevations are faring worse than those at low elevations and communities at mid-elevations (below the tree line) are changing towards higher abundance of species with preference from closed habitats. Combined effects of amplified climate change in mountains and habitat loss, due to abandonment of traditional management, appear to be affecting both individual species and community composition of butterflies in our study area.

Keywords: butterfly monitoring, population trends, multispecies indicator, insect decline, South European mountains, protected areas, elevational gradient, land-use change, abandonment, climate change

3.2 INTRODUCTION

Insect declines have been reported in many large-scale studies, though these are mainly from Western Europe and North America (Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020; Hallmann *et al.*, 2017; Seibold *et al.*, 2019). In Europe, the longest time series existing for insects are butterfly monitoring data from United Kingdom, Netherlands and Belgium. Butterflies are good insect models as they are easy to identify, popular, and they react quickly to environmental changes (Thomas, 2005). Data from existing monitoring schemes, including the recently assembled European Butterfly Monitoring Scheme (www.butterfly-monitoring.net), point to a global crisis of butterflies across Europe (Brereton *et al.*, 2019; Fox *et al.*, 2023; Van Strien *et al.*, 2019; Maes & Van Dyck, 2001; Van Swaay *et al.*, 2020). The main drivers, in line with global changes elsewhere, are habitat loss/degradation, climate change and chemical pollution (Warren *et al.*, 2021).

In Southern Europe, assessments of butterfly population trends have, to date, only been made in Catalonia (NE Spain) (Stefanescu *et al.*, 2011 a,b), reporting a worrying decline of a substantial component of the butterfly fauna. Stefanescu *et al.* (2011 b) suggest serious population declines in specialist species restricted to mountain areas, likely resulting from a combination of climate warming and habitat loss caused by the abandonment of traditional grazing and mowing. They also found negative trends for generalist species due to an increase in aridity in combination with an increase in intensification of human land use in lowland areas.

The impacts of abandonment of traditional management on Southern European mountain landscapes, harbouring a high diversity of both habitats and species, are not fully understood (but see MacDonald *et al.*, 2000). Generally, abandonment is leading to a loss of habitats dominated by sparse vegetation, thereby giving rise to a successional progression towards forest habitats (Poschlod *et al.*, 2005), with consequent changes in butterfly species composition (Balmer & Erhardt, 2000; Slancarova *et al.*, 2016; Mora *et al.*, 2022). In Spain, between 1962 and 2019, 4 million hectares of cultivated land were abandoned (around 8% of total national surface), leading to increasing forest cover, which now accounts for 55% of total national surface, of which around 80% is not managed (Greenpeace Spain, 2020). In the more humid Atlantic parts of Spain, the Cantabrian Mountains, recent studies have shown an increase of 16% of forest cover between 1990 and 2000 (García-Llamas *et al.*, 2019). Coupled to this advance of forests, the area of traditional hay meadows has been decreasing sharply (e.g. 70% lost between 1956 and 2017 in the Picos de Europa National Park, doubling the rate of decline in the last decade, García *et al*., 2018). The consequences of this land transformation on biodiversity are still largely unexplored.

Coupled to these land-use changes, climate change is acting upon mountain ecosystems. It is well known that the rate of temperature change with increased levels of greenhouse gases in the atmosphere is amplified at high latitudes (Previdi *et al*. 2021), but there is also growing evidence that the rate of warming is amplified with elevation, such as in mountain environments (Yan & Liu, 2014; Pepin *et al*. 2015; IPCC, 2022; Inouye, 2020). In recent decades, observed changes include increasing temperatures, changing seasonal weather patterns, and reductions in snow cover extent and duration (Klein *et al.*, 2016). Snow is a major component of weather in alpine ecosystems; it is a good insulator and can help protect the soil and its biota (e.g. overwintering pupae or larvae) from extreme cold winter temperatures (Inouye, 2020). Consequences of earlier snowmelt include advanced and perhaps longer growing seasons, more frequent frost damage and increased summer drought (Inouye, 2008, 2020; Edwards *et al.*, 2007). The spatial distributions of many plant and butterfly species have shifted to higher elevations in recent decades, consistent with rising temperatures across mountain regions (Grabherr *et al*., 1995; Gottfried *et al*., 2012; Jiménez-Alfaro *et al*., 2014; Wilson *et al.,* 2007). One estimate for European mountain plants is that 36-55% of alpine species, 31-51% of subalpine species and 19-46% of montane species will lose more than 80% of their suitable habitat by 2070-2100 (Engler *et al*., 2011). Although high-elevation ecosystems are predicted to be severely affected by environmental change, observations in these areas are typically sparse; we may not be monitoring some regions of the globe that are warming the most (Pepin *et al*., 2015).

Species responses to conversion of habitats and human-induced climate change are varied: such factors may cause species to move to areas where conditions are more favourable; remain where they are and adapt to the new conditions; or just decline and eventually go extinct. Species whose traits enable them to cope well with current pressures are expected to persist while others might face declines and, eventually, local extinction (Melero *et al*., 2016). In butterflies, the number of generations per year (voltinism), trophic range (in terms of number of larval host plants), and mobility (dispersal capacity), seem to determine their vulnerability to global changes (Slancarova *et al.*, 2016; Carnicer *et al*., 2013). Low number of generations, low mobility and narrow trophic range collectively define specialism (Slancarova *et al.,* 2016) and several studies have shown greater declines for habitat specialists than for habitat generalists (Stefanescu *et al*., 2011 a,b; DEFRA, 2021). For example, in the United Kingdom, population abundance of habitat specialist butterflies has declined significantly since

1976 (-61%), though species of the wider countryside show no significant change (DEFRA, 2021). In mountain areas, species thermal niche range has been shown to be an important trait determining response to climate change; and species with wider thermal tolerances are more likely to persist, moving both up or downhill (Rödder *et al*., 2021).

In order to detect significant change in butterfly communities as a result of species responses to environmental change, long-term data series are needed. The existing butterfly time series for western Europe come largely from densely populated, highly modified, and relatively flat areas. South European mountain ranges, which are much less populated and harbour one of the highest butterfly biodiversity of the continent (Van Swaay *et al*., 2010), have not been long-term monitored to produce population trends, due to the difficulty of setting up such monitoring programmes in difficult terrain and weather conditions. In particular, protected areas in these mountain ranges offer an opportunity to determine if butterfly species in these well-conserved areas, which are not subjected to an intense human pressure, are coping better than those elsewhere. They also offer an interesting contrast of different pressures from global drivers of change along elevational gradients.

Here, we analyse trends for butterfly populations in a Southwestern European mountain range (Picos de Europa, Northwest Spain) for 9 years (2013-2021), across an altitudinal gradient (80-2000 m), with different land use and climate change pressures. Picos de Europa was the first Spanish National Park, protected in 1918, more than 100 years ago. It is a very important area for butterflies (Van Swaay & Warren, 2006; Romo *et al*., 2007), holding 60% of all Ibero-Balearic species (García-Barros *et al*., 2013) and 28% of all European species (Van Swaay *et al*., 2010), including several rare species, three endemic and four legally protected species such as *Lopinga achine*, *Phengaris nausithous*, *Erebia palarica*, *Parnassius apollo* or *Lycaena helle*, many of which are at the southwestern edge of their distribution. The area has been very well conserved through millenia of sustainable traditional practices (shepherding, mowing, coppicing), practices which have been disappearing at an accelerated rate in the last decades (García *et al*., 2018). Forests are growing over grasslands because of rural abandonment of these cultural landscapes and our previous research has detected a significant change on butterfly community composition as a result (Mora *et al*., 2022). We hypothesize that:

1. Abundance trends will be positive for species associated with closed habitats, while species associated with open habitats will show negative abundance trends, due to the ongoing encroachment of vegetation resulting from abandonment of traditional land management.

2. Abundance trends (population growth rate) will be negatively related to species degree of specialisation, both in terms of habitat and host-plant specialisation.
3. Abundance trends will be negatively related to elevation because of amplified effects of climate change at higher elevations, with increasing temperatures, changing seasonal weather patterns and decreasing snow cover extent and duration.

3.3 METHODS

3.3.1 Study area

The study was carried out in the Picos de Europa National Park (PENP), located 20 km from the northern coast of Spain (centred on 43º15’ N, 5º00’W). Picos de Europa is a limestone mountain range extending approximately 30 km x 20 km. It receives Atlantic influences from the ocean on its northern slope and Mediterranean influences on its eastern part and southern slope. Its wide altitudinal range (70 - 2648 m) harbours extensive temperate forest and its substitution units; natural and seminatural grasslands; riverine, bog and lake vegetation; rocky and high mountain vegetation (Alonso *et al.*, 2011).

PENP presents a temperate macrobioclimate and its mediterranean variant (in less than 5% of the territory). All the territory has an oceanic character with asymmetric continental indexes between northern and southern slopes. In the northern, more oceanic slope, there is a substantial altitudinal decrease of vegetation bands (Jiménez-Alfaro *et al.*, 2010). Average annual temperatures range from 2.5 ºC at the higher elevations to 15 ºC in gorges dividing the mountain massifs (Ninyerola *et al.*, 2005).

In PENP are present all ombrotypes from Upper Subhumid to Lower Ultrahyperhumid (classification by Rivas-Martínez, 2007). Lower hyperhumid ombrotype is present in 62% of the territory (Jiménez-Alfaro *et al.*, 2010). Average rainfall is between 1100 and 1300 mm/year (Ninyerola *et al.*, 2005).

3.3.2 Butterfly data

Here we use monitoring data on butterfly populations from 11 sites in Picos de Europa National Park (Spain). Data were collected by the National Park staff led by Amparo Mora for the period 2013-2021 and contribute to the Butterfly Monitoring Scheme España (BMS España), a national butterfly recording network. Data series ranged from 3 to 9 years, depending on the site (Table 3.1, Figure 3.1). Monitoring sites cover an altitudinal range of 80 – 2.000 m, and represent most butterfly species (96%) and biotopes in the study area including mixed forests, beech and oak forests, seminatural grasslands (hay meadows and pastures), alpine shrubs and alpine grasslands (see Table S3.1 for the main habitat types and plant communities represented in the study area).

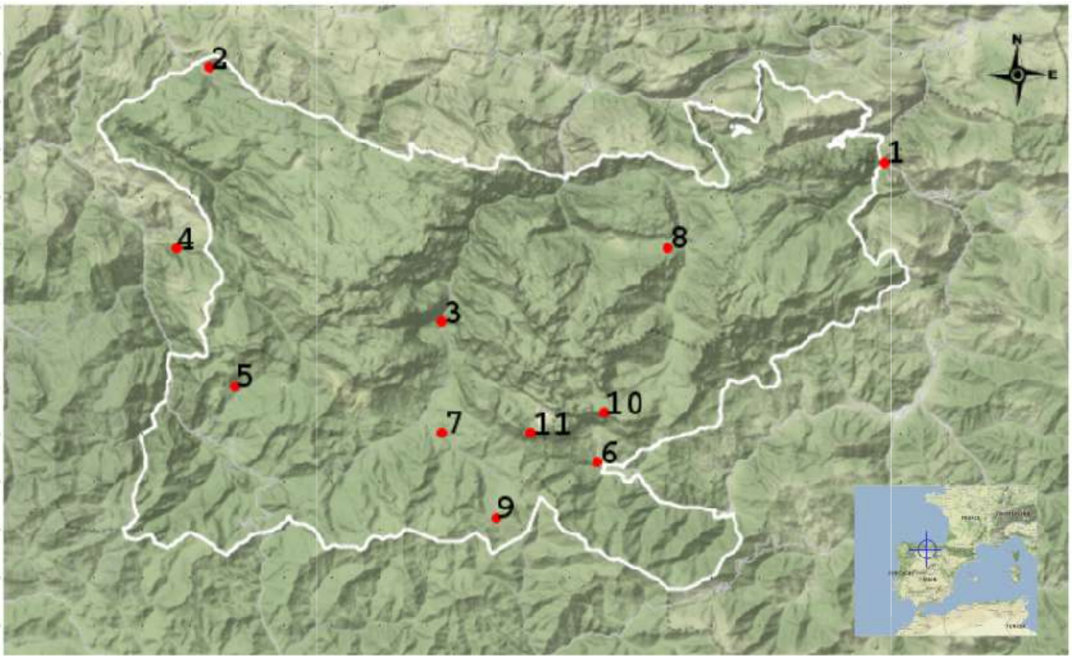


Fig. 3.1 Transect sites monitored in the Picos de Europa National Park (red points). Numbers correspond to column ID in Table 3.1 (1=Urdón, 2=Cuesta Ginés, 3=Sesanes, 4=Baenu, 5=Güembres, 6= Morrena Pido, 7=Prada, 8=Pandébano, 9=Pandetrave, 10=Lloroza, 11=Liordes). PENP limits in white.

Table 3.1 Transect sites for monitored butterfly populations in the PENP.

ID	Transect name	Coordinates (longitude, latitude)	Monitoring period	Number of years	Mean elevation (m)	Habitat types
1	Urdón	4º37’54,62555” W 43º16’1,81063” N	2015-2021	6	150	Mediterranean fluvial mosaic
2	Cuesta Ginés	5º3’5,56045” W 43º18’36,08561” N	2013-2021	9	200	Atlantic heaths
3	Sesanes	4º54’24,63581” W 43º11’42,14206” N	2013-2021	9	600	Atlantic mosaic
4	Baenu	5º4’18,64805” W 43º13’41,3103” N	2019-2021	3	760	Fagus woodland
5	Güembres	5º2’8,05956” W 43º9’57,68446” N	2014-2021	8	1000	Atlantic mosaic
6	Morrena Pido	4º48’35,38318” W 43º7’53,12269” N	2013-2016	4	1050	Atlantic mosaic
7	Prada	4º54’24,025” W 43º8’41,69134” N	2013-2021	9	1100	Atlantic mosaic
8	Pandébano	4º45’59,56362” W 43º13’42,51022” N	2013-2021	9	1140	Hay meadows
9	Pandetrave	4º52’23,75083” W 43º6’22,73198” N	2013-2021	9	1550	High mountain pastures
10	Lloroza	4º48’21,71657” W 43º9’14,63915” N	2014-2017	4	1850	High mountain (limestone)
11	Liordes	4º51’4,50011” W 43º8’40,20382” N	2019-2021	3	1900	High mountain (limestone)

Adult butterflies were counted along fixed transect routes using the standard BMS methodology (Pollard & Yates, 1993). Surveys took place every ten days from May to September (a total of 15 visits each season). In four of the transects (Pandetrave, Liordes, Lloroza and Baenu), we applied a reduced effort scheme with 5-6 surveys per season (Roy *et al*., 2007, 2015), because they were placed at high mountain locations with a shorter active period, and in one case (Baenu) because the transect was set up only to cover the flying period of the endangered species *Lopinga achine* between June and July. Recording routes were 1-2 km in length and were divided into several sections corresponding to different habitats. Throughout the study period, a total of 132 butterfly species were recorded (see the complete list in Table S3.2, nomenclature after Wiemers *et al*., 2018). Migratory species (*Lampides boeticus, Leptotes pirithous, Vanessa atalanta* and *Vanessa cardui*) were excluded from the analysis.

3.3.3 Species traits

For each species, we used a total of 10 traits related to morphology, life-history, climatic tolerances, habitat specialisation and distribution (Table S3.3). Trait information was obtained from the literature or from our own data. Trait descriptions are as follow:

- *Average forewing length* (mm), a proxy for dispersal ability. After Middleton-Welling *et al*. (2020).
- *Voltinism*, categorised as univoltine, bivoltine or variable (assigned to species showing univoltinism some years and bivoltinism others). From our own data.
- *Overwintering stage*, categorised as adult or immature (egg, larvae or pupae). After Middleton-Welling *et al*. (2020).
- *Hostplant specificity index*, calculated from the total number of hostplant species, genera and families used by a species with the following formula:

  HPI = 1/√(n hostplant species x n hostplant genera x n hostplant families)

  Hostplant index ranges from 0 for species which are highly polyphagous to 1 for species that are completely monophagous, providing a quantitative measure of overall hostplant specificity. After Middleton-Welling *et al*. (2020).
- *Habitat specialist/generalist* (several categories depending on the habitat). To classify species into specialists/generalists, we followed Stefanescu *et al.* (2011a). We analysed how the density of each species was partitioned across the habitats most widely represented in our transects. Density data from all transect sections, representing 22 EUNIS habitat types, were used. Habitat types were grouped into four broad categories

(scrub, grasslands, woodlands and almost bare rock pavements) and then the average abundance of each species was calculated for each category (expressed as the number of individuals/100 m per year). A species for which over 50% of its density was recorded in one particular habitat was considered a specialist of that habitat.

- *Species temperature index (STI)*, calculated as the mean temperature value (ºC) for the species across Europe. After Schweiger *et al*. (2014).
- *Species precipitation index (SPI)*, calculated as the mean precipitation (mm) for the species across Europe. After Schweiger *et al*. (2014).
- *Geographic distribution*, with five categories (pluriregional or widespread; eurosiberian; Iberian endemic; orophyte (living exclusively in mountains); and Mediterraean), taken from Kurdna *et al*. (2011).
- *Mean elevation* (m), the average of elevations at which a species is present in the study area (based on our butterfly database for the whole PENP which contains 15,138 records).
- *Elevation range* (m), the maximum elevation minus the minimum elevation at which a species occurs in the study area (based on our butterfly database for the whole PENP).

3.3.4 Data analyses

All statistical analyses were performed using the software RStudio for Statistical Computing (version 1.2.5019; RStudio Development Team 2019).

3.3.4.1 Climatic changes

We used the dataset CHELSAcruts (Climatologies at high resolution for the earth's land surface areas: Karger *et al.*, 2017) to obtain monthly maximum, mean and minimum temperatures over the period 1979-2019 for the whole of PNPE. We used these data to calculate the mean annual temperature (ºC) in each 10-km grid square. To test whether mean temperature has changed over time in the study area, we ran a generalised linear mixed model of mean annual temperature against time using the identity of the 10-km square as a random factor. We used lmer function in the "lme4" package (Bates *et al.*, 2015).

3.3.4.2 Species trends

Butterfly abundance in each year was calculated using the Generalised Abundance Index approach (Dennis *et al.*, 2016) implemented in "rbms" package in R (Schmucki *et al.*, 2022), which provides an efficient method for modelling seasonal count data. The method used all counts from all the sites in which a species occurred to describe the species phenology for each year, which was then used to estimate the abundance for any gaps in sampling. From the real and estimated counts, annual measures of relative abundance were produced for each monitored site. An overall abundance trend over time for each species was then calculated by applying a Poisson generalised linear model to the site-level annual abundance values. A bootstrapping procedure was used to determine the statistical significance of the abundance trends. This involved resampling the count data and estimating the trend 500 times, in order to evaluate the uncertainty associated with the species abundance trends. Trends were classified in different categories based on the multiplicative slope estimate (growth rate estimate) as follows (Pannekoek & Van Strien, 2005):

- Strong increase: Significant increase, more than 5% increase per year.
- Moderate increase: Significant increase, but less than 5% increase per year.
- Uncertain: No significant change, but changes (positive or negative) likely to be more than 5% per year.
- Stable: No significant change, but changes (positive or negative) likely to be less than 5% per year.
- Moderate decline: Significant decrease, but less than 5% decrease per year.
- Strong decline: Significant decrease, more than 5% decrease per year.

Growth rates below 1 indicate declining trends while values above 1 indicate positive trends.

A common phenology was considered for all sites, independent of the elevation of individual populations. It has been suggested that accounting for changes in phenology along the elevation gradient could improve estimates of species abundances particularly when the percentage of missing counts is higher than 40% (Schmucki *et al.*, 2016). It was not possible in our case to do this as there were only 11 sites, which is a limitation in our study. However, the average proportion of missing counts per site for the whole study period was 16% (± 5), which hopefully has minimised the effect of phenological patterns on our abundance estimates.

3.3.4.3 Multi-species abundance indicators

Multi-species abundance indicators were compiled for all butterfly species combined; species with preferences for open, intermediate or closed habitat (degree of encroachment) and for species occupying different elevation zones.

The collated abundance indices of the selected species for the multi-species indicator were combined by taking their geometric mean. A smoothed indicator was produced using a loess smooth with span=0.75 and degree=2 (as in Soldaat *et al.*, 2017). The same approach was applied to produce multi-species indices and smoothed indicators for each of 500 bootstraps, from which quantiles were taken to produce 95% confidence intervals around the indicators. All values were rescaled such that the smoothed indicator started at 100.

Trends were estimated by applying linear regression to the smoothed indicator. Trends were estimated for each bootstrap, from which 95% confidence intervals around the actual trend were produced and used to assess significance. Trends were classified based on the multiplicative slope estimate, as in TRIM (Pannekoek & Van Strien, 2005). Analyses were performed using the "rbms" package in R (Schmucki *et al.*, 2022).

To produce trends for open/closed/intermediate habitat indicators, we worked with TAO indices of species with significant trends. TAO index of species preferences for open/closed habitats has been developed by Ubach *et al.* (2020), and it is based on the Catalan Butterfly Monitoring Scheme data (1994-2017, 93 sites) (see details in www.catalanbms.org). Species showed great consistency in their preferences for open or closed habitats regardless of the climatic conditions in the different biogeographic regions analysed by Ubach *et al.* (2020), so we believe that this index is valid for our study area, and more appropriate than other indices used to describe butterfly habitat selection in Western Europe. The TAO index takes a " + 1" value when the butterfly species prefers completely open habitats and takes a " − 1" value when the butterfly species prefers completely closed habitats. Species with significant trends TAO indices ranged from -0.419 to 0.974 (-1 will be a completely closed habitat and +1 will be a completely open habitat). We split this range into three equal segments. The closed habitat indicator was based on 12 species with TAO indices between -0.419 and 0.200. The intermediate habitat indicator was based on 21 species with TAO indices between 0.210 and 0.500. The open habitat indicator was based on 19 species with TAO indices between 0.510 and 0.974.

To produce multispecies abundance indicators of species found at different elevations, we divided all species with significant trends into three groups depending on the mean elevation at which they are found. The elevations limits for each group also correspond with the bioclimatic vegetation zones (Alonso *et al.*, 2011) (see table S3.3 for species mean elevation and species elevation range):

- Lowland species: species with mean elevation below 900 m (15 species).
- Montane species: species with mean elevation below the treeline, 900-1200 m (25 species).
- Alpine species: species with mean elevation above the treeline, 1200-1500 m (14 species).

The average elevation of the treeline in the study area is around 1200 m, which is an artificial limit resulting from anthropogenic opening of the forests to create pastures. The natural treeline lies around 1400 m in the northern slope and 1700 m on the southern slope (Jiménez-Alfaro *et al.*, 2010).

3.3.4.4 Effect of species traits on abundance trends

The effects of the 10 species traits on growth rate estimates were tested using a generalised linear mixed model, with Family as a random factor to avoid pseudoreplication because of phylogenetic relatedness among species. A global model was first defined using all the 10 species traits. Function vif from package "car" (Fox & Weisberg, 2019) in R was used to discard highly correlated variables. Model simplification was performed by deletion of terms from the full model using function drop1 and the significance of terms assessed by likelihood ratio tests. Analyses were performed in R using package "lme4" (Bates *et al.*, 2015).

3.3.4.5 Changes in community indices over time

In order to assess if vegetation encroachment was playing a role in species trends, we also analysed trends at the community level for the TAO index, indicating preference for open/closed habitats over time. We followed Julliard *et al.* (2006) and Devictor *et al.* (2012) to develop a community index of preference for open/closed habitats (TAOc) for each transect (Table S3.5), by multiplying each species index by the square root of its abundance and then averaging across all species. The TAOc was thus obtained for each year of sampling for each butterfly transect.

The slopes of linear models with TAOc as the dependent variable and year as the independent variable showed the trends of each butterfly community towards openness/closeness over time (positive slopes, towards opened habitats; negative slopes, towards closed habitats). The change in TAOc over time was analysed using a generalised linear mixed-effects model (GLMM), with a Gaussian error structure. The site was assigned as a random effect. The statistical significance of the fixed factor (time) in the GLMM was tested with analysis of variance (ANOVA), comparing the fitted model containing the fixed factor with the null model containing only the random term. GLMMs analyses were performed with "lme4" package in R (Bates *et al.*, 2015).

Similarly, in order to assess if climate change was playing a role in species trends, we analysed changes in the community temperature index and in the community precipitation index over time (Table S3.5). These indices are based on the Species Temperature Index (STI) and the Species Precipitation Index (SPI), which indicate the species mean annual temperature and the species mean annual precipitation in the areas occupied by the species in the whole of Europe, after Schweiger *et al.* (2014). We followed the same procedure as with the TAOc index, to investigate if butterfly communities were changing towards warmer (positive STI slope) or colder (negative STI slope) communities over time, or towards more humid (positive SPI slope) or drier communities over time (negative SPI slope).

3.4 RESULTS

3.4.1 Climatic changes

Mean annual temperature in the study area increased annually by 0.021 ºC in the period 1979-2019 (χ^2=118.17, df=1, p < 0.001, Fig. S3.1), representing an increase of 0.21ºC per decade in the last 40 years.

3.4.2 Species trends

Abundance trends over the nine-year study period were produced for 55 species (Table S3.5) out of the 128 recorded species, for the rest (73 species) there were not enough data to produce a reliable trend. Among these 55 species: 39 species (71%) showed an "uncertain" trend; 8 species (14%) showed a "strong decline" trend (*Anthocharis cardamines, Cupido minimus, Laeosopis roboris, Melitaea diamina, Melitaea phoebe, Papilio machaon, Polyommatus dorylas, Speyeria aglaja*); 7 species (13%) a "moderate decline" trend (*Aporia crataegi, Brenthis ino, Hipparchia hermione, Issoria lathonia, Lasiommata maera, Lysandra coridon, Melitaea deione*); and 1 species (2%) a "stable" trend (*Maniola jurtina*).

3.4.3 Multispecies abundance indicators

The multispecies abundance indicator for all species combined showed a "moderate decline" trend (Fig. 3.2a). There was an overall decline of abundance in the period 2013-2021, of on average 5.7% per year (45.7 % cumulative) corresponding to an average annual growth rate of 0.936 (0.87-0.96).

The multispecies abundance indicators for preference for open (Fig. 3.2b), intermediate (Fig. 3.2c) and closed habitats (Fig. 3.2d), showed a "moderate decline" trend with percentages of change of -47.6, -40.6 and -49.9 respectively, over the 9 year study period.

The multispecies abundance indicator trend for lowland species (mean elevation 80-900 m), was "uncertain" with a percentage of change of -15.2 over the 9 year study period (Fig. 3.2e). The abundance indicator for montane species (mean elevation 900-1200 m) showed a “strong declining” trend with a percentage of change of -51.3 (Fig. 3.2f) and the abundance indicator for alpine species (mean elevation 1200-1500 m) showed a “moderate declining” trend with a percentage of change of -60.2 (Fig. 3.2g).

3.4.4 Effect of species traits on abundance trends

The minimum adequate model included mean elevation (coef.=-0.299, p=0.004), elevation range (coef.=0.165, p=0.003), distribution (coef.(eurosiberian=-0.083, mediterranean=-0.165, orophyte=-0.431, pluriregional=-0.171), p=0.016) as significant terms and dispersal, hostplant index and overwintering stage as marginally significant (see table S3.6). However, when removing two outliers (*Erebia triarius* and *Lycaena alciphron*), mean elevation remained strongly significant (coef.=-0.229, p=0.003), mean temperature became weakly significant (coef.=-0.022, p=0.049), and dispersal and elevation range became marginally significant (see table S3.7). Population growth rates decreased with the increase in species mean elevation, indicating species at higher elevations are faring worse than those at low elevations (Fig. 3.3a). On the other hand, species with higher mean temperatures (STI) had significantly lower population growth rates (Fig 3.3b).

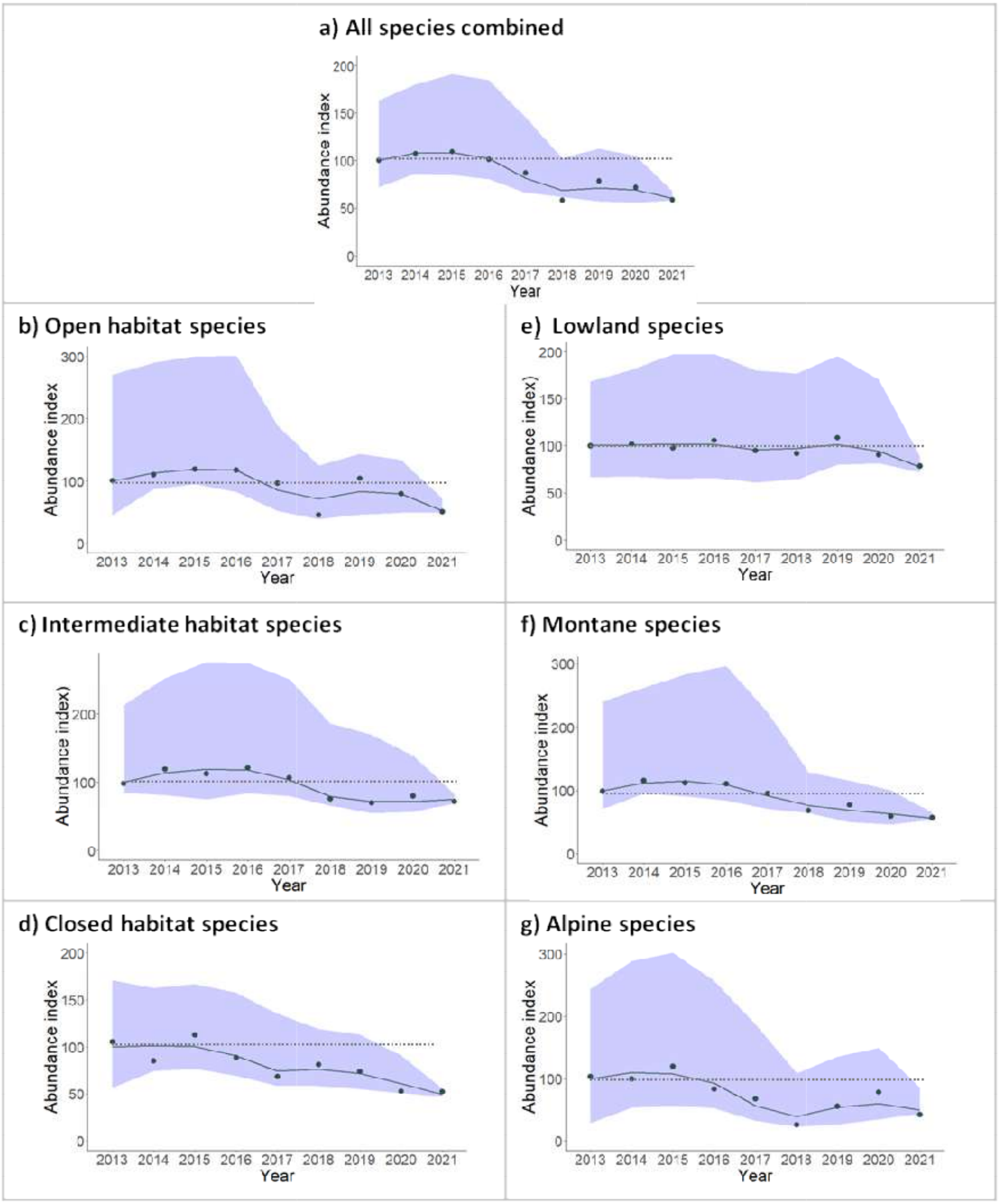


Fig. 3.2 Multispecies abundance indicators trends for the period 2013-2021. Multispecies indicator based on: a) all species for all surveyed sites together; b) species associated with open habitats (18 species); c) intermediate habitat species (20 species); d) species associated with closed habitats (12 species); e) lowland species (mean elevation 80-900 m; 15 species); f) montane species (mean elevation 900-1200 m; 25 species); g) alpine species (mean elevation 1200-1500 m; 14 species). The shaded area represents the 95% confidence limits surrounding the smoothed trend (line) and the dots represent the unsmoothed abundance index. The dotted line marks first year abundance level.

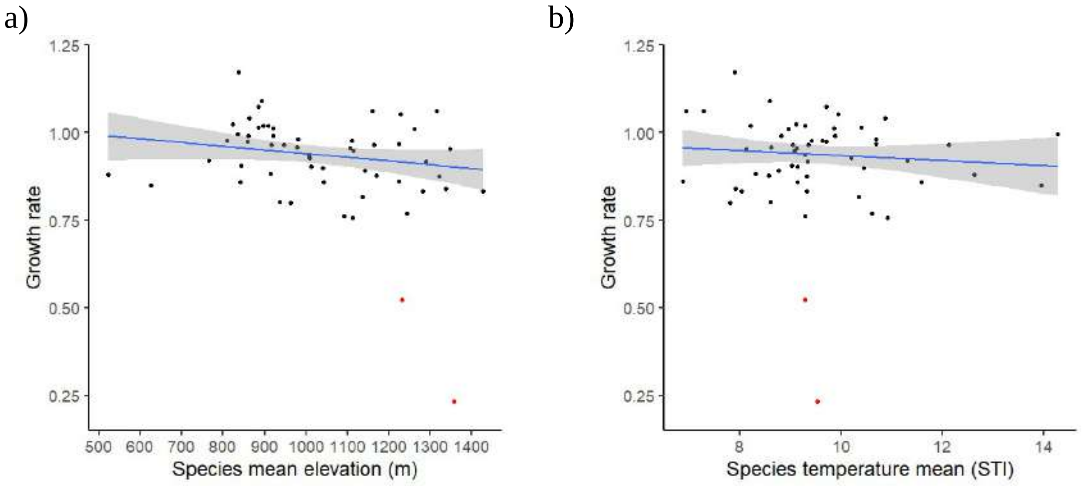


Fig 3.3 Species abundance trend (growth rate) against species mean elevation (a) and species Temperature mean (STI) (b). The shaded area represents the 95% confidence limits for the trend (line). Two outliers are represented in red but were excluded from the analysis.

3.4.5 Community changes over time

Among the 11 butterfly communities analysed, only three showed marginally significant trends in their preferences for open/closed habitats (Table 3.2; see Table S3.4 for TAOc values for each transect and year). Atlantic mosaic transects showed a change towards preference for closed habitats, while one high mountain pasture transect changed towards a preference for open habitats. When analysing all transects together, there was no significant effect of time on TAOc (χ^2=2.374, p=0.123). When considering only lowlands sites (80 - 900 m), there was a marginally significant effect of time on TAOc index (χ^2 = 3.340, p=0.067), changing at a negative rate of -0.008 per year, towards closed habitats (Fig. 3.4a). When considering montane sites below the tree line (900 - 1200 m), there was a significant effect of time on TAOc index (χ^2 = 4.200, p=0.04), changing at a negative rate of -0.005 per year, towards closed habitats (Fig. 3.4b). When considering montane sites above the tree line (1200-1900 m), there was no significant change in TAOc index over time (χ^2 = 0.205, p=0.650, Fig. 3.4c).

Among the 11 butterfly communities analysed, only one showed a significant trend in its temperature index (Table 3.2; see Table S4 for STIc and SPIc values for each transect and year). The butterfly community at Sesanes, an Atlantic mosaic transect at 600 m, showed a change towards a colder temperature community index. Moreover, the butterfly community at Baenu, a beech forest transect at 760 m, showed marginally significant trends also towards colder temperature community index. These two communities also showed significant trends towards lower precipitation community indices (drier conditions).

Table 3.2 TAOc (Community preference for open/closed habitats), STIc (Community temperature index) and SPIc (Community precipitation index) over time on each transect. Significant values are marked in bold.

Transect	Ecosystem	% hay meadows	Elevation (m)	Nº years	TAOc slope	TAOc p-value	STIc slope	STIc p-value	SPIc slope	SPIc p-value
Urdón	Mediterranean fluvial mosaic	0	150	6	-0.014	0.237	-0.304	0.315	-25.39	0.277
Cuesta Ginés	Heaths	0	200	9	-0.004	0.254	-0.028	0.800	-0.827	0.932
Sesanes	Atlantic mosaic	60	600	9	-0.021	**0.053**	-0.335	**0.040**	-27.37	**0.038**
Baenu	Fagus woodland	0	760	3	-0.023	0.435	-1.929	**0.057**	-115.8	**0.003**
Güembres	Atlantic mosaic	61	1000	8	-0.0008	0.855	0.142	0.154	10.793	0.165
Morrena Pido	Atlantic mosaic	18	1050	4	-0.032	**0.059**	-0.784	0.251	-66.02	0.227
Prada	Atlantic mosaic	29	1100	9	-0.003	0.452	0.102	0.326	8.829	0.301
Pandébano	Hay meadows	100	1140	9	-0.01	0.16	-0.010	0.949	-2.606	0.862
Pandetrave	High mountain pastures	0	1550	9	0.014	**0.088**	0.224	0.198	18.17	0.274
Lloroza	High mountain (limestone)	0	1850	4	0.051	0.52	0.322	0.774	34.74	0.762
Liordes	High mountain (limestone)	0	1900	3	0.07	0.256	0.944	0.128	84.13	0.242

When analysing all transects together, there was no significant effect of time on STIc (χ^2=0.356, p=0.550) nor on SPIc (χ^2=0.374, p=0.540). However, when considering only lowland sites (80 - 900 m), there was a significant effect of time on the STIc index (χ^2=5.103, p=0.023), changing at a negative rate of -0.219 per year towards a colder temperature community index, and also a significant effect on the SPIc index (χ^2=5.892, p=0.015) changing at a negative rate of -17.78 per year, towards a drier community index (Fig. 3.4). No significant effects of time on STIc index were observed for montane sites below (χ^2=0.166, p=0.683) or above the tree line (χ^2=0.201, p=0.653). Similarly, no significant effects of time on SPIc index were neither observed for montane sites below (χ^2=0.081, p=0.776) or above the tree line (χ^2=0.090, p=0.763).

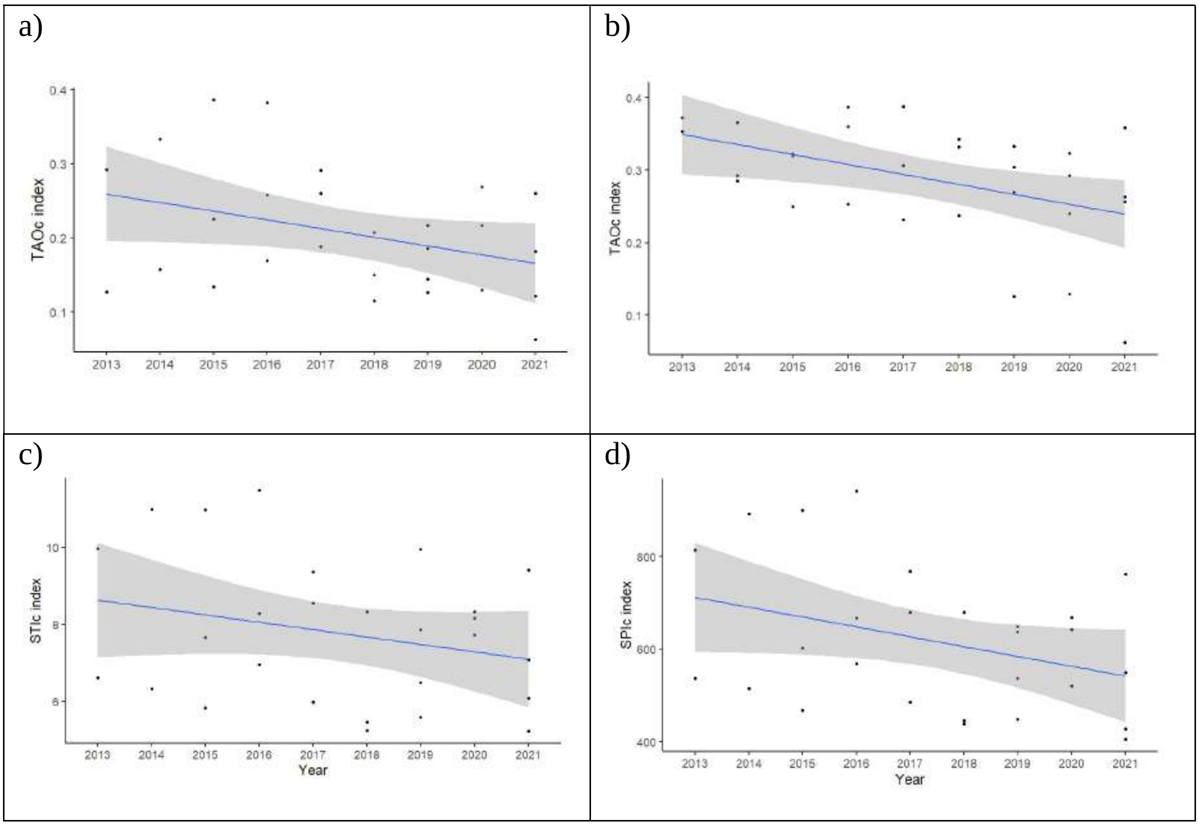


Fig 3.4 Changes in community indices over time for transects at different altitudinal zones: a) TAOc index over time in lowland transects (80 - 900 m), p=0.067; b) TAOc index over time in montane transects below the tree line (900 - 1200 m), p=0.04; c) STIc over time in lowland transects (80- 900m), p=0.023; and d) SPIc over time in lowland transects (80- 900m), p=0.015. The shaded area represents the 95% confidence limits for the trend (line).

3.5 DISCUSSION

The aim of this study was to investigate butterfly population trends from 2013-2021 along an elevational gradient (80-2000 m), in a European Southwestern mountain range, Picos de Europa. We found an overall decline in abundance of 5.7% per year (45.7% cummulative) in the study period. Species trends were produced for 55 species: 71% showed an uncertain trend while 26% of species were declining and none was increasing (Fig. 3.5). Multispecies abundance indicators for species with preferences for open, intermediate or closed habitats were all declining. Multispecies abundance indicators for species of low elevations (80 - 900 m) showed an uncertain trend, while indicators for species of higher altitudes showed declines (strong decline for 900 - 1200 m and moderate decline for 1200 – 1900 m). In montane sites below the treeline (900 - 1200 m), community composition changed in favour of species with preference for closed habitats in the nine-year period analysed, likely reflecting an effect of woodland and scrub encroachment. Whereas a marginal shift towards species characteristic of closed habitats was detected at lower elevations, and no effects were detected at higher elevations. Consistent with increasing vegetation encroachment, the Community Temperature Index also changed in favour of species preferring colder conditions in lowland sites (80 - 900 m), while no changes were detected at higher elevations. The Community Precipitation Index changed in favour of species preferring drier conditions in lowland sites (80-900 m). Population growth rate declined with species mean elevation and with species mean temperature.

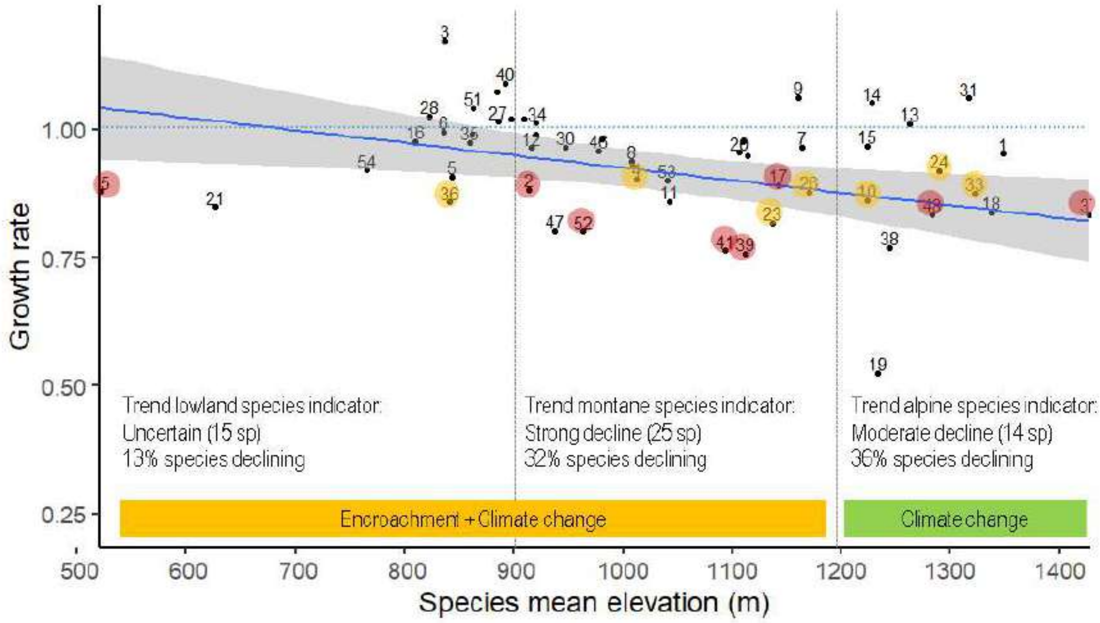


Fig 3.5 Species growth rate versus species mean elevation. Dots are labelled with numbers representing different species. Dotted grey lines separate different altitudinal bands in which multispecies indicators were calculated. Species with a red circle showed a Strong Decline trend. Species with a yellow circle showed a Moderate Decline trend. Dotted blue line marks growth rate value 1 across the graph. The shaded area represents the 95% confidence limits for the trend (line). 2=*Anthocharis cardamines*, 4=*Aporia* crataegi, 10=*Brenthis ino*, 17=*Cupido minimus*, 22=*Hipparchia hermione*, 23=*Issoria lathonia*, 24=*Laeosopis roboris*, 25=*Lasiommata maera*, 31=*Lysandra coridon*, 34=*Melitaea deione*, 35=*Melitaea diamina*, 37=*Melitaea phoebe*, 39=*Papilio machaon*, 46=*Polyommatus dorylas*, 50=*Speyeria aglaja*.

The decline found in Picos de Europa butterfly abundance in the last 9 years, is in line with previous studies from elsewhere (Fox *et al*., 2023; Brereton *et al*., 2018; Van Swaay *et al*., 2018; Melero *et al*., 2016; Wepprich *et al*., 2019; Van Swaay *et al*., 2020), confirming a global butterfly declining trend, even in well-established protected areas, which are nonetheless affected by global change drivers (Kuckerov *et al*., 2021; Colom *et al*., 2019). However, the annual 5.7% decline in abundance found, doubles the maximum annual decline rates found in other studies, which range from -2.6% to -0.8% (see Table 3 in Wepprich *et al*., 2019). Even if our results are limited in number of sites and years, which could affect the trends if more years were available, they strongly suggest that butterflies are declining in the study area. We argue that the butterfly abundance changes in the last decade in these cultural landscapes are due to rural abandonment, e.g. loss of 60% of hay meadows in the decade 2008-2017 (García *et al*., 2018; Mora *et al*., 2022), together with amplified effects of climate change at mountain ecosystems (IPCC, 2022; Pepin *et al*., 2015, 2022).

Depending on their specific traits, species will be more or less vulnerable to these global drivers of change. Based on previous butterfly studies (Brereton *et al*., 2018; DEFRA, 2021; Stefanescu *et al*., 2011b), we hypothesized that generalist species would fare better than specialists. Under a context of land abandonment and global warming, the abundance of specialist species (based on their food plants or on their elevational amplitude) is expected to experience a more negative trend than the abundance of species that can live in a wider elevational range or use a wider variety of food plants (Flousek *et al*., 2015, Filazolla *et al*., 2020; Rödder *et al*., 2021). A complex picture emerged from our results, where major factors as species mean elevation and species mean temperature significantly influenced species growth rates. In a sense, specialist species (alpine species and Mediterranean species at lower elevations) showed lower growth rates than species at mid-elevations and experiencing mid-temperatures across their geographic range in Europe. We argue that species at both extremes of the elevational range, which are not able to migrate because of their degree of specialism, are faring worse than species at mid-elevations.

Elevation is also an important factor when analysing the effects of land-use change (abandonment) over butterfly communities in mountains. We have shown that communities below 1200 m are changing composition in favour of species that prefer closed habitats, in line with our previous study in the area (Mora *et al*., 2022). Those communities are located below the treeline, where the landscape can potentially become dominated by forests. While community composition can change as a result of landscape changes (with species with greater preferences for closed habitats becoming more abundant), as shown in other studies (Van Strien *et al*., 2019; DEFRA, 2021), we found a general moderate decline trend for all species, independent of their preferences for open, intermediate or closed habitats, which is contrary to our initial hypothesis. As has been suggested for the United Kingdom (DEFRA, 2021), and generally for cultural landscapes in Europe (Warren *et al*., 2021), the long-term decline of butterflies with preference for closed habitats (woodland butterflies) may be due to a lack of woodland management and loss of open spaces in woods. *Lopinga achine*, *Hamearis lucina* or *Carterocephalus palaemon*, rare woodland species, deserve further investigations in Picos de Europa, as they are located near sites where encroachment is having an effect on butterfly communities.

Coupled to abandonment, climate change is expected to be driving substantial changes in butterfly populations in Picos de Europa. Temperatures in the study area have increased annually by 0.021 ºC in the period 1979-2019. This rate of warming of 0.21 ºC per decade in 40 years, is at the high end of estimates for the increase in global surface temperature of 0.18 ºC (± 0.04 ºC) per decade during a similar period (Leach *et al.*, 2018), consistent with the hypothesis that effects of climate change are amplified at mountain areas, as was highlighted by the IPCC in its latest report (IPCC, 2022). In our study, we found that at high elevations (above the treeline, 1200 - 1900 m) butterfly populations are declining and, climate change appears to be the main driver of changes to assemblages. At these elevations, land-use change has been minimal: grazing is relatively low intensity and the type of grazer (cow, sheep, horses and wild chamois) and livestock numbers has remained similar during the study period. Recent studies in Picos de Europa for alpine birds (De Gabriel *et al.*, 2022) showed a similar pattern of stronger effects of climate change at the highest elevations, with a decreasing abundance of alpine specialist bird species. Additional research is urgently needed on the impact of extreme weather events or prolonged stretches of weather outside of historical conditions on alpine populations (Halsch *et al.*, 2021). For example, an extreme frost event during the 2016 winter in Picos de Europa in which below-ground temperatures of -9ºC were reached in February in the absence of snow cover (Iglesias *et al.*, 2017), resulted in almost 50% decline in a long-term monitored high mountain specialist vascular plant (*Oxytropis foucadii*, Gillot) (Mora, unpublished data). Such extreme events may be also affecting butterflies, mediated by their hostplants or directly if they overwinter in the soil.

When analysing butterfly community temperature indices (STIc), we found significant changes towards colder communities at lower elevations (80-900 m), but no effects at higher elevations. The factors responsible for this finding remain unclear. Future research could explore if these results are due to: downslope migration of species from higher elevations and therefore with lower STI indices, looking for more open habitats (Lenoir *et al.*, 2010); microclimate effects i.e. habitats at lower elevations cooling because of encroachment of woody vegetation (Clavero *et al.*, 2011, Mingarro *et al.*, 2021); and/or changes on regional weather patterns, with more days of thermal inversion during the winter, and therefore lower temperatures at valley bottoms.

Protected areas are considered an essential tool to halt the collapse of biodiversity (Convention on Biological Diversity, 2020). Even if they are meant to preserve ecosystem functions and biodiversity, threats to insects have been shown to permeate their boundaries. Hallmann *et al*. (2017) showed a worrying decline of more than 75 percent of flying insect biomass in 27 years (1989-2016) in 63 nature protection areas in Germany, the majority of them of limited size and enclosed by agricultural fields. In Great Britain, Cunningham *et al*. (2021a) showed that the distributional trends of declining and priority species were similar in landscapes containing protected areas and in the wider countryside, implying that protected areas were not resilient to landscape-scale pressures. Picos de Europa was the first area in Spain to be declared National Park, in 1918, more than hundred years ago. However, our results show that the effectiveness of protected areas is also compromised in southern Europe highlighting the urgent need to improve conservation outcomes (Cunningham *et al*., 2021b). Specific measures to avoid further erosion of biodiversity include: continued monitoring, increasing the number of BMS-Spain volunteers in this area; increasing scientific knowledge of the species to guide actions, developing collaboration programmes among protected areas and academic institutions; maintaining open areas where traditional management has been abandoned (hay meadows and clearings in woods) at a landscape scale; and directing European funds to these objectives through CAP funds and Nature LIFE projects.

In conclusion, combined effects of amplified climate change and habitat loss appear to be affecting both individual species and community composition in our study area. It is of key importance to understand how the interplay of climate and land use, constraints biodiversity and ecosystem functions to determine the consequences of global change for mountain ecosystems (Peters *et al*., 2019). We have shown that these Southwestern Europe mountain ecosystems, with a long history of legal protection, are nonetheless under a great threat, with a decline of 45% of total butterfly abundance in the last 9 years. These southern mountain ranges harbour one of the highest butterfly biodiversity of the continent (Van Swaay *et al*., 2010) and are also centres of endemism not only for butterflies (Dennis & Schmitt, 2009; Rosso *et al*., 2017; Buira *et al*., 2017), having acted as refugia for many species during the last glacial oscillations (Gómez & Lunt, 2007). Landscape scale adaptative conservation measures, continued monitoring and increasing our scientific knowledge of the species living on these mountains will be essential for their conservation. But above all, urgent action is needed to reduce carbon emissions and avoid further climate change.

3.6 SUPPORTING INFORMATION

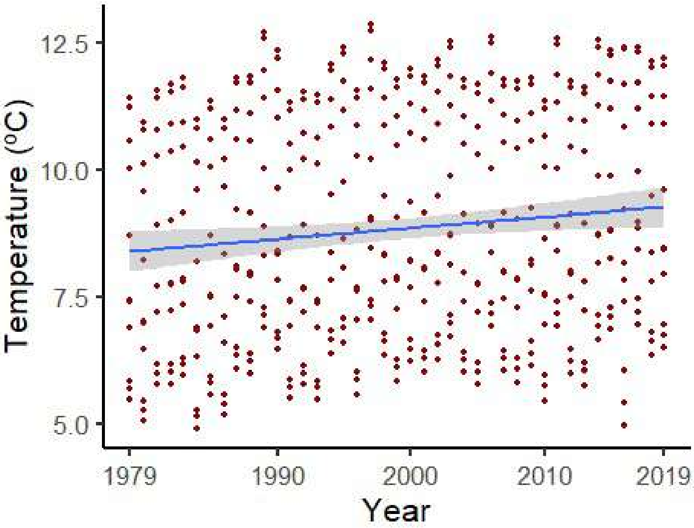


Figure S3.1 Changes in annual mean temperature in the study area over time for the period 1979-2019. Temperature has increased annually by 0.02 ºC. Data from Karger *et al*. (2017). The shaded area represents the 95% confidence limits surrounding the smoothed trend (line).

Table S3.1 Main habitats and plant communities at monitored sites.

TRANSECT	Habitat description EUNIS	EUNIS Code	Habitat category	Length (m)
Cuesta Gines	Western Cantabrian acidophilous oak forests	G1.8622	woodland	251
Cuesta Gines	Cantabro Pyrenean heaths (Erica mackaiana-Erica cinerea)	F4.236	scrub	1170
Pandebano	Atlantic hay meadows	E2.21	grassland	992
Guembres	Atlantic hay meadows	E2.21	grassland	258
Guembres	Cantabrian forests (Quercus pyrenaica)	G1.7B2	woodland	445
Guembres	Atlantic hay meadows	E2.21	grassland	600
Guembres	Cantabro Pyrenean heaths (Erica vagans-Erica cinerea)	F4.237	scrub	106
Prada	Atlantic hay meadows	E2.21	grassland	41
Prada	Bramble thickets	F3.131	scrub	140
Prada	Atlantic and subatlantic hazel tickets	F3.171	scrub	262
Prada	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	396
Prada	Atlantic hay meadows	E2.21	grassland	284
Pandetrave	Northwestern Iberian fields (Genist florida)	F3.252	scrub	108
Pandetrave	Permanent mesotrophic pastures and aftermath grazed meadows	E2.1	grassland	81
Pandetrave	Northwestern Iberian fields (Genist florida)	F3.252	scrub	82
Pandetrave	Nardus stricta swards and permanent mesotrophic pastures	E1.71, E2.1	grassland	283
Pandetrave	Northwestern Iberian fields (Genist florida)	F3.252	scrub	275
Sesanes	Atlantic hay meadows	E2.21	grassland	175
Sesanes	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	93
Sesanes	Atlantic hay meadows	E2.21	grassland	592
Sesanes	Meso and eutrophic Quercus, Carpinus, Fraxinus, Hacer, Tilia, Ulmus and related woodland	G1.A19	woodland	206
Sesanes	Spanish Quercus faginea forests	G1.771	woodland	116
Sesanes	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	92
Morrena Pido	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	467
Morrena Pido	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	348
Morrena Pido	Atlantic hay meadows	E2.21	grassland	181
Lloroza	Pavements and recreation areas	J4.6	other	89
Lloroza	Iberian montane Nardus stricta swards	E1.712	grassland	163
Lloroza	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	376
Lloroza	Iberian montane Nardus stricta swards	E1.712	grassland	77
Lloroza	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	359
Lloroza	Almost bare rock pavements, including limestone pavements	H3.5	other	335
Urdon	Basic and ultrabasic inland cliffs	H3.2	grassland	116
Urdon	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	96
Urdon	Calciphile western Mediterranean oak matorral	F5.113414	scrub	118
Urdon	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	176

TRANSECT	**Habitat description EUNIS**	**EUNIS Code**	**Habitat category**	**Length (m)**
Urdon	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	114
Urdon	Grasslands and lands dominated by forbs, mosses and lichens	E	grassland	210
Urdon	Calciphile western Mediterranean oak matorral	F5.113414	scrub	58
Urdon	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	32
Baenu	Fagus woodland	G1.6	woodland	1526
Liordes	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	218.81
Liordes	Iberian montane Nardus stricta swards and high mountain basic charmophyte communities	E1.712, H3.2	grassland	657.83
Liordes	Iberian montane Nardus stricta swards, permanent mesotrophic pastures and alkaline fens	E1.712, D4.1	grassland	366.76

Table S3.2 List of species recorded

Nº	Protec.	Endem.	Species	Family	Synonymous
1			*Aglais io (Linnaeus, 1758)*	*Nymphalidae*	*Inachis io*
2			*Aglais urticae (Linnaeus, 1758)*	*Nymphalidae*	
3		x	*Agriades pyrenaicus (Boisduval, 1840)*	*Lycaenidae*	*Plebejus pyrenaica*
4			*Anthocharis cardamines (Linnaeus, 1758)*	*Pieridae*	
5			*Anthocharis euphenoides Staudinger, 1869*	*Pieridae*	*Anthocaris belia*
6			*Apatura iris (Linnaeus, 1758)*	*Nymphalidae*	
7			*Aphantopus hyperantus (Linnaeus, 1758)*	*Satyridae*	
8			*Aporia crataegi (Linnaeus, 1758)*	*Pieridae*	
9			*Arethusana arethusa ([Denis & Schiffermüller], 1775)*	*Satyridae*	
10			*Argynnis pandora ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	*Pandoriana pandora*
11			*Argynnis paphia (Linnaeus, 1758)*	*Nymphalidae*	
12			*Aricia cramera (Eschscholtz, 1821)*	*Lycaenidae*	*Aricia agestis*
13			*Aricia montensis Verity, 1928*	*Lycaenidae*	*Aricia antaxerxes*
14		x	*Aricia morronensis (Ribbe, 1910)*	*Lycaenidae*	
15			*Boloria dia (Linnaeus, 1767)*	*Nymphalidae*	*Clossiana dia*
16			*Boloria euphrosyne (Linnaeus, 1758)*	*Nymphalidae*	
17			*Boloria pales ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	
18			*Boloria selene ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	*Clossiana selene*
19			*Brenthis daphne ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	
20			*Brenthis ino (Rottemburg, 1775)*	*Nymphalidae*	
21			*Brintesia circe (Fabricius, 1775)*	*Satyridae*	*Kanetisa circe*
22			*Callophrys rubi (Linnaeus, 1758)*	*Lycaenidae*	
23			*Carcharodus alceae (Esper, 1780)*	*Hesperiidae*	
24			*Carcharodus floccifera (Zeller, 1847)*	*Hesperiidae*	*Carcharodus flocciferus*
25			*Carcharodus lavatherae (Esper, 1783)*	*Hesperiidae*	
26			*Carterocephalus palaemon (Pallas, 1771)*	*Hesperiidae*	
27			*Celastrina argiolus (Linnaeus, 1758)*	*Lycaenidae*	
28			*Coenonympha arcania (Linnaeus, [1760])*	*Satyridae*	
29			*Coenonympha dorus (Esper, 1782)*	*Satyridae*	
30			*Coenonympha glycerion (Borkhausen, 1788)*	*Satyridae*	*Coenonympha iphioides*
31			*Coenonympha pamphilus (Linnaeus, 1758)*	*Satyridae*	
32			*Colias alfacariensis Ribbe, 1905*	*Pieridae*	
33			*Colias crocea (Geoffroy, 1785)*	*Pieridae*	*Colias croceus*
34			*Colias phicomone (Esper, [1780])*	*Pieridae*	
35			*Cupido argiades (Pallas, 1771)*	*Lycaenidae*	*Everes argiades*
36			*Cupido minimus (Fuessly, 1775)*	*Lycaenidae*	
37			*Cyaniris semiargus (Rottemburg, 1775)*	*Lycaenidae*	
38			*Erebia arvernensis Oberthür, 1908*	*Satyridae*	*Erebia cassioides*
39			*Erebia epiphron (Knoch, 1783)*	*Satyridae*	
40			*Erebia euryale (Esper, 1805)*	*Satyridae*	
41			*Erebia gorge (Hübner, [1804])*	*Satyridae*	
42			*Erebia lefebvrei (Boisduval, 1828)*	*Satyridae*	
43			*Erebia manto ([Denis & Schiffermüller], 1775)*	*Satyridae*	
44			*Erebia meolans (Prunner, 1798)*	*Satyridae*	
45		x	*Erebia palarica Chapman, 1905*	*Satyridae*	
46			*Erebia pronoe (Esper, 1780)*	*Satyridae*	
47			*Erebia triarius (Prunner, 1798)*	*Satyridae*	*Erebia triaria*
48			*Erynnis tages (Linnaeus, 1758)*	*Hesperiidae*	
49			*Euchloe crameri Butler, 1869*	*Pieridae*	
50			*Euchloe simplonia (Freyer, 1829)*	*Pieridae*	
51	x		*Euphydryas aurinia (Rottemburg, 1775)*	*Nymphalidae*	
52			*Fabriciana adippe ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	*Argynnis adippe*
53			*Favonius quercus (Linnaeus, 1758)*	*Lycaenidae*	*Quercusia quercus, Neozephyrus quercus*
54			*Glaucopsyche alexis (Poda, 1761)*	*Lycaenidae*	
55			*Glaucopsyche melanops (Boisduval, 1828)*	*Lycaenidae*	
56			*Gonepteryx cleopatra (Linnaeus, 1767)*	*Pieridae*	
57			*Gonepteryx rhamni (Linnaeus, 1758)*	*Pieridae*	
58			*Hamearis lucina (Linnaeus, 1758)*	*Lycaenidae*	

59			*Hesperia comma (Linnaeus, 1758)*	*Hesperiidae*	
60			*Heteropterus morpheus (Pallas, 1771)*	*Hesperiidae*	
61			*Hipparchia hermione (Linnaeus, 1764)*	*Satyridae*	*Hipparchia alcyone*
62			*Hipparchia semele (Linnaeus, 1758)*	*Satyridae*	
63			*Hipparchia statilinus (Hufnagel, 1766)*	*Satyridae*	
64			*Hyponephele lycaon (Kühn, 1774)*	*Satyridae*	
65			*Iphiclides feisthamelii (Duponchel, 1832)*	*Papilionidae*	*Iphiclides podalirius*
66			*Issoria lathonia (Linnaeus, 1758)*	*Nymphalidae*	
67			*Laeosopis roboris (Esper, [1793])*	*Lycaenidae*	
68			*Lampides boeticus (Linnaeus, 1767)*	*Lycaenidae*	
69			*Lasiommata maera (Linnaeus, 1758)*	*Satyridae*	
70			*Lasiommata megera (Linnaeus, 1767)*	*Satyridae*	
71			*Leptidea sinapis (Linnaeus, 1758)*	*Pieridae*	
72			*Leptotes pirithous (Linnaeus, 1767)*	*Lycaenidae*	
73			*Limenitis camilla (Linnaeus, 1764)*	*Nymphalidae*	
74	x		*Lopinga achine (Scopoli, 1763)*	*Satyridae*	
75			*Lycaena alciphron (Rottemburg, 1775)*	*Lycaenidae*	
76			*Lycaena hippothoe (Linnaeus, [1760])*	*Lycaenidae*	
77			*Lycaena phlaeas (Linnaeus, [1760])*	*Lycaenidae*	
78			*Lycaena tityrus (Poda, 1761)*	*Lycaenidae*	
79			*Lycaena virgaureae (Linnaeus, 1758)*	*Lycaenidae*	
80			*Lysandra bellargus (Rottemburg, 1775)*	*Lycaenidae*	*Polyommatus bellargus*
81			*Lysandra coridon (Poda, 1761)*	*Lycaenidae*	*Polyommatus coridon*
82			*Maniola jurtina (Linnaeus, 1758)*	*Satyridae*	
83			*Melanargia galathea (Linnaeus, 1758)*	*Satyridae*	
84			*Melanargia lachesis (Hübner, 1790)*		
85			*Melanargia russiae (Esper, 1783)*	*Satyridae*	
86			*Melitaea celadussa Fruhstorfer, 1910*	*Nymphalidae*	*Mellicta athalia, Melitaea nevadensis*
87			*Melitaea cinxia (Linnaeus, 1758)*	*Nymphalidae*	
88			*Melitaea deione (Geyer, [1832])*	*Nymphalidae*	*Mellicta deione*
89			*Melitaea diamina (Lang, 1789)*	*Nymphalidae*	
90			*Melitaea didyma (Esper, 1778)*	*Nymphalidae*	
91			*Melitaea parthenoides Keferstein, 1851*	*Nymphalidae*	*Mellicta parthenoides*
92			*Melitaea phoebe ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	
93			*Melitaea trivia ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	
94			*Minois dryas (Scopoli, 1763)*	*Satyridae*	
95			*Nymphalis antiopa (Linnaeus, 1758)*	*Nymphalidae*	
96			*Nymphalis polychloros (Linnaeus, 1758)*	*Nymphalidae*	
97			*Ochlodes sylvanus (Esper, 1777)*	*Hesperiidae*	*Ochlodes venata*
98			*Papilio machaon Linnaeus, 1758*	*Papilionidae*	
99			*Pararge aegeria (Linnaeus, 1758)*	*Satyridae*	
100	x		*Parnassius apollo (Linnaeus, 1758)*	*Papilionidae*	
101	x		*Phengaris nausithous (Bergsträsser, 1779)*	*Lycaenidae*	*Maculinea nausithous*
102			*Pieris brassicae (Linnaeus, 1758)*	*Pieridae*	
103			*Pieris mannii (Mayer, 1851)*	*Pieridae*	*Artogeia mannii*
104			*Pieris napi (Linnaeus, 1758)*	*Pieridae*	*Artogeia napi*
105			*Pieris rapae (Linnaeus, 1758)*	*Pieridae*	*Artogeia rapae*
106			*Plebejus argus (Linnaeus, 1758)*	*Lycaenidae*	
107			*Plebejus idas (Linnaeus, [1760])*	*Lycaenidae*	*Lycaeides idas*
108			*Polygonia c-album (Linnaeus, 1758)*	*Nymphalidae*	
109			*Polyommatus dorylas ([Denis & Schiffermüller], 1775)*	*Lycaenidae*	*Plebicula dorylas*
110			*Polyommatus icarus (Rottemburg, 1775)*	*Lycaenidae*	
111			*Pontia daplidice (Linnaeus, 1758)*	*Pieridae*	
112			*Pseudophilotes baton (Bergsträsser, 1779)*	*Lycaenidae*	*Scolitantides baton*
113			*Pyrgus alveus (Hübner, [1803])*	*Hesperiidae*	
114			*Pyrgus armoricanus (Oberthür, 1910)*	*Hesperiidae*	
115			*Pyrgus carthami (Hübner, [1813])*	*Hesperiidae*	
116			*Pyrgus cirsii (Rambur, 1839)*	*Hesperiidae*	
117			*Pyrgus malvoides (Elwes & Edwards, 1897)*	*Hesperiidae*	
118			*Pyrgus onopordi (Rambur, 1839)*	*Hesperiidae*	
119			*Pyrgus serratulae (Rambur, 1839)*	*Hesperiidae*	
120			*Pyronia tithonus (Linnaeus, 1771)*	*Satyridae*	

121			*Satyrium acaciae (Fabricius, 1787)*	*Lycaenidae*	
122			*Satyrium esculi (Hübner, [1804])*	*Lycaenidae*	
123			*Satyrium ilicis (Esper, 1779)*	*Lycaenidae*	
124			*Satyrium spini ([Denis & Schiffermüller], 1775)*	*Lycaenidae*	
125			*Speyeria aglaja (Linnaeus, 1758)*	*Nymphalidae*	*Argynnis aglaja,* *Mesoacidalia aglaja*
126			*Spialia sertorius (Hoffmansegg, 1804)*	*Hesperiidae*	
127			*Thecla betulae (Linnaeus, 1758)*	*Lycaenidae*	
128			*Thymelicus acteon (Rottemburg, 1775)*	*Hesperiidae*	
129			*Thymelicus lineola (Ochsenheimer, 1808)*	*Hesperiidae*	
130			*Thymelicus sylvestris (Poda, 1761)*	*Hesperiidae*	
131			*Vanessa atalanta (Linnaeus, 1758)*	*Nymphalidae*	
132			*Vanessa cardui (Linnaeus, 1758)*	*Nymphalidae*	

Nomenclature after: Wiemers M, Balletto E, Dincă V, Fric ZF, Lamas G, Lukhtanov V, Munguira ML, van Swaay CAM, Vila R, Vliegenthart A, Wahlberg N, Verovnik R (2018) An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea). ZooKeys 81: 9–45. https://doi.org/10.3897/zookeys.811.28712

In **column Protection**, legally protected species in Spain are marked with a cross.
In **column Endemisms**, Iberian endemic species are marked with a cross.

Table S3.3 Species trait values for species with significant population trends.

ID	SPECIES	Average forewing lenght (mm)	Voltinism	Overwintering stage	Hostplant specificity index	Habitat specialist/ generalist	Species temperature index (STI)	Species precipitation index (SPI)	TAO index	Geographic distribution	Mean elevation (m)	Elevation range (m)
1	*Aglais urticae*	23,5	changing	adult	0,707	G	8.12	781.52	0,448	plur	1348,033	2200
2	*Anthocharis cardamines*	21,5	univ	inmature	0,101	G	8.3	778.77	-0,027	plur	914,312	1770
3	*Aphantopus hyperantus*	22	univ	inmature	0,063	G	7.9	770.27	0,216	euro	837,227	1150
4	*Aporia crataegi*	31	univ	inmature	0,082	G	9.14	765.33	0,454	plur	1012,925	1361
5	*Argynnis paphia*	31,5	univ	inmature	0,258	S	9.02	777.2	0,044	plur	843,561	1250
6	*Aricia cramera*	12	changing	all	0,112	G	14.28	697	0,503	plur	835,4	634
7	*Aricia montensis*	15	changing	inmature	0,183	G	12.12	800.64	NA	endpi	1163,98	1498
8	*Boloria dia*	16,5	changing	inmature	0,447	G	9.28	784.27	0,535	euro	1007,645	1335
9	*Boloria selene*	19,5	univ	inmature	0,577	S	6.93	793.83	0,766	euro	1160,855	1550
10	*Brenthis ino*	18,5	univ	inmature	0,204	S	6.86	741.56	0,974	euro	1223,412	1110
11	*Celastrina argiolus*	15	changing	inmature	0,020	G	9.14	763.1	0,058	plur	1042,81	1550
12	*Coenonympha arcania*	18,5	univ	inmature	0,169	G	9.04	772.28	0,047	plur	916,363	1645
13	*Coenonympha pamphilus*	15	changing	inmature	0,096	S	8.96	793.06	0,654	plur	1262,397	1650
14	*Colias alfacariensis*	24	changing	inmature	0,167	G	9.94	811.35	0,545	plur	1228,592	1803
15	*Colias crocea*	25	biv	inmature	0,041	G	10.69	798.28	0,598	plur	1223,77	2050
16	*Cupido argiades*	12,5	changing	inmature	0,072	G	9.42	766.25	0,573	euro	809,833	1630
17	*Cupido minimus*	11	univ	inmature	0,105	G	8.76	817.26	0,274	plur	1142,968	1658
18	*Cyaniris semiargus*	15,5	univ	inmature	0,169	G	7.91	755.5	NA	plur	1337,368	1250
19	*Erebia triarius*	23,5	univ	inmature	0,289	S	9.28	957.83	0,451	orof	1233,381	1789
20	*Erynnis tages*	13,5	univ	inmature	0,129	G	9.12	807.99	0,631	med	1107,107	1550
21	*Gonepteryx cleopatra*	29	changing	adult	0,577	S	13.95	724.22	0,161	plur	626,285	1727
22	*Gonepteryx rhamni*	29,5	univ	adult	0,218	G	8.81	772.47	0,07	plur	920,852	1920
23	*Hipparchia hermione*	32,5	univ	inmature	0,408	G	10.34	810.98	0,111	plur	1137,27	1832
24	*Issoria lathonia*	21	changing	all	0,408	G	9.33	748.91	0,475	plur	1289,646	1627
25	*Laeosopis roboris*	13,5	univ	inmature	0,707	G	12.63	792.19	0,309	med	521,205	965
26	*Lasiommata maera*	25	changing	inmature	0,072	S	8.56	798.37	0,225	plur	1171,111	2080
27	*Lasiommata megera*	22	changing	inmature	0,120	G	10.39	775.99	0,116	plur	885,847	1830
28	*Leptidea sinapis*	21,5	biv	inmature	0,144	G	9.11	770.01	-0,099	plur	823,064	1730
29	*Lycaena alciphron*	17,5	changing	inmature	0,577	G	9.53	772.44	0,659	plur	1358,823	1040

ID	SPECIES	Average forewing lenght (mm)	Voltinism	Overwintering stage	Hostplant specificity index	Habitat specialist/ generalist	Species temperature index (STI)	Species precipitation index (SPI)	TAO index	Geographic distribution	Mean elevation (m)	Elevation range (m)
30	*Lycaena tityrus*	15	biv	inmature	0,136	G	9.35	778.38	0,852	euro	947,84	1146
31	*Lycaena virgaureae*	15	univ	inmature	0,408	S	7.27	757.44	0,669	euro	1316,956	1342
32	*Lysandra bellargus*	15,5	biv	inmature	0,183	G	10.19	800.09	0,613	plur	1008,933	1691
33	*Lysandra coridon*	16,5	univ	inmature	1,000	G	9.31	801.21	0,46	euro	1322,092	1850
34	*Maniola jurtina*	24	univ	inmature	0,289	G	9.85	797.53	0,257	plur	920,84	1650
35	*Melanargia galathea*	24,5	univ	inmature	0,107	G	9.71	782.6	NA	euro	859,178	1888
36	*Melitaea deione*	20,5	changing	inmature	0,120	G	11.58	850.16	0,504	plur	841,183	1358
37	*Melitaea diamina*	18,5	changing	inmature	0,126	G	8.03	817.02	0,5	euro	1427,5	620
38	*Melitaea parthenoides*	17	changing	inmature	0,105	G	10.61	842.52	0,596	plur	1244,836	1630
39	*Melitaea phoebe*	22,5	changing	inmature	0,154	G	10.91	810.61	NA	plur	1112,625	1500
40	*Ochlodes sylvanus*	15,5	univ	inmature	0,083	G	8.58	777.08	0,255	plur	892,382	1432
41	*Papilio machaon*	35	changing	inmature	0,053	S	9.28	737.43	0,517	plur	1093,216	1787
42	*Pararge aegeria*	19,5	changing	inmature	0,154	S	9.71	775.84	-0,419	plur	884,942	1697
43	*Pieris brassicae*	30,5	changing	inmature	0,115	G	9.29	789.63	0,244	plur	897,641	1600
44	*Pieris napi*	25	changing	inmature	0,114	G	8.21	793.11	0,05	plur	909,794	1930
45	*Pieris rapae*	25	changing	inmature	0,118	G	9.63	778.96	0,284	plur	1109,604	1836
46	*Plebejus argus*	14,5	univ	inmature	0,069	S	8.61	778.56	0,639	plur	978,078	1600
47	*Polygonia c-album*	23	univ	adult	0,050	G	8.6	759.35	-0,046	plur	937,166	1505
48	*Polyommatus dorylas*	16	univ	inmature	0,204	S	9.32	869.36	0,764	orof	1283,136	1600
49	*Polyommatus icarus*	16	changing	inmature	0,144	S	9.07	789.28	0,6	plur	1113,959	1820
50	*Pseudophilotes baton*	11	univ	inmature	0,124	S	10.68	904.69	NA	euro	981,5	753
51	*Pyronia tithonus*	18,5	univ	inmature	0,081	G	10.86	837.49	0,206	plur	863,381	1368
52	*Speyeria aglaja*	28,5	univ	inmature	0,500	G	7.79	814.41	0,34	euro	963,639	1467
53	*Spialia sertorius*	11	univ	inmature	1,000	G	10.44	849.15	0,54	plur	1040,553	1180
54	*Thymelicus acteon*	11,5	univ	inmature	0,118	G	11.31	763.51	0,394	plur	765,227	1239
55	*Thymelicus sylvestris*	14,5	univ	inmature	0,101	G	9.87	783.58	0,416	plur	861,855	1731

Average forewing lenght (mm), after Middleton-Welling *et al.*, 2020
Voltinism, as univoltine (univ), bivoltine (biv) or changing, after our own data.
Overwintering stage as adult or inmature (egg, pupae or larvae), after Middleton-Welling *et al.*, 2020
Hostplant specificity index, after Middleton-Welling *et al.*, 2020
Habitat specialist/generalist, after our own data.

Species temperature index (STI) and **Species precipitation index (SPI)**, after Schweiger *et al*., 2014
TAO index of preferences for open/closed habitats, after Ubach *et al*., 2020
Geographic distribution as Pluriregional (plur), Eurosiberian (euro), Iberian endemism (endpi), Orophyte (orof) and Mediterranean (med). After Kurdna *et al*., 2011
Mean elevation (m), after our own data.
Elevation range (m), after our own data.

Table S3.4 Community indices of preference for open/closed habitats (TAOc), Comunnity indices of Temperature (STIc) and Community índices of Precipittion (SPIc) for each transect over time (2013-2021).

TRANSECT	YEAR	TAOc	STIc	SPIc
Urdón	2015	0.217	7.673	602.297
Urdón	2016	0.266	8.286	666.197
Urdón	2017	0.266	8.550	680.021
Urdón	2018	0.15	5.478	445.803
Urdón	2019	0.14	5.587	447.274
Urdón	2021	0.187	7.076	549.694
Gines	2013	0.171	5.829	537.158
Gines	2014	0.186	6.954	515.000
Gines	2015	0.149	5.248	467.495
Gines	2016	0.163	6.614	569.027
Gines	2017	0.140	5.986	485.504
Gines	2018	0.090	6.331	439.139
Gines	2019	0.148	6.499	537.267
Gines	2020	0.180	7.720	642.508
Gines	2021	0.125	5.231	426.707
Sesanes	2013	0.374	9.968	813.269
Sesanes	2014	0.423	10.989	892.218
Sesanes	2015	0.494	10.970	900.001
Sesanes	2016	0.483	11.481	940.233
Sesanes	2017	0.364	9.366	767.911
Sesanes	2018	0.261	8.323	679.180
Sesanes	2019	0.27	7.865	649.018
Sesanes	2020	0.266	8.162	668.300
Sesanes	2021	0.334	9.403	761.376
Baenu	2019	0.107	9.950	637.107
Baenu	2020	0.117	8.320	520.092
Baenu	2021	0.06	6.090	443.999
Güembres	2014	0.377	7.771	647.838
Güembres	2015	0.324	7.563	626.160
Güembres	2016	0.333	7.316	608.857
Güembres	2017	0.3	6.880	596.702
Güembres	2018	0.317	7.121	645.733
Güembres	2019	0.339	7.763	571.843
Güembres	2020	0.371	8.747	718.866
Güembres	2021	0.328	8.414	691.786
Morrena Pido	2013	0.461	11.760	923.788
Morrena Pido	2014	0.422	9.685	801.696
Morrena Pido	2015	0.369	9.153	751.264
Morrena Pido	2016	0.371	7.913	595.036
Prada	2013	0.44	9.555	770.728
Prada	2014	0.431	9.446	775.947

TRANSECT	YEAR	TAOc	STIc	SPIc
Prada	2015	0.374	9.229	677.104
Prada	2016	0.461	10.917	893.892
Prada	2017	0.363	9.016	734.209
Prada	2018	0.408	9.472	767.553
Prada	2019	0.382	9.922	809.847
Prada	2020	0.389	9.985	817.505
Prada	2021	0.428	10.207	837.202
Pandebano	2013	0.353	8.414	720.560
Pandebano	2014	0.292	7.272	664.097
Pandebano	2015	0.319	10.745	648.822
Pandebano	2016	0.359	7.693	790.331
Pandebano	2017	0.387	8.905	930.683
Pandebano	2018	0.331	9.520	825.931
Pandebano	2019	0.304	6.941	695.559
Pandebano	2020	0.239	8.275	577.894
Pandebano	2021	0.262	8.048	713.860
Pandetrave	2013	0.374	7.703	674.942
Pandetrave	2014	0.42	7.708	685.464
Pandetrave	2015	0.395	6.940	616.464
Pandetrave	2016	0.44	7.552	650.250
Pandetrave	2017	0.315	6.047	532.086
Pandetrave	2018	0.461	9.742	925.031
Pandetrave	2019	0.532	9.765	835.780
Pandetrave	2020	0.493	9.437	808.616
Pandetrave	2021	0.459	7.816	676.769
Lloroza	2014	0.317	6.315	550.235
Lloroza	2015	0.516	9.406	874.946
Lloroza	2016	0.651	10.203	949.571
Lloroza	2017	0.445	7.124	641.163
Liordes	2019	0.297	5.292	558.114
Liordes	2020	0.42	5.904	583.856
Liordes	2021	0.438	7.180	726.371

Table S3.5 Long-term abundance trends for 55 species in the period 2013-2021.

ID	SPECIES	FLIGHT CURVE (YEARS)	N_BOOT_LT	GROWTH RATE	GROWTH RATE CHANGE (cummulative, %)	TREND CLASS
1	*Aglais urticae*	8	493	0.953 (0.315-1)	-31.657	uncertain
2	*Anthocharis cardamines*	9	499	0.882 (0.802-0.936)	-63.086	strong decline
3	*Aphantopus hyperantus*	9	498	1.173 (0.872-3)	258.713	uncertain
4	*Aporia crataegi*	9	373	0.903 (0.117-0.989)	-55.770	moderate decline
5	*Argynnis paphia*	9	500	0.907 (0,350-1)	-54.081	uncertain
6	*Aricia cramera*	9	500	0.996 (0.535-1.073)	-3.125	uncertain
7	*Aricia montensis*	9	500	0.996 (0.058-3.454)	-23.586	uncertain
8	*Boloria dia*	9	499	0.938 (0.231-1.231)	-36.600	uncertain
9	*Boloria selene*	9	62	1.063 (0.907-3.625)	62.095	uncertain
10	*Brenthis ino*	6	500	0.861 (0.132-0.983)	-69.775	moderate decline
11	*Celastrina argiolus*	9	500	0.859 (0.269-1)	-70.355	uncertain
12	*Coenonympha arcania*	9	500	0.964 (0.902-1.086)	-24.976	uncertain
13	*Coenonympha pamphilus*	9	491	1.011 (0.798-3.244)	10.012	uncertain
14	*Colias alfacariensis*	8	500	1.052 (0.133-2.923)	50.922	uncertain
15	*Colias crocea*	9	500	0.967 (0.939-1.008)	-23.189	uncertain
16	*Cupido argiades*	9	500	0.977 (0.287-1.04)	-16.381	uncertain
17	*Cupido minimus*	8	497	0.892 (0.771-0.932)	-59.881	strong decline
18	*Cyaniris semiargus*	3	494	0.839 (0.053-175.3)	-75.363	uncertain
19	*Erebia triarius*	4	183	0.524 (0.128-2.236)	-99.423	uncertain
20	*Erynnis tages*	8	184	0.955 (0.692-1.028)	-30.621	uncertain
21	*Gonepteryx cleopatra*	9	52	0.849 (0.392-1.977)	-72.918	uncertain
22	*Gonepteryx rhamni*	9	500	0.990 (0.929-1.063)	-7.588	uncertain
23	*Hipparchia hermione*	9	500	0.817 (0.36-0.968)	-79.982	moderate decline
24	*Issoria lathonia*	9	495	0.919 (0.177-0.96)	-48.904	moderate decline
25	*Laeosopis roboris*	9	53	0.879 (0.083-0.94)	-64.302	strong decline
26	*Lasiommata maera*	9	500	0.877 (0.786-0.974)	-64.721	moderate decline
27	*Lasiommata megera*	9	498	1.015 (0.804-1.119)	13.338	uncertain
28	*Leptidea sinapis*	9	498	1.025 (0.893-1.085)	22.417	uncertain
29	*Lycaena alciphron*	2	498	0.233 (0.035-7.456)	-99.999	uncertain
30	*Lycaena tityrus*	9	492	0.966 (0.791-1.03)	-24.055	uncertain
31	*Lycaena virgaureae*	8	498	1.061 (0.205-2.824)	60.888	uncertain
32	*Lysandra bellargus*	9	497	0.927 (0.651-1.008)	-45.381	uncertain
33	*Lysandra coridon*	9	500	0.875 (0.799-0.971)	-65.566	moderate decline
34	*Maniola jurtina*	9	500	1.013 (0.981-1.049)	11.127	stable
35	*Melanargia galathea*	9	500	0.975 (0.908-1.048)	-17.779	uncertain
36	*Melitaea deione*	6	500	0.858 (0.027-0.969)	-70.474	moderate decline
37	*Melitaea diamina*	9	101	0.834 (0.086-0.866)	-76.427	strong decline
38	*Melitaea parthenoides*	6	309	0.769 (0.033-2.58)	-87.674	uncertain

ID	SPECIES	FLIGHT CURVE (YEARS)	N_BOOT_LT	GROWTH RATE	ABUNDANCE CHANGE (cummulative, %)	TREND CLASS
39	*Melitaea phoebe*	8	500	0.757 (0.013-0.856)	-89.155	strong decline
40	*Ochlodes sylvanus*	9	500	1.09 (0.849-1.17)	100.694	uncertain
41	*Papilio machaon*	7	500	0.763 (0.184-0.891)	-88.414	strong decline
42	*Pararge aegeria*	9	500	1.073 (0.999-1.239)	76.061	uncertain
43	*Pieris brassicae*	9	498	1.02 (0.272-1.355)	17.664	uncertain
44	*Pieris napi*	9	500	1.02 (0.935-1.119)	17.336	uncertain
45	*Pieris rapae*	9	500	0.977 (0.916-1.047)	-16.659	uncertain
46	*Plebejus argus*	9	500	0.959 (0.281-2.828)	-27.928	uncertain
47	*Polygonia c-album*	9	378	0.801 (0.039-2.105)	-83.039	uncertain
48	*Polyommatus dorylas*	9	500	0.834 (0.043-0.928)	-76.563	strong decline
49	*Polyommatus icarus*	9	500	0.949 (0.897-1.003)	-33.755	uncertain
50	*Pseudophilotes baton*	1	492	0.982 (0.094-0.973)	13.266	uncertain
51	*Pyronia tithonus*	9	500	1.041 (0.904-1.115)	38.326	uncertain
52	*Speyeria aglaja*	9	500	0.8 (0.253-0.894)	-83.072	strong decline
53	*Spialia sertorius*	7	62	0.9 (0.146-1.022)	-56.678	uncertain
54	*Thymelicus acteon*	9	500	0.92 (0.293-2.958)	-48.641	uncertain
55	*Thymelicus sylvestris*	9	500	0.99 (0.908-1.144)	-7.338	uncertain

Flight curve (years) = Years used to build the flight curve.
N_boot_Lt = Number of bootstraps made to determine the statistical significance of the abundance trend.
Growth rate = Mean annual growth rate for the species
Abundance change (cummulative, %) = Percentage of Abundance change over the period 2013-2021.
Trend class = As in TRIM (Pannekoek & Strien, 2005).

Trend category	**Description**
Strong increase	Significant increase, more than 5% increase per year
Moderate increase	Significant increase, but less than 5% increase per year
Uncertain	No significant change, but changes (positive or negative) likely to be more than 5% per year
Stable	No significant change, but changes (positive or negative) likely to be less than 5% per year
Moderate decline	Significant decrease, but less than 5% decrease per year
Strong decline	Significant decrease, more than 5% decrease per year

Table S3.6 Parameter estimates and the associated standard error of the species traits retained in the model for population growth rate with outliers (*Erebia triarius* and *Lycaena alciphron*). Significant p values (<0.05) in bold.

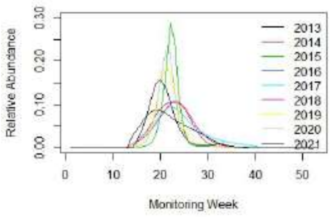
Parameter	**Estimates**	**Std. error**	**npar**	**LRT**	**p value**
Mean elevation	-0.299	0.121	1	8.508	**0.004**
Elevation range	0.165	0.064	1	8.828	**0.003**
Distribution			4	12.214	**0.016**
Distrib-euro	-0.083	0.147			
Distrib-med	-0.165	0.162			
Distrib-orof	-0.431	0.181			
Distrib-plur	-0.171	0.135			
Dispersal	-0.006	0.004	1	3.349	0.067
Hostplant index	-0.131	0.085	1	3.296	0.069
Overwintering stage			2	5.164	0.076
Overwint all	0.228	0.125			
Overwint inmature	0.006	0.073			

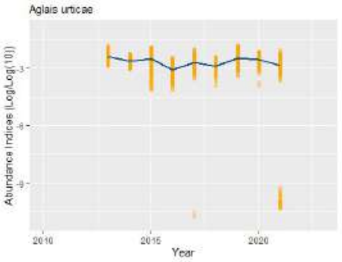
Table S3.7 Parameter estimates and the associated standard error of the species traits retained in the model for population growth rate without outliers (*Erebia triarius* and *Lycaena alciphron*). Significant p values (<0.05) in bold.

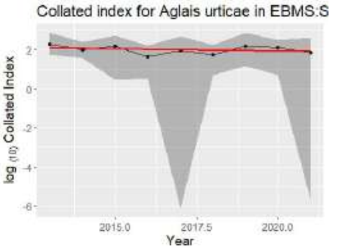
Parameter	**Estimates**	**Std. error**	**npar**	**LRT**	**p value**
Mean elevation	-0.299	0.091	1	8.788	**0.003**
Mean temperature (STI)	-0.022	0.014	1	3.875	**0.049**
Elevation range	0.072	0.049	1	2.923	0.087
Dispersal	-0.005	0.003	1	3.729	0.053

APPENDIX I. Flight curve, Abundance indices graph, Collated index graph and population trend for 55 species in the period 2013-2021.

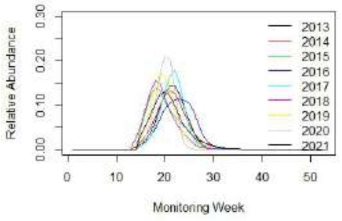
Aglais urticae **Flight curve:** 8 years. Univoltine (spring) **Date period:** 2013-2021 **N_Boot_Lt:** 493 **Rate of change:** 0.953 (0.315 – 1) **% of rate change:** -31.657 **Trend:** UNCERTAIN

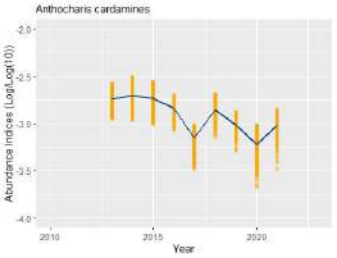


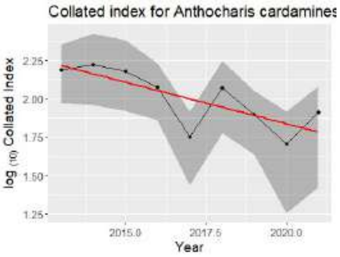




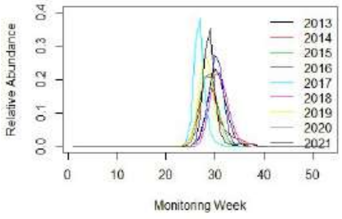
Anthocharis cardamines **Flight curve:** 9 years. Univoltine (spring) **Date period:** 2013-2021 **N_Boot_Lt:** 499 **Rate of change:** 0.882 (0.802 –0.9361) **% of rate change:** -63.086 **Trend:** STRONG DECLINE

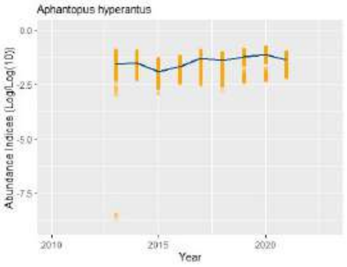


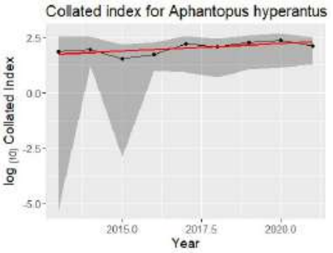




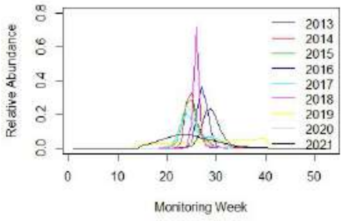
Aphantopus hyperantus **Flight curve:** 9 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 498 **Rate of change:** 1.173 (0.872 –3) **% of rate change:** 258.713 **Trend:** UNCERTAIN

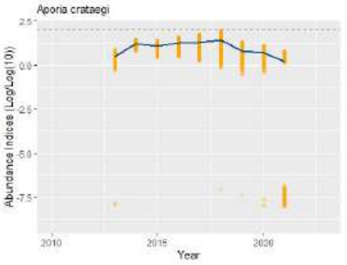


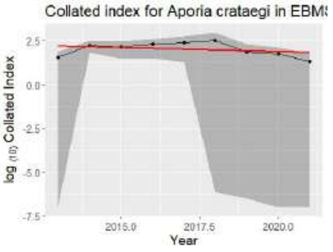




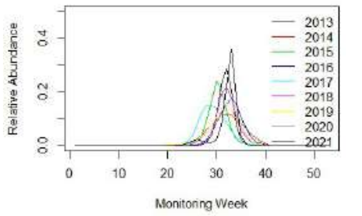
Aporia crataegi **Flight curve:** 9 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 373 **Rate of change:** 0.903 (0.117 –0.989) **% of rate change:** -55.770 **Trend:** MODERATE DECLINE

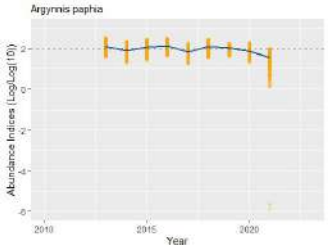


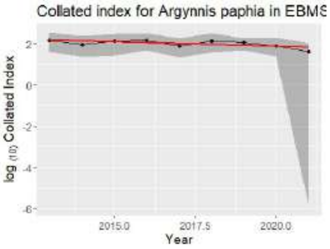




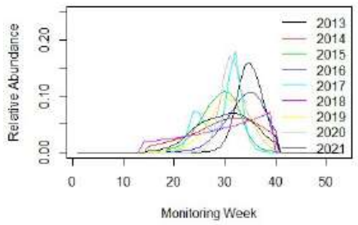
Argynnis paphia **Flight curve:** 9 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.907 (0.350 –1) **% of rate change:** -54.081 **Trend:** UNCERTAIN

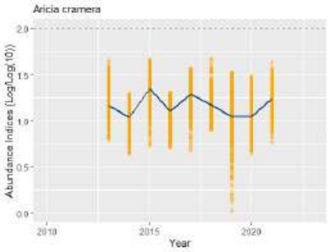


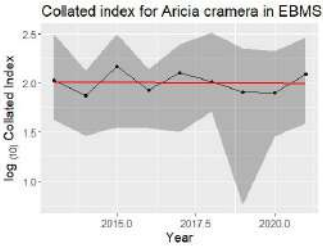




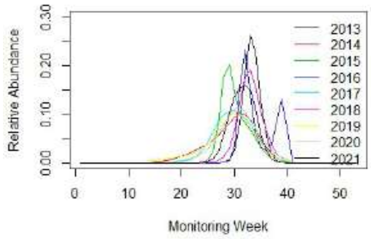
Aricia cramera **Flight curve:** 9 years. Univoltine (summer). Bilvoltine in 2017. **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.996 (0.535 –1.073) **% of rate change:** -3.125 **Trend:** UNCERTAIN

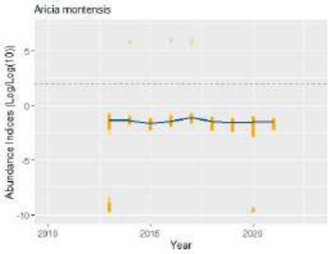


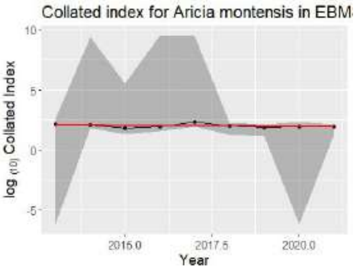




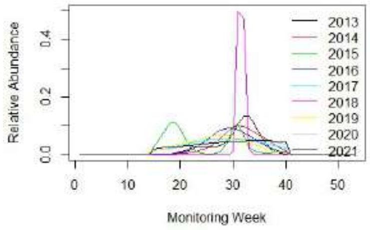
Aricia montensis **Flight curve:** 9 years. Univoltine (summer). Bilvoltine in 2016. **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.996 (0.058 –3.454) **% of rate change:** -23.586 **Trend:** UNCERTAIN

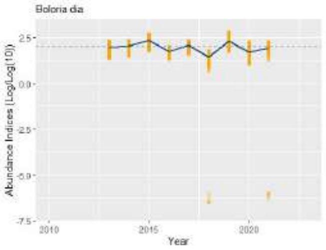


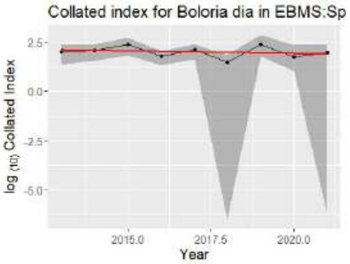




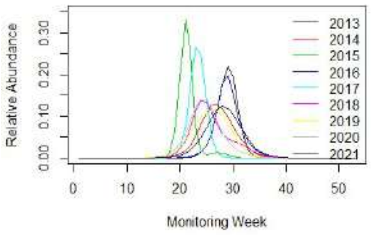
Boloria dia **Flight curve:** 9 years. Univoltine (summer). Bilvoltine (spring+ summer) in 2015 **Date period:** 2013-2021 **N_Boot_Lt:** 499 **Rate of change:** 0.938 (0.231–1.231) **% of rate change:**
-39.600 **Trend:** UNCERTAIN

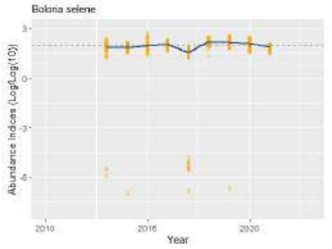


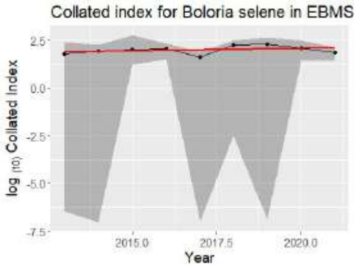




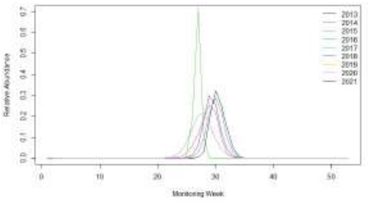
Boloria selene **Flight curve:** 9 years. Univoltine (summer). Bivoltine (spring+ summer) in 2015 **Date period:** 2013-2021 **N_Boot_Lt:** 62 **Rate of change:** 1.063 (0.907–3.625) **% of rate change:** 62.095 **Trend:** UNCERTAIN

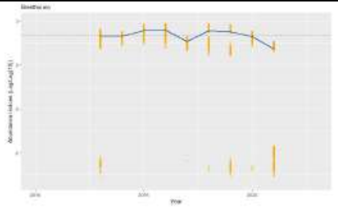


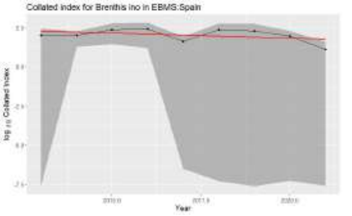




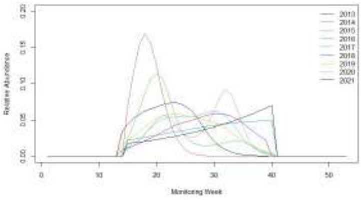
Brenthis ino **Flight curve:** 6 years. Univoltine (summer). **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.861 (0.132–0.983) **% of rate change:** -69.775 **Trend:** MODERATE DECLINE

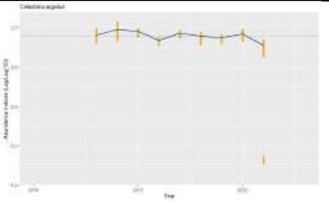


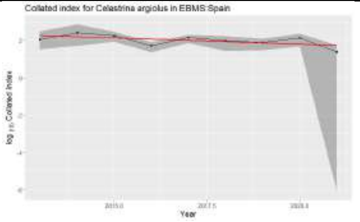




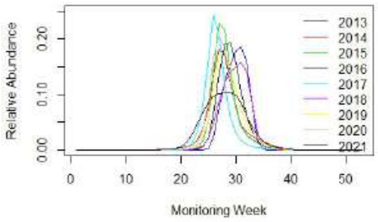
Celastrina argiolus **Flight curve:** 9 years. Univoltine (spring, summer) or bivoltine (spring-summer). **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.859 (0.269–1) **% of rate change:** -70.355 **Trend:** UNCERTAIN

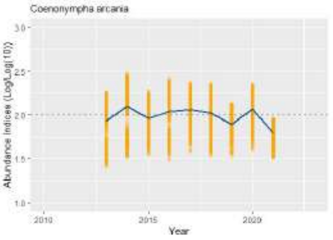


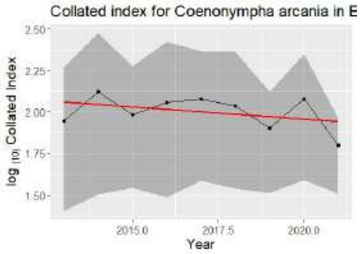




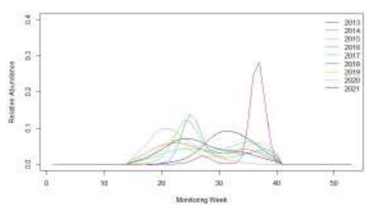
Coenonympha arcania **Flight curve:** 9 years. Univoltine (summer). **Date period:** 2013-2021 **N_Boot_Lt:**500 **Rate of change:** 0.964 (0.902–1.086) **% of rate change:** -24.976 **Trend:** UNCERTAIN

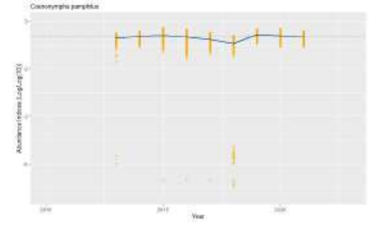


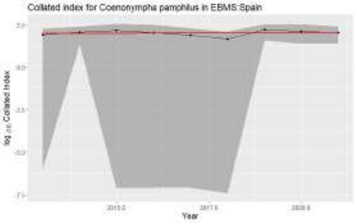




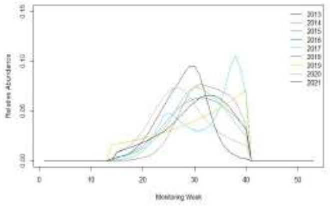
Coenonympha pamphilus **Flight curve:** 9 years. Univoltine (spring or summer) or bivoltine (early and late summer). **Date period:** 2013-2021 **N_Boot_Lt:** 491 **Rate of change:** 1.011 (0.798–3.244) **% of rate change:** 10.012 **Trend:** UNCERTAIN

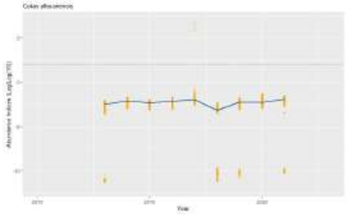


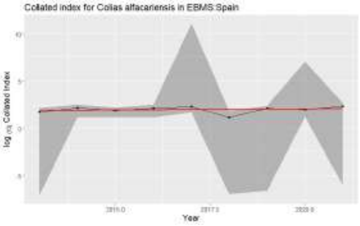




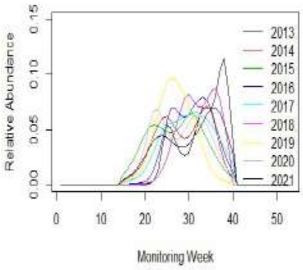
Colias alfacariensis **Flight curve:** 8 years. Univoltine (summer) but bivoltine (early and late summer) in 2017. **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 1.052 (0.133-2.923) **% of rate change:** 50.922 **Trend:** UNCERTAIN

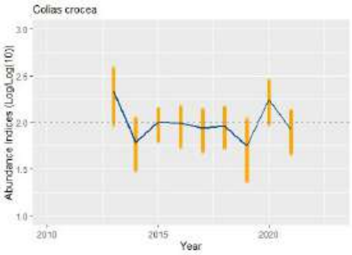


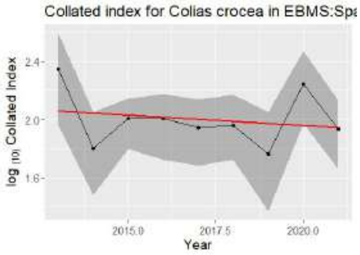




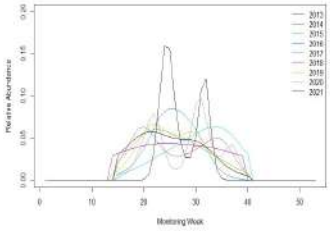
Colias crocea **Flight curve:** 9 years. Bivoltine (early and late summer). **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.967 (0.939-1.008) **% of rate change:** -23.189 **Trend:** UNCERTAIN

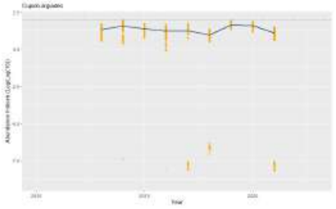


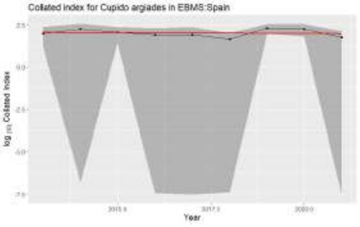




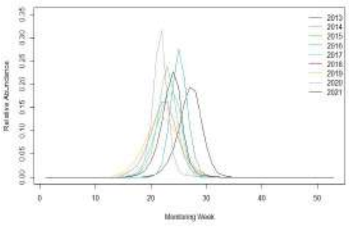
Cupido argiades **Flight curve:** 9 years. Monovoltine (early summer), bivoltine (early and late summer) or even trivoltine in 2020. **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.977 (0.287-1.04) **% of rate change:** -16.381 **Trend:** UNCERTAIN

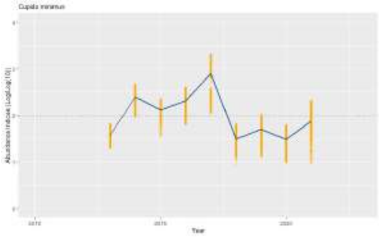


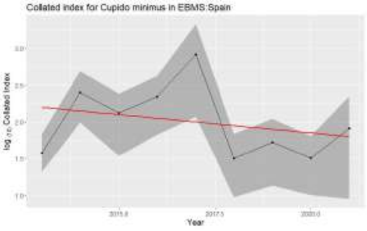




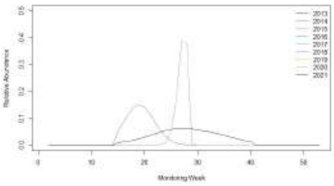
Cupido minimus **Flight curve:** 8 years. Univoltine (early summer). **Date period:** 2013-2021 **N_Boot_Lt:** 497 **Rate of change:** 0.892 (0.771-0.932) **% of rate change:** -59.881 **Trend:** STRONG DECLINE

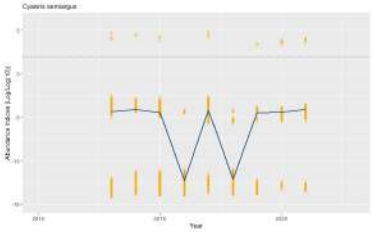


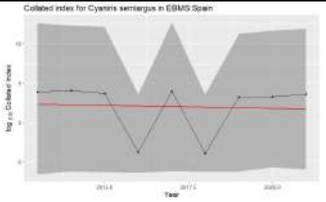




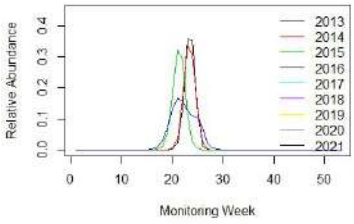
Cyaniris semiargus **Flight curve:** 3 years. Univoltine (spring or summer, depending on altitude). **Date period:** 2013-2021 **N_Boot_Lt:** 494 **Rate of change:** 0.839 (0.053-175.3) **% of rate change:** -75.363 **Trend:** UNCERTAIN

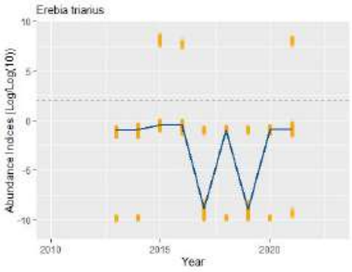


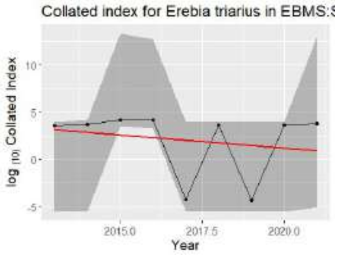




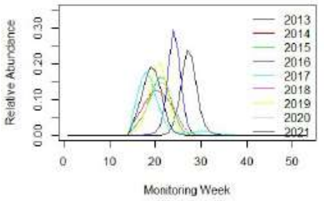
Erebia triarius **Flight curve:** 4 years. Univoltine (early summer). **Date period:** 2013-2021 **N_Boot_Lt:** 183 **Rate of change:** 0.524 (0.128-2.236) **% of rate change:** -99.423 **Trend:** UNCERTAIN

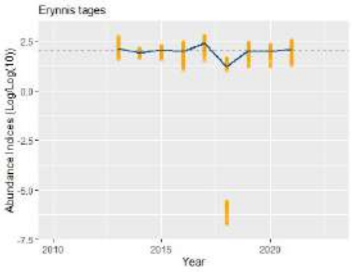


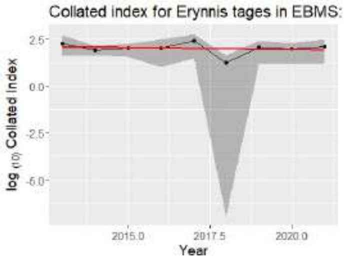




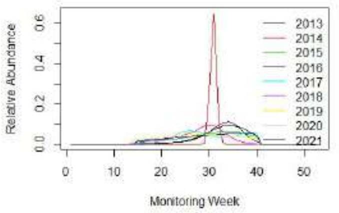
Erynnis tages **Flight curve:** 8 years. Univoltine (early or late summer). **Date period:** 2013-2021 **N_Boot_Lt:** 184 **Rate of change:** 0.955 (0.692-1.028) **% of rate change:** -30.621 **Trend:** UNCERTAIN

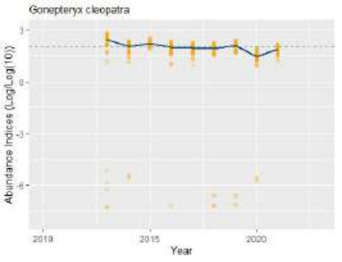


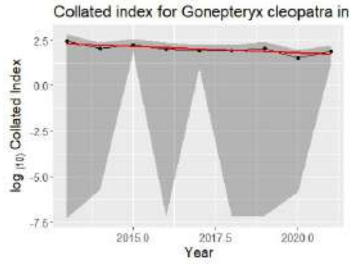




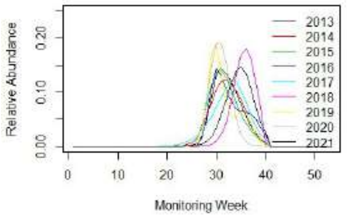
Gonepteryx cleopatra **Flight curve:** 8 years. Univoltine (early or late summer). **Date period:** 2013-2021 **N_Boot_Lt:** 184 **Rate of change:** 0.955 (0.692-1.028) **% of rate change:** -30.621 **Trend:** UNCERTAIN

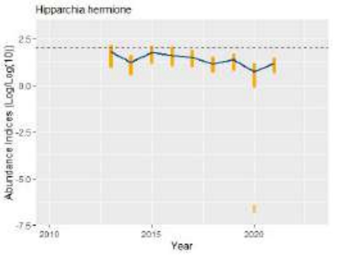


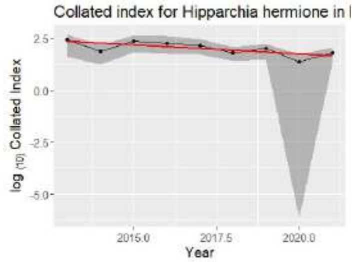




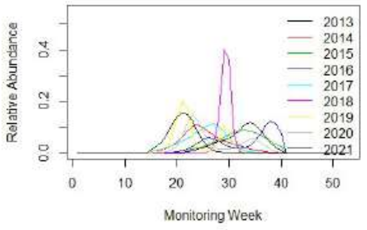
Hipparchia hermione **Flight curve:** 9 years. Univoltine (late summer, maybe with inmigrants in weeks 37-38, end september). **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.817 (0.36-0.968) **% of rate change:** -79.982 **Trend:**MODERATE DECLINE

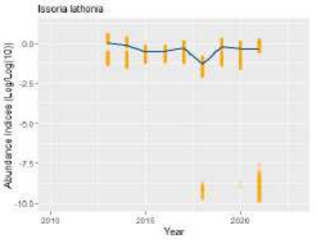


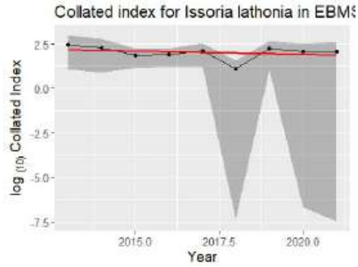




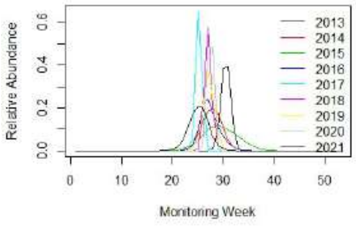
Issoria lathonia **Flight curve:** 9 years. Univoltine or bivoltine. **Date period:** 2013-2021 **N_Boot_Lt:** 495 **Rate of change:** 0.919 (0.177-0.96) **% of rate change:** -48.904 **Trend:** MODERATE DECLINE

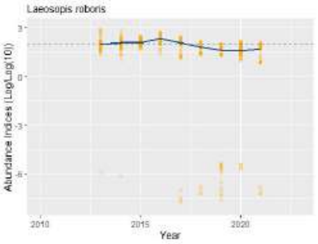


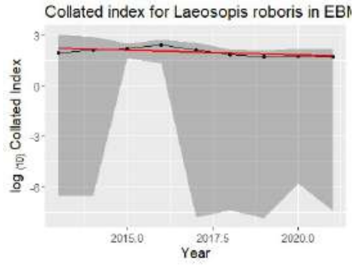




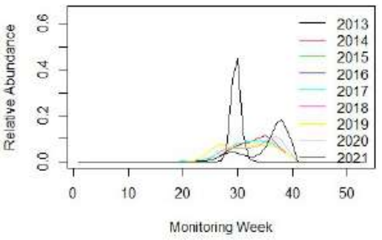
Laeosopis roboris **Flight curve:** 9 years. Univoltine (summer). **Date period:** 2013-2021 **N_Boot_Lt:** 53 **Rate of change:** 0.879 (0.083-0.94) **% of rate change:** -64.302 **Trend:** STRONG DECLINE

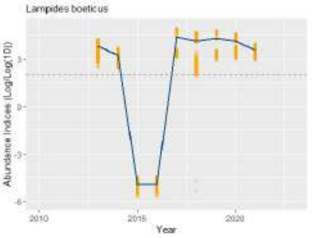


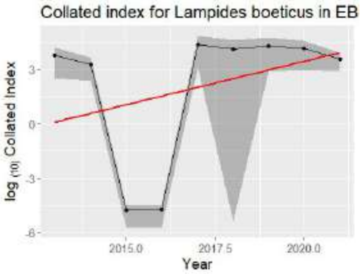




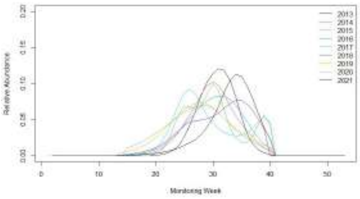
Lampides boeticus **Flight curve:** 6 years. Bivoltine (mid and late summer, plus migrants). **Date period:** 2013-2021 **N_Boot_Lt:** 499 **Rate of change:** 3.011 (2.031-3.917) **% of rate change:** 675656.3 **Trend:** STRONG INCREASE

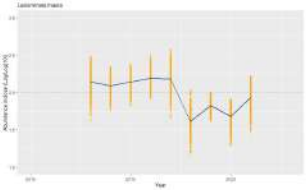


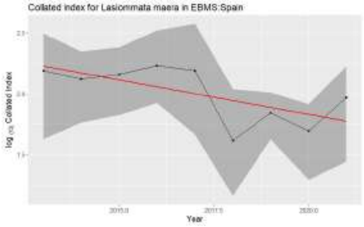




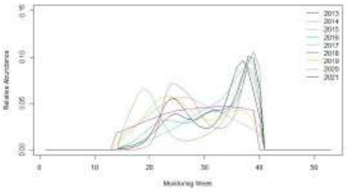
Lasiommata maera **Flight curve:** 9 years. Monovoltine (summer) or bivoltine (mid and late summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.877 (0.786-0.974) **% of rate change:** -64.721 **Trend:** MODERATE DECLINE

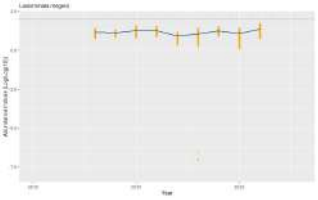


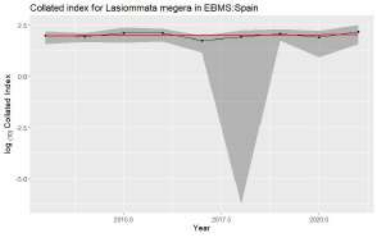




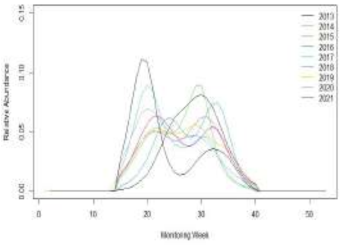
Lasiommata megera **Flight curve:** 9 years. Monovoltine (summer) or bivoltine (early and late summer) **Date period:** 2013-2021 **N_Boot_Lt:** 498 **Rate of change:** 1.015 (0.804-1.119) **% of rate change:** 13.338 **Trend:** UNCERTAIN

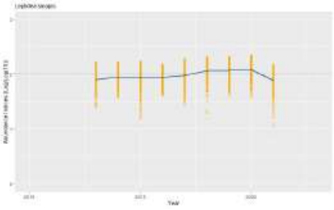


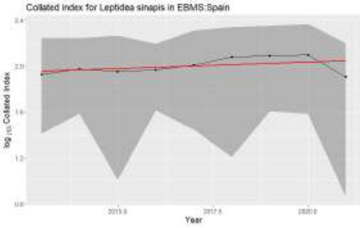




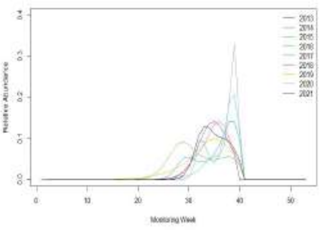
Leptidea sinapis **Flight curve:** 9 years. Bivoltine (early and late summer), but in 2013 monovoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 498 **Rate of change:** 1.025 (0.893-1.085) **% of rate change:** 22.417 **Trend:** UNCERTAIN

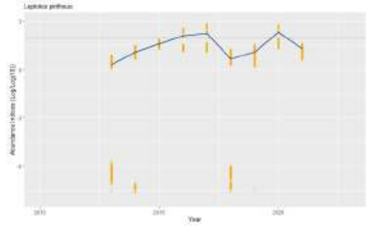


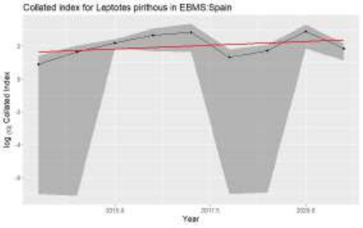




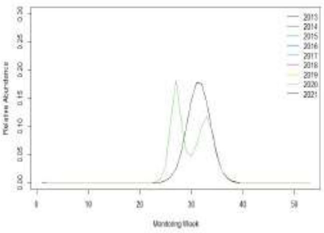
Leptotes pirithous **Flight curve:** 9 years. Univoltine (late summer), Bivoltine (mid and late summer) plus migrants in late summer **Date period:** 2013-2021 **N_Boot_Lt:** 499 **Rate of change:** 1.23 (0.877-3.591) **% of rate change:** 425.795 **Trend:** UNCERTAIN

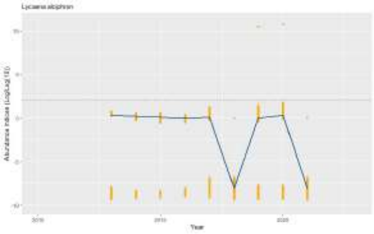


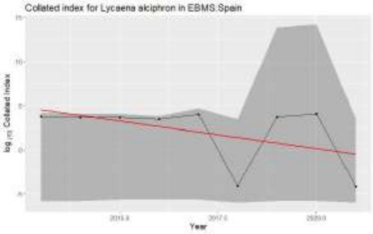




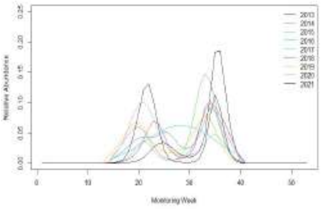
Lycaena alciphron **Flight curve:** 2 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 498 **Rate of change:** 0.233 (0.035-7.456) **% of rate change:** -99.999 **Trend:** UNCERTAIN

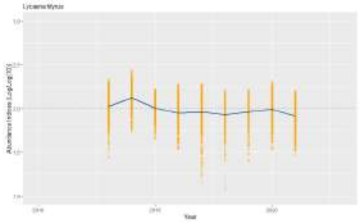


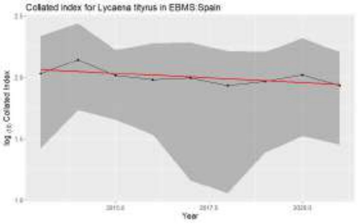




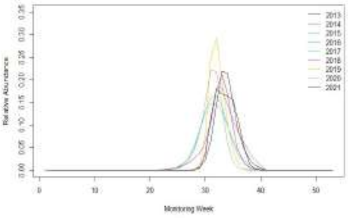
Lycaena tityrus **Flight curve:** 9 years. Bivoltine (early and late summer) but monovoltine (summer) in 2018 **Date period:** 2013-2021 **N_Boot_Lt:** 492 **Rate of change:** 0.966 (0.791-1.03) **% of rate change:** -24.055 **Trend:** UNCERTAIN

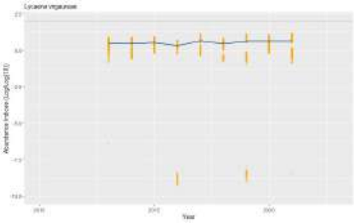


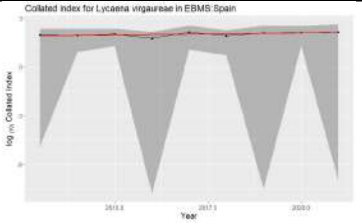




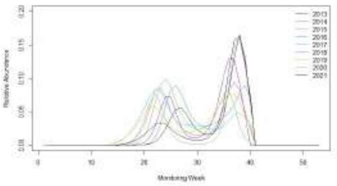
Lycaena virgaureae **Flight curve:** 8 years. Univoltine (late summer) **Date period:** 2013-2021 **N_Boot_Lt:** 498 **Rate of change:** 1.061 (0.205-2.824) **% of rate change:** 60.888 **Trend:** UNCERTAIN

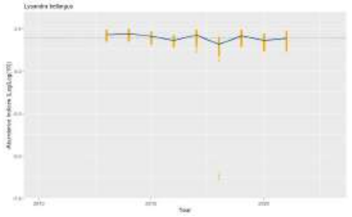


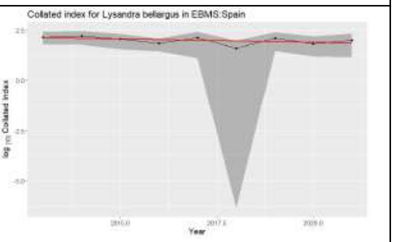




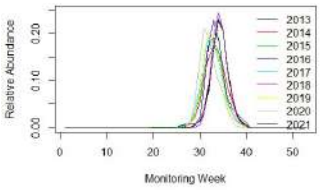
Lysandra bellargus **Flight curve:** 9 years. Bivoltine (early and late summer) **Date period:** 2013-2021 **N_Boot_Lt:** 497 **Rate of change:** 0.927 (0.651-1.008) **% of rate change:** -45.381 **Trend:** UNCERTAIN

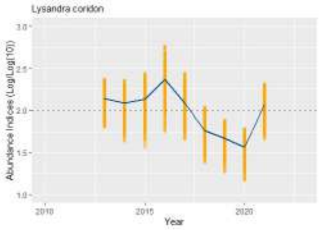


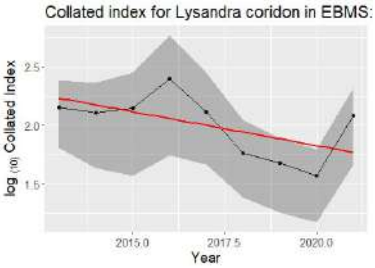




Lysandra coridon **Flight curve:** 9 years. Univoltine (late summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.875 (0.799-0.971) **% of rate change:** -65.566 **Trend:** MODERATE DECLINE

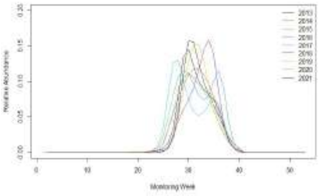


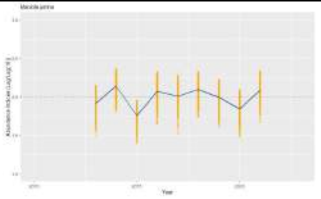


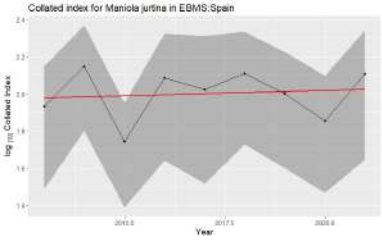


Maniola jurtina **Flight curve:** 9 years. Univoltine (summer) *

Date period: 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 1.013 (0.981-1.049) **% of rate change:** 11.127 **Trend:** STABLE

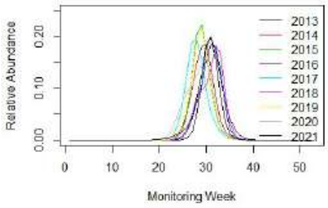


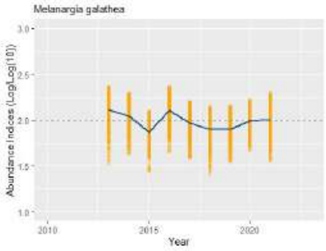


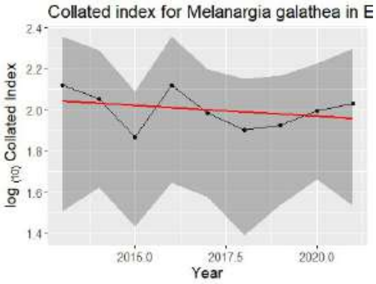


Melanargia galathea **Flight curve:** 9 years. Univoltine (summer)

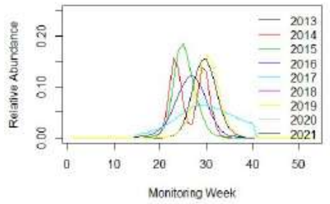
Date period: 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.975 (0.908-1.048) **% of rate change:** -17.779 **Trend:** UNCERTAIN

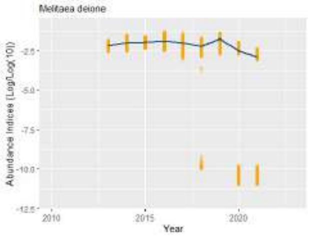


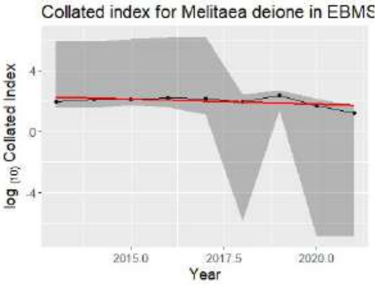




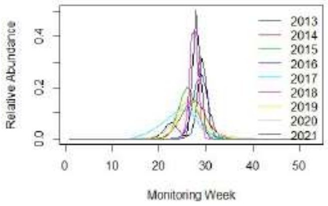
Melitaea deione **Flight curve:** 6 years. Univoltine (summer) but bivoltine in 2014 (early and mid summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.858 (0.027-0.969) **% of rate change:** -70.474 **Trend:** MODERATE DECLINE

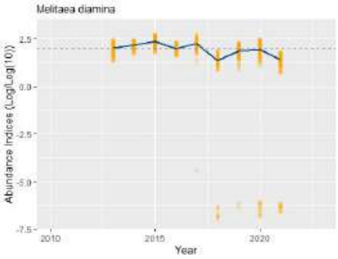


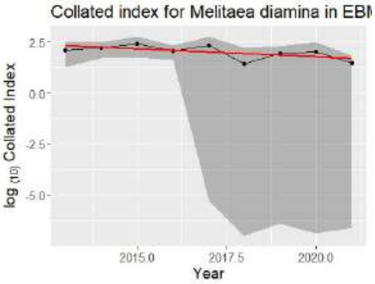




Melitaea diamina **Flight curve:** 9 years. Univoltine (summer) but bivoltine in 2013 (early and mid summer) **Date period:** 2013-2021 **N_Boot_Lt:** 101 **Rate of change:** 0.834 (0.086-0.866) **% of rate change:** -76.427 **Trend:** STRONG DECLINE

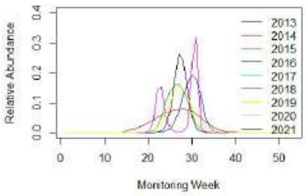


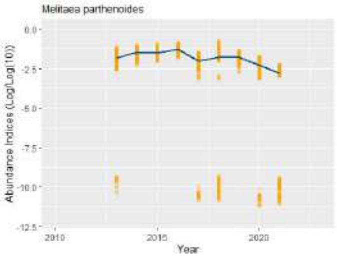


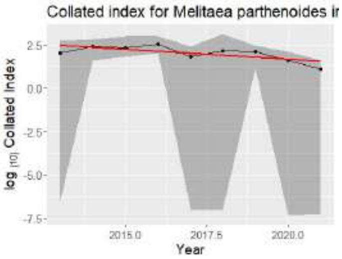


Melitaea parthenoides **Flight curve:** 6 years. Univoltine (summer) but bivoltine in 2018

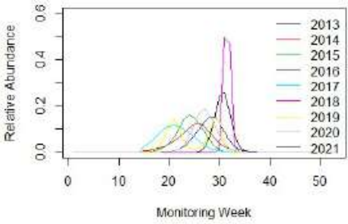
(early and mid summer) **Date period:** 2013-2021 **N_Boot_Lt:** 309 **Rate of change:** 0.769 (0.033-2.58) **% of rate change:** -87.674 **Trend:** UNCERTAIN

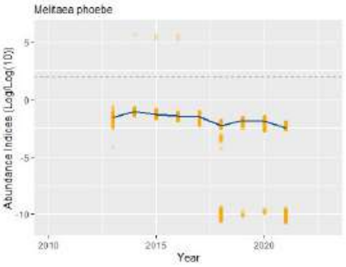


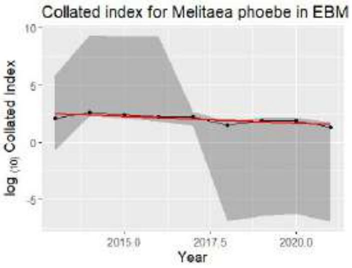




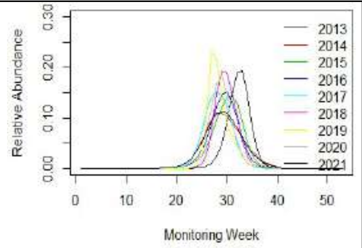
Melitaea phoebe **Flight curve:** 8 years. Univoltine (summer) but bivoltine in 2019 (early and mid summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.757 (0.013-0.856) **% of rate change:** -89.155 **Trend:** STRONG DECLINE

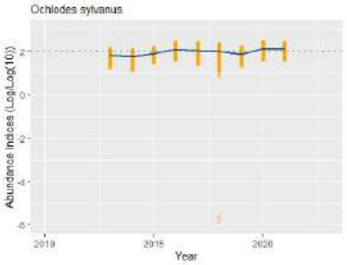


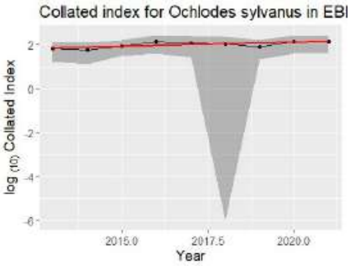




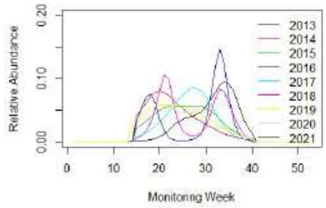
Ochlodes sylvanus **Flight curve:** 9 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 1.09 (0.849-1.17) **% of rate change:** 100.694 **Trend:** UNCERTAIN *

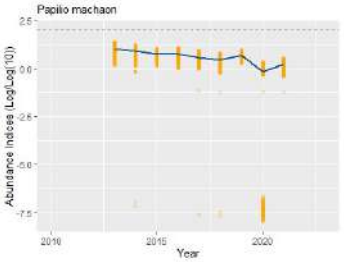


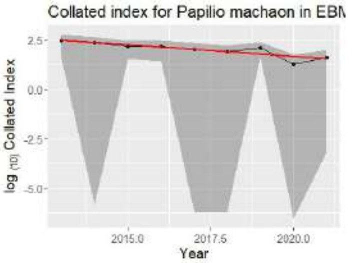




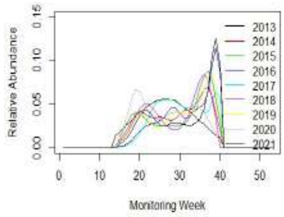
Papilio machaon **Flight curve:** 7 years. Univoltine (summer) but bivoltine (spring, late summer) in 2016 and 2018. **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.763 (0.184-0.891) **% of rate change:** -88.414 **Trend:** STRONG DECLINE

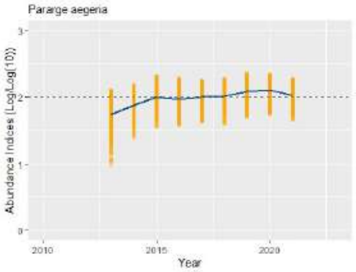


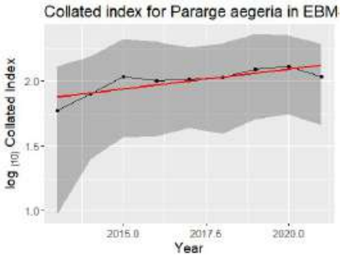




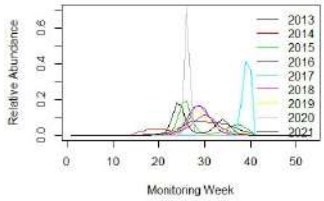
Pararge aegeria **Flight curve:** 9 years. Univoltine (summer) or bivoltine (early and late summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 1.073 (0.999-1.239) **% of rate change:** 76.061 **Trend:** UNCERTAIN

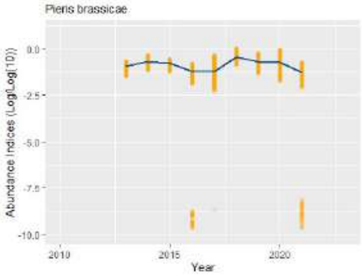


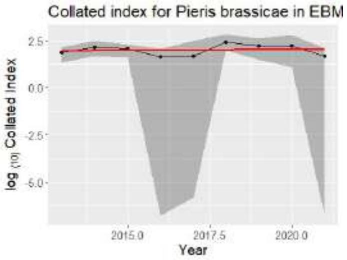




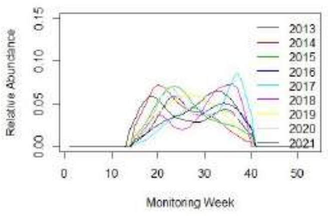
Pieris brassicae **Flight curve:** 9 years. Univoltine (summer) or bivoltine (early and late summer) Maybe also migrants in late summer **Date period:** 2013-2021 **N_Boot_Lt:** 498 **Rate of change:** 1.02 (0.272-1.355) **% of rate change:** 17.664 **Trend:** UNCERTAIN

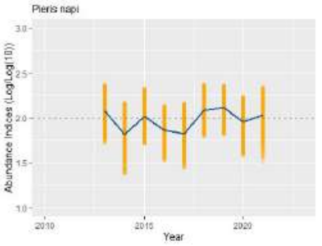


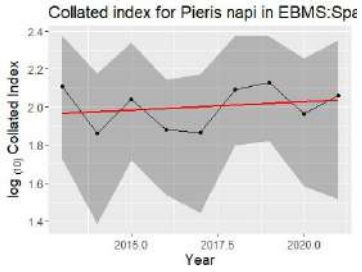




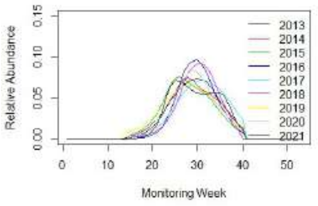
Pieris napi **Flight curve:** 9 years. Univoltine (summer) or bivoltine (early and late summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 1.02 (0.935-1.119) **% of rate change:** 17.336 **Trend:** UNCERTAIN

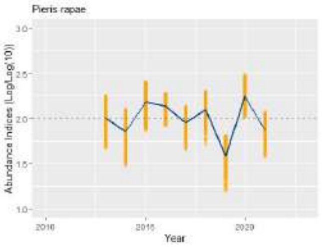


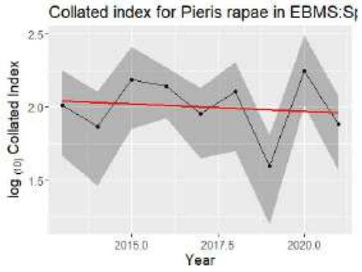




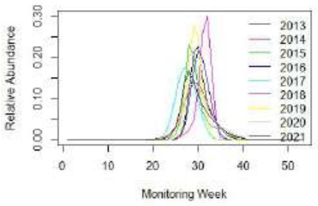
Pieris rapae **Flight curve:** 9 years. Univoltine (summer) or bivoltine (early and late summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.977 (0.916-1.047) **% of rate change:** -16.659 **Trend:** UNCERTAIN

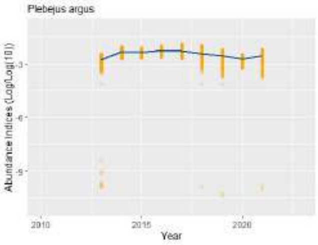


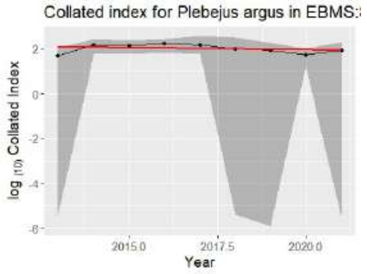




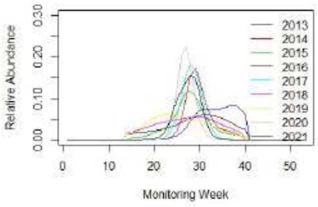
Plebejus argus **Flight curve:** 9 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.959 (0.281-2.828) **% of rate change:** -27.928 **Trend:** UNCERTAIN

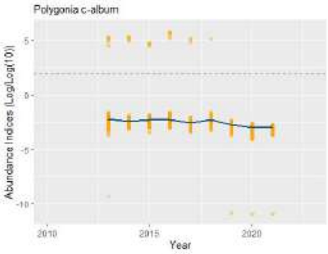


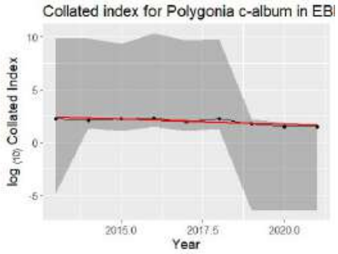




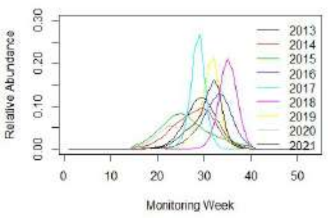
Polygonia c-album **Flight curve:** 9 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 378 **Rate of change:** 0.801 (0.039-2.105) **% of rate change:** -83.039 **Trend:** UNCERTAIN

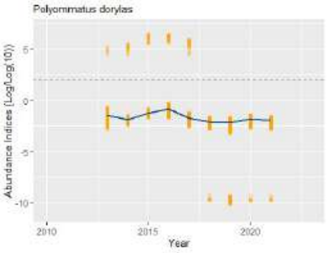


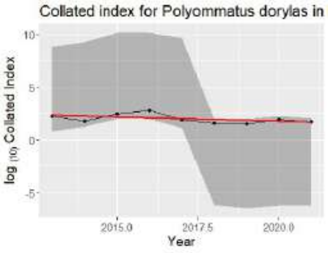




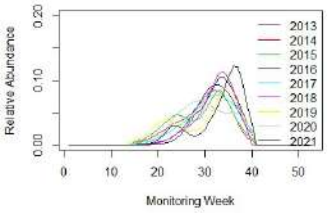
Polyommatus dorylas **Flight curve:** 9 years. Univoltine (summer) but bivoltine (early and late summer) in 2020 **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.834 (0.043-0.928)
% of rate change: -76.563 **Trend:** STRONG DECLINE

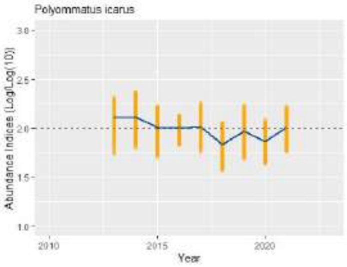


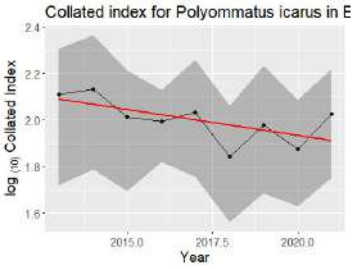




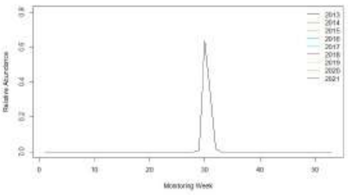
Polyommatus icarus **Flight curve:** 9 years. Univoltine (summer) ort bivoltine (early and late summer) in 2020 **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.949 (0.897-1.003)
% of rate change: -33.755 **Trend:** UNCERTAIN

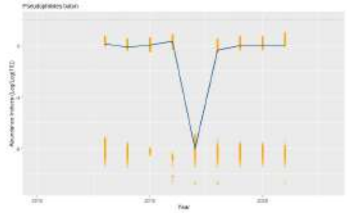


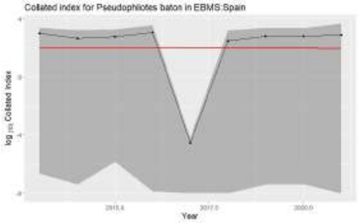




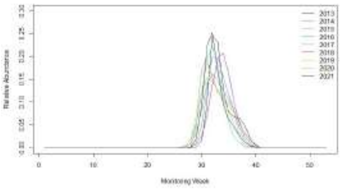
Pseudophilotes baton **Flight curve:** 1 year. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 492 **Rate of change:** 0.982 (0.094-6.973) **% of rate change:** -13.266 **Trend:** UNCERTAIN

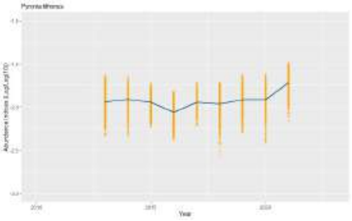


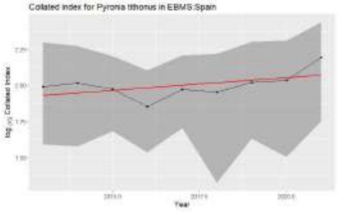




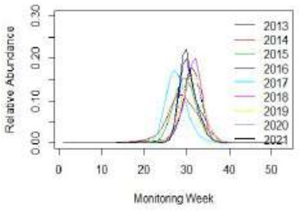
Pyronia tithonus **Flight curve:** 9 years. Univoltine (late summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 1.041 (0.904-1.115) **% of rate change:** 38.326 **Trend:** UNCERTAIN

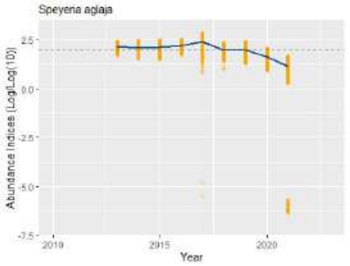


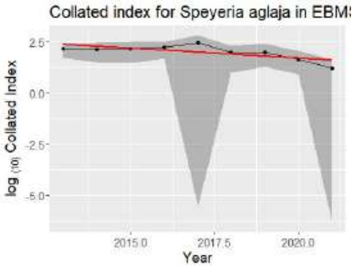




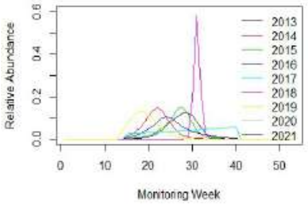
Speyeria aglaja **Flight curve:** 9 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.8 (0.253-0.894) **% of rate change:** -83.072 **Trend:** STRONG DECLINE

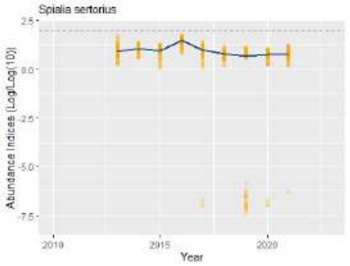


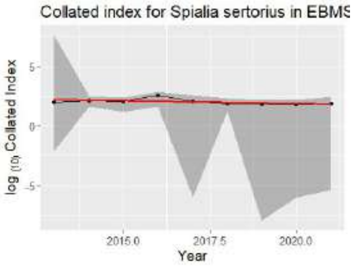




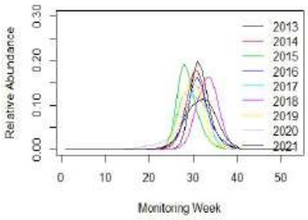
Spialia sertorius **Flight curve:** 7 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 62 **Rate of change:** 0.9 (0.146-1.022) **% of rate change:** -56.678 **Trend:** UNCERTAIN

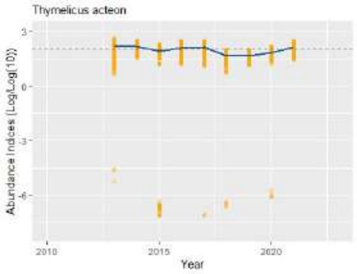


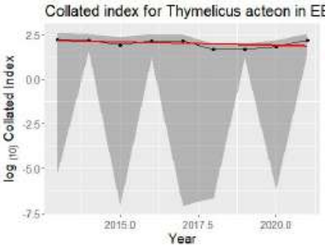




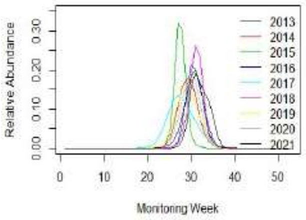
Thymelicus acteon **Flight curve:** 9 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.92 (0.293-2.958) **% of rate change:** -48.641 **Trend:** UNCERTAIN

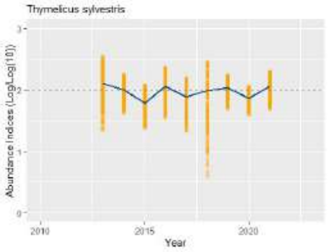


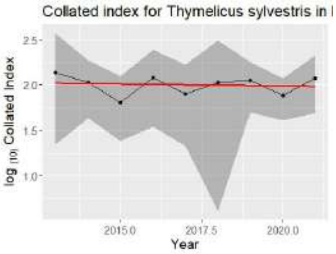




Thymelicus sylvestris **Flight curve:** 9 years. Univoltine (summer) **Date period:** 2013-2021 **N_Boot_Lt:** 500 **Rate of change:** 0.99 (0.908-1.144) **% of rate change:** -7.338 **Trend:** UNCERTAIN







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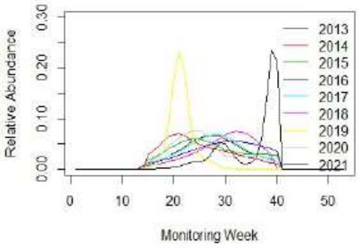
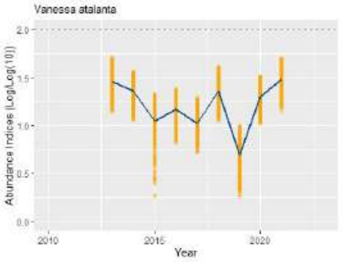
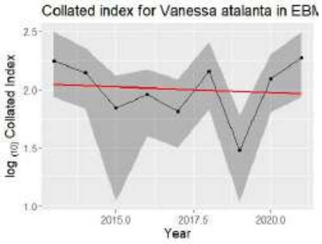
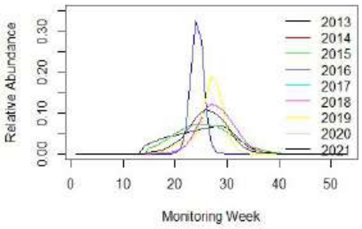
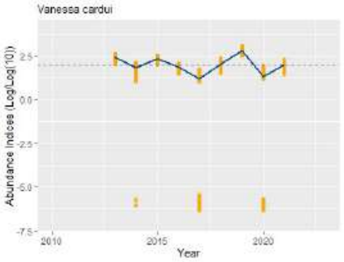
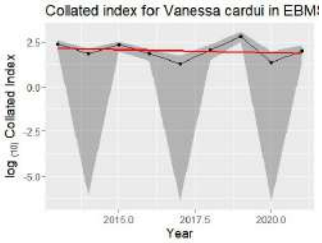
<tr><td colspan="3"><i>Vanessa atalanta</i> Flight curve: 9 years. Univoltine (summer) + migrants (spring, late summer) Date period: 2013-2021 N_Boot_Lt: 500 Rate of change: 0.978 (0.912-1.094)
% of rate change: -16.248 Trend: UNCERTAIN</td></tr>
<tr><td> </td><td> </td><td> </td></tr>
<tr><td colspan="3"><i>Vanessa cardui</i> Flight curve: 6 years. Univoltine (summer) + migrants (spring, late summer) Date period: 2013-2021 N_Boot_Lt: 500 Rate of change: 0.927 (0.366-2.271)
% of rate change: -45.175 Trend: UNCERTAIN</td></tr>
<tr><td> </td><td> </td><td> </td></tr>
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Chapter 4: Climate and topography as key drivers of butterfly diversity in a South European mountain range

Mountain clouded yellow (*Colias phicomone*) mating at Collado de Moñetas (Picos de Europa). Photo: Amparo Mora.

4.1 ABSTRACT

Mountains occupy around 25% of Earth's land but they hold disproportionate amounts of biodiversity. Elevation gradients encompass changes in temperature and humidity as well as in air pressure and UV exposure. As a result of both contemporary and past environmental drivers, spatial variation of diversity along elevation gradients can show different patterns. Determining those drivers is particularly relevant in a context of global change and global biodiversity decline. Here, we explored the patterns of butterfly diversity along elevation in a Southwestern European mountain range (Picos de Europa, Northwest Spain) and identified the environmental drivers of those patterns, and secondly, we investigated how diversity had changed over the last 14 years (2009-2023). The pattern of butterfly diversity versus elevation showed a cubic relationship peaking twice, at lower (150 m) and intermediate elevations (1500 m). The results showed that butterfly diversity was positively affected by near-surface relative humidity and distance to the coast, which is a surrogate for continentality. Species richness and Shannon diversity decreased significantly over the last 14 years, while Simpson diversity did not change, suggesting an ongoing faunal homogenization in the area, likely driven by climate change and land abandonment. Several lines of further research emerged from our study.

Keywords: mountain biodiversity, South European mountain ranges, butterfly diversity, elevation gradient, water-energy balances, continentality, relative humidity, faunal homogenization

4.2 INTRODUCTION

Mountains occupy around 25% of Earth's land but they hold disproportionate amounts of biodiversity: 87% of the world's species of amphibians, birds and mammals (Rahbek *et al*., 2019; Myers *et al*., 2000). Elevation gradients encompass changes in temperature and humidity as well as in air pressure and UV exposure. Moreover, differently orientated slopes receive different amounts of energy. This variety in climatic and physical attributes often results in a mosaic of different types of habitats in close proximity to each other in mountainous regions. In addition to the effect of current climate, historical climate change also drives biodiversity patterns. Mountains have had a crucial role as biodiversity refugia under climatic oscillations (Rahbek *et al*., 2019; Coelho *et al*., 2023; Dennis & Schmitt, 2009). As a result of both contemporary and past environmental drivers, spatial variation of diversity along elevation gradients shows a variety of patterns; decreasing species richness with increasing elevation and mid-elevation peak of species richness are the most commonly reported patterns (Rahbek, 1995). These patterns may be the result of differential contributions of environmental drivers depending on the geographic location of the mountain range, extent and topographical complexity (Hawkins *et al*., 2003b, Rahbek, 1995, Rahbek *et al*., 2019). Determining the main drivers of mountain biodiversity is particularly relevant in a context of global change (Brondizio *et al*., 2019) and global biodiversity decline (Wagner, 2020), as this may give us important clues to help conservation management and to make realistic projections into the future.

It is now well established that species diversity is often strongly correlated with climatic conditions, namely temperature, water availability and resulting ecosystem productivity (Hillebrand, 2004; Rohde, 1999; Bohdalková *et al*., 2021). At the global scale, Coehlo *et al*. (2023) have recently shown that climate and its geographical configuration and extension can explain as much as 90% of the variation in global species richness. For insects, and particularly butterflies, previous studies have explained species richness in mountains in the light of climate and topography (Gutiérrez & Menéndez, 1995, 2007; Stefanescu *et al*., 2004, 2011a,b; Romo *et al*., 2007; Illán *et al*., 2010; Pulido-Pastor *et al*., 2018), plant diversity (Gutiérrez & Menéndez, 1995, 2007; Hawkins & Porter, 2003a), heterogeneity of habitats (Janisová *et al*., 2014) and human-induced factors, such as traditional management by grazing or mowing (Dover *et al*., 2010b; Uchida & Ushimaru, 2014; Bonari *et al*., 2017; Trappe *et al*., 2017; Mora et al., 2022, 2023).

While the role of individual factors in driving species diversity is well established, an integrative approach which takes into account the interactions of topography with climate is lacking for many regions. Particularly, adiabatic lapse rates of air moving along slopes in mountains (Brun *et al.*, 2022; Díaz, 1996), which result in horizontal precipitation, mist, strong warm leeward winds, thermal inversions, cool air pools and other remarkable effects (Iglesias *et al*., 2017) are not usually considered in relation to biodiversity patterns (but see Chan *et al*., 2024). Neither is continentality, the influence of land masses on the climate, which results in lower cloudiness with increasing distances from the sea, and has been shown to have a positive effect on treeline elevation, likely by ameliorating thermal growing conditions at high elevations via reduced atmospheric absorption of solar radiation by clouds, air moisture or aerosols (Kienle *et al.*, 2023). Degree of continentality has been shown to positively relate to flying insect diversity in protected areas in Germany (Mühlethaler *et al.*, 2024) and to global patterns and drivers of bee distribution (Orr *et al.*, 2021).

In addition, while landscape composition and configuration have been extensively related to butterfly community dynamics at the local scale (Perovic *et al*., 2015; Seibold *et al*., 2019; Gámez-Virués *et al*., 2015; Dainese *et al*., 2017; Öckinger *et al*., 2012; Janisová *et al*., 2014), they have rarely been used as explanatory factors for diversity patterns at a regional scale (but see Bergman *et al*., 2004). Landscape heterogeneity can moderate the effects of local disturbances and influence species persistence, providing a diversity of habitat patches with different disturbance dynamics and encouraging spillover of organisms between complementary resources (van Halder *et al*., 2011; Tscharnke *et al*., 2012; Janisová *et al*., 2014). Movements of species between landscape elements may ensure community resilience, through the capacity to reorganise after disturbance in changing environments (Tscharnke *et al*., 2007). Links between landscape ecology and broader scale biodiversity patterns are still underexplored (Teng *et al*., 2020).

Human influence on European landscapes dates back for millennia. In Southern Europe, the components and dynamics of current biodiversity cannot be understood without taking into account the history of human induced changes, resulting in highly diverse cultural landscapes (Blondel, 2006; Pedroli *et al*., 2006). In the domain of temperate forests, human action by cattle grazing, mowing and coppicing has created diverse and heterogeneous landscapes: mosaics of forest patches intersected with seminatural grasslands (hay meadows or pastures). Nowadays, the abandonment of traditional land uses is giving rise to a succession towards forest habitats (Poschlod *et al*., 2005; Ubach *et al*., 2020; Mora *et al*., 2022). The effect of the disappearance of human disturbances on biodiversity after land abandonment is currently under debate (Daskalova & Kamp, 2023; Sartorello *et al*., 2020; Crawford *et al*., 2022), with long term studies in mountain sites still lacking.

Here, we explore the patterns of butterfly diversity in a Southwestern European mountain range (Picos de Europa, Northwest Spain) taking into account the influence of altitude on climatic conditions (temperature lapse rates), continentality and landscape configuration. Picos de Europa is a very important area for butterflies (Romo *et al*., 2007; Van Swaay & Warren, 2006), holding 60% of all Ibero-Balearic species (García-Barros *et al*., 2013) and 28% of all European species (Van Swaay *et al*., 2010), including several rare species such as *Lopinga achine, Phengaris nausithous, Erebia palarica, Parnassius apollo* and *Lycaena helle*. Our main aim is to assess how butterfly diversity varies with elevation across the mountain range and to disentangle the drivers of such diversity patterns. We hypothesise that:

1. Butterfly diversity will vary with elevation, showing a peak at middle elevations as has been shown in other studies in Iberian mountains (Wilson *et al*., 2007; Barea-Azcón *et al*., 2023; Álvarez *et al*., 2024).
2. Climate and topography will be major factors determining butterfly diversity.
3. Higher landscape heterogeneity will determine higher levels of butterfly diversity.
4. Human traditional land-use would have enhanced butterfly diversity.

Additionally, we investigate how butterfly diversity has changed in the last 14 years (2009-2023, our data period) and provide recommendations for future research.

4.3 METHODS

4.3.1 Study area

The study was carried out in the Picos de Europa National Park (PNPE), which is a mountain range, approximately 30 km x 20 km in area, running east to west 20 km inland from the northern coast of Spain (centred on 43°15’ N, 5°00’W) (Fig. 4.1). Due to its geographic location, it receives Atlantic influences from the ocean on its northern slopes and Mediterranean influences on its eastern and southern slopes. The mountain range has been traditionally managed for centuries by a combination of livestock grazing, mowing and coppicing resulting in a mosaic of habitats.

PNPE presents a temperate bioclimate and its mediterranean variant (in less than 5% of the territory). All the territory has an oceanic character, but southern slopes have less humidity as they are farther from the coast and the mountain barrier prevents the wet air coming from the sea to reach those southern slopes. In the northern, more oceanic slopes, there is a substantial increase in rainfall and combined with lower temperatures resulting in a altitudinal decrease of the treeline (Jiménez-Alfaro *et al*., 2010). Average annual temperatures range from 2.5 ºC at highest elevations to 15 ºC in the gorges which divide the mountain massifs (Ninyerola *et al.*, 2005). Average rainfall is between 1100 and 1300 mm/year (Ninyerola *et al.*, 2005).

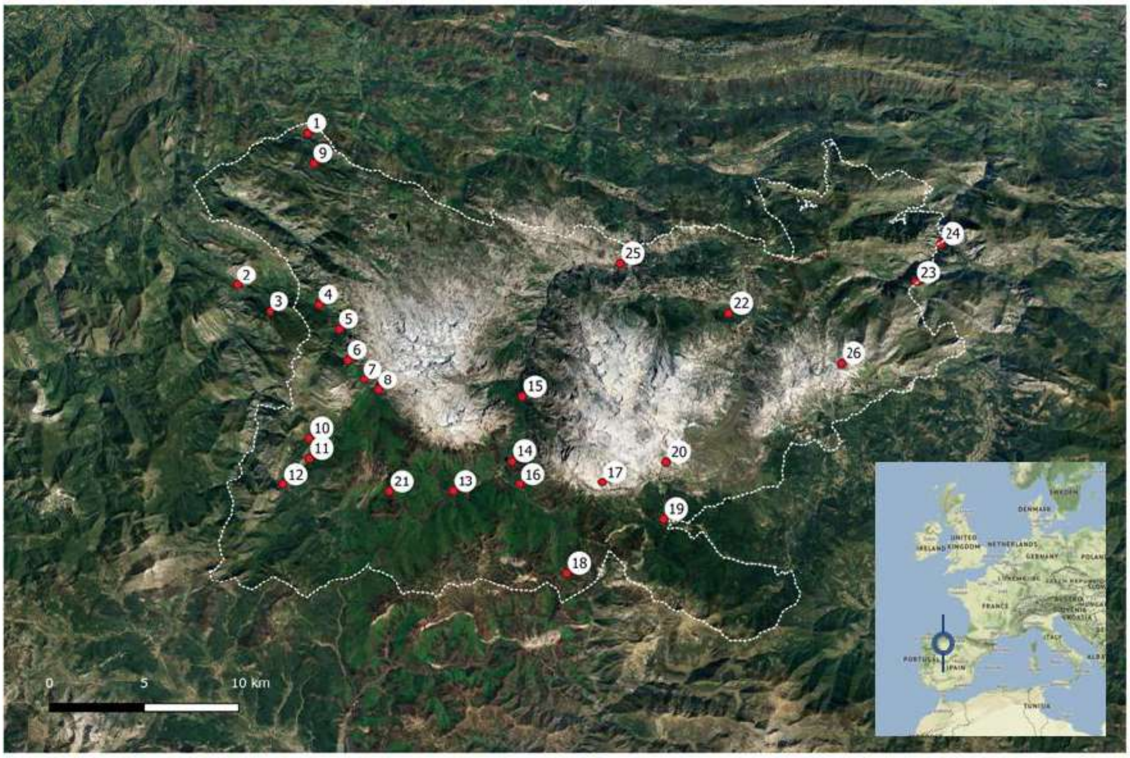


Fig. 4.1 Aerial photo of the study area, Picos de Europa National Park, showing the location of the 26 sites where butterfly data were collected (numbers as in Table S1). Inset map shows the location of the study area in Europe.

Based on the on the climatic stratification of the environment in Europe proposed by Metzger *et al*. (2005), Picos de Europa National Park covers three different climatic strata: Lusitanian climate at its northern slopes; alpine south climate at its highest elevations; and Mediterranean mountain climate at its southern slopes.

Due to the wide altitudinal range (70-2648 m), a high diversity of habitats is present in the study region. As we climb up the mountains, we find extensive patches of temperate deciduous forests (mixed, beech and oak forests), natural and seminatural grasslands, hazel thickets, bramble thickets*,* *Genista* and *Cytisus* scrub, Atlantic heaths, *Genista* cushion type scrub, rocky and high mountain vegetation, as well as riverine, bog and lake vegetation (Alonso *et al*., 2011).

A traditional land use system has been run in this territory for centuries, with pasturing (mainly sheep and goats in the past, substituted by cattle and horses at present), hay-making and woodland coppicing as the main human activities. Since the 1940s, sequential waves of rural depopulation have taken place with emigration to urban areas in the 1960s due to industrial development and poor living conditions in rural areas, resulting in a progressive abandonment of traditional land management. Currently, around 80% of the population in rural areas in the region works in tourism and services, 10% in agriculture and 10% in building and industrial activities (Rescia *et al.*, 2008; Sadei, 2024).

4.3.2 Butterfly data

Butterfly data for this study comes from different sources with a total of 26 sites: 12 sites are from the National Park monitoring network, which also contribute to the National Butterfly Monitoring Scheme (BMS Spain), and 14 sites in which butterflies were surveyed in different years for other purposes. Data series ranged from 3 to 11 years, depending on the site (Table S4.1, Figure 4.1) during the period 2009-2023. Monitoring sites cover an altitudinal range of 150-2000 m and represent most of biotopes present in the study region, including beech, oak and mixed deciduous forests, seminatural grasslands (hay meadows and pastures), alpine scrub and grasslands (see Table S4.2 for the main habitat types and plant communities represented in the study area). The dataset contains 96% of all butterfly species recorded in the National Park.

For the 12 sites of the National Park monitoring network, adult butterflies were counted along fixed transect routes using the standard BMS methodology (Pollard & Yates, 1993). Surveys took place every 10 days from May to September, which covers the full flight season of butterflies in the region (a total of 15 visits each year). In four of the transects (Pandetrave, Liordes, Lloroza and Baenu), we applied a reduced effort scheme with five to six surveys per year (Roy *et al.*, 2007, 2015), because they were placed at high mountain locations with a shorter active period, and in one case (Baenu) because the transect was set up only to cover the flying period of the endangered species *Lopinga achine* between June and July. Recording routes were 1-2 km in length and were divided into several sections corresponding to different habitats. Throughout the study period, a total of 132 butterfly species were recorded on these sites (see the complete list in Table S4.3, nomenclature follows Wiemers *et al.*, 2018).

BMS standard methodology was also used for the additional 14 sites, but the number of visits varied depending of the site (ranging 3-14 visits per year, Table S4.1). Two new butterfly species were added to the ones already recorded on the National Park monitoring sites (134 species in total).

4.3.3 Response variables: butterfly species richness and diversity

To measure butterfly diversity at each site and year we calculated Hill numbers: Hill Species Richness, Hill Shannon index and Hill Simpson index (Chao *et al.*, 2014), with samples rarefied by equal coverage (Chao & Jost, 2012). We used the function “estimateD” from package iNEXT (Hsieh *et al.*, 2022), fixing the parameters “base” as coverage and “level” for a sample coverage of 0.90. We also rarefied samples by equal number of individuals using the function “estimateD” from package iNEXT, fixing the parameters “base” as size and “level” as 307 individuals, which was the median of abundance per year among all sites. A Spearman Rank test revealed a correlation of 0.99 between diversity estimates using the two rarefaction methods, though confidence intervals were narrower for the coverage method, so only these data are presented here.

4.3.4 Environmental drivers: climate and landscape variables

Four groups of environmental variables that potentially affect butterfly diversity were used as explanatory variables:

(1) **Climate variables**. We used the dataset CHELSA 2.1 (Climatologies at high resolution for the Earth’s land surface areas: Karger *et al.*, 2017) to obtain monthly maximum, mean and minimum temperatures, monthly precipitation and monthly near-surface relative humidity over the period 2011-2015 for the whole of PNPE. We used these data to calculate the mean, maximum and minimum annual temperature, total annual precipitation, total precipitation of the driest month, total precipitation of the wettest month and mean annual near-surface relative humidity. The values for the 1 km squares that contained the transect centroids were used for the analyses.

Continentality was assessed by the distance of the transect centroids to the nearest coastline as in Kienle *et al.* (2023). These distances were extracted from Spanish National Topographic Maps (1:25.000) by the National Geographic Institute (www.ign.es).

(2) **Topography variables**: Elevation of sampling sites was extracted from Spanish National Topographic Maps (1:25.000) by the National Geographic Institute (www.ign.es).

(3) **Landscape variables**: A map of the PENP at 1:10.000 scale containing vegetation cover features was used to extract landscape variables (Alonso *et al.*, 2013). Vegetation was classified in 47 vegetation type categories and in four general habitat categories (grasslands, forest, scrub and other) (Table S4.2 for details). For each site, we drew a circular landscape of 500 m radius and extracted vegetation data from the vegetation

map. We did not examine larger radii because of the high patch heterogeneity in this mountain landscape and because some study sites were close in proximity (minimum distance apart of 1 km). The Shannon diversity index of vegetation types (based on the 47 categories) was used to represent compositional landscape heterogeneity. The average patch size inside the circular landscapes of 500 m radius was used to represent configurational landscape heterogeneity (Perovic *et al.*, 2015; Gámez-Virués *et al.*, 2015). For each landscape, the percentages of the three main habitat categories (grassland, forest and scrub) and the percentage of open habitat (which included grassland and scrub not exceeding 1.5 m in height) were also calculated. Landscape metrics were calculated using gvSIG2.5.1 (www.gvsig.com).

(4) **Land-use variables**: For each landscape, the percentage of seminatural grasslands used for mowing or pasturing was calculated, as a proxy for the extent of human traditional management.

4.3.5 Data analyses

All statistical analyses were performed using the software RStudio for Statistical Computing (version 2023.09.1 build 494; RStudio Development Team 2023). Butterfly diversity was calculated per site using Hill numbers (species richness, Shannon and Simpson diversity) and square-root transformed to follow a Gaussian error structure. The effect of elevation on the three butterfly diversity response variables was analysed using linear models incorporating linear, quadratic and cubic effects of elevation.

Generalized linear mixed models (GLMMs) were used to assess the response of butterfly diversity to the different environmental variables. Due to the high number of environmental variables and collinearity among them, two separate Principal Component Analyses (PCA) were performed, one for climatic variables and another for landscape variables. The climate PCA included six climatic variables: mean, maximum and minimum annual temperature, total annual precipitation, total precipitation of the driest month and total precipitation of the wettest month. Near surface relative humidity was not included in the climate PCA analysis as it is a composite variable that integrates climate and topography (it was calculated using atmospheric relative humidity, surface elevation and integrating in the formulas the orographic effects of wet and dry adiabatic lapse rates, see Brun *et al.*, 2022). The landscape PCA included five habitat variables (% forest, % grassland, % scrub, % open habitat, % seminatural grassland). Landscape heterogeneity in habitat composition and in habitat configuration were not included in the landscape PCA as they are composite variables that define diversity and configuration of habitats rather than individual habitat types. The PCA axes extracted from each analysis were used as fixed factors in the model. These analyses were performed using function “prcomp” in R.

A global Generalized Linear Mixed Model (GLMM) was first defined including the following fixed factors: Distance to the coast, near surface relative humidity, PC1_climate, landscape heterogeneity in composition, landscape heterogeneity in configuration, PC1_landscape and PC2_landscape; with a random effect of the year (see Table S4.4). Multicollinearity was tested by estimating the Variation Inflation Factor (VIF) between variables, using the function vif from package “car” (Fox & Weisberg, 2019) in R. Variables with an estimated VIF value above five were discarded from the analysis (Zuur et al. 2009). All the remaining variables were standardized before modelling through division by their standard deviation using the R base function “scale”. Modelling was perfomed using R’s “lme4” package (Bates *et al.*, 2015). Model selection was performed using an Information Criteria approach with the Akaike Information Criteria corrected for small samples (AICc). All produced models were ranked according to their ΔAICc (difference between each model AICc and the smaller AICc value), with models presenting ΔAICc < 2 being retained as the best models. Model selection procedures were implemented in R using the “MuMIn” package (Barton, 2022). Best models validation was tested by residual analysis using the R package “DHARMa” (Hartig, 2022) for Gaussian models.

The effect of time (years) on butterfly diversity was analysed using linear models. Analyses were performed with “lme4” package in R (Bates *et al.*, 2015).

4.4 RESULTS

In total, 72,390 individuals belonging to 134 butterfly species (Table S4.3) were recorded across the 26 sites surveyed in the period 2009-2023. Species accumulation curves for each site showed this to be a comprehensive representation of the butterfly community in the study area (Figure S4.2). The species recorded represented 98% of species present in the Picos de Europa National Park. The observed mean species richness per site was 40 species (±1.5), ranging between 12 species at Ándara in 2022, a high mountain location at 1950 m of altitude, and 75 species at Morrena de Pido in 2016, a heterogeneous landscape at 1050 m of altitude which includes an Atlantic mosaic of hay meadows, *Genista* scrub and oak forests.

4.4.1 Patterns of butterfly diversity along the elevation gradient

We found that butterfly species richness, Shannon diversity and Simpson diversity followed a cubic relationship with elevation (Fig. 4.2). Butterfly diversity was higher at the very low altitudes (150 m), corresponding to river gorges with Mediterranean influence, then declined until 650 m in altitude, where it started to rise again to reach its maximum value at around 1500 m in altitude, declining again to its minimum value at the highest altitudes (1950 m).

The cubic effect of elevation was highly significant for all diversity metrics and explained 36% of data variance in Species richness ($F_{3,22}$ =5.696, p=0.004, adjusted R^2=0.36) and 38% for both Shannon diversity ($F_{3,22}$ =6.139, p=0.003, adjusted R^2=0.38) and Simpson diversity ($F_{3,22}$=6.279, p=0.003, adjusted R^2=0.38). The quadratic or linear effects of elevation were not significant for any diversity metrics and explained only 3.5-6.4% of data variance in Species richness, 0.5-2.4% for Shannon diversity and 1.4-10% for Simpson diversity.

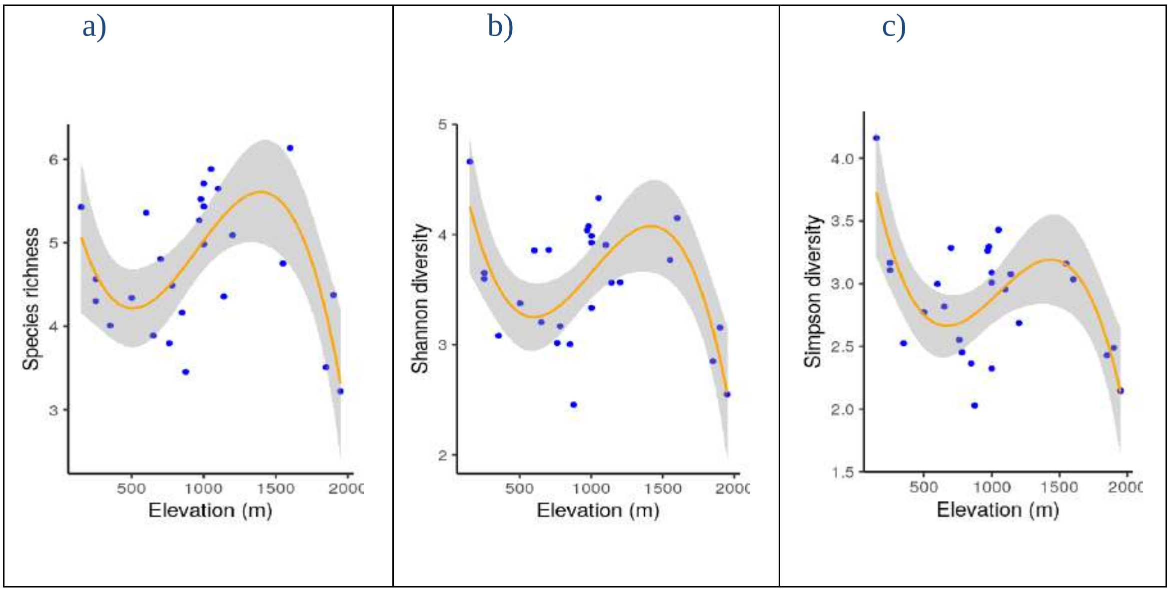


Fig. 4.2 Butterfly diversity versus elevation: a) Species richness, b) Shannon diversity and c) Simpson diversity.

4.4.2 Environmental drivers of butterfly diversity

We used the first two axes from the climate PCA to define a two-dimensional orthogonal space for climatic variables (Fig. S4.1a). First axis, named as "PC1_climate", explained 80% of the data variance and it was negatively correlated with temperature variables, whereas positively values correlated with precipitation variables (see S5.4a for coefficients of each variable on each principal component). Second axis, named PC2_climate, was used graphically but was discarded for further analysis because its eigenvalue was 1.04, the level expected for the null model if all variables were equally contributing to the principal component (Table S4.4a).

We also used the first two axes of the landscape PCA to define a two-dimensional orthogonal space for habitat variables (Fig. S4.1b). First axis, named “PC1_landscape”, separated closed (negative values) versus open habitat (positive values) and explained 58% of data variation. Second axis, named “PC2_landscape”, separated two types of open habitat: grassland (positive values) versus scrub (negative values) and explained 27% of data variation (see Table S4.4b for coefficients of each variable on each principal component).

The minimum adequate model to explain Hill species richness (Table S4.5a) included distance to coast (coef.= 0.459, t=-6.841, p=7.75e^{-10}, df=94.455), near-surface relative humidity (coef.= 0.2711, T=8.326, P=4.46e^{-13}, df=100.171), landscape heterogeneity in composition (coef.= 0.194, t=2.978, p=0.003, df=93.865) and pc1_lanscape (coef.=0.184, t=2.398, p=0.018, df=96.648) as significant terms (Fig. 4.3 a, c, f, j). Hill Shannon diversity (Table S4.5b) was also explained by distance to coast (coef.= 0.192, t=3.498, p=0.0007, df=93.064), near-surface relative humidity (coef.= 0.530, t=7.553, p=2.14e^{-11}, df=99.112), landscape heterogeneity in composition (coef.= 0.121, t=2.276, p=0.0251, df=92.431) and pc1_landscape (coef.=0.242, t=3.847, p=0.00021, df=95.549) (Fig. 4.3 b, d, g, j). Finally, Hill Simpson diversity (Table S4.5c) was explained by near-surface relative humidity (coef.=0.397, t=6.452, p=3.96e^{-09}, df=100.142), landscape heterogeneity in configuration (coef.=-0.170, t=-2.931, p=0.004, df=91.517) and pc1_landscape (coef.=0.178, t=2.662, p=0.009, df=93.435) (Fig. 4.3 c, e, h, k).

Table 4.1. Models for explaining Hill Species Richness, Hill Shannon Index and Hill Simpson Index by environmental variables selected according to the model's AIC and ΔAICc. The best model for each response variable is highlighted in blue.

Model	**df**	**AICc**	**ΔAICc**	**AICc weight**
Response variable: Hill Species Richness				
Distance to coast + relative humidity + landscape heterogeneity in composition + pc1_landscape	7	238.0	00	0.799
Distance to coast + relative humidity + landscape heterogeneity in composition + landscape heterogeneity in configuration + pc1_landscape	8	240.9	2.89	0.189
Distance to coast + relative humidity + landscape heterogeneity in composition + landscape heterogeneity in configuration + pc1_landscape + pc2_landscape	9	246.4	8.33	0.012
Response variable: Hill Shannon index				
Distance to coast + relative humidity + landscape heterogeneity in composition + pc1_landscape	7	199.0	0.00	0.893
Distance to coast + relative humidity + landscape heterogeneity in composition + landscape heterogeneity in configuration + pc1_landscape	8	203.3	4.33	0.103
Distance to coast + relative humidity + landscape heterogeneity in composition + landscape heterogeneity in configuration + pc1_landscape + pc2_landscape	9	209.6	10.56	0.005
Response variable: Hill Simpson index				
Relative humidity + landscape heterogeneity in configuration + pc1_landscape	6	183.7	0.00	0.915
Distance to coast + relative humidity + landscape heterogeneity in configuration + pc1_landscape	7	188.5	4.85	0.081
Distance to coast + relative humidity + landscape heterogeneity in configuration + pc1_landscape + pc2_landscape	8	194.8	11.08	0.004
Distance to coast + relative humidity + landscape heterogeneity in composition + landscape heterogeneity in configuration + pc1_landscape + pc2_landscape	9	200.8	17.16	0.000
Random terms (all models): 1|Year				

When Urdón site, an outlier site with very high values of landscape heterogeneity in configuration, was removed from the analysis, variables landscape heterogeneity in composition, landscape heterogeneity in configuration and pc1 landscape (representing closed versus open habitats) were no longer significant in any of the best models (see Table S4.6).

In summary, species richness and Shannon diversity increased with increasing distance from the coast; all diversity metrics increased with increasing near-surface relative humidity; and landscape effects (positive effects of a greater heterogeneity in composition or configuration and positive effects of a greater proportion of open habitats on all diversity metrics) didn’t held when the outlier site Urdón was removed from the analysis.

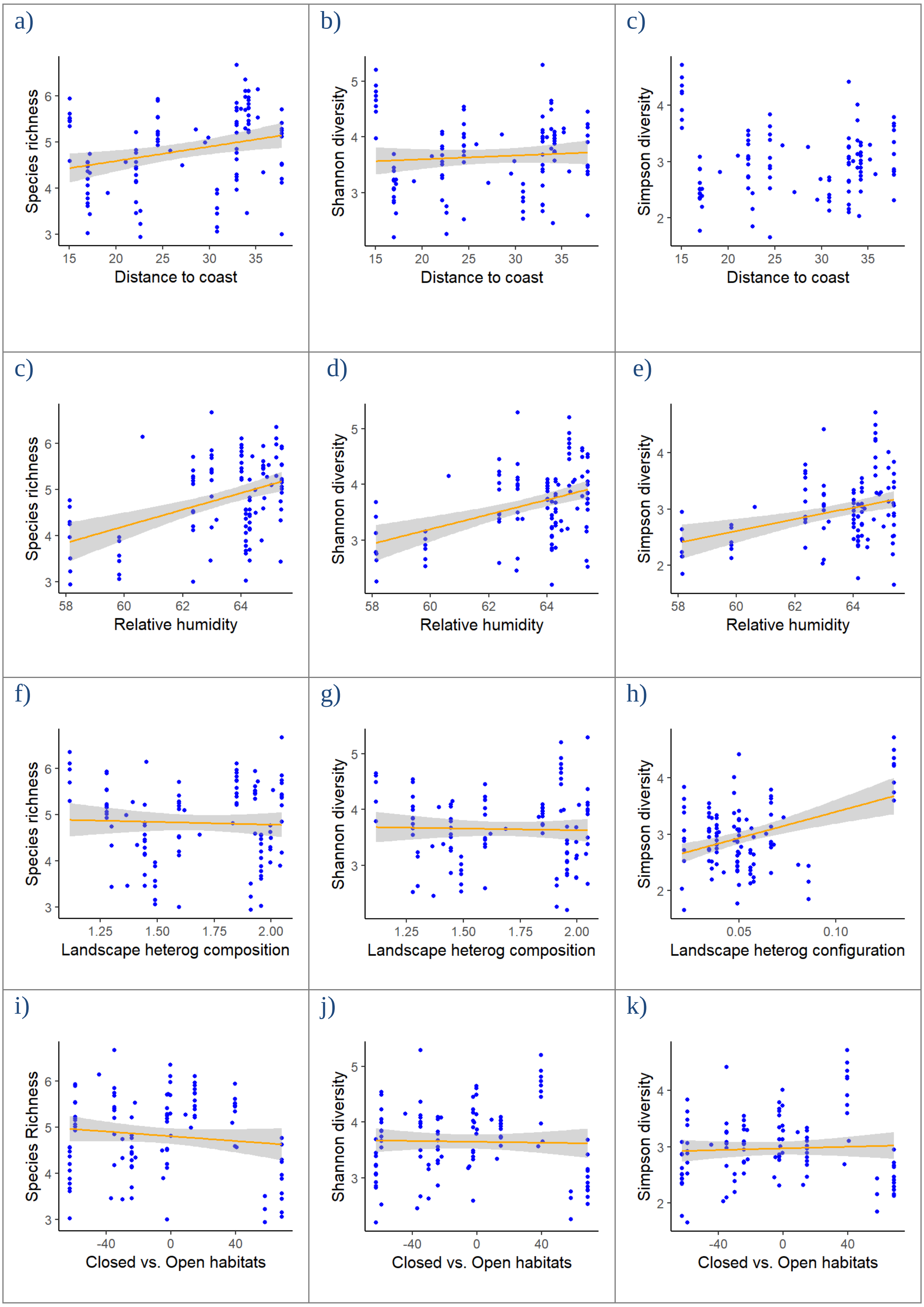


Fig. 4.3 Butterfly diversity versus main butterfly drivers in the study area: distance to coast (in km), relative humidity (in %), landscape heterogeneity in composition (calculated as the Shannon index of vegetation types), landscape heterogeneity in configuration (calculated as the inverse of average patch size) and pc1_landscape (representing closed vs. open habitats). a) Species richness versus distance to coast; b) Shannon diversity versus distance to coast;

c) Species richness versus relative humidity; d) Shannon diversity versus relative humidity; e) Simpson diversity versus relative humidity; f) Species richness versus landscape heterogeneity in composition; g) Shannon diversity versus landscape heterogeneity in composition; h) Simpson diversity versus landscape heterogeneity in configuration; i) Species richness versus pc1_landscape (representing open vs. closed habitats); j) Shannon diversity versus pc1_landscape; and k) Simpson diversity versus pc1_landscape.

4.4.3 Butterfly diversity changes over the last 14 years (2009-2023)

Butterfly species richness (Fig. 4.4a) and Shannon diversity (Fig. 4.4b) significantly declined over time (coef.= -0.059, $F_{1,111}$=7.61, p=0.006 and coef.= -0.035, $F_{1,111}$=4.636, p=0.033, respectively), while Simpson diversity (Fig. 4.4c) did not change (coef.=-0.018 , $F_{1,111}$=1.533, p=0.218).

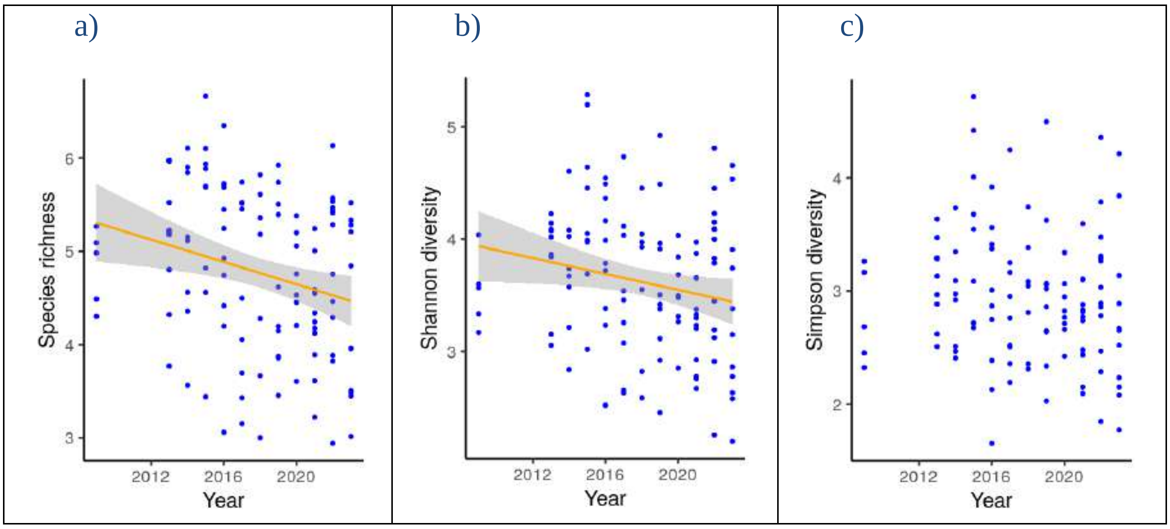


Fig. 4.4 Changes in butterfly diversity: a) Species richness, b) Shannon diversity and c) Simpson diversity over time (2009-2023).

4.5 DISCUSSION

The aim of this study was to assess butterfly diversity patterns along elevation gradients and to identify the environmental drivers of those patterns in the Picos de Europa National Park and secondly, to investigate how diversity has changed over the last 14 years (2009-2023). The pattern of butterfly diversity versus elevation showed a cubic relationship peaking twice, at lower (150 m) and intermediate elevations (1500 m). The results showed that butterfly diversity is positively affected by near-surface relative humidity and by continentality. Species richness and Shannon diversity decreased significantly over the last 14 years, while Simpson diversity did not change. Adding complexity to our expectations of a mid-elevation diversity peak, we reported two peaks in butterfly diversity with elevation, at lower (150 m) and intermediate altitudes (1500 m). The second diversity peak we have observed likely corresponds with that reported in other studies at intermediate altitudes (around 1500 m) (Álvarez *et al*., 2024; Wilson *et al*., 2007; Barea-Azcón *et al*., 2023), and may reflect the transition where cold temperatures start to be the primary limiting factor for organisms instead of water availability. However, the first peak in diversity at lower altitudes, often located in deep gorges that are warm and free from the effects of winter frost (sample sites Ginés, Ceneya, Urdón and Cares), would likely result from these areas acting as Tertiary refugia for tropical and Quaternary refugia for Mediterranean fauna and flora in the area (for example tree species like *Quercus ilex, Laurus nobilis* or *Arbutus unedo*; ferns like *Culcita macrocarpa* or *Woodwardia radicans*, amphibians like *Chioglossa lusitanica* or invertebrates as *Elona quimperiana)*. Typically, we find Mediterranean butterfly species like *Gonepteryx cleopatra* or *Laesopis roboris* in these gorges. Therefore, our data confirm that present climate is not enough to explain mountain diversity (Coehlo *et al*., 2023) and highlight the important role played by mountains as biodiversity refugia under climate oscillations (Rahbek *et al*., 2019).

The influence of climate on biodiversity has been recognised since the origin of biogeography (von Humboldt, 1808). Recently, Coehlo *et al*. (2023) have shown that climate and its geographical configuration and extension can explain as much as 90% of the variation in global species richness. But the specific aspects of climate that best explain richness are still unresolved. In our study, we have found that near-surface relative humidity, a climatic variable representing water-energy dynamics (solar energy and water availability) appears to be a key driver of regional butterfly diversity (Hawkins & Porter, 2003a). This result is in line with previous studies on western Palearctic butterflies (Hawkins & Porter, 2003b), European dung beetles (Hortal *et al*., 2011) and European and North African dragonflies (Keil *et al*., 2008).

Near-surface relative humidity is defined as water pressure deficit in the air (actual water pressure in the air divided by maximum water pressure of air for that temperature) (Díaz, 1996). It is calculated taking into account orographic effects (Brun *et al*., 2022), and is a synthetic variable in which temperature and availability of water are integrated as a function of altitude and adiabatic lapse rates. Moist air rising on the winward side of an orographic barrier, potentially loses moisture and cools with a wet-adiabatic lapse rate, and sinking on its leeward side, usually warms with a higher dry-adiabatic lapse rate (Díaz, 1996) (Fig. 4.5).

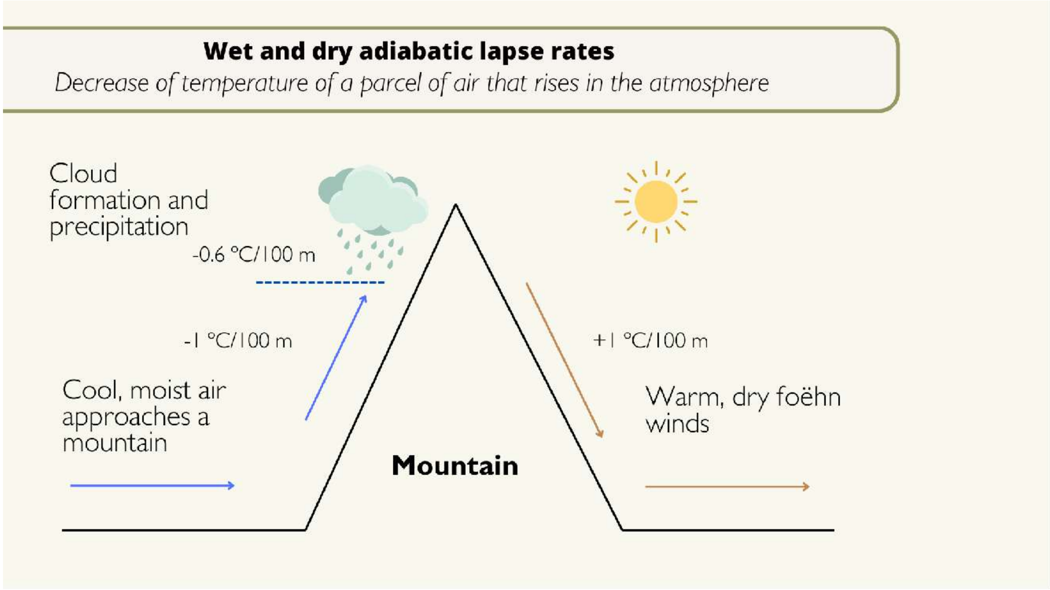


Fig. 4.5 When air rises on the winward side of an orographic barrier, it cools at a rate of 1ºC each 100 m of elevation (dry adiabatic lapse rate). If the air is moist, water condenses at a certain point and air cools at a lower rate of 0.6 ºC/100 m (wet adiabatic lapse rate), and sinks on the leeward side of the mountain, usually warming with a higher, dry-adiabatic lapse rate (1ºC/100 m). Based on: Oliver & Oliver (2018).

These effects are evident in our study region, in which the mountains form a parallel barrier to the coast, just 20 km from the sea (Cortesi *et al.*, 2014). It is likely that near-surface relative humidity operates both directly via physiological effects on butterflies and indirectly via effects on plant productivity (as it controls vapor pressure deficit for plants). For example, Bergman (2001) showed a 73% mortality of *Lopinga achine* eggs at 50% relative humidity while almost all eggs survived (97%) at higher relative humidity. However, Hawkins & Porter (2003b) suggest that plant productivity is the driving force of butterfly richness patterns in the Western Palearctic, given its strong link with evapotranspiration. Although the productivity hypothesis (Wright *et al.*, 1993; Huston, 1994; Mittelback *et al.*, 2001) could explain our results, we did not find a direct relationship between butterfly diversity and extent of seminatural grasslands (hay meadows), which are the most productive habitats in our study area.

As we have seen, the interaction between water and energy provides a good explanation for butterfly diversity patterns in our area, but we also found that distance to the coast as a measure of continentality contributes to butterfly diversity patterns. Continentality indicates the strength of the influence of land masses on the climate. We argue that it may influence positively butterfly diversity due to a decrease in cloudiness, leading to increased solar radiation in more continental locations and finally resulting in an increase of growing temperatures, as Kienle *et al.* (2023) showed for treelines in the Northern hemisphere. The same positive effect of continentality was found for flying insects across Germany in a gradient from northwest to southeast (Mühlethaler *et al.* 2024) and for global patterns of bee distribution (Orr *et al.* 2021).

Apart from climate, continentality and biogeographical history, butterfly diversity patterns in the region may also be affected by landscape variables such as land use and habitat heterogeneity. The idea that habitat diversity influences species diversity has been widely documented (Rosenzweig, 1995). We also found some evidence that open versus closed habitats could drive butterfly diversity in the Picos de Europa National Park, in line with many previous and recent studies (Kerr, 2001; Álvarez *et al*., 2024). Furthermore, the structural component of heterogeneity (landscape configuration measured as average patch size) showed a positive significant effect on Simpson butterfly diversity while heterogeneity in composition (measured as Shannon diversity of habitat types) showed a positive significant effect on Species richness and Shannon diversity. This result is similar to that reported by Álvarez *et al*. (2024) who found a positive relationship of butterfly species diversity with habitat heterogeneity, defining heterogeneity as the diversity of vegetation height classes (classification based on LIDAR data). Nevertheless, our results were not conclusive, as the positive relationship between butterfly diversity and landscape variables was influenced by an outlier site located in the easternmost part of the region and at low altitude. Future research is needed to assess if adding data from more sites with similarly higher landscape heterogeneity, rather than location, would confirm the pattern of a greater diversity with greater landscape heterogeneity. A diversity gradient, increasing from west to east, has already been shown for vascular plants in the area (Alonso *et al*., 2011).

Butterfly diversity was neither significantly explained by the percentage of seminatural grasslands, which is unexpected as we had hypothesised that traditionally managed grasslands, used for pasturing or hay making, would have promoted landscape heterogeneity by interspersing grassland patches (open habitat with relevant plants for butterflies) within what otherwise will be a relatively continuous forested landscape. Even if we could not find support for our predictions, we argue that this could be due to an extinction debt *(*Kuussaari *et al.* 2009, Figueiredo *et al.* 2019), with present butterfly diversity lagging behind the loss of grassland habitats, which have decreased by 70% in the last 60 years (García *et al*., 2018). Further research is needed to determine if current butterfly diversity in our region is better explained by historical rather than present seminatural grassland area and connectivity, as has been shown in other studies (Bommarco *et al*., 2014).

We have shown that water-energy balances (climate) and continentality drive butterfly diversity in the Picos de Europa National Park. We also provide evidence that species richness and Shannon diversity have decreased significantly over the last 14 years, while Simpson diversity did not change, suggesting that rare and specialist species (eg. *Melitaea deione, Hamearis lucina, Laeosopis roboris*) are disappearing while common species are thriving (eg. *Maniola jurtina, Melanargia galathea, Pieris rapae*), as Simpson's diversity is more sensitive to changes in common species than the other diversity measures. This likely reflects an ongoing process of butterfly fauna homogenization in the area, as reported in other European regions (Habel *et al*., 2022; Fox *et al*., 2023).

In conclusion, we have shown that the relationship between butterfly diversity and elevation in our study mountains follows a pattern of peaking twice, at lower (150 m) and intermediate elevations (1500 m). Butterfly diversity appears to be positively affected by near-surface relative humidity and continentality. Species richness and Shannon diversity decreased significantly over the last 14 years (2009-2023), while Simpson diversity did not change, suggesting an ongoing faunal homogenization in the area, likely driven by climate change and land abandonment (Mora *et al*., 2022, 2023). Several lines of further research emerged from our study. As we are living in a period of rapid global change and insect declines, it is critical that we understand what variables drive diversity and how organisms will respond when these variables change over time. As tackling climate change requires global approach, at the local scale, promoting landscape heterogeneity seems a sensible tool to conserve species as well as ecological processes. Pearce *et al*. (2023) suggest approaches aimed at restoring natural disturbance factors (such as large herbivores and fire) to restore European forest biomes because they directly increase habitat heterogeneity. Sound research together with ecological traditional knowledge and remarkable achievements made by some wilding experiences (Tree, 2018), could inspire us to find those much needed conservation approaches.

4.6 SUPPORTING INFORMATION

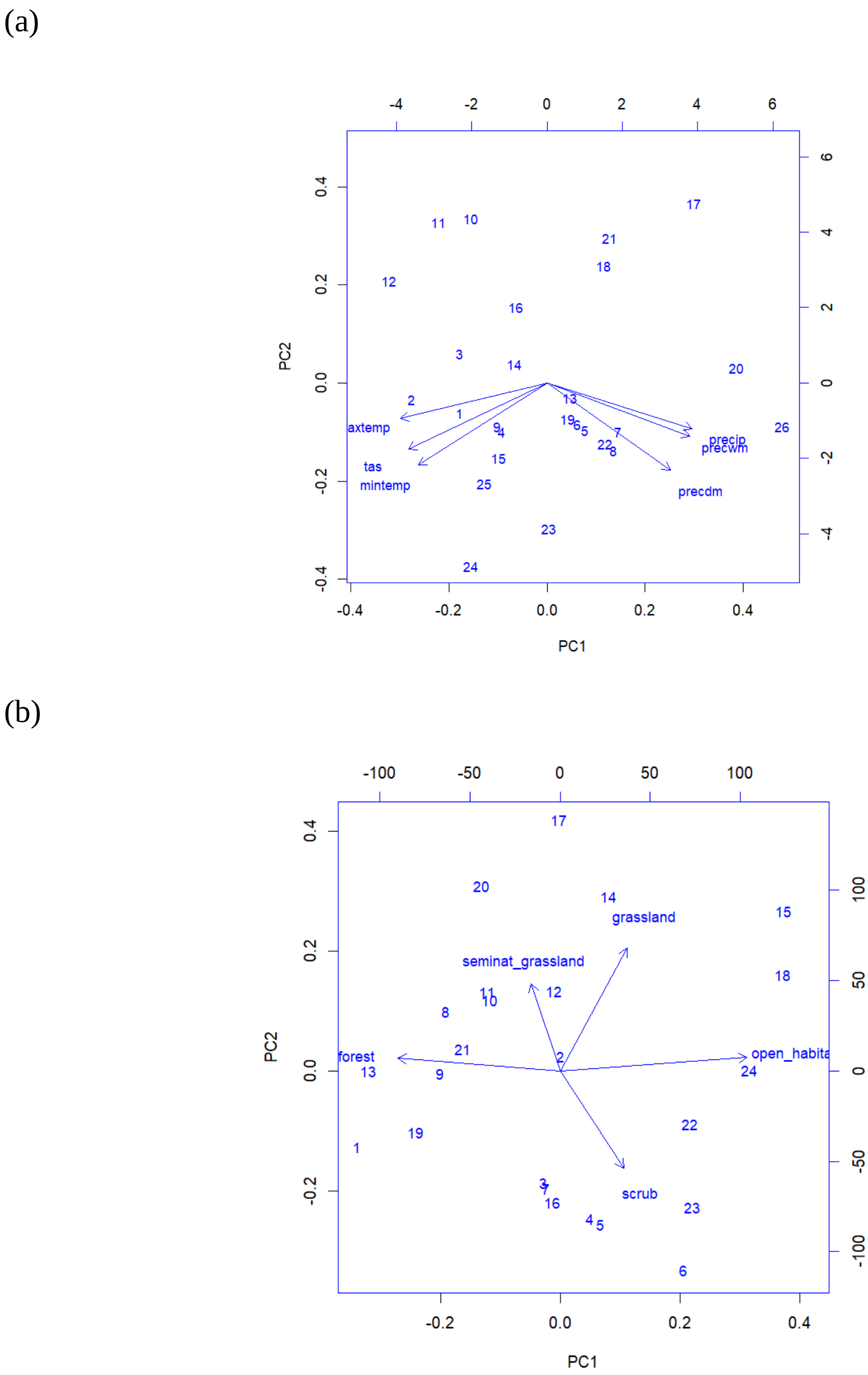
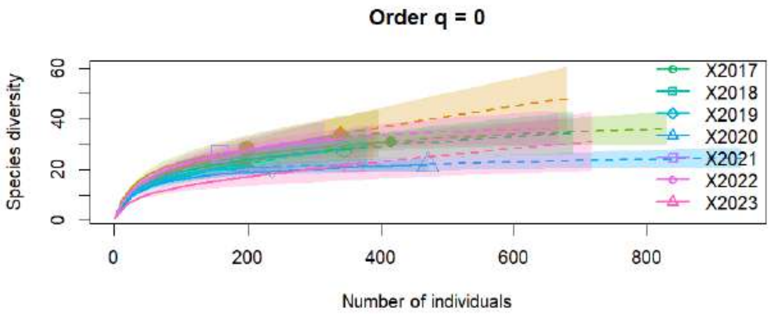
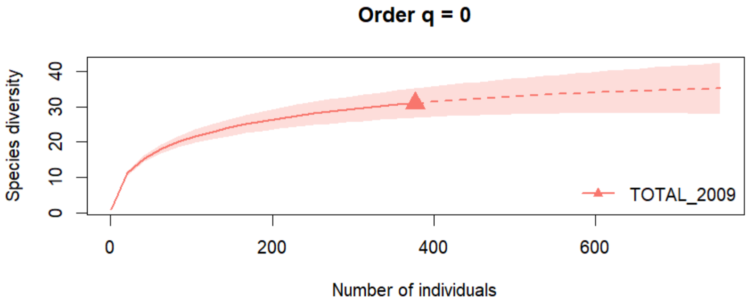


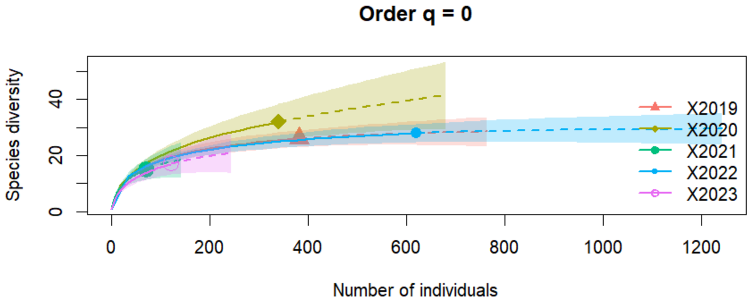
Fig. S4.1 Principal Component Analysis (PCA) for climate (a) and habitat (b) variables. The two first orthogonal axis are represented for each analysis. Climatic variables: mean annual temperature (tas), maximum annual temperature (maxtemp), minimum annual temperature (mintemp), annual total precipitation (precip), total precipitation of the wettest month (precwm), total precipitation of the driest month (precdm). Habitat variables: proportion of forest (forest), proportion of grassland (grassland), proportion of scrub (scrub), proportion of open habitat (open_habitat, including grassland and scrub not exceeding 1.5 m in height) and proportion of seminatural grassland used for mowing or pasturing (seminat_grassland).



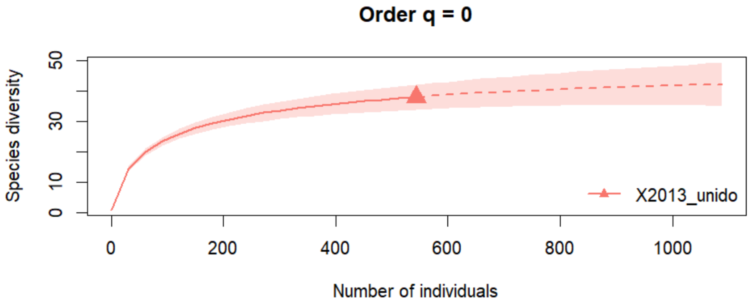
1. Ginés (mean nº individuals/year = 295, SE=31.32)



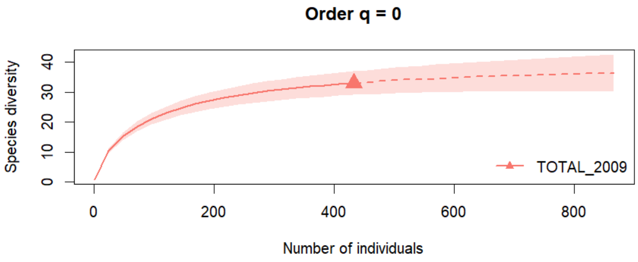
2. Ceneya (nº individuals in 2009 = 377)



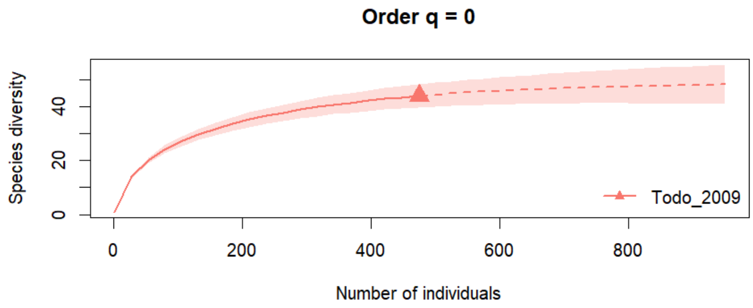
3. Baenu (mean nº individuals/year = 307, SE=98.80)



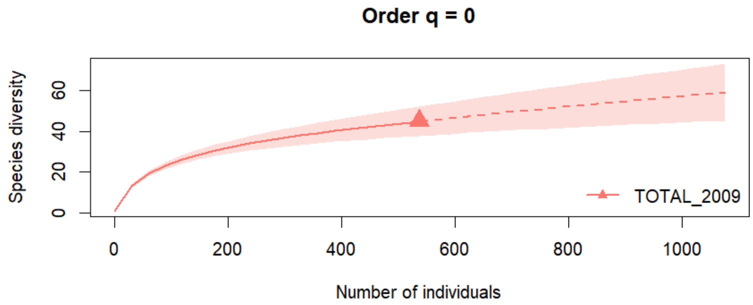
4. Angón (nº individuals in 2013 = 544)



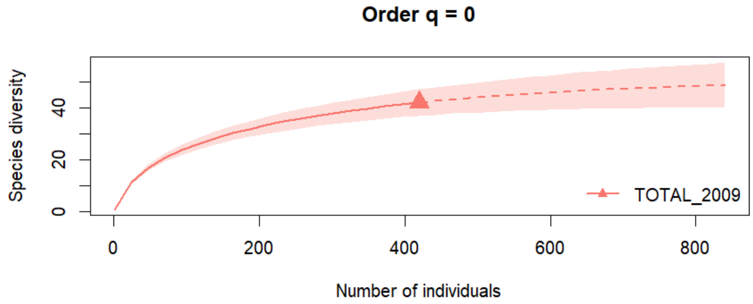
5. Fuente Prieta (nº individuals in 2009 = 115)



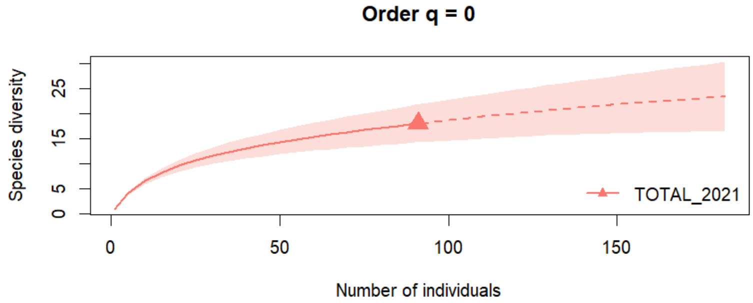
6. Camino a Carombo (nº individuals in 2009 = 166)



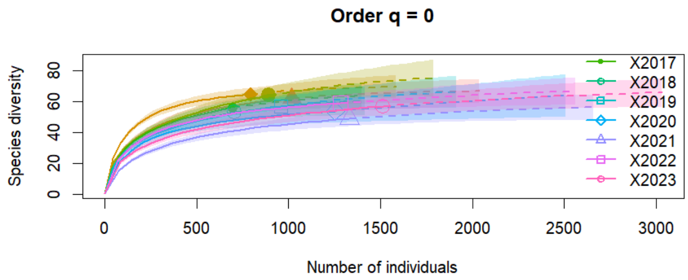
7. Dobraseca (nº individuals in 2009 = 538)



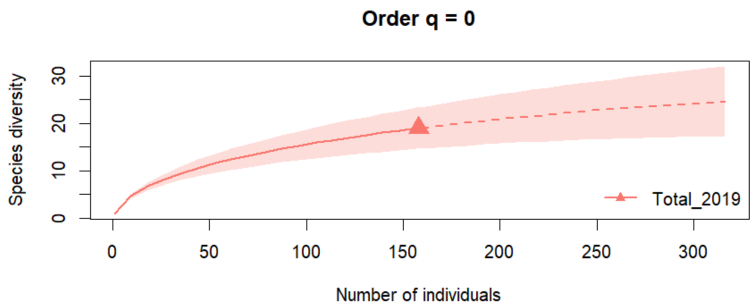
8. Carombo (nº individuals in 2009 = 148)



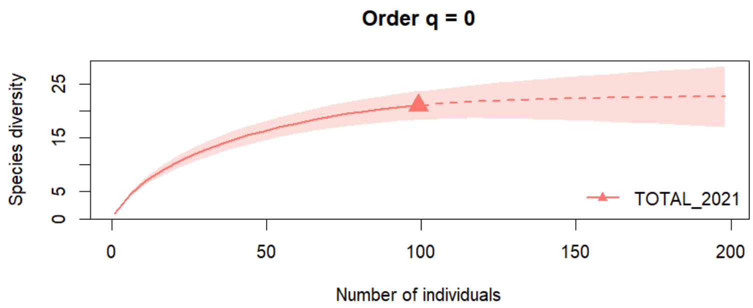
9. Bastañar (nº individuals in 2021 = 91)



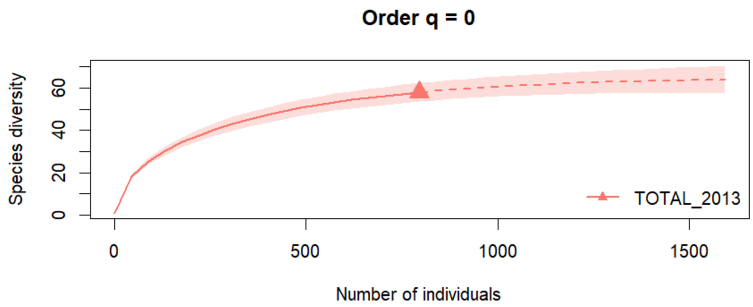
10. Güembres (mean nº individuals/year = 1044.6, SE=90.09)



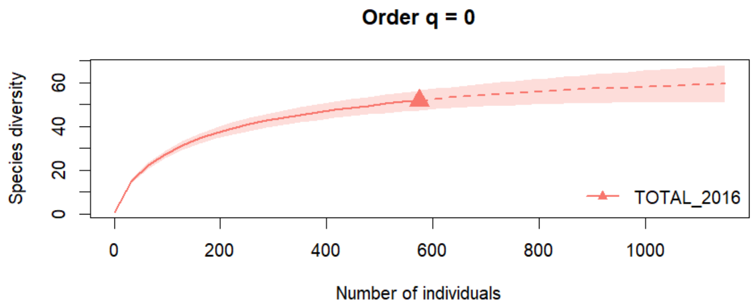
11. Soto prado experimento (nº individuals in 2019 = 157)



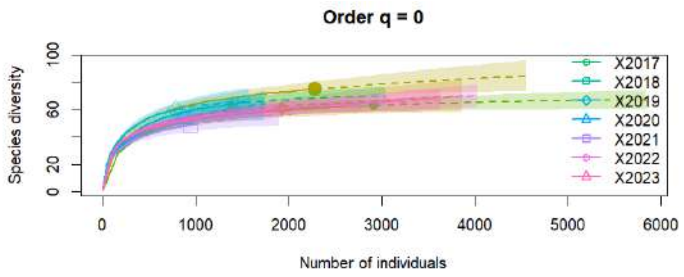
12. Ribota (nº individuals in 2021 = 99)



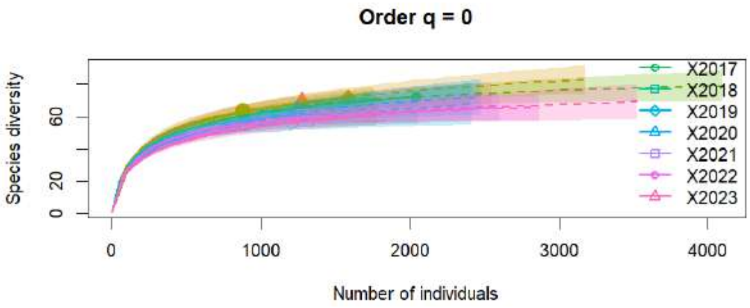
13. Caldevilla (nº individuals in 2013 = 796)



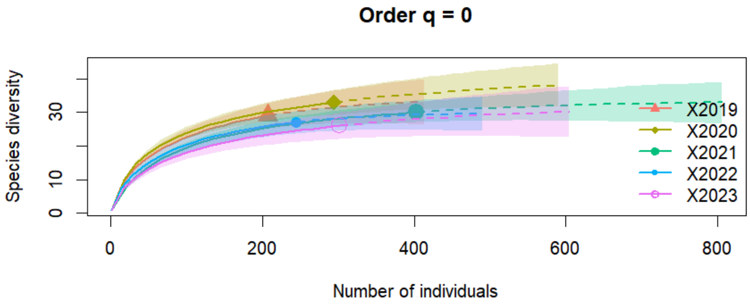
14. Los Llanos (mean nº individuals in 2016 = 575)



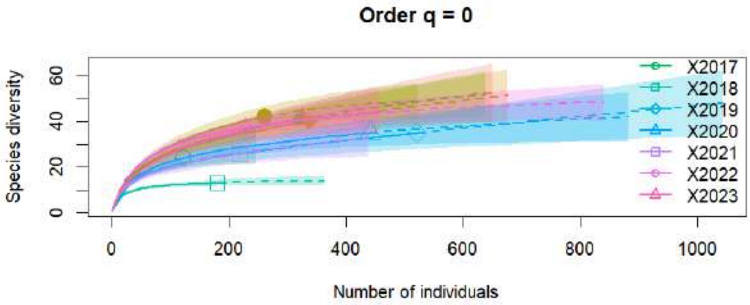
15. Sesanes (mean nº individuals/year = 1577, SE=206.91)



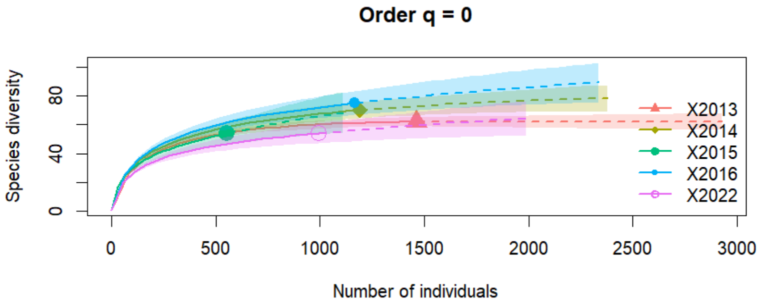
16. Prada (mean nº individuals/year = 1331, SE=108.36)



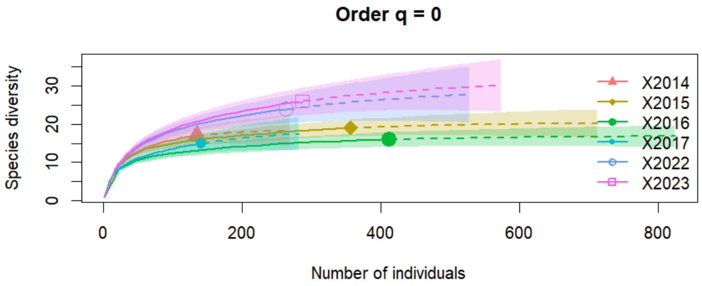
17. Liordes (mean nº individuals/year = 290, SE=33.05)



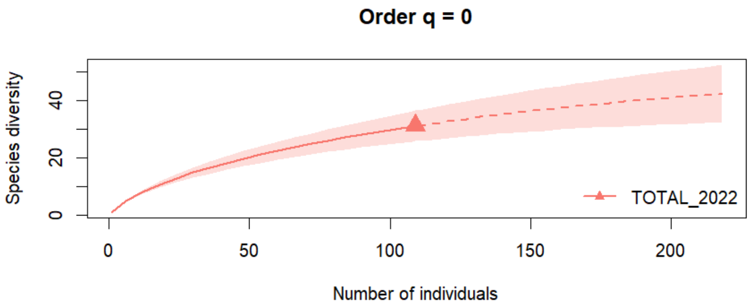
18. Pandetrave (mean nº individuals/year = 307, SE=36.15)



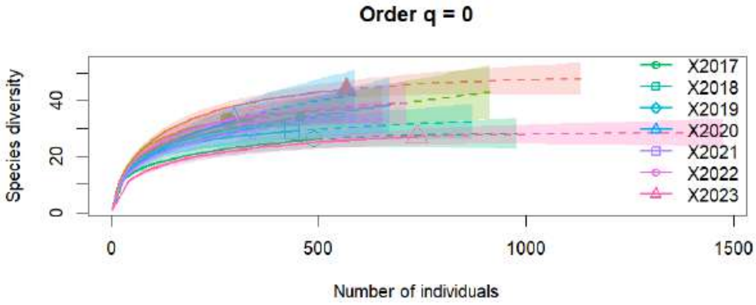
19. Morrena Pido (mean nº individuals/year = 1074, SE=149.83)



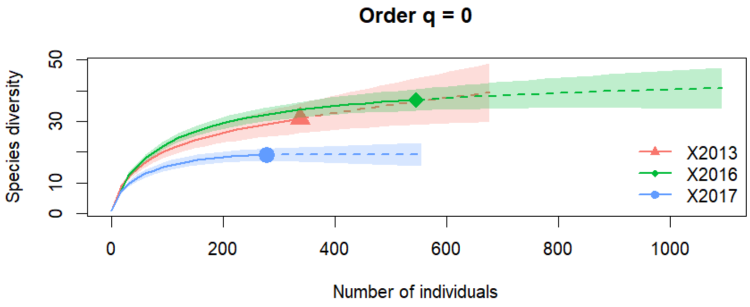
20. Lloroza (mean nº individuals/year = 266, SE=45.79)



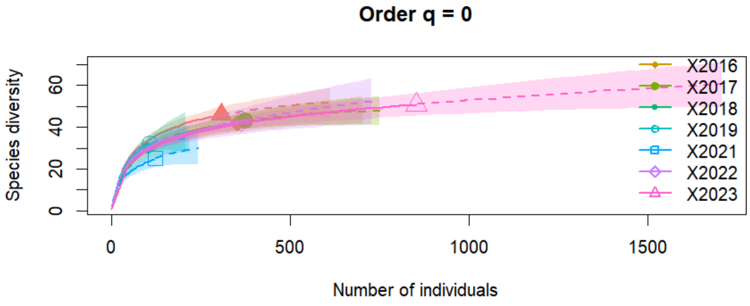
21. Panderruedas (nº individuals in 2022 = 109)



22. Pandébano (mean nº individuals/year = 418, SE=41.78)

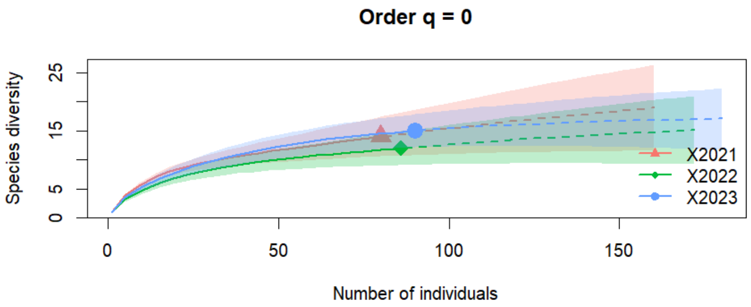


23. Collado Hoja (mean nº individuals/year = 387, SE=81.20)



24. Urdón (mean nº individuals/year = 323, SE=86.76)

25. Cares (nº individuals in 2021 = 167)



26. Ándara (mean nº individuals/year = 86, SE=2.90)

Fig. S4.2. Species accumulation curves for each sampled site. For sites in which more than a year was sampled, curves are calculated separate for each year.

Table S4.1 Study sites description

ID	Transect name	Coordinates (longitude, latitude)	Monitoring period	Nº years	Mean elevation (m)	Length (m)	Habitat types	Nº samples / year	Sampling dates	Nº individuals /year	Observers
1	Ginés	5°3’5.56045’’W 43°18’36.08561’’N	2013-2023	11	350	1421	Atlantic heaths	10	May - Sep	295	Manuel Díaz
2	Ceneya	5°5’24.22392’’W 43°14’20.61985’’N	2009	1	250	500	Mediterranean shrubs	14	Apr - Sep	377	Hugo Mortera
3	Baenu	5°4’5.803626’’W 43°13’36.30968’’N	2019-2023	5	760	1526	Fagus woodland	5	Jun - Jul	307	Manuel Díaz
4	Angón	5°2’11.04369’’W 43°13’49.58514’’N	2013	1	700	1489	Fagus woodland	9	Apr - Aug	544	Manuel Díaz
5	Fuente Prieta	5°1’23.12461’’W 43°13’9.39939’’N	2009	1	780	500	Mountain pastures, hazel and Genista scrub	14	Apr - Sep	115	Hugo Mortera
6	Camino a Carombo	5°1’1.767881’’W 43°12’17.16819’’N	2009	1	970	500	Hazel and Genista legionensis shrubland	14	Apr - Sep	166	Hugo Mortera
7	Dobraseca	5°0’23.08590’’W 43°11’44.75366’’N	2009	1	1000	500	Genista legionensis shrubland	14	Apr - Sep	538	Hugo Mortera
8	Carombo	4°59’46.31063’’W 43°11’26.98592’’N	2009	1	1200	500	Genista occidentalis shrubland	14	Apr - Sep	148	Hugo Mortera
9	Bastañar	5°2’31.49182’’W 43°17’52.61734’’N	2021	1	650	1300	Mixed forest regenerating over abandoned hay meadows	4	Jun - Jul	91	América Gonzalo
10	Güembres	5°2’8.05956’’W 43°9’57.68446’’N	2014-2023	10	1000	1409	Atlantic mosaic	10	May - Sep	1044.6	Amparo Mora

ID	Transect name	Coordinates (longitude, latitude)	Monitoring period	Nº years	Mean elevation (m)	Length (m)	Habitat types	Nº samples / year	Sampling dates	Nº individuals /year	Observers
11	Soto prado experimento	5°2’25.97450’’W 43°9’27.60468’’N	2019	1	875	1000	Hay meadows	3	May - Jul	157	Amparo Mora
12	Ribota	5°3’25.0357’’W 43°8’41.36038’’N	2021	1	500	555	Atlantic mosaic	4	Jun - Aug	99	Susana Bayón, José Manuel Castrillo
13	Caldevilla	4°56’48.79849’’W 43°8’36.88748’’N	2013	1	980	1120	Atlantic mosaic	12	Apr - Sep	796	Alicia García
14	Los Llanos	4°54’32.24175’’W 43°9’30.98879’’N	2016	1	1000	1410	Atlantic mosaic	7	May - Aug	575	Judit Blasco
15	Sesanes	4°54’24.63581’’W 43°11’42.14206’’N	2013-2023	11	600	1274	Atlantic mosaic	10	Apr - Sep	1577	Mar Matute
16	Prada	4°54’24.025’’W 43°8’41.69134’’N	2013-2023	11	1100	1123	Atlantic mosaic	10	May - Sep	1331	Félix Rojo, Miguel A. Bermejo
17	Liordes	4°51’4.50011’’W 43°8’40.20382’’N	2019-2023	5	1900	1243	High mountain (limestone)	5	Jun - Aug	290	Félix Rojo, Miguel A. Bermejo
18	Pandetrave	4°52’23.75083’’W 43°6’22.73198’’N	2013-2023	11	1550	829	High mountain pastures	5	Jun - Aug	446	Alicia García, Judit Blasco
19	Morrena Pido	4°48’35.38318’’W 43°7’53.12269’’N	2013-2016 + 2022	5	1050	996	Atlantic mosaic	10	May - Sep	1074	Sara González

ID	**Transect name**	**Coordinates (longitude, latitude)**	**Monitoring period**	**Nº years**	**Mean elevation (m)**	**Length (m)**	**Habitat types**	**Nº samples / year**	**Sampling dates**	**Nº individuals /year**	**Observers**
20	Lloroza	4°48’21.71657’’ W 43°9’14.63915’’ N	2014-2017 + 2022-2023	6	1850	1399	High mountain (limestone)	5	Jun - Aug	266	Teresa Farino, Gonzalo Gómez
21	Panderruedas	4°59’16.18160’’ W 43°8’33.50896’’ N	2022	1	1600	2000	High mountain (siliceous)	2	Jun	109	Susana Bayón, José Manuel Castrillo
22	Pandébano	4°45’59.56362’’ W 43°13’42.51022’’ N	2013-2023	11	1140	992	Hay meadows	10	May - Sep	418	Marino Sánchez, Jorge García
23	Collado de Hoja	4°38’57.23552’’ W 43°14’51.27152’’ N	2013 + 2016-2017	3	850	812	Quercus petraea woodlands with hay meadows	6	May - Sep	387	Rubén Varona, Saturnino González
24	Urdón	4°37’54.62555’’ N	2015-2019 + 2021-2023	8	150	920	Mediterranean fluvial mosaic	6	Apr - Sep	323	Teresa Farino, Conchi García, Pilar García
25	Cares	4°50’29.67942’’ W 43°15’13.53795’’ N	2021	1	250	542	Fluvial mosaic (Genista shrubland and rocky vegetation)	5	Jun - Aug	167	Félix Rojo, Miguel A. Bermejo
26	Ándara	4°41’47.46232’’ W 43°12’30.63025’’ N	2021-2023	3	1950	1183	High mountain (limestone)	3	Jun - Aug	86	César Obeso, Amparo Mora

Table S4.2. Vegetation categories. Plant community types based on the European Nature Information System Classification, EUNIS (https://eunis.eea.europa.eu) and habitat categories at study sites. Site name and length of the butterfly transect at each site are also provided.

SITE	Plant community type based on EUNIS	EUNIS Code	Habitat category	Length (m)
Cuesta Gines	Western Cantabrian acidophilous oak forests	G1.8622	woodland	251
Cuesta Gines	Cantabro Pyrenean heaths (Erica mackaiana-Erica cinerea)	F4.236	scrub	1170
Pandebano	Atlantic hay meadows	E2.21	grassland	992
Guembres	Atlantic hay meadows	E2.21	grassland	258
Guembres	Cantabrian forests (Quercus pyrenaica)	G1.7B2	woodland	445
Guembres	Atlantic hay meadows	E2.21	grassland	600
Guembres	Cantabro Pyrenean heaths (Erica vagans-Erica cinerea)	F4.237	scrub	106
Prada	Atlantic hay meadows	E2.21	grassland	41
Prada	Bramble thickets	F3.131	scrub	140
Prada	Atlantic and subatlantic hazel tickets	F3.171	scrub	262
Prada	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	396
Prada	Atlantic hay meadows	E2.21	grassland	284
Pandetrave	Northwestern Iberian fields (Genista florida)	F3.252	scrub	108
Pandetrave	Permanent mesotrophic pastures and aftermath grazed meadows	E2.1	grassland	81
Pandetrave	Northwestern Iberian fields (Genista florida)	F3.252	scrub	82
Pandetrave	Nardus stricta swards and permanent mesotrophic pastures	E1.71, E2.1	grassland	283
Pandetrave	Northwestern Iberian fields (Genista florida)	F3.252	scrub	275
Sesanes	Atlantic hay meadows	E2.21	grassland	175
Sesanes	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	93
Sesanes	Atlantic hay meadows	E2.21	grassland	592
Sesanes	Meso and eutrophic Quercus, Carpinus, Fraxinus, Acer, Tilia, Ulmus and related woodland	G1.A19	woodland	206
Sesanes	Spanish Quercus faginea forests	G1.771	woodland	116
Sesanes	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	92
Morrena Pido	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	467
Morrena Pido	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	348
Morrena Pido	Atlantic hay meadows	E2.21	grassland	181
Lloroza	Pavements and recreation areas	J4.6	other	89
Lloroza	Iberian montane Nardus stricta swards	E1.712	grassland	163
Lloroza	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	376
Lloroza	Iberian montane Nardus stricta swards	E1.712	grassland	77
Lloroza	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	359
Lloroza	Almost bare rock pavements, including limestone pavements	H3.5	other	335

Urdon	Basic and ultrabasic inland cliffs	H3.2	grassland	116
Urdon	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	96

SITE	**Plant community type based on EUNIS**	**EUNIS Code**	**Habitat category**	**Length (m)**
Urdon	Calciphile western Mediterranean oak matorral	F5.113414	scrub	118
Urdon	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	176
Urdon	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	114
Urdon	Grasslands and lands dominated by forbs, mosses and lichens	E	grassland	210
Urdon	Calciphile western Mediterranean oak matorral	F5.113414	scrub	58
Urdon	Pyreneo-Cantabrian forests (Quercus-Fraxinus)	G1.A19	woodland	32
Baenu	Fagus woodland	G1.6	woodland	1526
Liordes	Pyreneo-Cantabrian cushion heaths	F7.4451	scrub	218.81
Liordes	Iberian montane Nardus stricta swards and high mountain basic charmophyte communities	E1.712, H3.2	grassland	657.83
Liordes	Iberian montane Nardus stricta swards, permanent mesotrophic pastures and alkaline fens	E1.712, D4.1	grassland	366.76

Table S4.3. List of species recorded. Species scientific names follow nomenclature by Wiemers *et al*. (2018), the family and name synonymies are provided. Legally protected species in Spain are in red and endemic species to the Iberian Peninsula are marked in blue.

Nº	**Species**	**Family**	**Synonymous**
1	*Aglais io (Linnaeus, 1758)*	*Nymphalidae*	*Inachis io*
2	*Aglais urticae (Linnaeus, 1758)*	*Nymphalidae*	
3	*Agriades pyrenaicus (Boisduval, 1840)*	*Lycaenidae*	*Plebejus pyrenaica*
4	*Anthocharis cardamines (Linnaeus, 1758)*	*Pieridae*	
5	*Anthocharis euphenoides Staudinger, 1869*	*Pieridae*	*Anthocaris belia*
6	*Apatura iris (Linnaeus, 1758)*	*Nymphalidae*	
7	*Aphantopus hyperantus (Linnaeus, 1758)*	*Satyridae*	
8	*Aporia crataegi (Linnaeus, 1758)*	*Pieridae*	
9	*Arethusana arethusa ([Denis & Schiffermüller], 1775)*	*Satyridae*	
10	*Argynnis pandora ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	*Pandoriana pandora*
11	*Argynnis paphia (Linnaeus, 1758)*	*Nymphalidae*	
12	*Aricia cramera (Eschscholtz, 1821)*	*Lycaenidae*	*Aricia agestis*
13	*Aricia montensis Verity, 1928*	*Lycaenidae*	*Aricia antaxerxes*
14	*Aricia morronensis (Ribbe, 1910)*	*Lycaenidae*	
15	*Boloria dia (Linnaeus, 1767)*	*Nymphalidae*	*Clossiana dia*
16	*Boloria euphrosyne (Linnaeus, 1758)*	*Nymphalidae*	
17	*Boloria pales ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	
18	*Boloria selene ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	*Clossiana selene*
19	*Brenthis daphne ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	
20	*Brenthis ino (Rottemburg, 1775)*	*Nymphalidae*	
21	*Brintesia circe (Fabricius, 1775)*	*Satyridae*	*Kanetisa circe*
22	*Callophrys rubi (Linnaeus, 1758)*	*Lycaenidae*	
23	*Carcharodus alceae (Esper, 1780)*	*Hesperiidae*	
24	*Carcharodus floccifera (Zeller, 1847)*	*Hesperiidae*	*Carcharodus flocciferus*
25	*Carcharodus lavatherae (Esper, 1783)*	*Hesperiidae*	
26	*Carterocephalus palaemon (Pallas, 1771)*	*Hesperiidae*	
27	*Celastrina argiolus (Linnaeus, 1758)*	*Lycaenidae*	
28	*Coenonympha arcania (Linnaeus, [1760])*	*Satyridae*	
29	*Coenonympha dorus (Esper, 1782)*	*Satyridae*	
30	*Coenonympha glycerion (Borkhausen, 1788)*	*Satyridae*	*Coenonympha iphioides*
31	*Coenonympha pamphilus (Linnaeus, 1758)*	*Satyridae*	
32	*Colias alfacariensis Ribbe, 1905*	*Pieridae*	
33	*Colias crocea (Geoffroy, 1785)*	*Pieridae*	*Colias croceus*
34	*Colias phicomone (Esper, [1780])*	*Pieridae*	
35	*Cupido argiades (Pallas, 1771)*	*Lycaenidae*	*Everes argiades*
36	*Cupido minimus (Fuessly, 1775)*	*Lycaenidae*	
37	*Cyaniris semiargus (Rottemburg, 1775)*	*Lycaenidae*	
38	*Erebia arvernensis Oberthür, 1908*	*Satyridae*	*Erebia cassioides*
39	*Erebia epiphron (Knoch, 1783)*	*Satyridae*	
40	*Erebia euryale (Esper, 1805)*	*Satyridae*	
41	*Erebia gorge (Hübner, [1804])*	*Satyridae*	
42	*Erebia lefebvrei (Boisduval, 1828)*	*Satyridae*	
43	*Erebia manto ([Denis & Schiffermüller], 1775)*	*Satyridae*	
44	*Erebia meolans (Prunner, 1798)*	*Satyridae*	
45	*Erebia neoridas (Boisduval, 1828)*	*Satyridae*	*Satyrus neoridas*
46	*Erebia palarica Chapman, 1905*	*Satyridae*	
47	*Erebia pronoe (Esper, 1780)*	*Satyridae*	
48	*Erebia triarius (Prunner, 1798)*	*Satyridae*	*Erebia triaria*
49	*Erynnis tages (Linnaeus, 1758)*	*Hesperiidae*	
50	*Euchloe crameri Butler, 1869*	*Pieridae*	
51	*Euchloe simplonia (Freyer, 1829)*	*Pieridae*	
52	*Euphydryas aurinia (Rottemburg, 1775)*	*Nymphalidae*	
53	*Fabriciana adippe ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	*Argynnis adippe*
54	*Favonius quercus (Linnaeus, 1758)*	*Lycaenidae*	*Quercusia quercus, Neozephyrus quercus*
55	*Glaucopsyche alexis (Poda, 1761)*	*Lycaenidae*	
56	*Glaucopsyche melanops (Boisduval, 1828)*	*Lycaenidae*	
57	*Gonepteryx cleopatra (Linnaeus, 1767)*	*Pieridae*	

58	*Gonepteryx rhamni (Linnaeus, 1758)*	*Pieridae*	
59	*Hamearis lucina (Linnaeus, 1758)*	*Lycaenidae*	
60	*Hesperia comma (Linnaeus, 1758)*	*Hesperiidae*	
61	*Heteropterus morpheus (Pallas, 1771)*	*Hesperiidae*	
62	*Hipparchia hermione (Linnaeus, 1764)*	*Satyridae*	*Hipparchia alcyone*
63	*Hipparchia semele (Linnaeus, 1758)*	*Satyridae*	
64	*Hipparchia statilinus (Hufnagel, 1766)*	*Satyridae*	
65	*Hyponephele lycaon (Kühn, 1774)*	*Satyridae*	
66	*Iphiclides feisthamelii (Duponchel, 1832)*	*Papilionidae*	*Iphiclides podalirius*
67	*Issoria lathonia (Linnaeus, 1758)*	*Nymphalidae*	
68	*Laeosopis roboris (Esper, [1793])*	*Lycaenidae*	
69	*Lampides boeticus (Linnaeus, 1767)*	*Lycaenidae*	
70	*Lasiommata maera (Linnaeus, 1758)*	*Satyridae*	
71	*Lasiommata megera (Linnaeus, 1767)*	*Satyridae*	
72	*Leptidea sinapis (Linnaeus, 1758)*	*Pieridae*	
73	*Leptotes pirithous (Linnaeus, 1767)*	*Lycaenidae*	
74	*Limenitis camilla (Linnaeus, 1764)*	*Nymphalidae*	
75	*Lopinga achine (Scopoli, 1763)*	*Satyridae*	
76	*Lycaena alciphron (Rottemburg, 1775)*	*Lycaenidae*	
77	*Lycaena hippothoe (Linnaeus, [1760])*	*Lycaenidae*	
78	*Lycaena phlaeas (Linnaeus, [1760])*	*Lycaenidae*	
79	*Lycaena tityrus (Poda, 1761)*	*Lycaenidae*	
80	*Lycaena virgaureae (Linnaeus, 1758)*	*Lycaenidae*	
81	*Lysandra bellargus (Rottemburg, 1775)*	*Lycaenidae*	*Polyommatus bellargus*
82	*Lysandra coridon (Poda, 1761)*	*Lycaenidae*	*Polyommatus coridon*
83	*Maniola jurtina (Linnaeus, 1758)*	*Satyridae*	
84	*Melanargia galathea (Linnaeus, 1758)*	*Satyridae*	
85	*Melanargia lachesis (Hübner, 1790)*	*Satyridae*	
86	*Melanargia russiae (Esper, 1783)*	*Satyridae*	
87	*Melitaea celadussa Fruhstorfer, 1910*	*Nymphalidae*	*Mellicta athalia, Melitaea nevadensis*
88	*Melitaea cinxia (Linnaeus, 1758)*	*Nymphalidae*	
89	*Melitaea deione (Geyer, [1832])*	*Nymphalidae*	*Mellicta deione*
90	*Melitaea diamina (Lang, 1789)*	*Nymphalidae*	
91	*Melitaea didyma (Esper, 1778)*	*Nymphalidae*	
92	*Melitaea parthenoides Keferstein, 1851*	*Nymphalidae*	*Mellicta parthenoides*
93	*Melitaea phoebe ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	
94	*Melitaea trivia ([Denis & Schiffermüller], 1775)*	*Nymphalidae*	
95	*Minois dryas (Scopoli, 1763)*	*Satyridae*	
96	*Nymphalis antiopa (Linnaeus, 1758)*	*Nymphalidae*	
97	*Nymphalis polychloros (Linnaeus, 1758)*	*Nymphalidae*	
98	*Ochlodes sylvanus (Esper, 1777)*	*Hesperiidae*	*Ochlodes venata*
99	*Papilio machaon Linnaeus, 1758*	*Papilionidae*	
100	*Pararge aegeria (Linnaeus, 1758)*	*Satyridae*	
101	*Parnassius apollo (Linnaeus, 1758)*	*Papilionidae*	
102	*Phengaris nausithous (Bergsträsser, 1779)*	*Lycaenidae*	*Maculinea nausithous*
103	*Pieris brassicae (Linnaeus, 1758)*	*Pieridae*	
104	*Pieris mannii (Mayer, 1851)*	*Pieridae*	*Artogeia mannii*
105	*Pieris napi (Linnaeus, 1758)*	*Pieridae*	*Artogeia napi*
106	*Pieris rapae (Linnaeus, 1758)*	*Pieridae*	*Artogeia rapae*
107	*Plebejus argus (Linnaeus, 1758)*	*Lycaenidae*	
108	*Plebejus idas (Linnaeus, [1760])*	*Lycaenidae*	*Lycaeides idas*
109	*Polygonia c-album (Linnaeus, 1758)*	*Nymphalidae*	
110	*Polyommatus dorylas ([Denis & Schiffermüller], 1775)*	*Lycaenidae*	*Plebicula dorylas*
111	*Polyommatus icarus (Rottemburg, 1775)*	*Lycaenidae*	
112	*Pontia daplidice (Linnaeus, 1758)*	*Pieridae*	
113	*Pseudophilotes baton (Bergsträsser, 1779)*	*Lycaenidae*	*Scolitantides baton*
114	*Pyrgus alveus (Hübner, [1803])*	*Hesperiidae*	
115	*Pyrgus armoricanus (Oberthür, 1910)*	*Hesperiidae*	
116	*Pyrgus carthami (Hübner, [1813])*	*Hesperiidae*	
117	*Pyrgus cirsii (Rambur, 1839)*	*Hesperiidae*	
118	*Pyrgus malvoides (Elwes & Edwards, 1897)*	*Hesperiidae*	
119	*Pyrgus onopordi (Rambur, 1839)*	*Hesperiidae*	

120	*Pyrgus serratulae (Rambur, 1839)*	*Hesperiidae*	
121	*Pyronia tithonus (Linnaeus, 1771)*	*Satyridae*	
122	*Satyrium acaciae (Fabricius, 1787)*	*Lycaenidae*	
123	*Satyrium esculi (Hübner, [1804])*	*Lycaenidae*	
124	*Satyrium ilicis (Esper, 1779)*	*Lycaenidae*	
125	*Satyrium spini ([Denis & Schiffermüller], 1775)*	*Lycaenidae*	
126	*Satyrium w-album (Knoch, 1782)*	*Lycaenidae*	*Papilio w-album*
127	*Speyeria aglaja (Linnaeus, 1758)*	*Nymphalidae*	*Argynnis aglaja,* *Mesoacidalia aglaja*
128	*Spialia sertorius (Hoffmansegg, 1804)*	*Hesperiidae*	
129	*Thecla betulae (Linnaeus, 1758)*	*Lycaenidae*	
130	*Thymelicus acteon (Rottemburg, 1775)*	*Hesperiidae*	
131	*Thymelicus lineola (Ochsenheimer, 1808)*	*Hesperiidae*	
132	*Thymelicus sylvestris (Poda, 1761)*	*Hesperiidae*	
133	*Vanessa atalanta (Linnaeus, 1758)*	*Nymphalidae*	
134	*Vanessa cardui (Linnaeus, 1758)*	*Nymphalidae*	

Wiemers M, Balletto E, Dincă V, Fric ZF, Lamas G, Lukhtanov V, Munguira ML, van Swaay CAM, Vila R, Vliegenthart A, Wahlberg N, Verovnik R (2018) An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea). ZooKeys 81: 9–45. https://doi.org/10.3897/zookeys.811.28712

Table S4.4. Results of PCA for climate (a) and habitat (b) variables.

(a) **Climatic variables** included in the PCA were**:** mean annual temperature (tas), maximum annual temperature (maxtemp), minimum annual temperature (mintemp), annual total precipitation (precip), total precipitation of the wettest month (precwm), total precipitation of the driest month (precdm).

Importance of components:

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Standard deviation	2.1947	1.0239	0.30997	0.18931	0.05227	0.01413
Proportion of variance	0.8028	0.1747	0.01601	0.00597	0.00046	0.00003
Cumultive proportion	0.8028	0.9775	0.99354	0.99951	0.99997	1.00000

Relative contribution of each variable on each principal component (“vector rotation”):

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
tas	-0.4113709	-0.4182747	0.08058842	-0.11397573	0.30960486	0.73517352
maxtemp	-0.4338533	-0.2255446	0.53937160	0.57925616	0.05314501	-0.36279073
mintemp	-0.3813739	-0.5216303	-0.25128251	-0.46166984	-0.39437764	-0.38812383
precip	0.4297340	-0.2897093	0.47096393	0.01753758	-0.64774690	0.29951049
precwm	0.4225996	-0.3372053	0.37939018	-0.40432597	0.55954097	-0.29529589
precdm	0.3658381	-0.5517597	-0.52316053	0.52397113	0.11456255	-0.01888053

Eigenvalues (relative lenght of each principal component axis):

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Deviation	4.8167	1.0483	0.0960	0.0358	0.0027	0.0001

(b) **Habitat variables** included in the PCA were**:** % of forest (forest), % of grassland (grassland), % of scrub (scrub), % of open habitat (open_habitat, including grassland and scrub not exceeding 1.5 m in height) and % of seminatural grassland used for mowing or pasturing (seminat_grassland).

Importance of components:

	PC1	**PC2**	**PC3**	**PC4**	**PC5**
Standard deviation	37.6620	25.4416	14.46726	10.23458	5.08641
Proportion of variance	0.5896	0.2691	0.08701	0.04354	0.01075
Cumulative proportion	0.5896	0.8587	0.94570	0.98925	1.00000

Relative contribution of each variable on each principal component (“vector rotation”):

	PC1	**PC2**	**PC3**	**PC4**	**PC5**
forest	-0.6112279	0.07042624	-0.3386392	0.18835734	-0.68650245
scrub	0.2394234	-0.53882914	0.5909599	0.03944038	-0.54913611
grassland	0.2523017	0.68101598	0.1885139	-0.53119959	-0.39351060
open_habitat	0.7024050	0.07610659	-0.4830519	0.44940248	-0.25599474
seminat_grassland	-0.1097635	0.48490033	0.5169267	0.69197570	0.08234092

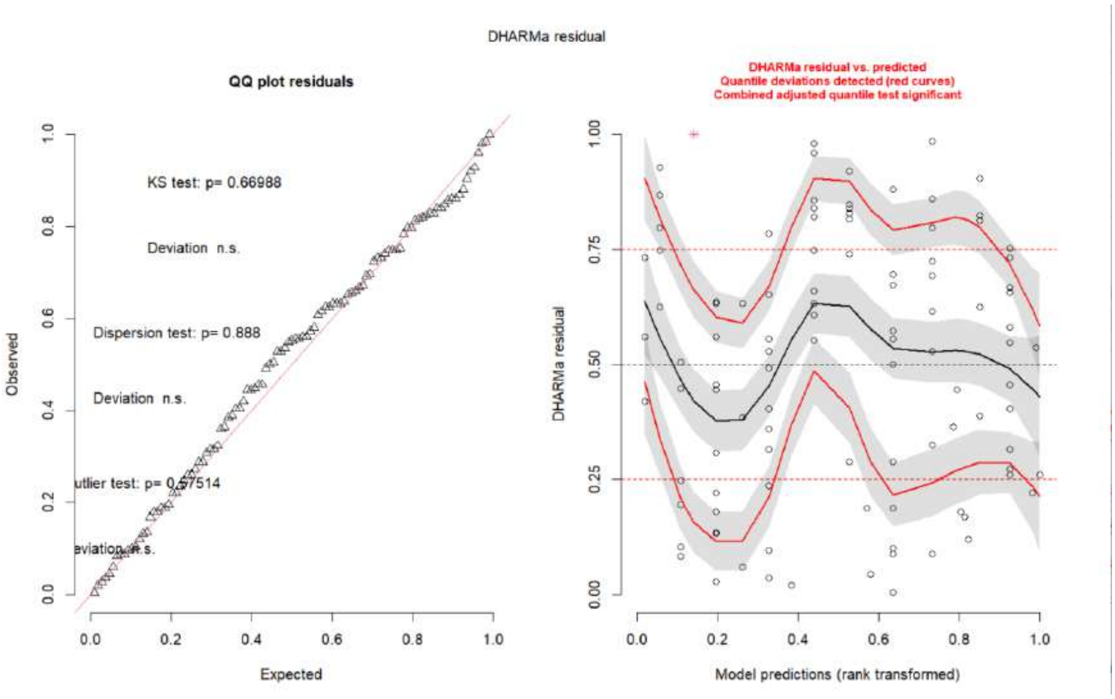
Eigenvalues (relative lenght of each principal component axis):

	PC1	**PC2**	**PC3**	**PC4**	**PC5**
Deviation	1418.4245	647.2748	209.3015	104.7466	25.87158

Table S4.5. Best models for butterfly diversity drivers, their parameters and validation by residuals.

(a) Response variable: Hill species richness
Best model: Hill Species richness ~ Distance to coast + near surface relative humidity + landscape heterogeneity in composition + pc1_landscape + (1|year)

Variable	**Estimate**	**Standard error**	**df**	**t value**	**p**
Distance to coast	0.459	0.067	94.455	6.841	**7.75e^{-10}**
Relative humidity	0.711	0.085	100.171	8.326	**4.46e^{-13}**
Landscape heterogeneity in composition	0.194	0.065	93.865	2.978	**0.003**
pc1_landscape	0.184	0.076	96.648	2.398	**0.018**



Asymptotic one-sample Kolmogorov-Smirnov test:
D=0.070056, p-value= 0.6699

DHARMa outlier test based on exact binomial test with approximate expectations:
Outliers at both margins=1, observations=107, p-value=0.5751
Frequency of outliers (expected: 0.007): 0.009

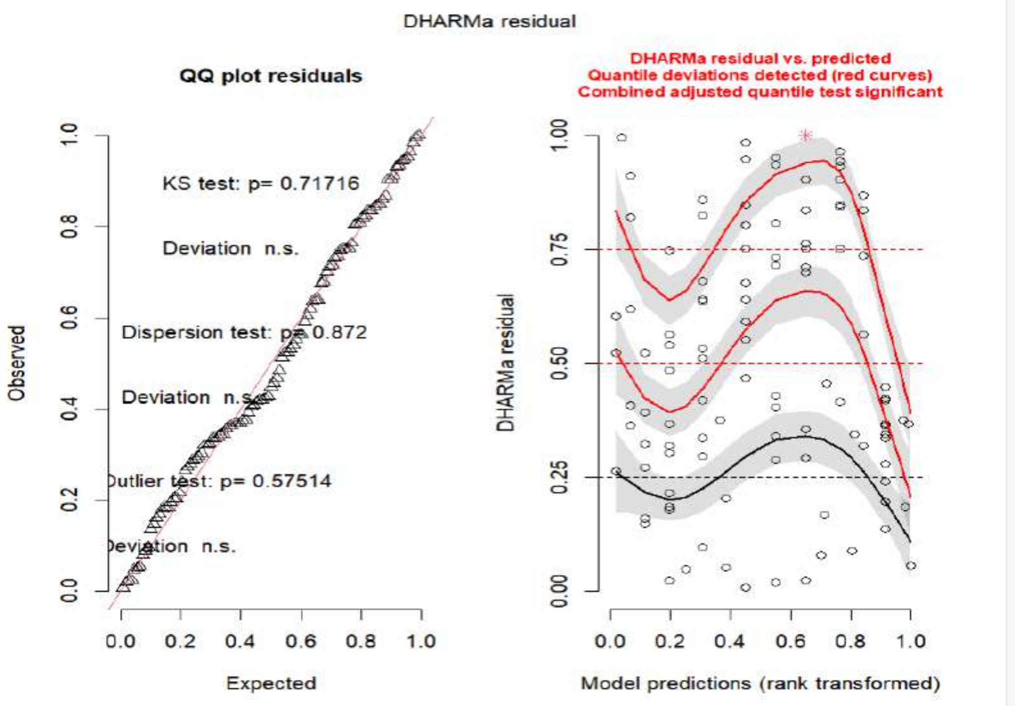
DHARMa nonparametric dispersion test via sd of residuals fitted vs. simulated:
dispersion=0.966, p-value=0.888

Test for location of quantiles via qgam:
p-value= 0.00277

(b) Response variable: Hill Shannon index

Best model: SHill Shannon index ~ Distance to coast + near surface relative humidity + landscape heterogeneity in composition + pc1_landscape + (1|year)

Variable	Estimate	Standard error	df	t value	p
Distance to coast	0.192	0.055	93.064	3.498	**0.0007**
Relative humidity	0.530	0.070	99.112	7.553	**2.14e-11**
Landscape heterogeneity in composition	0.121	0.053	92.431	2.276	**0.0251**
pc1_landscape	0.242	0.063	95.549	3.847	**0.00021**



Asymptotic one-sample Kolmogorov-Smirnov test:
D=0.067327, p-value= 0.7172

DHARMa outlier test based on exact binomial test with approximate expectations:
Outliers at both margins=1, observations=107, p-value=0.5751
Frequency of outliers (expected: 0.007): 0.009

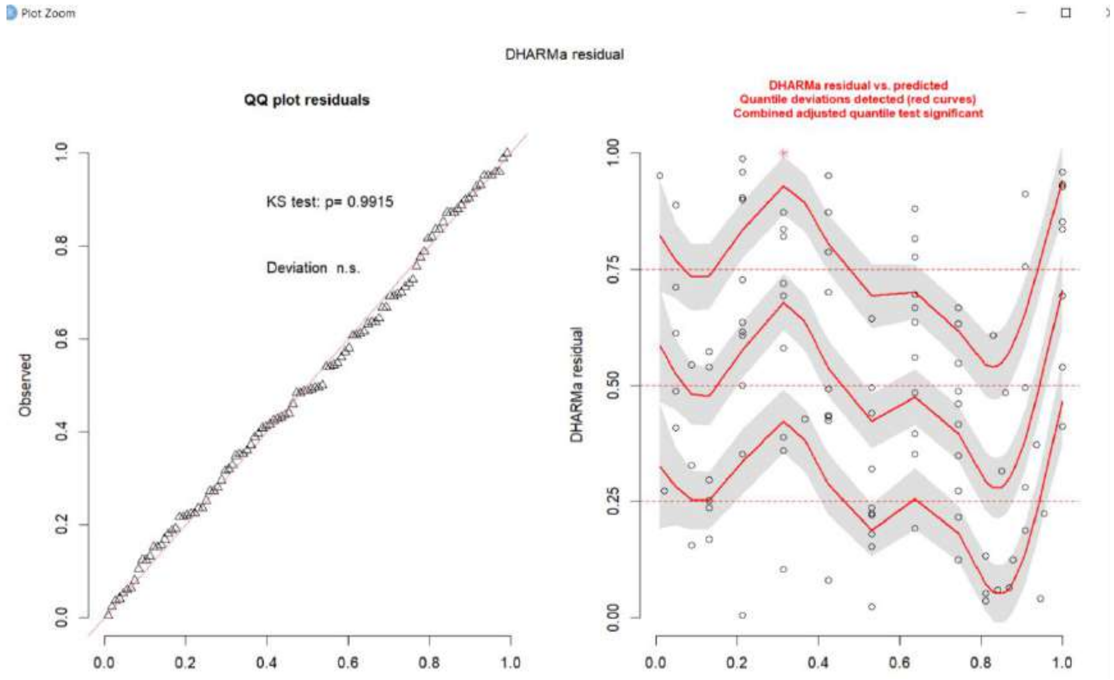
DHARMa nonparametric dispersion test via sd of residuals fitted vs. simulated:
dispersion=0.963, p-value=0.872

Test for location of quantiles via qgam:
p-value= 2.078e^{-05}

(c) Response variable: Hill Simpson index

Best model: Hill Simpson index ~ Near surface relative humidity + lanscape heterogeneity in configuration + pc1_landscape + (1|year)

Variable	**Estimate**	**Standard error**	**df**	**t value**	**p**
Relative humidity	0.397	0.061	100.142	6.452	**$3.96e^{-09}$**
Landscape heterogeneity in configuration	-0.170	0.058	91.517	-2.931	**0.004**
pc1_landscape	0.178	0.067	93.435	2.662	**0.009**



Asymptotic one-sample Kolmogorov-Smirnov test:
D=0.042056, p-value= 0.9915

DHARMa outlier test based on exact binomial test with approximate expectations:
Outliers at both margins=1, observations=107, p-value=0.5751
Frequency of outliers (expected: 0.007): 0.009

DHARMa nonparametric dispersion test via sd of residuals fitted vs. simulated:
dispersion=0.966, p-value=0.888

Test for location of quantiles via qgam:
p-value= 0.002

Table S4.6. Comparison of best models for butterfly diversity drivers using all sites or taking out Urdón, the outlier at heterogeneity graphs.

(a) Response variable: Hill species richness
Best model: Hill Species richness ~ Distance to coast + near surface relative humidity + landscape heterogeneity in composition + pc1_landscape + (1|year)

Using all sites:

Variable	**Estimate**	**Standard error**	**df**	**t value**	**p**
Distance to coast	0.459	0.067	94.455	6.841	**$7.75e^{-10}$**
Relative humidity	0.711	0.085	100.171	8.326	**$4.46e^{-13}$**
Landscape heterogeneity in composition	0.194	0.065	93.865	2.978	**0.003**
pc1_landscape	0.184	0.076	96.648	2.398	**0.018**

Without Urdón:

Variable	**Estimate**	**Standard error**	**df**	**t value**	**p**
Distance to coast	0.614	0.074	86.288	8.263	**$1.52e^{-12}$**
Relative humidity	0.509	0.095	93.995	5.352	**$6.12e^{-07}$**
Landscape heterogeneity in composition	0.100	0.066	86.894	1.517	0.133
pc1_landscape	-0.077	0.097	92.937	-0.795	0.428

(b) Response variable: Hill Shannon index
Best model: SHill Shannon index ~ Distance to coast + near surface relative humidity + landscape heterogeneity in composition + pc1_landscape + (1|year)

Using all sites:

Variable	**Estimate**	**Standard error**	**df**	**t value**	**p**
Distance to coast	0.192	0.055	93.064	3.498	**0.0007**
Relative humidity	0.530	0.070	99.112	7.553	**$2.14e^{-11}$**
Landscape heterogeneity in composition	0.121	0.053	92.431	2.276	**0.0251**
pc1_landscape	0.242	0.063	95.549	3.847	**0.00021**

Without Urdón:

Variable	**Estimate**	**Standard error**	**df**	**t value**	**p**
Distance to coast	0.367	0.055	85.772	6.590	**$3.40e^{-09}$**
Relative humidity	0.295	0.071	93.929	4.105	**$8.61e^{-05}$**
Landscape heterogeneity in composition	0.014	0.049	86.351	0.083	0.778
pc1_landscape	-0.059	0.072	92.682	-0.807	0.422

(c) Response variable: Hill Simpson index

Best model: Hill Simpson index ~ Near surface relative humidity + lanscape heterogeneity in configuration + pc1_landscape + (1|year)

Using all sites:

Variable	**Estimate**	**Standard error**	**df**	**t value**	**p**
Relative humidity	0.397	0.061	100.142	6.452	**$3.96e^{-09}$**
Landscape heterogeneity in configuration	-0.170	0.058	91.517	-2.931	**0.004**
pc1_landscape	0.178	0.067	93.435	2.662	**0.009**

Without Urdón:

Variable	**Estimate**	**Standard error**	**df**	**t value**	**p**
Relative humidity	0.216	0.071	93.746	3.018	**0.003**
Landscape heterogeneity in configuration	0.057	0.061	89.687	-0.936	0.351
pc1_landscape	0.048	0.071	91.769	0.686	0.494

Chapter 5: General discussion

Red admiral (*Vanessa atalanta*) feeding on meadow cress (*Cardamine pratensis)*
at Lago La Ercina (Picos de Europa). Photo: Amparo Mora.

5.1. CONTEXT OF STUDY AND RESEARCH AIMS

Mountains worldwide are biodiversity hotspots, they hold a huge variety of organisms despite occupying only 25% of planet's surface (Rahbek *et al.*, 2019; Myers *et al.*, 2000). Southwestern European mountain ranges, included in the Mediterranean Basin biodiversity hotspot, are among the richest areas on butterflies in Europe (Van Swaay *et al.*, 2010). Abandonment of traditional land management is facilitating forest growth over grasslands in these mountains (Slancarova *et al.*, 2016; Ubach *et al.*, 2020; Mora *et al.*, 2022). The consequences of lack of human management are a current subject of debate (Daskalova & Kamp, 2023; Sartorello *et al.*, 2020; Crawford *et al.*, 2022), with very few long-term mountain studies contributing, due to the difficult terrain and weather conditions (but see Rödder *et al.*, 2021; Caro-Miralles *et al.*, 2023). Besides rural abandonment, climate change is predicted to have amplified effects on mountain ecosystems (Pepin *et al.*, 2015). Nevertheless, observations in these areas are particularly scarce, we may not be placing focus on those regions in the world that are warming more rapidly.

The general aim of this thesis was to investigate the conservation status of butterflies at Picos de Europa National Park, a South European mountain range claimed as a priority area for butterflies in Europe, under changes driven by land abandonment and climate change. Firstly, a regional analysis of butterfly diversity drivers was accomplished, looking for a better understanding of the spatial variation of diversity along the elevation gradient. Secondly, the influence of land abandonment on butterfly communities was assessed examining both local hay meadow characteristics with different periods of abandonment and landscape variables (Mora *et al.*, 2022). Finally, by analysing long-term butterfly monitoring data, population trends in the last decade were obtained and key environmental factors explaining those changes were discussed (Mora *et al.*, 2023). New insights gained from meeting the initial aims have helped to elaborate conclusions, raise new questions for research, and to develop a 5-year management plan for Picos de Europa National Park, all of which will inform future conservation efforts not only in the study region, but are also applicable to other mountain ranges in Southern Europe.

5.2 DRIVERS OF BUTTERFLY COMMUNITIES IN MOUNTAINS: PICOS DE EUROPA NATIONAL PARK AS A CASE STUDY

Determining the main drivers of mountain biodiversity is particularly relevant in a context of global change (Brondizio *et al.*, 2019) and biodiversity decline (Wagner, 2020).

Mountains have been long recognised as hotspots of biodiversity (Rahbek *et al*., 2019; Myers *et al*., 2000), with environmental variables and human pressures changing along the elevation gradient.

Although most commonly reported biodiversity patterns in mountains are decreasing species richness with increasing elevation and a mid-elevation peak of species richness (Rahbek 1995), we found a more complex pattern, with butterfly diversity peaking twice. We found diversity to show a peak at middle elevations (around 1500 m) as reported in other mountain ranges in the Iberian Peninsula (Álvarez *et al*., 2024; Wilson *et al*., 2007; Barea-Azcón *et al*., 2022). This peak may reflect the transition where cold temperatures start to be the primary limiting factor for organisms instead of water availability. The second unexpected peak was found at the lower end of the elevation gradient (150 m), in deep gorges free from the effects of frost during the winter. This peak could reflect the effect of past climate, as Mediterranean species may have found refuge in these locations during the Pleistocene climatic oscillations. Other studies in Europe (Gallou *et al*., 2017) report patterns differing from the classical middle-altitude peak, suggesting that incomplete sampling of elevation gradients, missing the lowest elevations, may mislead interpretations.

Several factors have been proposed as major drivers of diversity patterns in mountains, including climate, geographic position of the mountain range and historic context, as well as landscape heterogeneity and human traditional land-use (see McCain & Grytnes, 2010 for a review). At a global scale, Coehlo *et al*. (2023) have recently shown that climate and its geographical configuration and extension can explain as much as 90% of the variation in global species richness. In mountains, where topography is complex, an integrative approach considering climate and topography is needed, particularly taking into account adiabatic lapse rates in mountain slopes.

We found that near-surface relative humidity and continentality were major drivers of butterfly diversity in Picos de Europa National Park. Butterfly species richness and Shannon diversity increased with the distance to the coast in our study area, in line with patterns reported in previous studies (Kienle *et al.* 2023, Mühlethaler *et al.* 2024, Orr *et al.* 2021). On the other hand, near-surface relative humidity, which takes into account orographic effects (Brun *et al*., 2022), had a positive effect on butterfly diversity. Near-surface relative humidity is a synthetic variable in which temperature and water availability are integrated as a function of altitude and adiabatic lapse rates. Adiabatic lapse rates of air moving along slopes in mountains (i.e. changes of air temperature with altitude) (Brun *et al*., 2022; Díaz, 1996), are important as they result in an array of remarkable local meteorological phenomena such as horizontal precipitation, mist, strong warm winds leewards, thermal inversions and cool air pools (Iglesias *et al*., 2017), which have not usually been considered in relation to biodiversity patterns (but see Chan *et al*., 2024). These phenomena have emerged as critical for understanding the distribution of butterfly biodiversity in Picos de Europa, a mountain range just 20 km from the sea, where these effects are evident (Cortesi *et al*., 2014).

Apart from climate and continentality, we had hypothesised than landscape heterogeneity would determine butterfly diversity. Butterfly local populations are related in the landscape by some degree of migration, forming a metapopulation (Levins, 1970; Hanski, 2001). Landscape attributes, such as landscape connectivity and heterogeneity affect metapopulations (Wiens, 1997). While landscape attributes have been extensively related to butterfly community dynamics (Perovic *et al*., 2015; Seibold *et al*., 2019; Gámez-Virués *et al*., 2015; Dainese *et al*., 2017; Öckinger *et al*., 2012; Janisová *et al*., 2014) at the local scale, they have rarely been used as explanatory factors for diversity patterns at a regional scale (but see Bergman *et al*., 2004). Links between landscape ecology and broader scale biodiversity patterns are still underexplored (Teng *et al*., 2020). We found some, though inconclusive, evidence that landscape heterogeneity could drive butterfly diversity in Picos de Europa, in line with many recent studies (Kerr, 2001; Álvarez *et al*., 2024). Nevertheless, our results were not conclusive, as the positive relationship between butterfly diversity and landscape heterogeneity was influenced by an outlier site. We neither found a significant effect of habitat heterogeneity on butterfly species richness nor diversity within seminatural grasslands, despite this factor being a major driver of changes in species composition. It is possible that a high level of landscape heterogeneity is present across the whole of our study area. Because spatial heterogeneity is highly scale dependent (Kumar *et al*., 2009), future research quantifying it at a larger spatial scale or in larger time lapses (exploring possible extinction debt processes) would shed light on the relationship between landscape heterogeneity and butterfly diversity in NW Spain.

Linked to landscape heterogeneity, human traditional land-use was investigated as an influential variable on butterfly diversity at regional and local levels. In the domain of temperate forests, human action by cattle grazing, mowing and coppicing has created heterogeneous mosaics of forest patches intersected with seminatural grasslands. Nowadays, the abandonment of traditional land uses is giving rise to a succession towards forest habitats, homogenising landscapes (Poschlod *et al*., 2005; Ubach *et al*., 2020; Mora *et al*., 2022). The effect of the disappearance of human disturbances on biodiversity after land abandonment is currently under debate (Daskalova & Kamp, 2023; Sartorello *et al*., 2020; Crawford *et al*., 2022), with long term studies in mountain sites still lacking. Unexpectedly, we did not find any significant relationship between butterfly diversity at the regional level and the percentage of seminatural grasslands. We argue that this could be due to an extinction debt (Kuussaari *et al*. 2009, Figueiredo *et al.* 2019), with present butterfly diversity lagging behind the loss of grassland habitats, which have decreased by 70% in the last 60 years (García *et al*., 2018).

Landscapes that have recently experienced substantial habitat loss and fragmentation are expected to show a transient excess of rare species, which represents a signature of extinction debt (Hanski & Ovaskainen, 2002). This is the case of seminatural grasslands (hay meadows) in Picos de Europa, where communities are composed by six to ten abundant species and a long tail of rare species. These landscapes may be in the process of crossing the boundary between the states in which they are and are not able to support viable populations for these rare species (Hanski & Ovaskainen, 2002). This scenario of many “living dead” species is particularly worrying as rare climatic events, able to wipe out large metapopulations (Thomas *et al.* 1996, Ehrlich *et al.* 1980), are predicted to become more frequent (IPCC, 2022). Perturbations are not isolated and occur across various spatial and temporal scales, from local habitat losses to global warming (Figueiredo *et al.* 2019).

The issue is how fast butterfly species are tracking changing environments (loss of seminatural grasslands, climate change) at the metapopulation level, on an extended landscape bigger than the scale within which most individuals disperse. Reported causes of delayed extinctions are life-history traits that prolong individual survival and metapopulation dynamics that maintain populations under deteriorated conditions (Figueiredo et al. 2019). Landscape attributes, like the percentage of remaining focal habitat and landscape heterogeneity (in composition and configuration) would also influence time delay to extinction. Further research is needed to determine if current butterfly diversity in our region is better explained by historical rather than present seminatural grassland area and connectivity, as has been shown in other studies (Bommarco *et al*., 2014).

At a local scale, our study has shown that butterfly communities associated with seminatural grasslands are going through massive changes in Picos de Europa because of rural abandonment, in line with other studies in the north east corner of the Iberian Peninsula (Stefanescu *et al*., 2009; Herrando *et al*., 2016). We recorded a species turnover of around 52% in the first years of abandonment and around 48% after 18 years of abandonment. Although changes were not detected in species richness or diversity, community composition analysis revealed a tendency for communities to lose grassland specialists in the short term (3-7 years) but to reorganise in the long term (18 years) by gaining species with preference for closed habitats. It appears that a large species pool, supported by a highly heterogeneous landscape, allowed butterfly communities to reorganise in a relatively short period of time, after human perturbation ceased. Several authors remark that aspects of biodiversity other than species richness, particularly those based on abundance-based trait composition of communities, can be a promising approach to advance current research on the responses of biodiversity and ecosystem functioning to changes in the environment (Rotchés-Ribalta *et al*., 2018; Dainese *et al*., 2017; Valiente-Banuet *et al*., 2015). Throughout this thesis, the use of this approach, particularly the calculation of community indices based on butterfly preferences for open or closed habitats, has advanced significantly the understanding of the effect of land abandonment on butterfly communities.

Both butterfly and vascular plant species richness and diversity exhibited a pattern of change with time since abandonment, which conformed to the Intermediate Disturbance Hypothesis (Connell, 1978). This hypothesis, developed by Connell for sessile animals or plants, which determine much of habitat structure in local areas, sustains that communities seldom or never reach an equilibrium state and that high diversity is a consequence of continually changing conditions. Organisms are killed or badly damaged in all communities by disturbances that happen at various scales of frequency and intensity. This hypothesis suggests that the highest diversity is maintained at intermediate scales of disturbance (Connell, 1978). Disturbances interrupt and set back the process of competitive elimination among species.

Translated to a seminatural grassland, this would mean that disturbance caused by mowing would cause a certain amount of direct mortality on butterflies (Humbert *et al.* 2010, 2012; Berger *et al*. 2024) and on plants (the amount depending on the mowing technique, its timing on the season, and the synchrony of the disturbance on different grassland patches across the landscape). But in turn, annual mowing would reduce competition among species setting back the advance of herbs like *Brachypodium pinnatum* over other species (Stampfly & Zeiter, 1999) and facilitating the coexistence of different vascular plants needed as nectar or host plants for butterflies and many other insects. Traditionally, mountain meadows were mowed at the end of the butterfly reproductive season and after most of plants had thrown their mature seeds (end of August or beginning of September), in an asynchronous way across the landscape due to distinct management regimes among various owners and different years, so that a “refuge effect” would be allowed to happen. Our results were similar to those obtained in Southern Finland by Pöyry (2004) and PyKälä (2003), in a restauration experience of previously pastured grasslands with cattle grazing. They also compared grasslands at different stages of abandonment and concluded that butterfly (Pöyry, 2004) and vascular plant (Pykälä, 2003) species richness followed an intermediate disturbance pattern, being higher on grasslands that had been traditionally managed continually for decades. Even if we recognize the pattern of species richness with time in presence/absence of disturbances, different landscapes with different type, intensity and spatial location of disturbances don't allow for easy or direct comparisons.

In our study area, vascular plant communities in seminatural grasslands also changed quickly after abandonment, with significant differences in both species richness and diversity. However, these changes in the plant community within meadows did not have a significant effect on the butterfly communities, contrary to other previous studies (Pöyry *et al*., 2009; Uchida *et al*., 2016; Dainese *et al*., 2017). We argue that such studies were conducted in landscape matrices where remaining grasslands where a small percentage of total land cover (2-3%). In our study, with a remaining mean grassland cover of around 40%, mobility of butterflies across the landscape could be buffering the negative effect of plant diversity loss in abandoned meadows. Another potential and possibly complementary explanation is that even if butterflies have an obvious dependence on their host-plant species, these species may be a small percentage of the total plant diversity in an area (Hawkins & Porter, 2003b). For example, 2076 plant species are present in Britain (Stace, 2019) and only 145 (7% of them) are identified as host plants for butterfly larvae (Eeles, 2019). Future research is needed on host and nectar plants for butterflies in our study region, to tackle this issue appropriately.

We also found that landscape variables had a larger impact on butterfly community composition than local management. As we had hypothesised, landscape heterogeneity and the extent of open versus closed habitats in the landscape influenced the response of butterfly communities to abandonment. The butterfly community index of preference for open habitats increased when the landscape around the meadow was more heterogeneous in spatial configuration and when there was a higher proportion of grassland and scrub (open habitats) around the meadow. In opposition, the butterfly community index of preference for closed habitats increased when the landscape around the meadow was less heterogeneous in configuration and when there was a higher proportion of woodland around it. In other words, heterogeneous cultural landscapes (produced by combination of traditional farming practices, livestock grazing and forest management) are moderating the negative effects of local land-use abandonment and influencing grassland species persistence. The advance of forest over grasslands will homogenise landscapes, which may lead to a decline of open habitat specialist butterflies. Woodland specialists may also be at risk as they rely on woodland clearings

(Settele *et al*., 2009), which are also disappearing all around Europe because of lack of coppicing (Warren *et al*., 2021). In fact, our results on population trends using multispecies abundance indicators confirmed that species with preference for closed habitats are declining in the area, despite an increase of forest habitat. Furthermore, when analysing butterfly diversity trends over the last 14 years, we showed a decrease on species richness and Shannon diversity index while Simpson diversity index didn't change, suggesting rare and specialist species are disappearing while common species are thriving, confirming a process of homogenisation of butterfly fauna in the area, as reported in other European regions (Habel *et al*., 2022; Fox *et al*., 2023).

5.3 THE CONSERVATION STATUS OF BUTTERFLIES IN PICOS DE EUROPA NATIONAL PARK

Data from existing monitoring schemes point to a global crisis of butterflies across Europe (Stefanescu *et al*., 2011a,b, Brereton *et al*., 2019; Fox *et al*., 2023; Van Swaay *et al*., 2020), and our results corroborate this view. We found that over the last decade butterfly species richness and diversity across the region declined significantly: total butterfly abundance declined by 5.7% annually, and 26% of species for which population trends could be produced, showed a significant negative population trend. These results not only mirrored those reported in previous studies from elsewhere (Melero *et al*., 2016; Van Swaay *et al*., 2017; Wepprich *et al*., 2019), but the annual decline in abundance found in our study region also doubled the decline found in other studies, which ranged from 2.6% to 0.8% decline (see table 3 in Wreppich *et al*., 2019). This is particularly worrying as it confirms a global butterfly declining trend, even in well-established protected areas like Picos de Europa National Park, which has been protected for more than 100 years. Rural abandonment (García *et al*., 2018) together with amplified effects of climate change at mountains ecosystems (IPCC, 2022; Pepin *et al*., 2022) seem to be causing these accelerated declining rates.

We found a general moderate declining trend for all species, independent of their preference for open, intermediate or closed habitats, which was contrary to our initial hypothesis, assuming that species with preferences for closed habitats would be faring better than those preferring open habitats due to vegetation encroachment. As it has been suggested generally for cultural landscapes in Europe (Warren *et al*., 2021), and as previously discussed, woodland species may be at risk because of a lack of woodland management. Rare woodland species, such as *Lopinga achine*, *Hamearis lucina* or *Carterocephalus palaemon*, deserve further studies in Picos de Europa to ensure their persistence.

Based on previous studies (Brereton *et al*., 2019; DEFRA, 2021; Stefanescu *et al*., 2011a), we hypothesised that species with wider preferences (habitat generalist and/or widespread species) would fare better than those with narrow niches. However, a complex picture emerged with elevation, with population growth rates decreasing with increasing species mean elevation. Besides that, species with higher mean temperature index (STI) had significantly lower population growth rates. We argue that species at both extremes of the elevation gradient, that is, alpine species (over 1800 m) and mediterranean species (below 200 m), are faring worse than species at the rest of the elevation gradient, which have wider elevation ranges and so wider climatic tolerances, as it has been shown for butterflies and birds in other mountain areas in Europe (Rödder *et al*., 2021, Flousek *et al*., 2015).

When analysing data using multispecies abundance indicators, trends were of strong or moderate decline in sites above 900 meters, while the abundance indicator at lower elevations showed an uncertain trend, confirming our hypothesis of a negative relationship between abundance and elevation. Picos de Europa has experienced an increase in temperature of 0.21 °C per decade in the last 40 years, so climate change is likely responsible for the decline in alpine species above the treeline, as land use change has been minimal at this altitude. The same pattern has been confirmed recently for alpine birds in Picos de Europa (De Gabriel *et al*., 2022), adding evidence to the general consensus that mountains are affected by amplified effects of climate change (Pepin *et al*., 2022; IPCC, 2022). In our study, mountain butterfly species below the treeline (between 900-1200 m) showed the worst tendencies, with climate change and abandonment effects (vegetation encroachment and habitat loss) acting together, as already shown in other Mediterranean regions (Stefanescu *et al*., 2011a,b). Further research on the impacts of extreme weather events or prolonged stretches of weather outside of historical conditions on alpine populations is urgently needed (Halsh *et al*., 2021). Specifically, frost events during the winter in the absence of snow impose important challenges to alpine fauna and flora (Konvicka *et al*., 2021), as has been already shown in Picos de Europa alpine plant communities, undergoing a process of thermophilization or replacement of high-elevation species by low-elevation ones (Jiménez-Alfaro *et al*., 2024).

5.4 MANAGEMENT PLAN PROPOSAL FOR PICOS DE EUROPA NATIONAL PARK

The general aim of this thesis was to investigate the conservation status of butterflies at Picos de Europa National Park, claimed as a priority area for butterflies in Europe. New insights gained from meeting the initial aims have helped to elaborate conclusions and gain understanding of ecological processes on the study system. Conservation action must be based on sound scientific evidence if it is to be effective. The magnitude of butterfly abundance, species richness and species diversity loss found, have motivated the proposal of a five year Butterfly Conservation Plan for Picos de Europa National Park, to apply the scientific knowledge gathered throughout this thesis to conservation action. It has been directly written under the structure of European funded LIFE Nature projects (https://cinea.ec.europa.eu/programmes/life_en), with the intention of gathering the financial support from different institutions to set it up in the next years.

Butterfly monitoring in Picos de Europa has been active since 2013, contributing data to the Butterfly Monitoring Scheme Spain (BMS Spain) and to the European Butterfly Monitoring Scheme (eBMS). This data are used to elaborate the European Grassland Butterfly Index for the European Environmental Agency. The elaboration of a national grassland butterfly index and the aim of putting measures in place to increase its trend by 2030 and thereafter, has been included in the recent EU regulation on nature restoration (Regulation (EU) 2024/1991 on nature restoration and amending Regulation (EU) 2022/869), which opens the door for a broad range of ecosystems to be restored. Our project is in line with this regulation.

Our project aims are to:

- Restore seminatural grasslands habitats for butterflies on a landscape scale, opening areas where traditional management has been abandoned, both directly and through land management agreements with landowners. Our results show that landscape characteristics act as a strong filter of functional-trait diversity for butterfly communities within seminatural grasslands and dominate over local effects. This emphasizes the importance of landscape-scale management (Gámez-Virués *et al.* 2015, Ellis *et al.* 2012).

  The obvious measure for restoring hay meadows is going back to its traditional management. Our results suggest than delayed mowings, every 3-7 years, better than annually can increase butterfly density in the meadows. Through rotative mowing of different meadows in the landscape each year, insects would always have uncut refuges to buffer the impact of mowing mortality. Promoting landscape heterogeneity, in space and time, to enhance biodiversity has been a recurrent conclusion throughout all our study.

  Furthermore, our results show that standard BMS protocol (Pollard & Yates, 1993) is useful for monitoring restauration actions and their effects on butterflies. It provides data on butterfly species abundance, useful to analyse community trait based indices like TAO Index of preferences for open and closed habitats, which are informative of community composition changes in short periods of time, unlike species richness or species diversity, which need longer periods to reflect environmental changes.

- Carry out ecological applied studies on endangered species (high mountain, woodland and grassland specialists). We have shown that species at both extremes of the elevational range, which are not able to migrate because of their degree of specialism, are faring worse than species at mid elevations. Also, we demonstrated that common species are faring better than specialist as Simpson diversity index did not change along the study period while species richness and Shannon diversity index decreased. So ecological studies are needed on species like *Parnassius apollo* (high mountain) or *Laeosopis roboris* (gorges with Mediterranean characterictics) to disentangle the complex relationships between temperature, vegetation changes and each species particular ecological requirements. This is extensive to other specialist species at habitats like woodlands (*Lopinga achine*) or grasslands (*Speyeria aglaja*).
- Establish a captive breeding programme, both to increase scientific knowledge on target species life cycles and to reinforce natural populations at risk. The alarming results shown throughout this study in terms of butterfly species richness, diversity and abundance loss call for action. Species like *Lycaena helle*, at its European southernmost location and with only a few individuals, could greatly benefit from a captive breeding program. Previous successful experiences in the UK (Thomas & Harrison, 1992) are extremely valuable to inform these actions.
- Give support to a shift in agricultural practices both facilitating education for present and future farmers and recovering traditional ecological knowledge. Specifically, offering grants to local young and future farmers to accomplish a professional education degree on agriculture, looking for an integrative and sustainable approach; and holding workshops on regenerative and sustainable agriculture, and the use of butterflies as indicators for local landowners. Finally, a special effort will be dedicated to recover ecological traditional knowledge on landscape management from local communities. Previous work has been done on this issue, indicating a very important potential source of useful guidelines for restoration of butterfly habitats.

The target species, all protected by the European Habitat Directive, will be *Lopinga achine, Phengaris nausithous, Parnassius apollo, Lycaena helle* and *Euphydryas aurinia*. Nonetheless, all 137 butterfly species in Picos de Europa National Park would be held into account, as the project aims to have a community approach. Target habitats, also protected under Habitats Directive, will be 6510 Lowland hay meadows and 6520 Mountain hay meadows.

Hopefully, an evidence based management plan, grounded on previous and contrasted research, would allow for an efficient allocation of financial resources to butterfly conservation, while being the frame permitting extended studies on butterfly populations to close the circle of continuous monitoring, data analysis, extraction and discussion of results, and application to conservation management.

5.5 FUTURE RESEARCH

Several lines of research emerged from our studies, some of them highlighting the need to widen the scientific knowledge on South European butterfly ecology and others imposed by the urgent need to investigate how global climate change is acting upon ecosystems. Questions are also posed on the possible role of historical landscape factors in explaining current butterfly diversity. Therefore, further research is proposed on:

- **Increasing knowledge on host and nectar plants for butterflies in Southern Europe**. Our studies have pointed out that butterfly diversity may not be directly related to plant diversity in an area, but rather with diversity of their host and nectar plants, which may be a tiny fraction of total plant diversity in an area. Recent studies have succeeded in relating plant and butterfly diversity when using these more targeted variables (Kerner *et al.*, 2023; Sánchez-Davila *et al.*, 2024).

  Although there is scattered information about certain species (Baz, 2002; Stefanescu, 1997; Munguira *et al.*, 1993) or certain regions inside the Iberian Peninsula (Gutiérrez *et al.*, 2016), as a starting point a literature review on Iberian host and nectar plants for butterflies is needed to put together all the existing knowledge and highlight knowledge gaps to be covered.

- **Woodland butterfly species status**. European woodland butterflies utilise sunny habitats within woodlands, such as sparse stands, bogs, stream sides, clearings, rides or edges. Managing woodlands for many threatened species consists of maintaining relatively low tree density and forest clearings (Settele *et al.*, 2009). Our results pointed to a global decline of butterflies, independent of their preferences for open or closed habitats. Woodland specialists may not be benefiting from the advance of forest over grasslands, but suffering due to lack of management on woodlands because of rural abandonment (Warren *et al*., 2021). Further research is needed in rare species like *Lopinga achine*, *Carterocephalus palaemon* or *Hamearis lucina*, which are dependent on woodland clearings, to elucidate these issues.

- **Impact of extreme weather events or prolonged stretches of weather outside of historical conditions on alpine populations** (Halsch *et al*., 2021). Recent evidence in Picos de Europa points to the effects of frost without the protection of snow cover over alpine ecosystems during the winter period. This may drive plant species turnover from alpine species (adapted to the buffering protection of snow) to lower altitude Mediterranean species, more adapted to frost in the winter and warmer temperatures all year round (Jiménez-Alfaro *et al*., 2024). The impact of extreme frost events on alpine ecosystems needs to be assessed urgently, as they could be affecting alpine butterfly species lethally while they overwinter in the soil as larvae or pupae (Konvicka *et al*., 2021).

- **Lowland butterfly community composition changes**. We showed that lowland butterfly communities in Picos de Europa were changing towards communities with preference for colder temperatures and for drier conditions. Further research is needed to disentangle the drivers of lowland community compositional change. We propose possible explanations as downslope migration of species from higher elevations (Lenoir *et al*., 2010), microclimate effects because of vegetation encroachment (Clavero *et al*., 2011; Mingarro *et al*., 2021) and changes in regional weather patterns, with more days of thermal inversion and lower temperatures during the winter (sunny weather preventing cold air at valley bottoms to rise up).

- **Landscape heterogeneity as biodiversity driver.** We could not present concluding evidence of landscape heterogeneity being a significant driver of regional butterfly diversity, although results on the rapid butterfly community reorganisation after abandonment point to heterogeneous landscapes maintaining a large species pool and influencing grassland species persistence (Tscharntke *et al*., 2012; Oliver *et al*., 2010). Further sampling to add more sites and statistical power to the study may shed light onto this question.

- **Extinction debt processes: Is butterfly diversity lagging behind seminatural grasslands losses?** We showed butterfly diversity at the regional level was not significantly explained by the percentage of seminatural grasslands (a proxy for traditional management), which was unexpected as we had hypothesised that traditionally managed grasslands would have promoted landscape heterogeneity by interspersing grassland within a continuous forested landscape. Further research is needed to determine if current butterfly diversity in Picos de Europa is better explained by historical rather than present seminatural grassland area (because of an extinction debt process), as it has been shown in other studies (Bommarco *et al.*, 2014).

5.6 CONCLUDING REMARKS

Overall, a rapidly declining status of Picos de Europa (Southwestern Europe mountain range) butterfly populations was found: 45% of butterfly abundance lost and species richness and Shannon diversity declining in the last 14 years. This was one of the first long-term monitoring studies made in Europe specifically focused on mountain butterflies (Rödder *et al.*, 2021; Caro-Miralles *et al.*, 2023; Mora *et al.*, 2023). Two potential main drivers of the decline appear to be climate change and the abandonment of traditional management. Butterfly species with broader thermal ranges (capable of shifting in elevation) seem to be faring better than those at both extremes of the elevation gradient and forest are advancing over grasslands, homogenising landscapes and reorganising communities. In order to help reverting this negative trend, the findings of this thesis are being used to develop a 5-year management plan for Picos de Europa NP, which is outlined in Appendix 1.

Finally, land abandonment and amplified effects of climate change are acting not only upon our study region, but also other mountain ranges in Europe (Pyrenees, Carpathian mountains, Balkan mountains and the Alps, among many others). More focus is needed on mountain ecosystems, European biodiversity hotspots that are undergoing accelerated major changes. We may not be monitoring some of the richest regions in Europe that are under a high risk, both of losing biodiversity and irreplaceable traditional knowledge on mountain ecosystem management.

Appendix 1: Five year Butterfly Conservation Plan for Picos de Europa National Park

Dusky large blue (*Phengaris nausithous*) on great burnet (*Sanguisorba officinalis)*, its hostplant, in Valdeón (Picos de Europa). Photo: Amparo Mora.

TECHNICAL DESCRIPTION

PROJECT	
Project name:	Butterflies in their landscapes
Project acronym:	BELLE (**B**utterflies, **E**ducation, **L**andowners, **L**andscapes, **E**cological traditional knowledge)
Coordinator contact:	Amparo Mora, Picos de Europa National Park (amora@pnpeu.es)

PROJECT SUMMARY

Project summary (2000 characters)

Southwestern Europe mountain ecosystems are under a great threat. In Picos de Europa (NW Spain), protected as National Park since 1918, a decline of 45% in total butterfly abundance has been documented in the period 2013-2021, parallel to a decline on species richness and diversity (Mora et al. 2023). Combined effects of amplified climate change and habitat loss because of rural abandonment appear to be affecting butterfly populations (Mora et al. 2022). Previous EU funded projects have shown a decrease of 70% of seminatural grasslands (particularly relevant habitats for butterflies) in the area since 1959 (García et al. 2018; www.sospraderas.eu).

Project BELLE is grounded on sound research and monitoring on Picos de Europa butterflies, their habitats and on previous collaboration with local communities through landscape management. The project aims to act on a landscape scale, opening areas where traditional management has been abandoned, both directly and through land management agreements with landowners. Education for landscape is proposed as a major part of BELLE, offering grants to local young and future farmers to accomplish a professional education degree on agriculture, looking for an integrative and sustainable approach. Also, workshops on regenerative and sustainable agriculture, and the use of butterflies as indicators will be held for local landowners.

Regarding applied research on butterfly populations, three main actions are foreseen: continued butterfly monitoring in the area (active since 2013), increasing the number of volunteer and professional recorders; developing ecological applied research on endangered species (high mountain, woodland and grassland specialists); and captive breeding of target species both to enlarge scientific knowledge on their life cycles and to reinforce natural populations at risk.

Finally, a special effort will be dedicated to recover ecological traditional knowledge on landscape management from local communities. Previous work has been done on this issue, indicating a very important potential source of useful guidelines for restoration of butterfly habitats.

Focus will be placed on sustainability throughout the project as halting CO_2 emissions and further climate change is vital for butterfly conservation.

1. RELEVANCE

1.1 Background and general project objectives

Background and general project objectives

Butterfly monitoring and ecological applied research has been accomplished in Picos de Europa since 2011. Picos de Europa has been recognised as a priority area for butterflies in Europe, holding 60% of all Ibero-Balearic species (García-Barros et al. 2013) and 28% of all European species (Van Swaay et al. 2010), including several rare species, three endemic and four legally protected species such as *Lopinga achine*, *Phengaris nausithous*, *Erebia palarica*, *Parnassius apollo* or *Lycaena helle*, many of which are at the southwestern edge of their distribution.

Traditional practices (shepherding, mowing and coppicing) are disappearing at an accelerated rate in the last decades (García et al. 2018). Rural abandonment together with the effects of climate change are causing a dramatic decline of 45% butterfly abundance in the period 2013-2021 (Mora et al. 2022, 2023), species richness and diversity.

Butterfly monitoring in Picos de Europa is active since 2013, contributing data to the Butterfly Monitoring Scheme Spain (BMS Spain) and to the European Butterfly Monitoring Scheme (eBMS). This data are used to elaborate the European Grassland Butterfly Index, a European Environmental Agency official index. Reversing the decline of pollinators is an objective of the EU Biodiversity Strategy for 2030 and the EU Pollinators Initiative. The EU regulation on nature restoration opens the door for a broad range of ecosystems to be restored. The grassland butterfly index is included among three indicators in agricultural ecosystems out of which Member States have to select at least two, with the obligation to put measures in place which aim to achieve an increasing trend in the chosen indicators by 2030 and thereafter until satisfactory levels are achieved. Project BELLE is absolutely in line with recent EU regulation and provides grounded experience to achieve improvements by restoring grassland butterfly populations and their ecosystems.

Previous Interreg SUDOE project SOS Praderas, held in Picos de Europa in 2016-2019, paved the way to project BELLE, implementing restoring measures for abandoned seminatural grasslands in Picos de Europa in different and relevant landscape units. Picos de Europa is protected as National Park, it is part of Natura 2000 network and it is designated also as a Man and Biosphere Reserve.

Project BELLE aims to restore seminatural grasslands habitats for butterflies on a landscape scale, to run ecological applied studies on endangered species, to run a captive breeding programme to reinforce endangered populations, and to give support to a shift in agricultural practices both facilitating education for present and future farmers and recovering traditional ecological knowledge.

Target species:
Lopinga achine, annex IV Habitats Directive
Phengaris nausithous, annexes II and IV Habitats Directive
Parnassius apollo, annex IV Habitats Directive
Lycaena helle, annex II Habitats Directive
Euphydryas aurinia, annex II Habitats Directive
All 137 butterfly species in Picos de Europa National Park, the project aims to have a community approach, especially focusing on grassland, woodland and high mountain

specialists.
Target habitats:
6510 Lowland hay meadows, annex I Habitats Directive.
6520 Mountain hay meadows, annex I Habitats Directive.

1.2 Specific project objectives

Specific project objectives

- **Maintaining open areas** where traditional management has been abandoned (hay meadows and clearings in woods) at a landscape scale. 3 landscape units (aprox. 1000 hectares each) with increased % of open areas and increased connectivity.
- **Education** for landscape. Support future local farmers by granting access to formal education on **professional agricultural degrees** with a focus on **sustainable agriculture**. Education for landowners on sustainable agriculture and butterflies as environmental indicators. 4 two-year grants for future farmers along project and 5 workshops for landowners.
- Continued **monitoring of** Picos de Europa **butterflies** and increase the number of recorders. At least 25 new recorders and 10 new transect along project.
- **Ecological studies of endangered butterfly species**, mainly grassland, woodland and high mountain specialists listed in the Habitats Directive. At least 3 species covered.
- **Captive breeding programme** for target species to gain knowledge on their life cycles and reinforce natural populations. At least 3 species covered.
- **Recovering ecological traditional knowledge** from local communities developing traditional land management maps using GIS (geographic information system). At least 3 landscape units (same as chosen for maintaining open areas).

a. Concept and methodology

Concept and methodology

A skilled team is already assembled in Picos de Europa National Park, composed by administrative personnel (office support), rangers (monitoring), guides (education and communication) and conservation technicians (project coordinators), which has been running butterfly monitoring and ecological applied studies since 2011. Also, landscape management actions to maintain open areas have been run in the period 2015-2019. Rangers and guides establish direct links with local farmers. Further coordination and networking with other institutions is accomplished by conservation technicians and Park authorities (director).

Further scientific and education capacities will be covered by academic institutions and ngos in the consortium (other beneficiaries). A realistic timetable, clear division of tasks, two in person meetings per year plus online meetings each month will guarantee appropriate timing of milestones and deliverables. A technical assistance for administrative project management support and another technical assistance for communication activities will be contracted.

Proposed work packages are all directed towards an enriching interaction with local communities looking after cultural landscapes that are most significant for them, offering education opportunities, proposing participation through volunteering in butterfly monitoring and appreciating and adding value to their traditional knowledge. If these actions are welcomed it is probable that they could be implemented in wider areas, being easy to disseminate the results through Spanish and European protected areas networks and scientific networks.

2. IMPLEMENTATION

2.1 Work packages and activities

Work plan

WP1 → Project management and coordination activities.
WP2 → Maintaining open areas.
WP3 → Education for landscape.
WP4 → Butterfly monitoring.
WP5 → Ecological studies on butterfly species.
WP6 → Captive breeding of target species.
WP7 → Recovering of ecological traditional knowledge.
WP8 → Sustainability, replication and exploitation of project results.

Work Package 1: Project management and coordination

Duration:	60 months	**Lead Beneficiary:**	PENP	Picos de Europa National Park

Objectives and results

- Guarantee appropiate timing of milestones and deliverables.
- Guarantee appropiate payment times.
- Guarantee alternative solutions to the original plan if needed.
- Guarantee appropiate communication among beneficiaries and with financing authorities.

Activities and division of work (WP description)

T.1.1 Project management and coordination:
Two in person meetings per year plus online meetings each month will guarantee appropriate financial management, communication among beneficiaries and appropriate timing of milestones and deliverables. A technical assistance for administrative project management support will be contracted.

T.1.2 Project monitoring and evaluation:
Milestones and deriverables from all work packages will be assessed on a 6-month basis.

Work Package 2: Maintaining open areas				
Duration:	M9 – M48	**Lead Beneficiary:**	PENP	Picos de Europa National Park
Objectives and results				
・ Maintaining open areas where traditional management has been abandoned (hay meadows and clearings in woods) at a landscape scale. ・ Action over 3 landscape units (aprox. 1000 hectares) with increased % of open areas and increased connectivity at the end of the project.				
Activities and division of work (WP description)				
T.2.1 Landscape units selection and landowners engagement. **T.2.2 Direct actions with project resources: mowing/pruning with landowners permission.** **T.2.3 Indirect actions through landscape management agreements with landowners.**				

Work Package 3: Education for landscape				
Duration:	M12 – M51	**Lead Beneficiary:**	PENP	Picos de Europa National Park
Objectives and results				
・ Provide present and future farmers with education on sustainable agriculture and butterflies as biodiversity indicators. ・ Support young future farmers in their access to a formal professional degree on agriculture, with a special focus on sustainable agriculture through grants.				
Activities and division of work (WP description)				
T.3.1 Workshops on sustainable agriculture. **T.3.2 Grants programme for young locals to access formal agricultural education.**				

Work Package 4: Butterfly monitoring				
Duration:	M1 – M57	**Lead Beneficiary:**	PENP	Picos de Europa National Park
Objectives and results				
・ Continued monitoring of PENP butterflies. ・ Increasing the number of Butterfly Monitoring Scheme recorders in the area.				
Activities and division of work (WP description)				
T.4.1 Continued monitoring at PENP. **T.4.2 Expanding BMS volunteer network in the area (butterfly workshops and volunteer support group)** **T.4.3 Implementing of BMS monitoring at Parque Regional Montaña de Riaño y Mampodre (annexed protected area)**				

Work Package 5: Ecological studies of target butterfly species				
Duration:	M1 – M57	**Lead Beneficiary:**	PENP	Picos de Europa National Park
Objectives and results				
・ Increase scientific knowledge on woodland specialists (*Lopinga achine, Hamearis lucina, Carterocephalus palaemon*); grassland specialists (*Lycaena helle, Phengaris nausithous, Euphydryas aurinia*) and high mountain specialists (*Parnassius apollo, Agriades pyrenaicus*) ・ Developing conservation plans for target habitats with specific measures for each target species.				
Activities and division of work (WP description)				
T.5.1 Literature review and study design. **T.5.2 Field data gathering and field experiments.** **T.5.3 Data analysis, discussion and writing of conservation plans.**				

Work Package 6: Captive breeding of target species				
Duration:	M1– M57	**Lead Beneficiary:**	PENP	Picos de Europa National Park
Objectives and results				
・ Developing butterfly captive breeding capacities. ・ Increase scientific knowledge on life cycles of target species (*Lycaena helle, Lopinga achine, Parnassius apollo*). ・ Reinforce natural populations (coupled with habitat management measures when necessary, included in WP2).				
Activities and division of work (WP description)				
T.6.1 Literature review, programme design and ex-situ preparations. **T.6.2 Environmental authorities permission gathering.** **T.6.3 Captive breeding ex-situ and population reinforcement.** **T.6.4. Manual for butterflies captive breeding and population reinforcement writing.**				

<table>
<tr><td colspan="5">Work Package 7: Recovering of ecological traditional knowledge</td></tr>
<tr><td>Duration:</td><td>M13– M48</td><td>Lead Beneficiary:</td><td>PENP</td><td>Picos de Europa National Park</td></tr>
<tr><td colspan="5">Objectives and results</td></tr>
<tr><td colspan="5">・ To gather ecological traditional knowledge on landscape management in collaboration with local communities.</td></tr>
<tr><td colspan="5">Activities and division of work (WP description)</td></tr>
<tr><td colspan="5">T.7.1 Building of contacts, networking with townhalls, local associations, etc and meetings plan designing.
T.7.2 Workshops with local communities to gather information based on GIS/aerial photographs of landscape units.
T.7.3 Specific meetings with local women on traditional knowledge held by women.
T.7.4. Maps editing.</td></tr>
</table>

<table>
<tr><td colspan="5">Work Package 8: Sustainability, replication and exploitation of project results.</td></tr>
<tr><td>Duration:</td><td>M51– M60</td><td>Lead Beneficiary:</td><td>PENP</td><td>Picos de Europa National Park</td></tr>
<tr><td colspan="5">Objectives and results</td></tr>
<tr><td colspan="5">・ To explore future financial resources to continue project actions.
・ Networking with other protected areas, academic institutions and agricultural organisations to replicate project actions elsewhere.</td></tr>
<tr><td colspan="5">Activities and division of work (WP description)</td></tr>
<tr><td colspan="5">T.7.1 Future financial resources search and building of new propositions/consortiums.
T.7.2 Final project seminar to disseminate results.
T.7.3 Dissemination of results in the following networks: Spanish National Park’s; Spanish Butterfly Monitoring Scheme Annual Meetings; European Butterfly Monitoring Scheme; ESPARC (Spanish network of protected areas); Europarc (European network of protected areas); LTER-Spain (Long Term Ecological Research-Spain)</td></tr>
</table>

2.2 Timetable

Timetable																				
ACTIVITY	YEAR 1				YEAR 2				YEAR 3				YEAR 4				YEAR 5			
	M1	M4	M7	M10	M13	M16	M19	M22	M25	M28	M31	M34	M37	M40	M43	M46	M49	M52	M55	M58
WP1 – Project management and coordination	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
WP2 – Maintaining open areas			■	■			■	■			■	■			■	■				
WP3 – Education for landscape	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
WP4 – Butterfly monitoring		■	■			■	■			■	■			■	■			■	■	
WP5 – Ecological studies on butterfly species			■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		
WP6 – Captive breeding of target species	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		
WP7 – Recovering of traditional knowledge				■	■			■	■			■	■			■	■			
WP8 – Sustainability, replication and exploitarion of project results															■	■	■	■	■	■

2.3 Budget

Estimated budget — Resources				
Work package	**Cost (€)**	**Category**	**Subcontracted (Y/N)**	**Justification**
WP1 - Coordination	192,000	1	N	Personnel costs for project coordination.
	96,000	4	Y	Technical assistance for administrative support.
WP2 – Open areas	40,000	4	Y	Technical assistance to accomplish works.
WP3 – Education for landscape	32,000	1	N	Personnel costs.
	10,000	4	N	Workshops different costs.
	80,000	5	N	Grants for agriculture students.
WP4 – Butterfly monitoring	4,000	4	N	Workshops different costs.
	9,600	4	Y	Technical assistance to expand BMS network.
WP5 – Ecological studies	40,000	2	N	Travel and subsistence to accomplish field studies.
WP6 – Captive breeding programme	96,000	1	N	Personnel costs.
	25,000	3	N	Equipment (incl, Infrastructure).
WP7 – Recovering traditional knowledge	12,000	4	N	Workshops different costs.
WP8 - Replication	48,000	4	Y	Technical assistance for communication tasks.
TOTAL (€)	**684,600**		193,600	
	100%		28,27%	

Categories: 1= Personnel; 2=Travel and subsistence; 3=Equipment (incl. Infrastructure); 4=Other goods, works and services; 5=Financial support to third parties.

BIBLIOGRAPHY

Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002). Global biodiversity, biochemical kinetics and the energetic-equivalence rule. *Science*, 297 (5586), 1545-1548.

Alonso Felpete, J.I., González Robinson, S.L., Fernández Rodríguez, A., Sanzo Rodríguez, I., Mora Cabello de Alba, A., Bueno Sánchez, A. & Díaz González, T.E. (2011). Catálogo florístico del Parque Nacional Picos de Europa. *Documentos del Jardín Botánico Atlántico de Gijón*, 8. Ayuntamiento de Gijón. https://parquenacionalpicoseuropa.es/wp-content/uploads/2016/01/Catalogo_publ_JBA_2011.pdf

Alonso, J.I. (Coord). (2013). *Mapa de vegetación 1:10.000 del Parque Nacional Picos de Europa*. Memoria de análisis global de la vegetación del Parque Nacional Picos de Europa. Organismo Autónomo Parques Nacionales.

Álvarez, H.A., Walker, E., Mingarro, M., Ursul, G., Cancela, J.P., Bassett, L., & Wilson, R.J. (2024). Heterogeneity in habitat and microclimate delay butterfly community tracking of climate change over an elevation gradient. *Biological Conservation*, 289, 110389.

Araújo, M.B., Lobo, J.M. & Moreno, J.C. (2007). The effectiveness of Iberian protected areas in conserving terrestrial biodiversity. *Conservation Biology*, 21: 1423–1432.

Atleo, E.R. (2011). *Principles of tsawalk: an indigenous approach to global crisis*. Vancouver, Canada: University of British Columbia Press.

Balmer, O. & Erhardt, A. (2000). Consequences of succession on extensively grazed grasslands for central european butterfly communities: rethinking conservation practices. *Conservation Biology*, 14, 746-757. https://doi.org/10.1046/j.1523-1739.2000.98612.x

Barea-Azcón, J. M., Pérez-Luque, A. J., Olivares, F. J., Guerrero, M., Galiana-García, M., Chaves, M. D., ... & Munguira, M. L. (2023). Butterfly diversity, richness, and density patterns in Sierra Nevada (SE Spain): Conservation implications under a global change scenario. Insect Conservation and Diversity, 16(2), 217-230.

Barton, K., 2022. MuMIn: Multi-Model Inference (version 1.47.1).

Bates, D., Maechler, M. Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Baz, A. (2002). Nectar plant sources for the threatened Apollo butterfly (Parnassius apollo L. 1758) in populations of central Spain. *Biological Conservation*, 103(3), 277-282.

Berger, J. L., Staab, M., Hartlieb, M., Simons, N. K., Wells, K., Gossner, M. M., Vogt, J., Achury, R., Seibold, S., Hemp, A., Weisser, W.W. & Blüthgen, N. (2024). The day after mowing: Time and type of mowing influence grassland arthropods. *Ecological Applications*, 34(6), e3022.

Bergman, K.O. (1999). Habitat utilisation by Lopinga achine (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. *Biological Conservation*, 88: 69-74.

Bergman, K.O. (2001). Population dynamics and the importance of habitat management for conservation of the butterfly Lopinga achine. *Journal of Applied Ecology*, 38(6), 1303-1313.

Bergman, K.O., Askling, J., Ekberg, O., Ignell, H., Wahlman, H., & Milberg, P. (2004). Landscape effects on butterfly assemblages in an agricultural region. *Ecography*, 27(5), 619-628.

Berkes, F. (2018). *Sacred ecology*. London, UK: Routledge.

Blondel, J. (2006). The 'design'of Mediterranean landscapes: a millennial story of humans and ecological systems during the historic period. *Human ecology*, 34, 713-729.

Blowes, S.A., McGill, B., Brambilla, V., Chow, C.F., Engel, T., Fontrodona-Eslava, A., ... & Chase, J.M. (2024). Synthesis reveals approximately balanced biotic differentiation and homogenization. *Science Advances*, 10(8), eadj9395.

Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., ... & Dornelas, M. (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science*, 366(6463), 339-345.

Bohdalková, E., Toszogyova, A., Šímová, I., & Storch, D. (2021). Universality in biodiversity patterns: variation in species–temperature and species–productivity relationships reveals a prominent role of productivity in diversity gradients. *Ecography*, 44(9), 1366-1378.

Bommarco, R., Lindborg, R., Marini, L., & Öckinger, E. (2014). Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. *Diversity and Distributions*, 20(5), 591-599.

Bonari, G., Fajmon, K., Malenovský, I., Zelený, D., Holuša, J., Jongepierová, I., ... & Chytrý, M. (2017). Management of semi-natural grasslands benefiting both plant and insect diversity: The importance of heterogeneity and tradition. *Agriculture, Ecosystems & Environment*, 246, 243-25

Bourn, N.A. & Bulman, C.R. (2005). Landscape scale conservation, theory into practice. *Studies on the ecology and conservation of butterflies in Europe*, 1, 111-112.

Brereton, T.M., Botham, M.S., Middlebrook, I., Randle, Z., Noble D., Harris, S., Dennis, E.B., Robinson, A.E., Peck, K. & Roy, D.B. (2019). *United Kingdom Butterfly Monitoring Scheme report for 2018*. Centre for Ecology & Hydrology, Butterfly Conservation, British Trust for Ornithology and Joint Nature Conservation Committee.

Brondizio ES, Settele J, Ngo Ht (Eds.) (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES Secretariat, Bonn, Germany.

Brun, P., Zimmermann, N.E., Hari, C., Pellissier, L., & Karger, D.N. (2022). Global climate-related predictors at kilometer resolution for the past and future. *Earth System Science Data*, 14(12), 5573-5603.

Bruppacher, L., Pellet, J., Arlettaz, R. & Humbert, J. (2016). Simple modifications of mowing regime promote butterflies in extensively managed meadows: Evidence from field-scale experiments. *Biological Conservation*, 196, 196-202. http://dx.doi.org/10.1016/j.biocon.2016.02.018

Buira, A., Aedo, C. & Medina, L. (2017). Spatial patterns of the Iberia and Balearic endemic vascular flora. *Biodiversity Conservation*, 26, 479-508.

Carnicer, J., Stefanescu, C., Vila, R., Dinca, V., Font, X. & Peñuelas, J. (2013). A unified framework for diversity gradients: the adaptive trait continuum. *Global Ecology and Biogeography*, 22, 6–18.

Caro-Miralles, E., & Gutiérrez, D. (2023). Butterfly population trends track vegetation encroachment but not climate warming in a Mediterranean mountain. *Biodiversity and Conservation*, 32(6), 2017-2035.

Chan, W.P., Lenoir, J., Mai, G.S., Kuo, H.C., Chen, I.C., & Shen, S.F. (2024). Climate velocities and species tracking in global mountain regions. *Nature*, 629(8010), 114-120.

Chao, A., Gotelli, N.J., Hsieh T.C., Sande E.L., Ma K.H., Colwell, R.K. & Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45–67.

Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93, 2533–2547.

Chowdhury, S., Jennions, M.D., Zalucki, M. P., Maron, M., Watson, J.E., & Fuller, R.A. (2023). Protected areas and the future of insect conservation. *Trends in Ecology & Evolution*, 38(1), 85-95.

Clavero, C., Villero, D. & Brotons, L. (2011). Climate change or land use dynamics: do we know what climate change indicators indicate? *PloSOne*, 6, e18581.

Coelho, M.T.P., Barreto, E., Rangel, T.F., Diniz-Filho, J.A.F., Wüest, R.O., Bach, W., ... & Graham, C.H. (2023). The geography of climate and the global patterns of species diversity. *Nature*, 622(7983), 537-544.

Colom, P., Carreras, D. & Stefanescu, C. (2019). Long-term monitoring of Menorcan butterfly populations reveals widespread insular biogeographical patterns and negative trends. *Biodiversity and Conservation*, 28(7), 1837-1851.

Colom, P., Traveset, A. & Stefanescu, C. (2021). Long-term effects of abandonment and restoration of Mediterranean meadows on butterfly-plant interactions. *Journal of Insect Conservation*. https://doi.org/10.1007/s10841-021-00307-w

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. Science, vol. 199, nº 4335: 1302-1310.

Convention of Biological Diversity (2020). *Update of the zero draft of the Post-2020 Global Biodiversity Framework*, Convention on Biological Diversity, UN Environment Programme.

Cortesi, N., González-Hidalgo, J.C., Brunetti, M. & de Luis, M. (2014). Spatial variability of precipitation in Spain. *Regional environmental change*, 14: 1743-1749.

Crawford, C.L., Yin, H., Radeloff, V.C., & Wilcove, D.S. (2022). Rural land abandonment is too ephemeral to provide major benefits for biodiversity and climate. *Science advances*, 8(21), eabm8999.

Cunningham, C.A., Crick, H.Q.P., Morecroft, M.D., Thomas, C.D. & Beale, C.M.. (2021a). Translating area-based conservation pledges into efficient biodiversity protection outcomes. *Communications Biology*, 4, 1043. https://doi.org/10.1038/s42003-021-02590-4

Cunningham, C.A., Thomas, C.D., Morecroft, M.D., Crick, H.Q.P. & Beale, C.M. (2021b). The effectiveness of the protected area network of Great Britain. *Biological Conservation*, 257, 109146, ISSN 0006-3207. Available from: https://doi.org/10.1016/j.biocon.2021.109146

Cuttelod, A., García, N., Abdul Malak, D., Temple, H. & Katariya, V. (2008). *The Mediterranean: a biodiversity hotspot under threat. In The 2008 Review of The IUCN Red List of Threatened Species.* Vie, J.-C., Hilton-Taylor, C. and Stuart, S.N. (Eds). Gland: IUCN.

Dainese, M., Isaac, N.J.B, Powney, G, Bommarco, R., Öckinger, E., Kuussaari, M., Pöyry, J., Benton, T.G., Gabriel, D., Hodgson, J.A., Kunin, W.E., Lindborg, R., Sait, S.M. & Marini, L. (2017). Landscape simplification weakens the association between terrestrial producer and consumer diversity in Europe. *Global Change Biology* 23, 3040–3051.

Dantas de Miranda, M., Pereira, H.M., Corley, M.F.V. & Merckx, T. (2019). Beta diversity patterns reveal positive effects of farmland abandonment on moth communities. *Scientific Reports* 9, 1549. https://doi.org/10.1038/s41598-018-38200-3

Daskalova, G. N. & Kamp, J. (2023). Abandoning land transforms biodiversity. *Science*, 380(6645), 581-583.

De Cáceres, M. & Legendre, P. (2009). *Associations between species and groups of sites: indices and statistical inference*. http://sites.google.com/site/miqueldecaceres/.

De Cáceres, M. (2020). *How to use the indicspecies package.* https://cran.r-project.org/wweb/packages/indicspecies/vignettes/indicspeciesTutorial.pdf Accessed online: 29/01/2021.

De Gabriel, M., Roa, I., Fernández-Gil, J., Juan, J., Fuertes, B., Reguera, B. & Revilla, E. (2022). Trends in weather conditions favor generalist over specialist species in rear-edge alpine bird communities. *Ecosphere*, 13, e3953. https://doi.org/10.1002/ecs2.3953

DEFRA (2021). *UK Biodiversity Indicators 2021.* Department for Environment, Food and Rural Affairs, UK.

Dennis, E.B., Morgan, B.J., Freeman, S.N., Brereton, T.M., & Roy, D.B. (2016). A generalized abundance index for seasonal invertebrates. *Biometrics*, 72(4), 1305-1314.

Dennis, E.B., Morgan, B.J.T., Brereton, T.M., Roy, D.B. & Fox, R. (2017). Using citizen science butterfly counts to predict species population trends. *Conservation Biology*, 31(6), 1350-1361.

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

Dennis, R.L.H., Williams, W.R. & Shreeve, T.G. (1991). A multivariate approach to the determination of faunal structures among European butterfly species (Lepidoptera: Rhopalocera). *Zoological Journal of the Linnean Society* 101:1-49.

Dennis, R.L.H. & T. Schmitt (2009). *Faunal structures, phylogeography and historical inference*. In: Settele, J., T. Shreeve, M. Konvicka & H. Van Dyck. Ecology of butterflies in Europe. Cambridge University Press, 250-280.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, B., Schweiger, O., Settele, J., Stefanescu, C., van Strien, A., van Turnhout, C., Vermouzek, Z., Wallis De Vries, M., Wynhoff, I., Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change,* 2:121. https://doi.org/10.1038/nclimate1347

Diamond, J. M. (1969). Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proceedings of the National Academy of Sciences*, 64: 57–63.

Díaz Pineda, F. (1996). *Ecología I: Ambiente físico y organismos vivos*. Ed. Síntesis.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., and Collen, B. (2014). Defaunation in the Anthropocene. *Science* 345, 401–406. https://doi.org/10.1126/science.1251817.

Dornelas, M., Chase, J. M., Gotelli, N. J., Magurran, A. E., McGill, B. J., Antão, L. H., ... & Vellend, M. (2023). Looking back on biodiversity change: lessons for the road ahead. *Philosophical Transactions of the Royal Society B*, 378(1881), 20220199.

Dover, J.W., Rescia, A., Fungariño, S., Fairburn, J., Carey, P., Lunt, P., Dennis, R.L.H. & Dover, C.J. (2010a). Can hay harvesting detrimentally affect adult butterfly abundance? *Journal of Insect Conservation,* 14:413–418. https://doi. org/ 10. 1007/ s10841- 010- 9267-5

Dover, J.W., Spencer, C., Collins, S., Hadjigeorgiou, I. & Rescia, A. (2010b). Grassland butterflies and low intensity farming in Europe. *Journal of Insect Conservation*, 15: 129-137.

Dufrêne, M. & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67(3): 345-366.

Eeles, P. (2019). *Lyfe cycles of British and Irish butterflies*. Ed. Nature Bureau.

Edwards, A.C., Scalenghe, R. & Freppaz M. (2007). Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. *Quaternary International,* 162-163, 172-181.

Ehrlich, P.R., Murphy, D.D., Singer, M.C., Sherwood, C.B., White, R.R., Brown, I.L. (1980) Extinction, reduction, stability and increase: The responses of checkerspot butterfly (*Euphydryas editha*) populations to California drought. *Oecologia*, 46: 101-105.

Ellis, S., Bourn, N.A. & Bulman, C.R. eds. (2012). *Landscape-scale conservation for butterflies and moths: lessons from the UK*. Wareham: Butterfly Conservation.

Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmerman, N.E., Araújo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnböck, T., Gégout, J., Gómez-García, D., Grytnes, J., Heegaard, E., Høistad, F., Nogués-Bravo, D., Normand, S., Puscas, M., Sebastiá, M.T., Stanisi, A., Theurillat, J., Trivedi, M.R., Vittoz, P., Guisan, S. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, 17, 2330-2341.

Eriksson, B. K. & Hillebrand, H. (2019). Rapid reorganization of global biodiversity. *Science*, 366(6463), 308-309.

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., ... & Martin, J. L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology letters*, 14(2), 101-112.

Farina, A. (2000). The cultural landscape as a model for the integration of ecology and economics. *BioScience*, 50(4): 313-320. https://doi.org/10.1641/0006-3568(2000)050[0313:TCLAAAM]2.3.CO;2

Figueiredo, L., Krauss, J., Steffan-Dewenter, I., & Sarmento Cabral, J. (2019). Understanding extinction debts: spatio–temporal scales, mechanisms and a roadmap for future research. *Ecography*, 42(12), 1973-1990.

Filazzola, A., Matter, S. F. & Roland, J. (2020). Inclusion of trophic interactions increases the vulnerability of an alpine butterfly species to climate change. *Global Change Biololgy*, 26, 2867–2877.

Flousek, J., Telenský, T., Hanzelka, J. & Reif, J. (2015). Population trends of Central European montane birds provide evidence for adverse impacts of climate change on high-altitude species. *PLoS One*, 10, e0139465.

Fox, J. & Weisberg, S. (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Fox, R., Dennis, E.B., Purdy, K.M., Middlebrook, I., Roy, D.B., Noble, D.G., Botham, M.S. & Bourn, N.A.D. (2023). *The State of the UK's Butterflies 2022.* Butterfly Conservation, Wareham, UK.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E. M., Steffan-Dewenter, I., Emmerson, M., Potts, S. G., Tscharntke, T., Weisser, W. & Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society of London B: Biological Sciences*, 282, 20142620.

Gallou, A., Baillet, Y., Ficetola, G. F., & Després, L. (2017). Elevational gradient and human effects on butterfly species richness in the French Alps. *Ecology and evolution*, 7(11), 3672-3681.

Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H., Simons, N.K., Klein, A., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C.N., Weisser, W., Werner, M., Tscharntke, T., Westphal, C. (2015). Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*. https://doi.org/10.1038/ncomms9568

García, P., García, L. & González, V. (2018). Diagnóstico de la situación de prados de siega en el suroeste europeo: análisis diacrónico en el Parque Nacional de los Picos de Europa. *Naturalia Cantabricae*, 6(1):1-21.

García-Barros, E., Gurrea, P., Luciáñez, M. J., Cano, J. M., Munguira, M. L., Moreno, J. C., ... & Simón, J. C. (2002). Parsimony analysis of endemicity and its application to animal and plant geographical distributions in the Ibero-Balearic region (western Mediterranean). *Journal of Biogeography*, 29(1), 109-124.

García-Barros, E., Munguira, M.L., Stefanescu, C. & Vives Moreno, A. (2013). Lepidoptera, Papilionoidea. In: *Fauna Ibérica*, vol 37. Ramos, MA et al (Eds.). Museo Nacional de Ciencias Naturales. CSIC. Madrid.

García-Barros, E., Cancela, J.P., Lobo, J.M., Munguira, M.L. & Romo, H. (2022). Forecasts of butterfly future richness change in the southwest Mediterranean. The role of sampling effort and non-climatic variables. *J. Insect Conserv*. 26, 639–650. https://doi.org/10.1007/s10841-022-00406-2.

García-Llamas, P., Geijzendorffer, I.R., García-Nieto, A.P., Calvo, L., Suárez-Seoane, S. & Cramer, W. (2019). Impact of land cover change on ecosystem service supply in mountain systems: a case study in the Cantabrian Mountains (NW of Spain). *Regional Environmental Change*, 19, 529–542. https://doi.org/10.1007/s10113-018-1419-2

García-Perea, R. & Gisbert, J. (1997). Lista patrón de los mamíferos de la Península Ibérica, Islas Baleares y Canarias. *Galemys*, 9: 1-38.

Gómez, A. & Lunt, D.H. (2007). Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula. In: Weiss, S. & Ferrand, N. (Eds.). *Phylogeography in Southern European Refugia*. The Netherlands. Springer. Pp: 155-188.

Gómez-Campo, C., Bermudez-de-Castro, L., Cagiga, M.J., & Sánchez-Yélamo, M.D. (1984). Endemism in the Iberian peninsula and Balearic Islands. *Webbia*, 38(1), 709-714.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J.L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M.R., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., M erzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.-P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I. & Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2, 111–115. doi:10.1038/nclimate1329

Goulson, D. (2021). *Silent Earth: averting the insect apocalypse*. Random House.

Grabherr, G., Gottfried, M., Gruber, A. & Pauli, H. (1995). *Patterns and current changes in alpine plant diversity.* Springer Berlin Heidelberg, pp. 167–181. doi:10.1007/978-3-642-78966-3_12

Greenpeace Spain (2020). https://es.greenpeace.org/es/sala-de-prensa/informes/proteger-el-medio-rural-es-protegernos-del-fuego-hacia-paisajes-y-poblacion-resilientes-frente-a-la-crisis-climatica/ Accessed online: 22/02/2021.

Grytnes, J.A. & Romdal, T.S. (2008). Using museum collections to estimate diversity patterns along geographical gradients. *Folia Geobotanica*, 43: 357–359

Gutiérrez, D. (1997). Importance of historical factors on species richness and composition of butterfly assemblages (Lepidoptera: Rhopalocera) in a northern Iberian mountain range. *Journal of Biogeography*, 24: 77-88.

Gutiérrez, D. (2009). Butterfly richness patterns and gradients, 281-295. In: Settele, J., Shreeve, T., Konvicka, M. & Van Dyck, H. (editors). *Ecology of butterflies in Europe.* Cambridge University Press.

Gutiérrez, D. & Menéndez, R. (1995). Distribution and Abundance of Butterflies in a Mountain Area in the Northern Iberian Peninsula. *Ecography*, Vol. 18, No. 3, 209-216.

Gutiérrez, D. & Menéndez, R. (2007). Regional hotspots of butterfly diversity in a protected area: Are they indicators of unique assemblages and areas with more species of conservation concern? *Acta Oecologica* 32, 301–311.

Gutiérrez, D., Vila, R. & Wilson, R.J. (2016). Asymmetric constraints on limits to species ranges influence consumer-resource richness over an environmental gradient. *Global Ecology and Biogeography,* 25:1477–1488. https://doi.org/10.1111/geb.12510

Habel, J. C., Schmitt, T., Gros, P., & Ulrich, W. (2022). Breakpoints in butterfly decline in Central Europe over the last century. *Science of the Total Environment*, 851, 158315.

Hallett L, Avolio M, Carroll I, Jones S, MacDonald A, Flynn D, Slaughter P, Ripplinger J, Collins S, Gries C, Jones M (2020). codyn: Community Dynamics Metrics. doi:10.5063/F1N877Z6, R package version 2.0.5, https://github.com/NCEAS/codyn.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. & De Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *Plos One*. https://doi.org/10.1371/journal.pone.0185809

Halsch, C.A., Shapiro, A.M., Fordyce, J.A., Nice, C.C., Thorne, J.H., Waetjen, D.P. & Forister, M.L. (2021). Insects and recent climate change. *Proceedings of the National Academy of Sciences*, 118, 2, e2002543117. https://doi.org/10,1073/pnas.2002543117

Hanski, I. (1999). *Metapopulation Ecology*. Oxford University Press

Hanski, I. (2001). Spatially realistic theory of metapopulation ecology. *Naturwissenschaften,* 88: 372-381.

Hanski, I. & Ovaskainen, O. (2002). Extinction debt at extinction threshold. Conservation Biology, vol. 16, nº 3: 666-673.

Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.4.6

Hawkins, B.A. & Porter, E. (2003a). Does herbivore diversity depend on plant diversity? The case of California butterflies. *American Naturalist*, 161, 40-49.

Hawkins, B.A. & Porter, E.E. (2003b). Water-energy balance and the geographic pattern of species richness of western Palearctic butterflies. *Ecological Entomology*, 28: 678-686.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., ... & Turner, J.R. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84(12), 3105-3117.

Hawkins, B.A., Rodríguez, M.A., & Weller, S.G. (2011). Global angiosperm family richness revisited: linking ecology and evolution to climate. *Journal of Biogeography*, 38(7), 1253-1266.

Herrando, S., Brotons, L., Anton, M., Páramo, F., Villero, D., Titeux, N., Quesada, J. & Stefanescu, C. (2016) Assessing impacts of land abandonment on Mediterranean biodiversity using indicators based on bird and butterfly monitoring data. *Environmental Conservation*, https://doi.org/10.1017/S0376892915000260

Hewitt, G.M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnaean Society*, 58:247-276.

Hewitt, G.M. (1999). Post-glacial recolonization of European biota. *Biological Journal of the Linnaean Society*, 68: 87-112.

Hewitt, G.M. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, 405:907-913.

Hewitt, G.M. (2011). Mediterranean Peninsulas: the evolution of hostpots. In: Zachos, FE, Habel, JC (eds) *Biodiversity hospots: distribution and protection of conservation priority areas*. Springer, Heidelberg, pp 123-147.

Hill, R., Nates-Parra, G. & Quezada-Euán, JJG. (2019). Biocultural approaches to pollinator conservation. *Nature Sustainability,* 2: 214.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *American Naturalist*, 163: 192-211.

Hodapp, D., Borer, E. T., Harpole, W. S., Lind, E. M., Seabloom, E. W., Adler, P. B., ... & Hillebrand, H. (2018). Spatial heterogeneity in species composition constrains plant community responses to herbivory and fertilisation. *Ecology letters*, 21(9), 1364-1371.

Holyoak, M., Leibold, M.A. & Holt, R.D. (2005). *Metacommunities: Spatial Dynamics and Ecological Communities*. The University of Chicago Press, Chicago, IL and London.

Hortal, J., Diniz-Filho, J. A. F., Bini, L. M., Rodríguez, M. Á., Baselga, A., Nogués-Bravo, D., ... & Lobo, J. M. (2011). Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, 14(8), 741-748.

Hsieh, T.C., Ma, K.H. & Chao, A. (2022). *iNEXT: Interpolation and Extrapolation for Species Diversity. R package version 3.0.0*, http://chao.stat.nthu.edu.tw/wordpress/software_download/.

Humbert, J. Ghazoul, J., Richner, N. & Walter, T. (2012). Uncut grass refuges mitigate the impact of mechanical meadow harvesting on orthopterans. *Biological Conservation*, 152: 96-101.

Humbert, J., Ghazoul, J., Sauter, G.J. & Walter, T. (2010). Impact of different meadow mowing techniques on field invertebrates. *Journal of Applied Entomology*, 134: 592-599.

Huston, M.A. (1994). *Biological diversity*. Cambridge University Press, Cambridge, UK.

Iglesias González, M., Yagüe, C., & Maqueda, G. (2017). Temperature inversions and cold-air pools study in Picos de Europa surroundings. In EGU General Assembly Conference Abstracts (p. 15768)

Illán, J. G., Gutiérrez, D. & Wilson, R.J. (2010). Fine-scale determinants of butterfly species richness and composition on a mountain region. *Journal of Biogegraphy* 37, 1706-1720.

Inouye, D.W. (2008). Effects of climate change on phenology, frost damage and floral abundance of montane wildflowers. *Ecology*, 89, 353-362.

Inouye, D.W.(2020). Effects of climate change on alpine plants and their pollinators. *Annals of the New York Academy of Sciences*, 1469, 26-37. doi: 10.1111/nyas.14104

IPCC (2022). Cross-Chapter 5: Mountains. In: *Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S.Langsdorf, S. Löschke, V. Möller, A. Okem & B. Rama (eds.). Cambridge University Press. In Press.

Izquierdo, J. & Barrena, G. (2006). *Marqueses, funcionarios, políticos y pastores*. Ed. Nobel. Oviedo.

Jackson, S.T., & Sax, D.F. (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in ecology and evolution*, 25(3), 153-160.

Janišová, M., Michalcová, D., Bacaro, G., Ghisla, A. (2014). Landscape effects on diversity of semi-natural grasslands. *Agriculture, ecosystems and environment,*182: 47–58

Jessen, T.D., Ban, N.C., Claxton, N.X., Darimont, C.T. (2022). Contributions of indigenous knowledge to ecological and evolutionary understanding. *Frontiers in Ecology and the Environment*, 20(2), 93-101.

Jiménez-Alfaro, B., Abajo, A., Alonso, I., Bueno, A., Fernández, A., Marcenó, C., Obeso, J.R. & Recondo, C. (2010). *Bases para el seguimiento de los cambios en la flora y vegetación como consecuencia del cambio climático en el Parque Nacional de los Picos de Europa.* Universidad de Oviedo. Fundación Biodiversidad. Unpublished report.

Jiménez-Alfaro, B., Fernández-Pascual, E., Espinosa Del Alba, C., & Marcenò, C. (2024). Spatiotemporal patterns of microclimatic buffering in relict alpine communities. *Journal of Vegetation Science*, 35(2), e13242

Jiménez-Alfaro, B., Gavilán, R. G., Escudero, A., Iriondo, J. M. & Fernández-González, F. (2014). Decline of dry grassland specialists in Mediterranean high-mountain communities influenced by recent climate warming. *Journal of Vegetation Science*, 25, 1394–1404.

Johst, K., Drechsler, M.,Thomas, J. & Settele, J. (2006). Influence of mowing on the persistence of two endangered large blue butterfly species. *Journal of Applied Ecology*, 43: 333–342.

Jubete, F., Barea, J.M., Escobés, R., Galante, E. Gómez-Calmaestra, R., Manceñido, D.C., Monasterio, Y., Mora, A., Munguira, M.L., Stefanescu & C., Tinaut, A. (2019). *Bases técnicas para la conservación de los lepidópteros amenazados en España*. Asociación de Naturalistas Palentinos.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F. & Couvet, D. (2006). Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, 9:1237–1244

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, P., & Kessler, M. (2017). Climatologies at high resolution for the Earth land surface areas. *Scientific Data*, 4, 170122. https://doi.org/10.1038/sdata.2017.122 Dryad Digital Repository. http://dx.doi.org/doi:10.5061/dryad.kd1d4

Keil, P., Simova, I., & Hawkins, B. A. (2008). Water-energy and the geographical species richness pattern of European and North African dragonflies (Odonata). *Insect Conservation and Diversity*, 1(3), 142-150.

Kerner, J. M., Krauss, J., Maihoff, F., Bofinger, L., & Classen, A. (2023). Alpine butterflies want to fly high: Species and communities shift upwards faster than their host plants. *Ecology,* 104(1), e3848.

Kerr, J. T. (2001). Butterfly species richness patterns in Canada: energy, heterogeneity, and the potential consequences of climate change. *Conservation Ecology*, 5(1).

Kienle, D. R., Irl, S. D., & Beierkuhnlein, C. (2023). Mass elevation effect and continentality have a stronger impact on global treelines than spatial isolation. *Global Ecology and Biogeography*, 32(7), 1087-1097.

Kimmerer, R.W. & Artelle, K.A. (2024) Time to support indigenous science. *Science*, 383 (6680): 243.

Klein, G., Vitasse, Y., Rixen, C., Marty, C. & Rebetez, M. (2016). Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. *Climatic Change*, 139, 637.

Knepp (2024). https://knepp.co.uk/rewilding/ecosystem-services/soil-restoration (accessed on 15 May 2024)

Konvicka, M., Kuras, T., Liparova, J., Slezak, V., Horázná, D., Klečka, J. & Kleckova, I. (2021). Low winter precipitation, but not warm autumns and springs, threatens mountain butterflies in middle-high mountains. *PeerJ,* 9: e12021 https://doi.org/10.7717/peerj.12021

Konvicka, M., Benes, J., Cizek, O., Kopecek, F., Konvicka, O. & Vitaz, L. (2008). How too much care kills species: grassland reserves, agri-environmental schemes and extinction of Colias myrmidone (Lepidoptera: Pieridae) from its former stronghold. *Journal of Insect Conservation*, 12: 519–525.

Krauss, J., Steffan-Dewenter, I. & Tscharntke, T. (2003). How does landscape context contribute to effects of habitat fragmentation on diversity and population density? *Journal of Biogeography*, 30: 889-900.

Kuckerov, N.B., Minor, E.S., Johnson, P.P., Taron, D., & Matteson, K.C. (2021). Butterfly declines in protected areas of Illinois: Assessing the influence of two decades of climate and landscape change. *PloS one*, 16(10), e0257889.

Kudrna, O., Harpke, A., Lux, K., Pennerstorfer, J., Schweiger, O., Settele, J. & Wiemers, M. (2011). *Distribution atlas of butterflies in Europe.* – Gesellschaft für Schmetterlingschutz, Halle, Germany.

Kumar, S., Simonson, S.E., & Stohlgren, T.J. (2009). Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, USA. *Biodiversity and Conservation*, 18, 739-763.

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodá, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009). Extinction debt: a challenge for biodiversity conservation. Trends in ecology & evolution, 24(10), 564-571.

Lauber, K. & Wagner, G. (1998) *Flora Helvetica. Flore illustrée de Suisse*. Editions Paul Haupt.

Leach, N.J., Millar, R.J., Haustein, K., Jenkins, S., Graham, E. & Allen, M.R. (2018). Current level and rate of warming determine emissions budgets under ambitious mitigation. *Nature Geoscience*, 11: 574–579, doi:10.1038/s41561-018-0156-y.

Lee, L.C., Thorley, J., ... & Watson, J. (2018). Diverse knowledge systems reveal social–ecological dynamics that inform species conservation status. *Conservation Letters*, 12: e12613.

Lenoir, J., Gégout, J., Guisan, A., Vittoz, A., Wohlgemuth, T., Zimmermann, N.E., Dullinger, S., Pauli, H., Willner, W. & Svenning, J. (2010). Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, 33-2, 295-303. https://doi.org/10.1111/j.1600-0587.2010.06279.x

Levins, R. (1970). Extinction. *Lect. Notes Math*. 2: 75-107.

MacArthur, R. H., and E. O. Wilson (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17: 373–387.

MacDonald, D., Crabtree, J.R., Wiesinger, G.,Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J. & Gibon, A. (2000). Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *Journal of Environmental Management*, 59, 1, 47-69, https://doi.org/10.1006/jema.1999.0335.

Maes, D., Verovnik, R., Wiemers, M., Brosens, D., Beshkov, S., Bonelli, S., ... & Warren, M. S. (2019). Integrating national Red Lists for prioritising conservation actions for European butterflies. *Journal of insect conservation*, 23(2), 301-330.

Maes, D. & Van Dyck, H. (2001). Butterfly diversity loss in Flanders (North Belgium): Europe's worst case scenario? *Biological Conservation*, 99, 263-276.

Marini, L., Fontana, P., Battisti, A. & Gaston, K.J. (2009). Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland-forest mosaic: a multi-scale approach. *Insect Conservation and Diversity*, 2: 213-220.

McCain, C.M. & Grytnes, J.A. (2010). Elevational gradients in species richness. In: *Encyclopedia of Life Sciences (ELS).* John Wiley & Sons, Ltd, Chichester. https://doi.org/10.1002/9780470015902.a0022548

McKenney, M.L. & Lockwood, J.L. (1999). Biotic homogeneization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, 14: 450-453.

Medail, F., & Quezel, P. (1997). Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Annals of the Missouri Botanical Garden*, 112-127.

Melero, Y., Stefanescu, C. & Pino, J. (2016). General declines in Mediterranean butterflies over the last two decades are modulated by species traits. *Biological Conservation*, 201: 336-342.

Menéndez, M. (2020). Un siglo de investigaciones arqueológicas en la cueva del Buxu (Cangas de Onís, Asturias). *Nailos*, 275-291.

Metzger, M. J., Bunce, R. G. H., Jongman, R. H., Mücher, C. A., & Watkins, J. W. (2005). A climatic stratification of the environment of Europe. *Global ecology and biogeography*, 14(6), 549-563.

Middlebrook, I., Botham, M.S., Conway, R., Fox, R., Heywood, J., Noble, D., Peck, K., Salvati, J. & Roy, D.B. (2023). *United Kingdom Butterfly Monitoring Scheme report for 2022*. Butterfly Conservation, UK Centre for Ecology and Hydrology, British Trust for Ornithology and Joint Nature Conservation Committee.

Middleton-Welling, J., Dapporto, L., García-Barros, E., Wiemers, M., Nowicki, P., Plazio, E., Bonelli, S., Zaccagno, M., Šašić, M., Liparova, J., Schweiger, O., Harpke, A., Musche, M., Settele, J., Reto Schmucki, R. & Shreeve, T. (2020). A new comprehensive trait database of European and Maghreb butterflies, Papilionoidea. *Scientific Data*, 7(1), 1-10.

Mingarro, M., Cancela, J.P., Burón-Ugarte, A., García-Barros, E., Munguira, M.L., Romo, H. & Wilson, R.J. (2021). Butterfly communities track climatic variation over space but not time in the Iberian Peninsula. *Insect Conservation and Diversity*, 14, 647-660. https://doi.org/10.1111/icad.12498

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson & L. Gough. (2001). What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.

Mittermeier, R.A., Turner, W.R., Larsen F.W., Brooks T.M. & Gascon, C. (2011). Global biodiversity conservation: the critical role of hotspots. In: Zachos, F.E. & Habel, J.C. (eds.). *Biodiversity hotspots: distribution and protection of conservation priority areas.* Springer, Heidelberg, pp 2-22.

Mora, A., Wilby, A., & Menéndez, R. (2022). Abandonment of cultural landscapes: butterfly communities track the advance of forest over grasslands. *Journal of Insect Conservation*, 26(1), 85-96.

Mora, A., Wilby, A., & Menéndez, R. (2023). South European mountain butterflies at a high risk from land abandonment and amplified effects of climate change. *Insect Conservation and Diversity*, 16(6), 838-852.

Moreno, A., López-Merino, L., Leira, M., Marco-Barba, J., González-Sampériz, P., Valero-Garcés, B. L., ... & Ito, E. (2011). Revealing the last 13,500 years of environmental history from the multiproxy record of a mountain lake (Lago Enol, northern Iberian Peninsula). *Journal of Paleolimnology*, 46, 327-349.

Moretti, M., Dias, A.T.C., Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., Bell, J.R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J.P., Ellers, J. & Berg, M.P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, 31:558–567

Mühlethaler, R., Köthe, S., Hörren, T., Sorg, M., Eichler, L., & Lehmann, G. U. (2024). No recovery in the biomass of flying insects over the last decade in German nature protected areas. *Ecology and Evolution*, 14(3), e11182.

Munguira, M. L., & Martín, J. (1993). The conservation of endangered lycaenid butterflies in Spain. *Biological Conservation*, 66(1), 17-22.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.

Nieuwendam, A., Ruiz-Fernández, J., Oliva, M., Lopes, V., Cruces, A., & da Conceição Freitas, M. (2016). Postglacial landscape changes and cryogenic processes in the Picos de Europa (Northern Spain) reconstructed from geomorphological mapping and microstructures on quartz grains. *Permafrost and Periglacial Processes*, 27(1), 96-108.

Ninyerola, N., Pons, X. & Roure, J.M. (2005). *Atlas Climático Digital de la Península Ibérica.* Metodología y aplicaciones en bioclimatología y geobotánica. ISBN 932860-8-7. Universidad Autónoma de Barcelona, Bellaterra.

Nogués-Bravo, D., Araújo, M. B., Romdal, T., & Rahbek, C. (2008). Scale effects and human impact on the elevational species richness gradients. *Nature*, 453(7192), 216-219.

Öckinger, E., Bergman, K.O., Franzén, M., Kadlec, T., Krauss, J., Kuussaari, M., Pöyry, J., Smith, H.G., Steffan-Dewenter, I. & Bommarco, R. (2012). The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. *Landscape Ecology*, 27:121–131

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S. & Bommarco, R. (2010). Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters*, 13:969–979

Öckinger, E., Smith, G, Eriksson, K. & Henrik, A. (2006). Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biological Conservation*, 133: 291-300.

Oksanen, J., F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry., M., Stevens, H., Szoecs, E. & Wagner, H. (2019). *Vegan: Community Ecology Package*. R package version 2.5-6. https://CRAN.R-project.org/package=vegan

Oliver, T., Roy, D.B., Hill, J.K., Brereton, T. & Thomas, C.D. (2010). Heterogeneous landscapes promote population stability. *Ecology Letters*, https://doi.org/10.1111/j.1461-0248.2010.01441.x

Orr, M. C., Hughes, A. C., Chesters, D., Pickering, J., Zhu, C. D., & Ascher, J. S. (2021). Global patterns and drivers of bee distribution. *Current Biology*, 31(3), 451-458.

Pannekoek, J. & van Strien, A. (2005). *TRIM 3 Manual. TRends & Indices for Monitoring data*. Voorburg, the Netherlands: Statistics Netherlands. P. 58

Pearce, E. A., Mazier, F., Normand, S., Fyfe, R., Andrieu, V., Bakels, C., ... & Svenning, J. C. (2023). Substantial light woodland and open vegetation characterized the temperate forest biome before Homo sapiens. *Science advances*, 9(45), eadi9135

Pedroli, B., Pinto-Correia, T., & Cornish, P. (2006). Landscape–what's in it? Trends in European landscape science and priority themes for concerted research. *Landscape Ecology*, 21, 421-430.

Pepin, N. C., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C., ... & Adler, C. (2022). Climate changes and their elevational patterns in the mountains of the world. *Reviews of geophysics*, 60(1), e2020RG000730.

Pepin, N., Bradley, R. S., Diaz, H. F., Baraër, M., Caceres, E. B., Forsythe, N., Fowler, H. ; Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M. B., Williamson, S. N. & Yang, D. Q. (Mountain Research Initiative EDW Working Group) (2015). Elevation-dependent warming in mountain regions of the world. *Nature climate change*, 5(5), 424-430.

Perović, D., Gámez-Virués, S., Börschig, C., Klein, A., Krauss, J., Steckel, J., Rothenwöhrer, C., Erasmi, S., Tscharntke, T. & Westphal, C. (2015). Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *Journal of Applied Ecology*, 52:505–513

Peters, M.K., Hemp, A., Appelhans, T., Becker, J.N., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S.W., Frederiksen, S.B., Gebert, F., Gerschlauer, F., Gütlein, A., Helbig-Bonitz, M., Hemp, C., Kindeketa, W.J., Kühnel, A., Mayr, A.V., Mwangomo, E., Ngereza, C., Njovu, H.K., Otte, I., Pabst, H., Renner, M., Röder, J., Rutten, G., Costa, D.S., Sierra-Cornejo, N., Vollstädt, M.G.R., Dulle, H.I., Eardley,C.D., Howell, K.M., Keller, A., Peters, R.S., Ssymank, A., Kakengi, V., Zhang, J., Bogner, C., Böhning-Gaese, K., Brand, R., Hertel, D., Huwe, B., Kiese, R., Kleyer, M., Kuzyakov, Y., Nauss, T., Schleuning, M., Tschapka, M., Fischer, M. & Steffan-Dewenter, I. (2019). Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature*, 568, 88–92. https://doi.org/10.1038/s41586-019-1048-z

Pinkert, S., Barve, V., Guralnick, R., & Jetz, W. (2022). Global geographical and latitudinal variation in butterfly species richness captured through a comprehensive country-level occurrence database. *Global Ecology and Biogeography*, 31(5), 830-839

Polfus, J.L., Heinemeyer, K., Hebblewhite, M. & Taku River Tlingit First Nation. (2014). Comparing traditional ecological knowledge and Western science woodland caribou habitat models: TEK caribou habitat models. *Journal of Wildlife Management*, 78: 112–21.

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

Poschlod, P., Bakket, J.P. & Kahmen, S. (2005). Changing land use and its impact on biodiversity. *Basic and Applied Ecology,* 6, 93-98.

Pöyry, J., Lindgren, S., Salminen, J., & Kuussaari, M. (2004). Restoration of butterfly and moth communities in semi-natural grasslands by cattle grazing. *Ecological Applications*, 14(6), 1656-1670.

Pöyry, J., Paukkunen, J., Heliölä, J. & Kuussaari, M. (2009). Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. *Oecologia*, 160, 577-587.

Previdi, M., Smith, K.L. & Polvani, L.M. (2021). Arctic amplification of climate change: a review of underlying mechanisms. *Environmental Research Letters*, 16, 9. Doi: 10.1088/1748-9326/ac1c29

Pulido-Pastor A, Márquez AL, García-Barros E & Leal R (2018). Identification of potential source and sink areas for butterflies on the Iberian Peninsula. *Insect Conservation and Diversity*, 11, 479-492.

Pullin, A.S. & Knight, T.M. (2001) Effectiveness in conservation practice: pointers from medicine and public health. *Conservation Biology*, 15: 50-54

Pykälä, J. (2003). Effects of restoration with cattle grazing on plant species composition and richness of semi-natural grasslands. *Biodiversity & Conservation*, 12, 2211-2226.

R Core Team (2019). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rada, S., Schweiger, O., Harpke, A., Kühn, E., Kuras, T., Settele, J. & Musche, M. (2019). Protected areas do not mitigate biodiversity declines: A case study on butterflies. *Diversity and distributions*, 25(2), pp.217-224.

Rahbek, C. (1995). The elevation gradient of species richness: an uniform pattern? *Ecography*, 18, 200-205.

Rahbek, C., Borregaard, M.K., Colwell, R.K., Dalsgaard, B., Holt, B.G., Morueta-Holme, N., Nogués-Bravo, D., Whittaker, R.J. & Fjeldsa, J. (2019). Hulmboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, 365: 1108-1113.

Reichholf, J. H. (2020). *The disappearance of butterflies*. John Wiley & Sons.

Rescia, A. J., Pons, A., Lomba, I., Esteban, C., & Dover, J. W. (2008). Reformulating the social–ecological system in a cultural rural mountain landscape in the Picos de Europa region (northern Spain). *Landscape and Urban Planning*, 88(1), 23-33.

Rivas-Martínez, S. (2007). Mapa de series, geoseries y geopermaseries de vegetación de España [Memoria del Mapa de vegetación Potencial de España] Parte I. *Itinera Geobotanica*, 17.

Rivas-Martínez, S., Díaz. T.E., Prieto, J.A.F., Loidi, J. & Penas, A. (1984*). La vegetación de la alta montaña cantábrica. Los Picos de Europa*. Ed. Leonesas.

Rödder, D., Schmit, T., Gros, P., Ulrich, W. & Habel, J.C. (2021). Climate change drives mountain butterflies towards the summits. *Scientific Reports, Nature*, 11, 14382. https://doi.org/10.1038/s41598-021-93826-0.

Rodríguez, M. Á., Belmontes, J. A., & Hawkins, B. A. (2005). Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. *Acta Oecologica*, 28(1), 65-70.

Rohde, K. (1999). Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients. *Ecography*, 22(6), 593-613.

Romo, H., Munguira, M.L. & García-Barros, E. (2007). Area selection for the conservation of butterflies in the Iberian Peninsula and Balearic Islands. *Animal Biodiversity and Conservation*, 30(1):7–27

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.

Rosso, A., Aragón, P., Acevedo, F., Doadrio, I., García-Barros, E., Lobo, J.M., Munguira, M.L., Monserrat, V.J., Palomo, J., Pleguezuelos, J.M., Romo, H., Triviño, V. & Sánchez-Fernández, D. (2018). Effectiveness of the Natura 2000 network in protecting Iberian endemic fauna. *Animal Conservation*, 21, 262-271. https://doi.org/10.1111/acv.12387

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, 130(3), 321-338.

Rotchés-Ribalta, R., Winsa, M., Roberts, S.P.M. & Öckinger, E. (2018). Associations between plant and pollinator communities under grassland restoration respond mainly to landscape connectivity. *Journal of Applied Ecology*, 55, issue 6: 2822-2833. https://doi.org/10.1111/1365-2664.13232

Roy, D. B., Ploquin, E. F., Randle, Z., Risely, K., Botham, M. S., Middlebrook, I., ... & Brereton, T. M. (2015). Comparison of trends in butterfly populations between monitoring schemes. *Journal of Insect Conservation*, 19, 313-324.

Roy, D.B., Rothery, P. & Brereton, T. (2007). Reduced-effort schemes for monitoring butterfly populations. *Journal of Applied Ecology*, 44, 993–1000.

RStudio Team (2019). *RStudio: Integrated Development for R. RStudio*, Inc., Boston, MA URL https://www.rstudio.com/

Ruggiero, A., & Hawkins, B. A. (2008). Why do mountains support so many species of birds? *Ecography*, 31(3), 306-315.

Sadei (2024). *Anuario estadístico de Asturias, 2022*. Sociedad Asturiana de Estudios Económicos e Industriales. Principado de Asturias.

Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019). Worlwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8-27.

Sánchez-Dávila, J., Traveset, A., & Colom, P. (2024). Effects of food availability on butterfly diversity and network specialization across altitudinal levels in a Mediterranean landscape. *Biodiversity and Conservation*, 33(1), 239-256

Sartorello, Y., Pastorino, A., Bogliani, G., Ghidotti, S., Viterbi, R., & Cerrato, C. (2020). The impact of pastoral activities on animal biodiversity in Europe: A systematic review and meta-analysis. *Journal for Nature Conservation*, 56, 125863.

Savo, V., Lepofsky, D., Benner, J. P., Kohfeld, K. E., Bailey, J., & Lertzman, K. (2016). Observations of climate change among subsistence-oriented communities around the world. *Nature Climate Change*, 6(5), 462-473.

Schmitt, T. & Hewitt, G.M. (2004). The genetic pattern of population threat and loss: a case study of butterflies. *Molecular Ecology*, 13: 21-31.

Schmucki, R., Harrower, C.A. & Dennis, E.B. (2022). *rbms: Computing generalised abundance indices for butterfly monitoring count data.* R package version 1.1.3. https://github.com/RetoSchmucki/rbms

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

Schweiger, O., Harpke, A., Wiemers, M., & Settele, J. (2014). CLIMBER: Climatic niche characteristics of the butterflies in Europe. *ZooKeys*, 367, 65.

Seibold, S., Gossner, M.M., Simons, N.K, Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E., Vogt, J., Wöllauer, S. & Weisser, W.W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, 574, 671–674. https://doi.org/10.1038/s41586-019-1684-3

Settele, J., Dover, J., Dolek, M. & Konvicka, M. (2009) Butterflies of European ecosystems: impact of land use and options for conservation management, 353-370. In: Settele, J., Shreeve, T., konvicka, M. & Van Dyck, H. (eds.). *Ecology of butterflies in Europe*. Cambridge University Press.

Sevilleja, C. G., Collins, S., Warren, M. S., Wynhoff, I., Van Swaay, C. A. M., Dennis, E. B., ... & Roy, D. B. (2020). *European Butterfly Monitoring Scheme (eBMS): network development*. Technical report.

Skórka, P., Settele, J. & Woyciechowski, M. (2007). Effect of management cessation on grassland butterflies in southern Poland. *Agriculture, ecosystems and environment*, 121:319-324.

Slancarova, J., Bartonova, A., Zapletal, M., Kotilinek, M., Fric, Z.F., Micevski, N., Vasiliki, K. & Konvicka, M. (2016). Life history traits reflect changes in Mediterranean butterfly communities due to forest encroachment. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0152026

Soldaat, L.L., Pannekoek, J., Verweij, R.J., van Turnhout, C.A. & van Strien, A.J. (2017). A Monte Carlo method to account for sampling error in multi-species indicators. *Ecological indicators*, 81, 340-347.

Soulé, M. & Noss, R. (1998). Rewilding and biodiversity: complementary goals for continental conservation. *Wild Earth*, 8, pp.18-28.

Stace, C. (2019). *New Flora of the British Isles*, 4th edition. Ed. C&M Floristics.

Stampfli, A., & Zeiter, M. (1999). Plant species decline due to abandonment of meadows cannot easily be reversed by mowing. A case study from the southern Alps. *Journal of Vegetation Science*, 10(2), 151-164.

Stefanescu, C., Carnicer, J. & Peñuelas, J. (2011a). Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. *Ecography* 34, 353-363.

Stefanescu, C., Herrando, S. & Páramo, F. (2004). Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. *Journal of Biogeography* 31, 905-915.

Stefanescu, C., Torre, I., Jubany, J. & Páramo, F. (2011b). Recent trends in butterfly populations from north-east Spain and Andorra in the light of habitat and climate change. *Journal of Insect Conservation*, 15:83–93

Stefanescu, C. (1997). Migration patterns and feeding resources of the Painted Lady butterfly, Cynthia cardui (L.)(Lepidoptera, Nynphalidae) in the northeast of the Iberian peninsula. *Miscellània Zoològica*, 31-48.

Stefanescu, C., Peñuelas, J. & Filella, I. (2009). Rapid changes in butterfly communities following the abandonment of grasslands: a case study. *Insect Conservation and Diversity*, 2:261-269.

Teng, S. N., Svenning, J. C., Santana, J., Reino, L., Abades, S., & Xu, C. (2020). Linking landscape ecology and macroecology by scaling biodiversity in space and time. *Current Landscape Ecology Reports*, 5, 25-34.

Thomas, C.D., Singer, M.C., Boughton, D.A. (1996). Catastrophic extinction of population sources in a butterfly metapopulation. *American Naturalist*, 148: 957-975.

Thomas, J. A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R. & Goodger, B. (2001). The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society, London B.* 268: 1791-1796

Thomas, C.D., Gillingham, P.K., Bradbury, R.B., Roy, D.B., Anderson, B.J., Baxter, J.M., Bourn, N.A., Crick, H.Q., Findon, R.A., Fox, R. & Hodgson, J.A. (2012). Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences*, 109(35), pp.14063-14068.

Thomas, C.D., Harrison, S. (1992) Spatial dynamics of a patchily-distributed butterfly species. *Journal of Animal Ecology*, 61: 437-446.

Thomas, C.S. (2017). *Inheritors of the Earth: how Nature is thriving in an age of extinction*. Penguin. Random House. UK.

Thomas, J. A. (2005). Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1454), 339-357.

Trappe J, Kunz F, Weking S & Kamp J (2017). Grassland butterfly communities of the Western Siberian forest steppe in the light of post-Soviet land abandonment. *Journal of Insect Conservation*, 21, 813-826.

Tree, I. (2018). *Wilding. The return of nature to a British farm*. Picador, London.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S. & Vidal, S. (2007). Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, Volume 43, Issue 3: 294-309

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., ... & Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biological reviews*, 87(3), 661-685.

Ubach, A., Páramo, F., Gutiérrez, C., & Stefanescu, C. (2020). Vegetation encroachment drives changes in the composition of butterfly assemblages and species loss in Mediterranean ecosystems. *Insect Conservation and Diversity*, 13(2), 151-161. https://doi.org/10.1111/icad.12397

Uchida, K. & Ushimaru, A. (2014). Biodiversity declines due to abandonment and intensification of agricultural lands: patterns and mechanisms. *Ecological Monographs*, 84:637–658. https:// doi. org/ 10. 1890/13- 2170.1

Uchida, K., Takahashi, S., Shinohara, T. & Ushimaru, A. (2016). Threatened herbivorous insects maintained by long-term traditional management practices in semi-natural grasslands. *Agriculture, Ecosystems and Environment*, 221, 156-162.

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L., Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M. & Zamora, R. (2015). Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, 29, 299–307.

Van Halder, I., Barbaro, L. & Jactel, H. (2011). Conserving butterflies in fragmented plantation forests: Are edge and interior habitats equally important? *Journal of Insect Conservation*, 15: 591-601.

Van Strien, A.J., Van Swaay, C.A.M., Van Strien-van Liempt, W., Poot, M.J.M. & Wallis De Vries, M.F. (2019). Over a century of data reveal more than 80% decline in butterflies in the Netherlands. *Biological Conservation*, 234, 116-122. doi: 10.1016/j.biocon.2019.03.023

Van Swaay, C. & Warren, M.S. (2006). Prime butterfly areas of Europe: an initial selection of priority sites for conservation. *Journal of Insect Conservation*, 10: 5-11.

Van Swaay, C.A.M., Dennis, E.B., Schmucki, R., Sevilleja, C.G., Aghababyan, K., Åström, S., Balalaikins, M., Bonelli, S., Botham, M., Bourn, N., Brereton, T., Cancela, J.P., Carlisle, B., Chambers, P., Collins, S., Dopagne, C., Dziekanska, I., Escobés, R., Faltynek Fric, Z., ... Roy, D.B. (2020*). Assessing Butterflies in Europe - Butterfly Indicators 1990-2018: Technical report.* Butterfly Conservation Europe & ABLE/eBMS(www.butterfly-monitoring.net). https://butterfly-monitoring.net/sites/default/files/Pdf/Reports/Assessing%20Butterflies%20in%20Europe%20-%20Butterfly%20Indicators%20Revised.pdf

Van Swaay, C., Cuttelod, A., Collins, S., Maes, D., Munguira, M. L., Šašić, M., ... & Wynhoff, I. (2010) *European red list of butterflies.* Luxembourg: Publications Office of the European Union.

Van Swaay, C.A.M., Bos, G., Van Grunsven, R.H.A., Kok, J., Huskens, K. & Van Deijk, J.R.(2018) *Vlinders en libellen geteld: Jaarverslag (2017)* [Internet]. De Vlinderstichting, Wageningen; Report No.: Rapport VS2018.006. https://assets.vlinderstichting.nl/docs/6d51f174-b497-4777-b84a-362e344c3528.pdf

Vera, F.W.M., Bakker, E., & Olff, H. (2006). The influence of large herbivores on tree recruitment and forest dynamics. In: Danell, K., Duncan, P., Bergström, R. & Pastor, J. (eds) *Large Herbivore Ecology, Ecosystem Dynamics and Conservation.* Cambridge University Press, Cambridge, pp 203-231

Von Humboldt, A. (1808). *Ansichten der Natur mit wissenschaftlichen Erlauterungen*. J. G. Cotta, Tübingen, Germany.

Wagner, D.L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, 65, 457–480.

Warren, M.S., Kill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414: 65-69.

Warren, M.S., Maes, D., Van Swaay, C.A.M., Goffart, P., Van Dyck, H., Bourn, N.A.D., Wynhoff, I., Hoare, D. & Ellis, S. (2021). The decline of butterflies in Europe: Problems, significance and possible solutions. *Proceedings of the National Academy of Sciences*, 118, 2, e2002551117 https://doi.org/10.1073/pnas.2002551117

Weiss, S., & Ferrand, N. (2007). Current perspectives in phylogeography and the significance of South European refugia in the creation and maintenance of European biodiversity. *Phylogeography of Southern European Refugia: Evolutionary perspectives on the origins and conservation of European biodiversity*, 341-357

Wepprich, T., Adrion, J.R., Ries, L., Wiedmann, J. & Haddad, N.M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS ONE,*14(7), e0216270. https://doi.org/10.1371/journal.pone.0216270

Wiemers, M., Balletto, E., Dincă, V., Faltynek, F. Z., Gerardo Lamas, 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*, 811, 9-45. doi: 10.3897/zookeys.811.28712. PMID: 30627036; PMCID: PMC6323101.

Wiens, J.A. (1997). Metapopulation dynamics and landscape ecology. In “Metapopulation biology: Ecology, Genetics and Evolution” (I. Hanski and M.E. Gilpin, eds.), 43-62. Academic Press, San Diego.

Williams, P.H., Araújo, M.B., Humphries, C., Lampinen, R., Hagemeijer, W., Gasc, P.J. & Mitchell-Jones, T., (2000). European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. *Belgian Journal of Entomology* 2, 21–46.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J. & Monserrat, V.J., (2007). An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, 13: 1873-1887.

Wright, D. H., Currie, D.J. & Maurer, B.A. (1993). Energy supply and patterns of species richness on local and regional scales. Pages 66–74 in: Ricklefs, R.E. & Schluter, D. (eds.). *Species diversity in ecological communities: historical and geographical perspectives.* University of Chicago Press, Chicago, Illinois, USA.

WWF (2022). *Living Planet Report 2022 – Building a nature-positive society.* Almond, R.E.A., Grooten, M., Juffe Bignoli,D. & Petersen, T. (Eds). WWF, Gland, Switzerland.

Yan, L. & Liu, X. (2014). Has climatic warming over the Tibetan Plateau paused or continued in recent years? *Journal of Earth, Ocean and Atmospheric Sciences*, 1, 13-28.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.