





# Micro-habitat shifts by butterflies foster conservation strategies to preserve pollinator diversity in a warming Mediterranean climate

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## Highlights

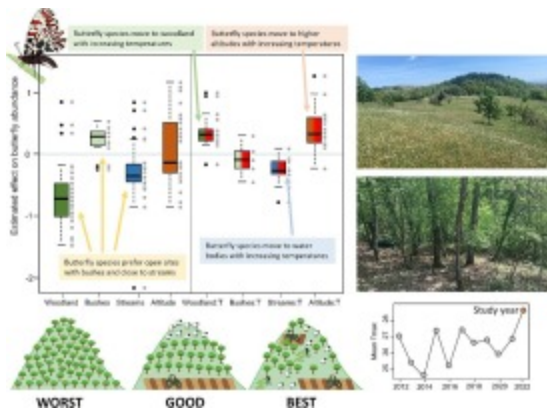
- Different environmental features determine Mediterranean butterfly richness across seasons.
- Cold-adapted species prefer humid areas with some woodland coverage.
- 80% of the community move to wet and shady areas in response to high temperatures.
- Geomorphological and vegetational heterogeneity mitigate extreme weather conditions.

- We present an evidence-based protocol to preserve butterflies within the resist-accept-direct framework.

## Abstract

The Butterfly Monitoring Scheme based on linear transects conducted by citizen scientists has become a fundamental indicator for understanding the impact of climate change on butterfly populations. A key finding is the fast poleward expansion of butterfly distributions in Europe, coupled with slower population declines in southern regions. Given that the Mediterranean region is a climate change hotspot, understanding the largely unknown mechanisms employed by butterflies to cope with increasing aridity is crucial for developing data-driven conservation strategies. To address this issue, we developed a monitoring approach based on 90 transects fully covering areas of 50m×50m squares instead of linear paths. This enabled us to explore the fine-scale dynamics of 80 butterfly species and their association with vegetational units in the Mediterranean hills (~800m a.s.l. as maximum altitude) of the MAB UNESCO Reserve of Monte Peglia (Central Italy). We sampled the transects from April to October 2022 (the locally hottest summer of the last decade) and documented three main patterns: 1) butterfly richness and abundance correlate with environmental features and these relationships vary across seasons. Richer sites consisted of some 30% of woodland and were those closer to water, mostly during summer (area-based analysis). 2) Environmental preferences vary with species traits. Specialist species and those adapted to colder climates and narrower temperature ranges were more abundant in higher altitudes sites, closer to water and with wider woodland coverage (fourth-quadrant analysis). 3) Although most species preferred meadows, when temperature increases, they increased their abundance in sites with wider tree coverage, closer to streams, and at higher altitude (species-based analysis). These dynamics demonstrate that butterflies opportunistically move to cooler micro-habitats to buffer elevated temperatures. This phenomenon potentially involves most of the community since the species showing significant effects encompass >80% of the observed individuals. Our analysis introduces new dimensions to the niche of Mediterranean butterflies, highlighting the significance of shady micro-habitats, altitudinal ranges, and water streams. These factors are likely to become increasingly critical with rising aridity levels. By combining our findings with existing literature data, we have provided a protocol aimed at preserving Mediterranean butterflies within the resist-accept-direct framework.

## Graphical abstract



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## Keywords

Lepidoptera; Climate buffering; Micro-habitat selection; Environmental heterogeneity; Site management; Woodland habitat; Conservation strategies; Species traits

## 1. Introduction

Current human-induced climatic changes are driving the planet far from its typical cyclic climatic history ([Steffen et al., 2018](#)). The rapid pace of climate change is significantly impacting insect populations, driving them out of their thermal niche and producing mismatches with resource phenologies ([Halsch et al., 2021](#), [Harvey et al., 2023](#), [Parmesan, 2007](#), [Settele et al., 2008](#), [Stange and Ayres, 2010](#)). The Butterfly Monitoring Scheme (BMS), operational since the early 1970s, produced quantitative and qualitative data based on repeated inspection of linear transects (about 1 km long) conducted mostly by citizen scientists. This huge dataset allows for precise spatial and temporal tracking of population trends and distributional changes, making butterflies a model group in understanding population dynamics ([Parmesan et al., 1999](#), [van Swaay et al., 2008](#), [Warren et al., 2021](#)). BMS data revealed poleward and upward distributional shifts in response to changing climate in many species ([Goded et al., 2024](#), [McCain and Garfinkel, 2021](#), [Parmesan et al., 1999](#)). For example, the number of species in Sweden and Finland increased from 108 to 131 since 1909 ([Pöyry et al., 2009](#),

Sunde et al., 2023). Shifts of approximately 5–10m per year in altitude were also recorded over the Alps, Apennines, Sierra Nevada, and Balkans, with populations tending to contract to smaller and restricted areas (Goded et al., 2024, Illán et al., 2012, Kerner et al., 2023, Rödder et al., 2021, Romo et al., 2023, Sistri et al., 2022, Wilson et al., 2007, Bonelli et al., 2022).

Current climate models consistently identify the Mediterranean region as a climate change hotspot (Cos et al., 2022), experiencing greater increases in aridity than the global average (Drobinski et al., 2020). Consequently, it is expected that southern European regions will face species depauperation and loss of ecosystemic functions due to poleward distributional shifts involving local extinctions at southern limits. Despite these expectations, the increase of species in northern communities is not mirrored by corresponding losses and community changes in Southern Europe (Devictor et al., 2012, Parmesan et al., 1999). In fact, while in the Mediterranean region population declines were detected mostly for specialist species (e.g. Melero et al., 2016) driving local extinctions (Bonelli et al., 2011, Gil-Tapetado et al., 2023), butterfly populations seem to have persisted, at least at the country level, in the last decades (Bonelli et al., 2018, Mora et al., 2023).

Therefore, investigating the adaptive strategies of butterfly populations in response to increased aridity in Mediterranean regions is necessary to develop evidence-informed conservation strategies aimed at preserving diversity of butterflies (and other pollinators) and the ecosystem functions they sustain. Possible adaptive strategies involve opportunistic shifting of micro-habitat. Adults of most European butterflies are dependent on open biotopes such as dry grassland and meadows. However, minor movements from meadows to bushes to woodland margins and to full woodland areas may allow survival on particularly hot days (Hayes et al., 2023). For instance, some univoltine species of butterflies, such as *Maniola jurtina* and *Brintesia circe* (Birch et al., 2021) have been found to display typical unimodal adult phenology in Central and Northern Europe and bimodal frequencies in southern regions where they survive the warmest months by moving to shady areas and reduce their activity through a process known as aestivation (Brakefield, 1982, Scali, 1971, Wiklund et al., 1983). These phenomena are likely common in butterflies and possibly represent fundamental mechanisms for survival in the Mediterranean under the current and future scenarios of climatic change. However, despite their significance, the extent of these phenomena remains largely unknown (van Swaay et al., 2008).

In fact, while the use of transects from BMS projects has provided invaluable insights on various aspects of butterfly ecology and conservation (Barea-Azcón et al., 2023,

Bubová et al., 2015, Caro-Miralles and Gutiérrez, 2023, Colom et al., 2021, Comay et al., 2021, Fartmann et al., 2013, Graser et al., 2023, Gutiérrez and Wilson, 2014, Slancarova et al., 2016, Stefanescu et al., 2004, Ubach et al., 2020, van Swaay et al., 2006, van Swaay and Warren, 2006, Zografou et al., 2014), its design typically does not allow for the recognition of subtle interactions between butterfly occurrence, environmental features, and functional traits. This limitation arises from the use of lengthy transects passing through (and mixing) different vegetational units and typically established by citizens without a standardized experimental design. In our study, we established squared transects measuring 50m×50m across 90 sites within the MAB UNESCO Reserve of Monte Peglia (Central Italy). This approach enabled us to account for the environmental settings within these small areas. The transects were surveyed bi-monthly from April to October. We designed the experimental setting to conduct a three-step analysis focusing on the following:

- Investigating how vegetational types and geographical features, such as altitude and distance from streams impact butterfly richness, diversity, and abundance across seasons (area-based analysis). Our aim is to pinpoint specific environmental features crucial for preserving butterfly communities during different periods characterised by different meteorological stresses.
- Exploring how species features, such as size, phenology, degree of generalism, type of host plant and temperature tolerance interact with vegetational types and geographical features to influence the abundance of individuals of each species in each area (fourth-quadrant analysis). This understanding of the relationship between environmental settings and species characteristics allows to identify the environments most crucial for the survival of species at higher risk of local extinction.
- Analysing the frequency of individual species in different environmental settings may be affected by temperature fluctuations, as individuals may move opportunistically between sites to cope with warmer days (species-focused analysis). This analysis will shed light on the availability of key micro-habitat among resources define butterfly niches.

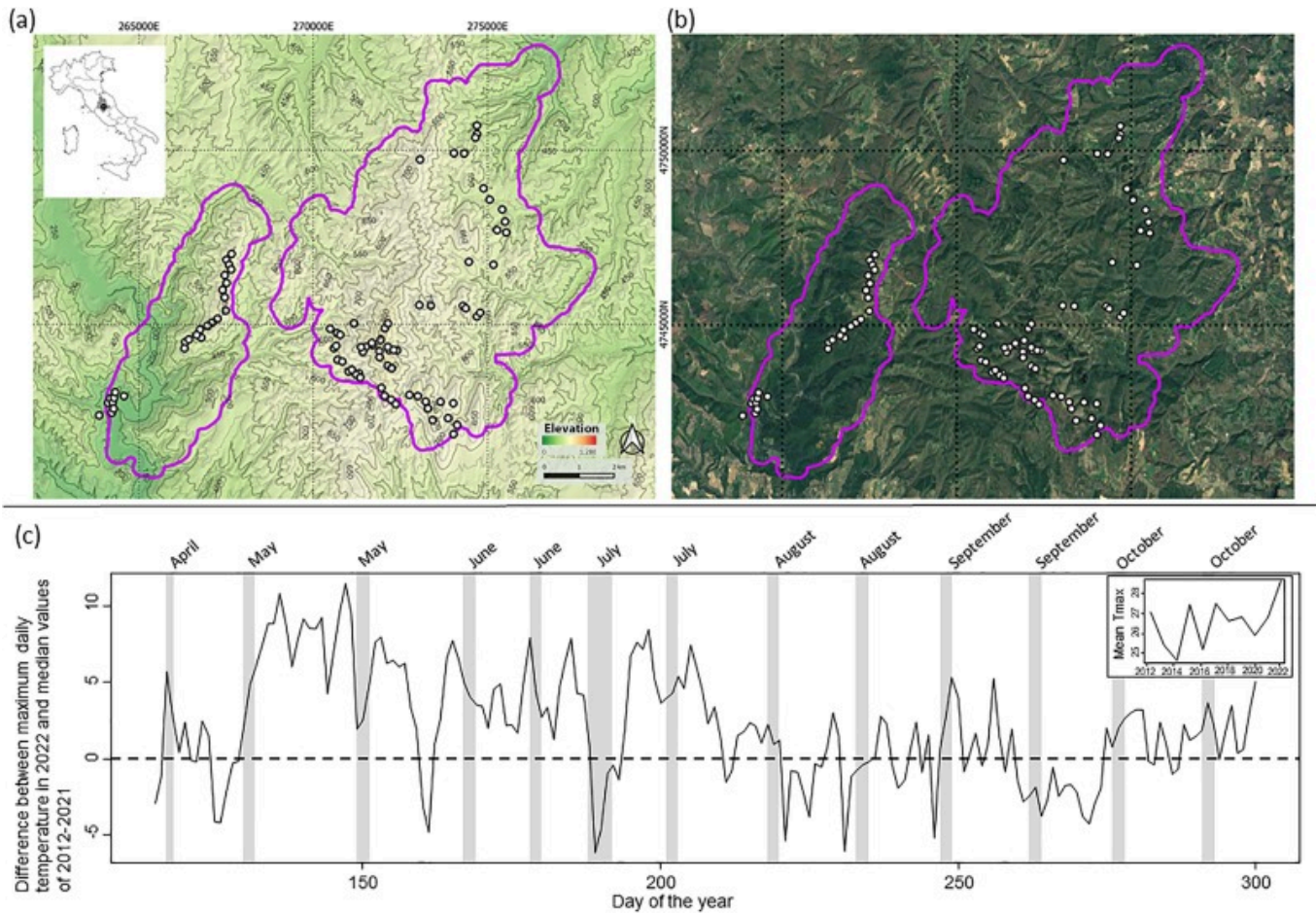
Once corroborated with literature data from other Mediterranean regions, this information will aid in formulating evidence-based guidelines for reserve design and site selection, as well as informing agri-environment schemes aimed at enhancing biodiversity. The ultimate goal of these guidelines is to preserve butterflies, both individual species and entire communities, in the face of increasing aridity in Mediterranean hills.

## 2. Methodology



## 2.1. Study area

The study was conducted within the Monte Peglia MAB UNESCO World Biosphere Reserve which spans approximately 60km<sup>2</sup> (Fig. 1a,b).



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Fig. 1. The study area depicts the boundaries of the Monte Peglia UNESCO Reserve, with the 90 squared transects represented by white circles. a) Contour lines indicating altitude and b) satellite land cover image of the area. c) Difference between daily maximum temperatures in 2022 during the survey period (April 28th – October 20th) and the median of the last ten years (2012–2021) in the Monte Peglia area. Shady areas correspond to our field work sessions. The inset graph on top right represents the trend of the average maximum temperatures between 2012 and 2022 in the same period.

The Reserve is characterized by a system of low hills, with the Peglia mountain (837 m a.s.l., 42° 49' N 12° 12' E) dominating the southern part (Stoppa, 1996, Stoppa, 2014). According to the Köppen-Geiger climate classification, the Monte Peglia Reserve falls into the Csa

category, indicating a temperate region with dry and hot summers (Koppen, 1936). The Reserve primarily comprises extensive forested areas, occasionally interspersed with meadows and pastures, and harbors a diverse array of flora and fauna, with habitats that are largely intact and well-preserved (Italian MAB National Committee, 2019).

## 2.2. Data collection

Field surveys were conducted every two weeks from April to October 2022 in five macro-areas spanning the altitudinal gradient of the Reserve (from 150 to 837m). Since several sectors were inaccessible, we optimized sampling efficiency within each session (limited to a maximum of 2–3 days) and cover a wide range of altitudes and environmental settings, selecting 90 sites at different altitudes, including open areas and various types of woodlands (Fig. 1a,b) (Bruschini et al., 2023). A typical linear BMS transect spans at least 500m in length and 5m in width, traversing various vegetational units at potentially different altitudes and distances from environmental features like water bodies. This variability complicates the possibility to precisely associate butterfly frequencies with specific environmental settings. Since our aim was to identify micro-habitat buffering acted by butterflies, we adapted the standard BMS methodology (Pollard and Yates, 1993) by implementing squared transects of 50m×50m (Fig. S1). Butterflies encountered in the site were counted by walking along ten designated paths 5m wide (like in BMS) within the survey area at a slow and steady pace in approximately 10min to cover the entire square (Fig. S1). The individuals were captured using a butterfly net for identification and were promptly released, except for those of uncertain species, which were collected and subsequently identified in the laboratory. All sites were visited regularly and in random order throughout the sampling season during the central hours of the day (from 10:00 a.m. to 4:30 p.m.), when wind speeds were below four on the Beaufort scale and when temperatures reached at least 17°C on cloudy days (Sevilleja et al., 2019).

## 2.3. Environmental features

We obtained temperature records every 10min and daily maximum temperatures from two available weather stations within the area: Pornello (504m, 42°52'32.0"N 12°12'02.0"E) and Bagni (156m, 42°46'58.0"N 12°07'44.0"E). The historical data from these stations enabled us to compare the mean temperatures of 2022 with those from previous years (Fig. 1c).

The altitude above sea level in meters (*Alt*) for each site was determined using Google Earth, while the distance from the nearest water stream in meters (*DisW*) was obtained from the hydrographic network layer at national scale (HydRet – SINAnet 2020; Rete del Sistema

Informativo Nazionale Ambientale-SINAnet,

<http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais/reticolo-idrografico/view> ↗  
)

In the Reserve, where agricultural activities are limited, we focused on semi-natural grasslands characterized by low-intensity exploitation for pastures and/or hay meadows. To gather information on vegetation cover and its structure, we identified the land types, classifying the physiognomic vegetation cover of each plot, through the interpretation of orthophotos from Google Satellite (acquired between 2021 and 2022). This was performed at a scale of 1:1000 in GIS environment using QGIS, version 3.34.6 LTR. The land type identification was fine-tuned with ground-surveys conducted in spring 2023, and on-site photos of each plot taken during the sampling process, also in GIS environment. We calculated the percentage of coverage in different land types, including shrubland (*Bu*) and woodlands (*Wo*); the remaining fraction was represented by meadows and very minor elements such as bare ground, roads, roofs. We further classified woodlands into the following stages: (i) young coppice (<5 years, *W1*), representing dense monostratified formations with a considerable shrub coverage, resulting from the first dynamic stages following the coppicing; (ii) mid-aged coppice (5–15 years, *W2*), denoting a more evolved formation with a clear differentiation of canopy and a sparser, dominated shrub layer; (iii) older trees (>15 years, *W3*), characterized by a typically evolved woodland formation with full developed canopy differentiation and a very sparse, dominated shrub layer.

## 2.4. Butterflies' traits

We assembled a comprehensive set of butterfly traits encompassing various ecological and physiological aspects (feeding, morphology, life history and physiology), known to be sensitive to global stressors (Moretti et al., 2017). Trophic generalism and preferences were evaluated using two measures: the number of host plant genera used by a species (*HP*) and an index (*HN*) ranging from 1 to 5, indicating the growth forms of the host plants and the extent to which these are associated with open or closed vegetation types (*HN*: 1, herb growing in grasslands; 2, herbs/shrubs mainly found in grasslands and secondarily in shrublands; 3, shrubs/herbs also growing in woodlands; 4, shrubs also growing in woodlands; 5, trees). Mobility was evaluated through wingspan (*WS*), correlated with the ability to move efficiently (Middleton-Welling et al., 2020, Sekar, 2012). Species phenology (*Ph*) was identified as the first Principal Component axis among: (i) the number of months during which adults occur in Europe, (ii) the first and the last month when adults fly, and (iii) voltinism (i.e. the maximum number of generations per year recorded in Europe). Temperature tolerance (*T95* and *TSD*) includes the upper 95% confidence limit of



temperature mean ( $T95$ ) and standard deviation of mean temperature ( $TSD$ ) experienced by European populations of each species (Platania et al., 2020, Schweiger et al., 2014). While not representing functional traits (Moretti et al., 2017), they serve as widely used proxies for eco-physiological responses to temperatures (Dapporto et al., 2017, Devictor et al., 2012, Slancarova et al., 2016). Additionally, we computed averaged maximum temperatures experienced by each species ( $T_{exp}$ ) during the surveys as follows:

$$T_{exp} = \frac{\sum_{i=1}^n T_{max_i} * Ab_i}{\sum_{i=1}^n Ab_i}$$

Where  $T_{max_i}$  represents the average maximum temperature of the two weather stations for each day(i) when that species has been observed, and  $Ab_i$  denotes the total number of individuals observed that day. A summary of the definitions of the variables used in this study is provided in Table 1.

Table 1. Definitions of the variables used in this study.

Name	Abbr.	Definition	Type
Species	Sp	The scientific name of a species	Taxonomic datum
Genus	Gn	The genus of a species	Taxonomic datum
Wingspan	WS	The wing size as in <a href="#">Middleton-Welling et al. (2020)</a>	Species functional trait
Host plants	HP	The number of known plant genera used by larvae	Species functional trait
Host plant type and habitat	HN	The growth forms of the host plants and the extent to which these are associated with open or closed vegetation types, ranging from 1 (grasslands) to 5 (woodlands)	Species feeding feature
Phenology	Ph	First principal component score among various phenology traits. It encompasses the length of period during which adults occur	Species functional trait
Upper 95% c.i. of mean temperature experienced in Europe	T95	An index of heat tolerance for butterfly species – updated version of <a href="#">Platania et al. (2020)</a>	Species physiological feature
Standard deviation of mean temperature	TSD	An index of temperature range for butterfly species – updated version of	Species physiological feature

<b>Name</b>	<b>Abbr.</b>	<b>Definition</b>	<b>Type</b>
experienced in Europe		<a href="#">Platania et al. (2020)</a>	
Temperature experienced	<i>Temp</i>	The average maximum temperature experienced by individuals of a species in the study area	Species environmental feature
Shrubland	<i>Bu</i>	The percentage of a site occupied by bushes	Environmental site feature
Total of woodlands	<i>Wo</i>	The percentage of a site occupied by woodlands. It can be divided in three categories	Environmental site feature
Young coppice	<i>W1</i>	The percentage of a site occupied by young coppice (<5 years)	Environmental site feature
Mid coppice	<i>W2</i>	The percentage of a site occupied by mid aged coppice (5–15 years)	Environmental site feature
Old coppice	<i>W3</i>	The percentage of a site occupied by old coppice (>15 year)	Environmental site feature
Altitude	<i>Alt</i>	The altitude of a site	Geomorphological site feature
Distance to water stream	<i>DisW</i>	Minimum distance between a site and a water stream	Geomorphological site feature
Latitude and Longitude	<i>Lat and Long</i>	The Latitude and Longitude of a site in decimal degrees	Geomorphological site feature
Day	<i>Day</i>	The day of the year (in sequential number) when a site has been surveyed	Collection datum
Time	<i>Tm</i>	The time when a site has been surveyed	Collection datum
Session	<i>Ses</i>	The session (fortnightly) of the survey	Collection datum
Maximum Temperature	<i>Tmax</i>	The maximum temperature of a given day	Collection datum
Temperature	<i>T</i>	The temperature recorded at the time of a visit (average between two weather stations)	Collection datum
Recorder	<i>Rec</i>	The operator who surveyed the site	Collection datum

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## 2.5. Statistical analyses

### 2.5.1. Beta diversity and area-based analyses

In the area-based analyses, each site represented a case, with response variables being alpha diversity indexes derived from single or multiple visits. Initially, we computed three indices of butterfly diversity and quantity for each site by aggregating all data of the observed butterflies over the seven months of survey period: 1) the total number of individuals observed (*Ab*), 2) species richness (*Rich*, Hill number  $q=0$ ); 3) Shannon index (*Sh*, Hill number  $q=1$ ). These indices were then compared with site features (*Alt*, *DisW*, *Wo*, *Bu*) by Generalized Additive Models (GAMs) using the *gam* function of the *mgcv* R package (Wood and Wood, 2015), employing the formula provided in Appendix A, Eq. (S1). For *Rich* and *Ab*, a Poisson family was used for the response variable, while for *Sh*, a Gaussian family was employed. Additionally, we examined whether these relationships were influenced by seasons by fitting another series of models incorporating interactions between site features and collection day (*Day*) (Appendix A, Eq. S2).

To highlight differences among the three stages of coppice forests (*W1*, *W2*, *W3*), we first eliminated sites with less than 10% of woodland coverage (pure meadows). Subsequently, we applied a model to identify potential trends based on the various stages of coppice (*W1*, *W2* and *W3*) (Stages in Appendix A, Eq. S3), as well as to assess overall diversity differences among sites dominated by different stages of coppice. This approach was implemented for both the fixed-effect model and an interaction model (Appendix A, Eq. S3-S4). In the event of significant differences among stages, we conducted post-hoc Tukey tests using the *emmeans* and the *pair* R functions from the *emmeans* package (Lenth, 2022).

Subsequently, we replicated the analysis by grouping the collection sessions into seven months from April to October. This approach enabled us to describe the interactions between environmental features and seasons, thereby observing changes in the shape of the relationships between richness/abundance indexes and site features. Additionally, we reran the models after eliminating the sites with less than 10% of woodland coverage to search for different trends based on the stage of coppice forests (*W1*, *W2* and *W3*).

Differences in faunal composition among sites (beta diversity) were calculated by summing the observed number of individuals of every species in each site, resulting in a typical community matrix with sites in rows and species in columns. Our objective was to understand whether differences in composition among sites were primarily driven by differences in nestedness (i. e., an ordered loss of individuals and species among sites) or

turnover (i. e., individuals and species replacement among sites). To achieve this, we utilized the Sorensen qualitative index, which can be partitioned into two additive components of the Simpson index of turnover, encompassing species replacing each other among sites, and the nestedness component, encompassing the ordered loss of species among sites. Similarly, the Bray-Curtis quantitative dissimilarity was partitioned into a turnover component, measured by how much individuals of certain species in one site are substituted by the same number of individuals of different species from another site, and a quantitative nestedness component, measuring the loss of individuals from one site to another ( [Baselga, 2017](#)). Finally, we assessed the ratio between the sum of cells representing turnover and nestedness with respect to overall dissimilarity. These analyses provided insights into the relative contributions of turnover and nestedness to overall beta diversity.

### 2.5.2. Fourth-quadrant analysis

Fourth-quadrant analysis is designed to elucidate which species traits influence species occurrence or abundance in sites with varying environmental characteristics ( [Legendre et al., 1997](#)). Traditionally, the analysis integrates three known matrices: species traits, site features, and the presence/absence of species in each site to generate a fourth matrix summarizing the significant association between environmental variables and species traits. However, in transect surveys where a quantitative evaluation of species abundance is available, it can be modelled as a function of environmental features, species traits, and their interactions, representing the fourth corner (e.g. [Brown et al., 2014](#), [Jamil et al., 2013](#)). Previous studies have employed various forms of generalized linear mixed models for this purpose. In this study, considering the potential for nonlinear fixed influences as mentioned earlier, we employed a GAM which enabled us to simultaneously model nonlinear fixed effects and linear interactions. While species were included as a random factor, the inclusion of random factor for sites is contentious. Following the recommendation of [Brown et al. \(2014\)](#), we did not include it. However, we accounted for the possibility that site location influences abundance by incorporating a covariance structure for site location, thereby addressing spatial autocorrelation. The resulting GAM formula can be found in [Appendix A](#), Eq. S5. A positive significant interaction between a site feature and a species trait indicates that as the given feature increases among sites, species with higher values for that trait tend to be more abundant. In a subsequent analysis, we removed sites with less than 10% of woodland (pure meadows) and applied a model to explore different interaction between species traits and *W1*, *W2* and *W3* to highlight distinct trends among coppice stages.

### 2.5.3. Species-focused analysis

For the species-focused analysis, a series of GAMs were conducted for individual species where cases were represented by the number of individuals observed in each visit to each site. The analysis considered the abundance (including absence) of each species in each day of collection between the first and the last appearance during the surveys. The primary focus was on examining how temperature interacts with environmental and geomorphological features in altering the abundance of individual species among sites. To control for overall changes in frequency due to phenology, the day of the year was included as a smooth term. All predictors were centered and scaled to allow for a direct comparison of their effects (estimates). The resulting model is described in [Appendix A](#), Eq. S6. GAMs were conducted for all species observed with at least 20 individuals. The investigation aiming to discern whether most of the significant responses revealed either positive or negative fixed effects and their interactions.

### 3. Results

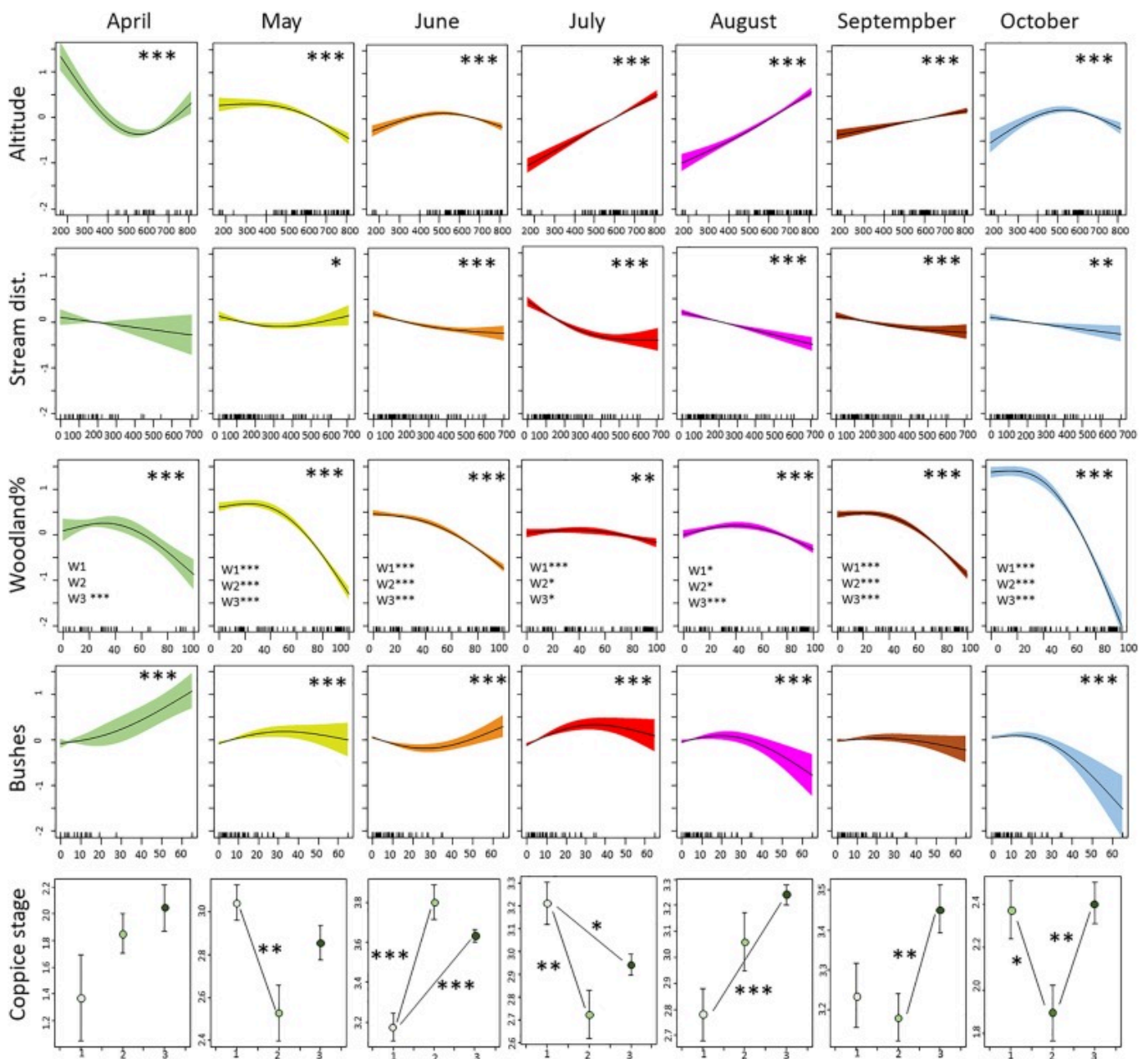
#### 3.1. Area focused analyses

A total of 80 species were spotted during the surveys. Most of the beta diversity among sites, considering the total number of individuals per species observed from April to October, was encompassed by turnover dissimilarity for both presence-absence (65.7%) and abundance data (64.3%). This suggests that even sites with low species richness and abundance contribute significantly to overall diversity in the study area.

A series of GAMs revealed that environmental factors strongly influence butterfly richness, Shannon index, and number of individuals observed over the entire study period. Tree coverage and distance to water bodies showed a negative effect, while altitude was more clearly positively related to abundance, than to richness and finally to the Shannon index ([Appendix A, Fig. S2-S4](#)). Bushes showed weaker effects, being only significant for abundance ([Appendix A, Fig. S2-S4](#); [Appendix B, Table S1](#)). Interactions between these environmental variables and day of collection revealed strongly significant different effects on butterfly diversity across different time periods ([Appendix B, Table S2](#)). Coverages in all coppice stages showed significant relationships, as showed by overall woodland ([Appendix A, Fig. S5](#) ; [Appendix B, Table S3](#)). Differences among stages revealed a weak effect on richness due to higher richness in *W3* compared to *W2* and a strong effect on abundance due to a higher richness in *W3* and *W1* compared to *W2* ([Appendix B, Table S4](#)). Only abundance showed a significant interaction between coppice stage and day of collection ([Appendix B, Table S2](#)).



When richness was analysed in different months, GAMs revealed that altitude exhibited a positive relationship during the hottest months (July and August) ([Appendix A, Fig. S6](#); [Appendix B, Table S5](#)), while showing negative trends in May, bell shaped patterns in June and October and no significant relationship in April (likely due to fewer records) and September. Distance from streams was negatively correlated with richness in the hottest months (June to August) peaking in July. Woodland coverage ( $W_0$ ) showed a curvilinear effect throughout the period (except in April) with maximum richness in areas with intermediate woodland coverage: this trend flattened in the hottest months when completely closed areas appeared as rich as open areas. In cooler months (May, September, October) the lowest richness was recorded in completely closed areas. Significant differences among the coppice stages emerged, but they varied among months, with special reference to  $W_1$ . Similar trends were observed for the Shannon index ([Appendix A, Fig. S7](#); [Appendix B, Table S5](#)). Similar patterns were also observed for abundance, with more significant relationships ([Fig. 2](#); [Appendix B, Table S5](#)). Notably distance to water streams showed a consistent negative relationship from May to October and significant overall differences in abundance among sites with different coppice stages. Again, the direction of these significant relationships varied among months ([Fig. 2](#), [Appendix B, Table S5](#)).



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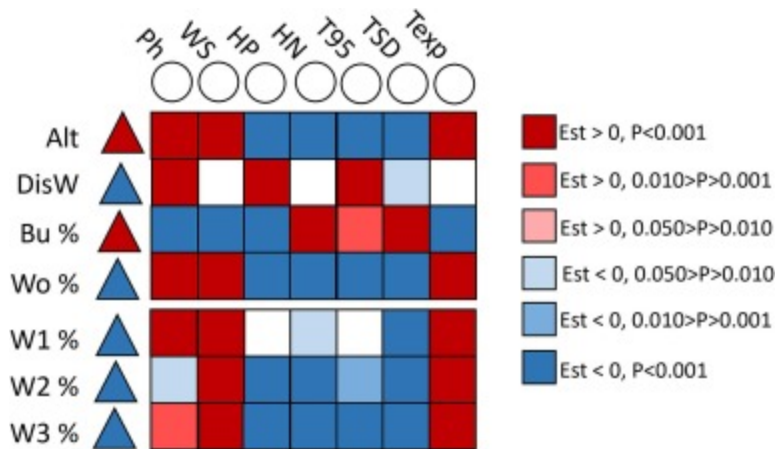
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Fig. 2. The effect of altitude, distance from water bodies, tree coverage, bushes and type of coppice on species abundance during the study period (from April to October) in a series of GAMs. \*  $P < 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P < 0.001$ .

### 3.2. Area $\times$ species (fourth-quadrant) analysis

A GAM testing smoothed fixed effects for species traits and site features and their linear interactions on species abundance on individual sites over the study period confirmed area-based analyses. Sites at higher altitude, closer to water with a fraction of shrubs and a lower

fraction of woodland hosted a higher general abundance of butterflies (triangles in Fig. 3). Species traits did not reveal any significant effect as fixed factors (circles in Fig. 3) but many significant interactions between site features and species traits emerged (squares in Fig. 3) (Appendix B, Table S6-S7).



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Fig. 3. Fixed effect of species traits (circles) and site features (triangles) and their interactions (squares) in determining overall species abundance. *Alt*: altitude, *DisW*: distance from the nearest water stream, *Bu*: percentage of coverage of shrubland, *Wo*: percentage of coverage of woodlands, *W1*: young coppice (<5 years), *W2*: mid-aged coppice (5–15 years), *W3*: older trees (>15 years), *Ph*: species phenology, *WS*: wingspan of a butterfly, *HP*: the number of host plant genera used by a species, *HN*: degree to which host plants are linked to open or closed vegetation, *T95*: upper 95% confidence limit of mean temperature, *TSD*: standard deviation of mean temperature, *Texp*: averaged maximum temperatures experienced by each species. The colour gradient represents the degree of p-value in the Generalized Additive Model (GAM).

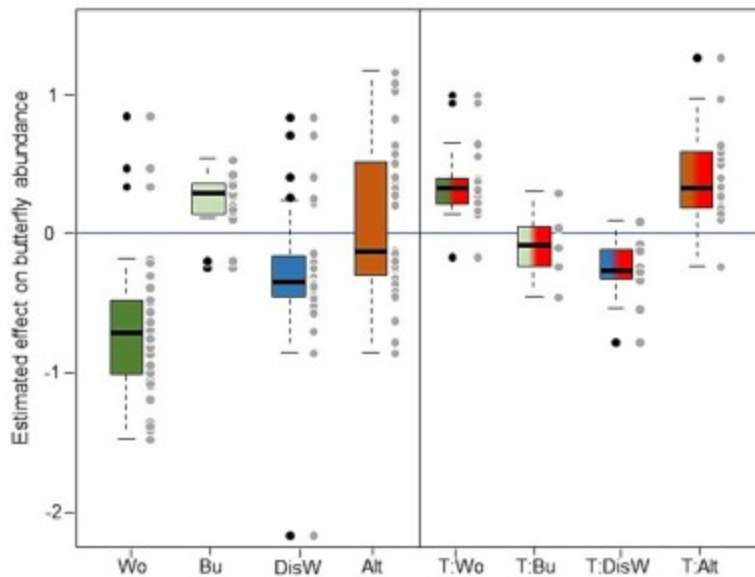
Larger species tended to be more common at high altitude, far from water, in woody areas and in areas with fewer shrubs. Specialist species and those adapted to colder climates are more frequent at higher altitudes, closer to water streams and in areas with higher wood coverage (and bushes for specialists). Species adapted to a narrow temperature range are found more frequently at higher altitude and in woody areas and less frequently in shrub areas where high temperature tolerant species prevail. The species experiencing higher temperatures (those with summer centered phenologies) were more frequent at higher altitudes, occupying sites with a lower fraction of bushes and a higher fraction of woodland. Hostplants associated with high hostplant index, tend to occur at lower altitudes, in sites with higher fraction of bushes but with less wood coverage, probably because most species

with high index (4) are bush specialist and only three species of the reserve are specialized tree feeders (5). When the different stages of coppice are considered, a similar result among coppice stages is found, thus implying that they function in a similar manner in allowing occurrence of species with different traits.

### 3.3. Species-focused analysis

A series of individual GAMs ([Appendix B, Table S8](#)) were performed on the 50 species with at least 20 individuals. All these species, except two (*Melitaea cinxia*, *Leptotes pirithous*), showed at least one significant effect for environmental features. Eighteen species did not show any significant interaction between environmental preferences and temperature at the time of each visit ([Appendix B, Table S8](#)).

Fourteen species were not affected by the quantity of woodland at each site. Among the significant effects woodland had a significant negative impact on 33 species and a positive impact on only three species ([Fig. 4](#)), confirming the tendency of European-Mediterranean butterflies to prefer open areas. The total number of observed individuals of species showing a preference for open areas was 10,521, representing 79.2% of the total individuals observed. Conversely, most of the significant effects of bushes were positive (18 species vs 2 species), potentially affecting 32.9% of the butterflies observed. Similarly, species were more abundant close (21 species) than far (6 species) from water bodies, and presence of water bodies potentially had a positive effect on 48.2% of individuals. Altitude had a mixed effect, with 18 species occurring more frequently at lower altitudes and 15 at higher altitudes. Despite most species preferring open areas, when higher temperatures occurred, 16 species (representing 60.1% of individuals) were found significantly more abundant in areas with higher woodland coverage and only one in areas with lower coverage. Bushes showed a significant positive interaction in two species and negative in three (21.7% and 8.9% of individuals appeared in sites with wider bush coverage, respectively, with increased temperatures). A total of 10 species (encompassing 40.4% of individuals) were more frequent closer to water bodies at higher temperatures, as opposed to one showing the opposite pattern. Finally, 16 species tended to be more frequent at higher altitudes with increasing temperatures (38.8% of individuals) while only 2 showed the opposite pattern ([Fig. 4; Appendix B, Table S8](#)). The species that showed at least one interaction becoming more common in site covered with a higher fraction of tree or bushes or closer to water bodies or at higher altitude was 30, potentially covering the 82.3% of the individuals observed in the survey.



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Fig. 4. The significant estimated effects from individual species GAMs environmental features as fixed effects and their interactions with temperature. Each grey dot represents the estimated abundance of a species showing a significant effect for the specific environmental feature. Dark green: Woodland, light green: Bushes, blue: Distance from the nearest stream, brown: Altitude. The interactions of these variables with temperature (red) are represented by the combination of the colours.

## 4. Discussion

### 4.1. Main findings

The use of Pollard transects in Europe has provided high-quality data for evaluating butterfly occurrence and local density, ultimately aiding in understanding their interaction with environmental features and climatic change. Since 1994 the Butterfly Monitoring Scheme (BMS) in Catalunya, expanded across Spain in 2014, has furthered the understanding of these phenomena from Northern and Central Europe (Lee et al., 2020) to the Mediterranean region, one of the major biodiversity hotspot (Myers et al., 2000). Moreover, populations from Southern Europe exhibit increased genetic diversity compared to those in Northern Europe (Dincă et al., 2021). Since southern populations are anticipated to become more widespread at higher latitudes and altitudes in the future, they will likely serve as reservoirs of genetic variance adapted to warm climates (Brooks et al., 2015).



In contrast to previous studies ([Barea-Azcón et al., 2023](#)), which primarily examined BMS data across large altitudinal gradients ([Table 2](#)), we examined the fine-scale dynamics of butterfly populations within purely Mediterranean hills below 1000m altitude. Additionally, we specifically designed an experiment by including a balanced number of open, closed and mixed areas and we did not aggregate samples across seasons to focus on shifts in site occupancy across periods and with varying temperatures. This allowed us to demonstrate that, for many species, environmental preferences change with the temperature experienced at a given moment. Indeed, in response to increased temperatures, adult butterflies of most examined species were opportunistically more common at higher altitudes, closer to woodlands, and to water bodies. The species involved in these phenomena encompassed more than the 80% of the individuals observed, thus possibly affecting a significance portion of the ecosystem functioning sustained by diurnal Lepidoptera. This finding significantly broadens the dimensionality of the butterfly niche of many species, for which vital resources include not only host plants for larvae, nectar resources for adults, reproductive sites, and climatic envelopes ([Dennis et al., 2003](#), [Sánchez-Dávila et al., 2023](#)) but also geomorphological and vegetational heterogeneity to buffer extreme weather conditions. We expect that this phenomenon will be increasingly important for survival in the Mediterranean area due to forecasts of increased aridity in this region ([Cos et al., 2022](#), [Drobinski et al., 2020](#)). Noteworthy, spring, summer and autumn 2022, when the experiment took place, were particularly hot and dry, with maximum daily temperatures surpassing the median of the previous 10 years for 10 sessions over 13 (average +2.03 °C). This resulted in 2022 showing the highest mean for the maximum daily temperatures between 2012 and 2022 ([Fig. 1c](#)). The response of butterflies to 2022 temperatures likely represents a preview of what will happen in the next decades.

Table 2. The actions suggested (first column) based on our evidence (second column) and the literature demonstrating a efficacy Southern Europe (third column).

<b>Suggested action</b>	<b>This study evidence</b>	<b>Literature evidence</b>
Select management sites at various altitudes	1) Different altitudes show distinct species richness and the relationship interact with seasons  2) Species increase frequency at higher altitudes during warmer	1) Spain: different altitude host different communities ( <a href="#">Barea-Azcón et al., 2023</a> ).  2) Spain: uphill migration in summer of <i>Gonepteryx rhmani</i> ( <a href="#">Gutiérrez and Wilson, 2014</a> ).

Suggested action	This study evidence	Literature evidence
	<p>days/seasons. for altitudinal shifts or delayed emergence</p> <p>3) Cold-adapted species are more commonly found at higher altitudes and are declining due to climatic changes.</p>	<p>3) Greece: increased abundance of low-elevation species, decline of species occurring at higher elevations (<a href="#">Zografou et al., 2014</a>).</p>
<p>Select management sites that include both dry areas and water bodies</p>	<p>1) Locations close to water bodies support a higher diversity of butterfly species compared to dry sites</p> <p>2) Specialist and cold-adapted species are more likely to be found in the vicinity of water bodies</p> <p>3) Species opportunistically move to humid areas during warm days/periods</p>	<p>1) Balkans: lack of humidity restricts local species richness (<a href="#">Slancarova et al., 2016</a>).</p> <p>2) Spain: wetness increases abundance but reduces diversity (<a href="#">Barea-Azcón et al., 2023</a>). Richness is positively correlated with rainfall (<a href="#">Stefanescu et al., 2004</a>).</p> <p>3) Menorca island: ravine populations increase with temperature suggesting that butterflies disperse to humid and shady areas (<a href="#">Colom et al., 2021</a>).</p>
<p>Implement management practices for open sites to enhance resource heterogeneity incorporating marginal and wooded areas around them. Prioritize the presence of bushes/shrubs within the meadows</p>	<p>1) Open sites host a greater diversity of butterfly species compared to wooded areas</p> <p>2) Marginal sites contribute to increased richness due to higher number of resources;</p>	<p>1) General: (<a href="#">Bubová et al., 2015</a>, <a href="#">van Swaay and Warren, 2006</a>, <a href="#">van Swaay et al., 2006</a>).</p> <p>2) Italy: (<a href="#">Luppi et al., 2018</a>); Sicily: (<a href="#">Fileccia et al., 2015</a>). Balkans: (<a href="#">Slancarova et al., 2016</a>). Israel: (</p>

Suggested action	This study evidence	Literature evidence
	bush show lower positive effect	Pe'er et al., 2011). Spain: (Atauri and De Lucio, 2001).
	3) Specialist and cold-adapted species are more likely to be found in proximity of closed areas	3) Spain: (Ubach et al., 2020). Sierra Nevada: bushes increase abundance and diversity (Caro-Miralles and Gutiérrez, 2023).
	4) Species opportunistically move to shaded areas during warm days/periods	4) Spain: distance to woodland reduces density and diversity (Barea-Azcón et al., 2023). Israel: meadow, forests and meadow-forest have more species than forest-bushland (Comay et al., 2021). Menorca island (Colom et al., 2021). Italy: with increased yearly temperatures, species richness disproportionately increased in wooded areas (Bonelli et al., 2022). Aestivation (e.g. <i>M. jurtina</i> (Scali, 1973)).
Manage the coppice to foster diversification among its stages	1) Different coppice stages have a slight overall effect and show similar response to climatic buffering.	1) Germany: <i>M. athalia</i> and <i>S. ilicis</i> prefer intermediate coppice stages (Graser et al., 2023).
	2) Different coppice stages provide different resources and buffering in different periods/weather conditions	2) France: richness and abundance highest in early and mid-successional stages (Fartmann et al., 2013). Austria: richness highest in early stages and lowest in intermediate stages (Weiss et al., 2021).

Conservation practices at the local scale underlay a first step identifying areas with invariant geomorphological features, such as altitude and distance to water bodies to select priority areas (site selection). Site management, on the other hand, involves potential interventions on vegetation and/or land use. The guidelines we propose are not only based on our

findings; we also considered similar evidence from other Mediterranean contexts to broaden their applicability ([Table 2](#)).

## 4.2. Site selection

The diversity of Lepidopteran communities along altitudinal gradients typically follows a bell-shaped curve in the Mediterranean region, and species composition is influenced primarily by turnover phenomena, although nestedness also plays a role. In communities primarily differentiated by nestedness, conservation efforts should concentrate on the richest areas while, more complex strategies are required for communities predominantly differentiated by turnover ([Socolar et al., 2016](#)). Therefore, we propose a protocol for preserving entire local communities of butterflies rather than focusing solely on managing individual species or richer sites. It's important to note that these two strategies are not mutually exclusive. In the presence of particularly endangered taxa, species-specific actions can complement community-wide conservation efforts.

The decline in richness at high altitudes typically occurs over 1600m ([Barea-Azcón et al., 2023](#)). Most Mediterranean hills have a much lower maximum altitude, likely representing only the left part of this bell-shaped relationship. Nonetheless, we did not find consistent evidence for a uniform trend in richness with altitude. Instead, the relationship between diversity and altitude varied across months. In spring, we observed higher richness of butterfly species in low-altitude areas, whereas this trend reversed in summer (area-focused analysis). Thus, we demonstrate that an altitudinal range of a few hundred meters still plays a crucial role in buffering different temperatures throughout the flight season.

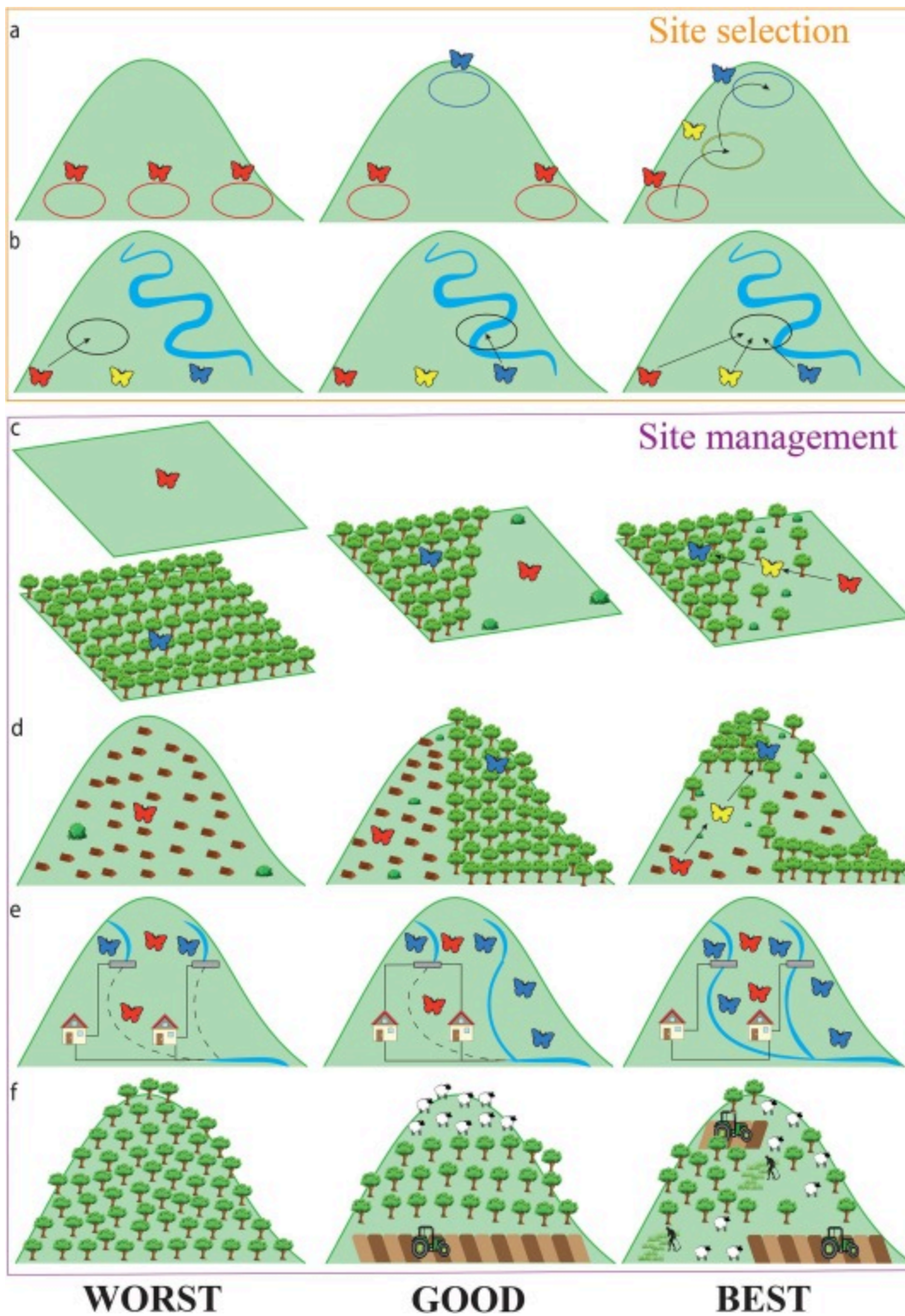
Richness variations across altitudinal strata also reflects the environmental preference of cold-adapted species for higher altitudes and of warm adapted species for low altitudes (fourth-quadrant analysis). The consistent positive interaction between temperature and altitude in species-focused analysis also suggests that butterflies opportunistically shift their distribution along the altitudinal gradient ([Colom et al., 2024](#)). While it is challenging to determine whether this result is due to sequential emergence, aestivation of individuals at lower altitude, or to active altitudinal migration of individuals, the practical implications for conservation remain clear: adult butterflies of many species (potentially the 43.8% of individuals) benefit for the presence of suitable areas across an altitudinal range.

If high altitude areas host the species most vulnerable to climatic changes, they are likely to become the only suitable habitats for many other taxa in a warmer future. For instance, previous studies documented the occurrences of two orophilous species (*Chazara briseis* and

*Euphydryas aurinia*) near the summit of Monte Peglia in 1978 and 2009 respectively ( [Bruschini et al., 2023](#)). Despite our intensive sampling efforts, we did not observe these species during our study. Therefore, it is possible that they have become locally extinct, indicating the loss of species over time when compared to historical data.

From a site selection perspective, we recommend choosing conservation sites at various altitudes to broaden the range of species benefiting from conservation measures and to facilitate opportunistic altitudinal movements ([Table 2](#), [Fig. 5a](#)). It could be argued that high altitude areas hold special conservation value and are typically smaller in size, due to the conical shape of mountains, making them less suitable for agricultural use. As a result, the costs associated with their protection may be significantly reduced.





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Fig. 5. Protocol guidelines for site selection and site management strategies for butterfly conservation in low-altitude Mediterranean areas. We examined six site-related features (a-f) and assessed how site selection and their management affect butterfly communities (butterfly icons represent species adapted to different climates and environments from red

(warm and/or open), to yellow (intermediate), to blue (cold and/or closed). The representation for each feature represent decisions ranging from the least favorable to the most favorable. a) altitudinal gradient; b) distance from water streams; c) environmental heterogeneity; d) coppicing management; e) water diversion; f) agro-silvo-pastoral practices.

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Based on our data, increasing aridity will likely strongly affect butterfly populations. In Spain a linear negative relationship was documented between butterfly richness and aridity (Stefanescu et al., 2011). There can be both direct physiological effects and indirect effects on host-plants and nectar resources that may explain the importance of water availability (Hawkins and Porter, 2003). In Mediterranean landscapes, many plants which are important as food for larvae and nectar sources for adults (including species that we could observe in our study area such as *Lythrum* spp., *Mentha* spp., *Aristolochia* spp., *Carex riparia*) are particularly frequent around streams being much less common only a few meters away (Bruno et al., 2014, Cini et al., 2021, Nardi, 1984). Water also has a direct impact on the survival of many species. For example, mud-puddling, primarily observed in males, is believed to facilitate the acquisition of essential resources such as sodium for adult butterflies (Molleman, 2010). Finally, the vegetation around the streams can contribute to creating shady areas where resources can be found in a relatively cooler micro-habitat (Fig. 5b).

We confirm all these hypotheses since sites closer to water streams were richer in individuals from May to October and richer in species during the most arid months of July and August (area-based analysis). Moreover, several species moved closer to water bodies when higher temperatures were experienced (species-focused analysis). The effect of uncommon resources around water streams is confirmed by the observation that specialist species tend to occur more frequently close to water streams (fourth-quadrant analysis). Finally, the hypothesis that some species can find a cooler micro-habitat along water streams is supported by the occurrence of more cold-adapted species in proximity to streams (fourth-quadrant analysis).

We conclude that together with high altitude areas, sites close to water streams should be considered a high priority in site selection. We suggest including the streams at the margin of a selected site to protect both species linked to resources found close and relatively far from them, while allowing their opportunistic movements (Fig. 5b). Movements along an altitudinal gradient require longer distances and are likely limited by philopatry and the dispersal abilities typical of each species. In contrast, movement from a grassland area to an adjacent waterline can be undertaken by a wider range of species. Clearly, there can be other geomorphological features not considered in our study (exposure, slope, soil and

substrate quality) but in any case, the general recommendation is to select sites in order to obtain the highest possible heterogeneity.

### 4.3. Site management and biodiversity friendly strategies

After identifying sites for implementing conservation measures, the necessity for appropriate management becomes evident. Within the array of management decisions and actions, the Resist-Accept-Direct framework posits that management actions can be categorized into three fundamental types: 1) Resist to changing ecological trajectories and restore pristine conditions; 2) Accept the trajectory, allowing ecosystems to transform into new conditions; or 3) Intervene in the trajectory to direct transformations toward new states better suited to sustain biodiversity and ecosystem services than pristine ones ( [Schoorman et al., 2022](#)).

Identifying the pristine conditions for butterflies in the Mediterranean region thus emerges as a prerequisite for site management. Over the last 3 million years, since the onset of the Pleistocene, the climate has been colder and drier than nowadays, and steppic and substeppic landscapes dominated southern Europe, mostly at low altitudes ( [Combourieu-Nebout et al., 2015](#)). During this period, European butterflies evolved to thrive in grassland biotas, leading to exceptional species diversity in open habitats ( [van Swaay and Warren, 2006](#), [van Swaay et al., 2006](#)) and we confirmed this preference for our study area. At the onset of the Holocene, temperate and mixed Mediterranean forests expanded in Southern Europe, with pollen-based reconstructions indicating the establishment of the modern Mediterranean climate, marked by an inversion of winter and summer precipitation trends, about 4 kyr BP ( [Combourieu-Nebout et al., 2015](#)). Human activities, such as deforestation for agri-silvo-pastoral system ( [Kaal et al., 2011](#)), interacted with the changing interglacial climate to maintain wide-open areas required by species adapted to the colder and drier Pleistocene conditions ( [Roberts et al., 2011](#)).

Vegetation encroachment threatens butterfly diversity in Europe, spreading woody plants in open areas, reducing resources for butterflies ( [Table 2](#)). Encroached meadows also rely more on deep water and exacerbate Mediterranean aridity ( [Rolo and Moreno, 2019](#)). In our study area, sites with greater bush coverage did not exhibit a generalised higher diversity (area-focused analysis) although a few species preferred bush-rich environments (species-focused analysis), for host plants or nectar sources. Specifically, areas abundant in bushes tend to harbor climatic generalist species compared to woodlands (fourth-quadrant analysis), while there is no evidence of opportunistic utilization of bushes in warmer temperatures (species-focused analysis).

However, the relationship between the predominance of open areas and butterfly diversity is not linear and varies across seasons. In the Reserve, butterfly richness and abundance increased with woodland cover up to approximately 30%, before slightly decreasing in fully open sites. The area-based results showing very low differences between fully open and fully closed sites in summer agree with results obtained in the arid southern Mediterranean Israel hills, where forest and grassland-forest sites showed similarly high richness while forest-shrubland areas showed the lowest richness (Comay et al., 2021).

An obvious explanation for these trends lies in the presence of transitional zones (ecotones). Ecotones are recognized as a key for maintaining rich insect communities for three main reasons (Luppi et al., 2018, Pe'er et al., 2011, Schlegel, 2022): provide a wide range of resources, offer a range of micro-temperatures suitable for various species, and act as climate buffers, enabling species to cope with momentary meteorological conditions.

In the context of preserving European and Mediterranean butterflies, passively accepting the transition to bushy and woody areas is thus deemed ineffective. A possible strategy would actively guide the change by creating mixed mosaics of woodlands, marginal bushes, and meadows (Table 2, Fig. 5c). This approach demands ongoing intervention and can be costly and its feasibility is evident only in specific cases (Cini et al., 2021). Over extensive Mediterranean landscapes, delaying encroachment may not be feasible unless there are socio-economic benefits associated with this management. Considering the historical establishment of the Mediterranean climate, the pristine environmental setting of this region is inherently linked to traditional agriculture and pastures which had an overall beneficial influence on biological diversity (Bagella et al., 2014a, Bagella et al., 2014b, Blondel and Aronson, 1995, Roberts et al., 2011). In 2010, the UNESCO recognized the Mediterranean diet as an Intangible Cultural Heritage of Humanity. The Mediterranean diet encompasses the entire set of “skills, knowledge, rituals, symbols and traditions concerning crops, harvesting, fishing, animal husbandry, conservation, processing, cooking, and particularly the sharing and consumption of food” (<https://ich.unesco.org/en/RL/mediterranean-diet-00884> ↗). Promoting the Mediterranean diet drives eco-tourism, boosting revenues and supporting traditional agriculture with minimal impact (Burlingame and Dernini, 2011, Mattas et al., 2023, Whitelaw et al., 2014) (Fig. 5f).

Other than traditional agricultural practices, coppicing is a self-sustaining activity maintaining environmental diversity and it has been proven to favor pollinators abundance in Mediterranean regions. However, different studies provided different results about which stage(s) offer higher opportunities for butterflies (references in Table 2). We confirmed this



pattern since different coppicing stages supported different butterfly richness and abundance in different months. This can be attributed to unique plants of varying coppice stages flowering at different times and attracting butterflies across distinct months as well as the diverse efficacy of these stages in buffering temperatures throughout the year. Nevertheless, all coppice stages increased the frequency of specialized species, larger in size, with low tolerance of high temperatures and facilitate the presence of species flying in the hottest months. So, we recommend coppicing activity over small spatially and temporally separated patches as a favorable practice to offer varied resources and climate buffering to pollinators (Fig. 5d) (Božek et al., 2023, Fartmann et al., 2013, Proesmans et al., 2019).

In contrast to the complex effect of wood coverage on butterfly abundance and richness (butterflies prefer open areas but move closer to woodland on hot days), the proximity of water bodies consistently had positive effect, particularly in the hottest periods. Preserving of at least a part of superficial water resources (Fig. 5e) is thus essential to provide butterflies with a primary climatic buffer. For this reason, water diversion practices pose a significant threat to biodiversity (Zhan et al., 2015) also in butterflies. While water is vital for agriculture and tourism, passive acceptance or resistance to aridity isn't enough to protect natural water bodies. Sustainable management, integrating technology and social solutions, is crucial. Despite bleak forecasts for the Mediterranean, there are opportunities and technical advancements to maintain agro-ecosystems.

Clearly, the hope for an increase in traditional agriculture and eco-tourism clashes with the need to maintain surface water bodies. Agriculture is responsible for more than 60% of water withdrawal, and municipal use of water in many Mediterranean countries contributes to another 30%. Tourism adds important demand to municipal water, especially during arid peak seasons (Fader et al., 2020). Addressing these challenges in the Mediterranean basins requires urgent attention and comprehensive solutions and sustainable practices, such as integrated water management. Solutions include: i) protecting and replenishing groundwater through managed aquifer recharge with treated wastewater; ii) implementing efficient wastewater reuse for irrigation (Bourziza and Burak, 2018) and iii) promoting rain water harvesting systems in buildings to allow household level water-saving (Fader et al., 2020). In seashore areas improvements and advancements in desalination technologies offer possibilities to minimize the impacts associated with this process and reduce water diversion (Elsaid et al., 2020). Additionally improving subsurface dams and check dams, can provide localized water storage solutions, while agricultural practices like minimum-tillage, mulching and efficient systems can optimize water usage. In eco-tourism, strategies include using recycled water and promoting water-saving technologies.

## 5. Conclusion

Based on our evidence, we envisage that shady areas are (and will continue to) become part of many species' niches, especially with increasing aridity in Mediterranean regions. We reinforce the paradigm that preserving traditional agro-ecosystems in the Mediterranean can maintain environmental heterogeneity and support functional, biodiverse landscapes. The complexity of the distributional dynamics we have highlighted calls for conservation strategies tailored to the Mediterranean region, informed by evidence-based studies. By identifying historical determinants for community richness, forecasting climate trends for the next decade, and identifying key environmental factors, we can propose practical management approaches and provide stakeholders with crucial resources for preserving butterfly populations and the ecosystem services they provide in this region.

## CRedit authorship contribution statement

**Claudia Bruschini:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Giulia Simbula:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Fulvia Benetello:** Writing – review & editing, Investigation. **Loirella Dell’Olmo:** Software. **Lorenzo Lazzaro:** Writing – review & editing, Investigation, Formal analysis. **Michele Mugnai:** Writing – review & editing, Investigation. **Francesco Paola:** Funding acquisition. **Lorenzo Pasquali:** Writing – review & editing, Investigation, Formal analysis. **Leonardo Dapporto:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Claudia Bruschini reports financial support was provided by Umbria Region. Leonardo Dapporto reports financial support was provided by Italian Ministry of University and Research. Giulia Simbula reports financial support was provided by Umbria Region. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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## Data availability

The data are available in Figshare at doi:10.6084/m9.figshare.25290592

## References

[Atauri and De Lucio, 2001](#) J.A. Atauri, J.V. De Lucio

The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes

Landsc. Ecol., 16 (2) (2001), pp. 147-159, [10.1023/A:1011115921050](#) ↗

[View in Scopus ↗](#) [Google Scholar ↗](#)

- [Bagella et al., 2014a](#) S. Bagella, M.C. Caria, E. Farris, I. Rossetti, R. Filigheddu  
**Traditional land uses enhanced plant biodiversity in a Mediterranean agro-silvo-pastoral system**  
Plant Biosyst., 150 (2) (2014), pp. 201-207, [10.1080/11263504.2014.943319](https://doi.org/10.1080/11263504.2014.943319) ↗  
[Google Scholar](#) ↗
- [Bagella et al., 2014b](#) S. Bagella, R. Filigheddu, M.C. Caria, M. Girlanda, P.P. Roggero  
**Contrasting land uses in Mediterranean agro-silvo-pastoral systems generated patchy diversity patterns of vascular plants and below-ground microorganisms**  
C. R. – Biol., 337 (12) (2014), pp. 717-724, [10.1016/j.crvi.2014.09.005](https://doi.org/10.1016/j.crvi.2014.09.005) ↗  
 [View PDF](#)   [View article](#)   [View in Scopus](#) ↗   [Google Scholar](#) ↗
- [Barea-Azcón et al., 2023](#) J.M. Barea-Azcón, A.J. Pérez-Luque, F.J. Olivares, M. Guerrero, M. Galiana-García, M.D. Chaves, M. Olvera, M.L. Munguira  
**Butterfly diversity, richness, and density patterns in Sierra Nevada (SE Spain): Conservation implications under a global change scenario**  
Insect Conserv. Divers., 16 (2) (2023), pp. 217-230, [10.1111/icad.12617](https://doi.org/10.1111/icad.12617) ↗  
[View in Scopus](#) ↗   [Google Scholar](#) ↗
- [Baselga, 2017](#) A. Baselga  
**Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients**  
Methods Ecol. Evol., 8 (7) (2017), pp. 799-808, [10.1111/2041-210X.12693](https://doi.org/10.1111/2041-210X.12693) ↗  
[View in Scopus](#) ↗   [Google Scholar](#) ↗
- [Birch et al., 2021](#) R.J. Birch, G. Markl, T.K. Gottschalk  
**Aestivation as a response to climate change: the Great Banded Grayling *Brintesia circe* in Central Europe**  
Ecol. Entomol., 46 (6) (2021), pp. 1342-1352, [10.1111/een.13081](https://doi.org/10.1111/een.13081) ↗  
[View in Scopus](#) ↗   [Google Scholar](#) ↗
- [Blondel and Aronson, 1995](#) Blondel, J., Aronson, J. 1995. *Biodiversity and Ecosystem Function in the Mediterranean Basin: Human and Non-Human Determinants*. 43–119.  
[https://doi.org/10.1007/978-3-642-78881-9\\_2](https://doi.org/10.1007/978-3-642-78881-9_2).  
[Google Scholar](#) ↗
- [Bonelli et al., 2011](#) S. Bonelli, C. Cerrato, N. Loglisci, E. Balletto

## Population extinctions in the Italian diurnal Lepidoptera: An analysis of possible causes

J. Insect Conserv., 15 (6) (2011), pp. 879-890, [10.1007/s10841-011-9387-6](https://doi.org/10.1007/s10841-011-9387-6) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Bonelli et al., 2018](#) S. Bonelli, L.P. Casacci, F. Barbero, C. Cerrato, L. Dapporto, V. Sbordoni, S. Scalercio, A. Zilli, A. Battistoni, C. Teofili, C. Rondinini, E. Balletto

## The first red list of Italian butterflies

Insect Conserv. Divers., 11 (5) (2018), pp. 506-521, [10.1111/icad.12293](https://doi.org/10.1111/icad.12293) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Bonelli et al., 2022](#) S. Bonelli, C. Cerrato, F. Barbero, M.V. Boiani, G. Buffa, L.P. Casacci, L. Fracastoro, A. Provenzale, E. Rivella, B. Zaccagno, E. Balletto

## Changes in Alpine Butterfly Communities during the Last 40 Years

Insects., 13 (1) (2022), p. 43, [10.3390/insects13010043](https://doi.org/10.3390/insects13010043) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Bourziza and Burak, 2018](#) Bourziza, H., Burak, S. 2018. *IPEMED Palimpsestes - Reuse of treated waste water in the Mediterranean and impacts on territories* EDITING Arthur DEBOOS, *IPEMED*. 1–20.

[http://www.ipemed.coop/adminIpemed/media/fich\\_article/1521051262\\_palimpseste-n19-en.pdf](http://www.ipemed.coop/adminIpemed/media/fich_article/1521051262_palimpseste-n19-en.pdf) ↗

.

[Google Scholar](#) ↗

[Bożek et al., 2023](#) M. Bożek, B. Denisow, M. Strzałkowska-Abramek, E. Chrzanowska, K. Winiarczyk

## Non-forest woody vegetation: a critical resource for pollinators in agricultural landscapes-A review

Sustainability (Switzerland), 15 (11) (2023), [10.3390/su15118751](https://doi.org/10.3390/su15118751) ↗

[Google Scholar](#) ↗

[Brakefield, 1982](#) P.M. Brakefield

## Ecological studies on the butterfly *Maniola jurtina* in Britain. Adult behaviour, microdistribution and dispersal

J. Anim. Ecol., 51 (3) (1982), pp. 713-726

[Crossref](#) ↗ [View in Scopus](#) ↗ [Google Scholar](#) ↗

[Brooks et al., 2015](#) T.M. Brooks, A. Cuttelod, D.P. Faith, J. Garcia-Moreno, P. Langhammer, S. Pérez-Espona

## Why and how might genetic and phylogenetic diversity be reflected in the identification of key biodiversity areas?

Philos. Trans. R. Soc., B, 370 (1662) (2015), pp. 1-7, [10.1098/rstb.2014.0019](https://doi.org/10.1098/rstb.2014.0019) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Brown et al., 2014](#) A.M. Brown, D.I. Warton, N.R. Andrew, M. Binns, G. Cassis, H. Gibb

## The fourth-corner solution - using predictive models to understand how species traits interact with the environment

Methods Ecol. Evol., 5 (4) (2014), pp. 344-352, [10.1111/2041-210X.12163](https://doi.org/10.1111/2041-210X.12163) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Bruno et al., 2014](#) D. Bruno, O. Belmar, D. Sánchez-Fernández, J. Velasco

## Environmental determinants of woody and herbaceous riparian vegetation patterns in a semi-arid mediterranean basin

Hydrobiologia, 730 (1) (2014), pp. 45-57, [10.1007/s10750-014-1822-8](https://doi.org/10.1007/s10750-014-1822-8) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Bruschini et al., 2023](#) C. Bruschini, L. Dapporto, L. Pasquali, F. Benetello, E. Balletto, F. Paola, G.

Simbula

## Intensive monitoring of the butterflies of the UNESCO MAB reserve of Monte Peglia (Central Italy) reveals strong potential for local extinctions in a Mediterranean area

J. Insect Biodivers., 40 (1) (2023), pp. 1-11, [10.12976/jib/2023.40.1.1](https://doi.org/10.12976/jib/2023.40.1.1) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Bubová et al., 2015](#) T. Bubová, V. Vrabec, M. Kulma, P. Nowicki

## Land management impacts on European butterflies of conservation concern: a review

J. Insect Conserv., 19 (5) (2015), pp. 805-821, [10.1007/s10841-015-9819-9](https://doi.org/10.1007/s10841-015-9819-9) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Burlingame and Dernini, 2011](#) B. Burlingame, S. Dernini

## Sustainable diets: the Mediterranean diet as an example

Public Health Nutr., 14 (12 A) (2011), pp. 2285-2287, [10.1017/S1368980011002527](https://doi.org/10.1017/S1368980011002527) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Caro-Miralles and Gutiérrez, 2023](#) E. Caro-Miralles, D. Gutiérrez

## Butterfly population trends track vegetation encroachment but not climate warming in a Mediterranean mountain

Biodivers. Conserv., 32 (6) (2023), pp. 2017-2035, [10.1007/s10531-023-02589-9](https://doi.org/10.1007/s10531-023-02589-9) ↗

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Cini et al., 2021](#) A. Cini, F. Benetello, L. Platania, A. Bordoni, S. Boschi, E. Franci, G. Ghisolfi, L. Pasquali, R. Negroni, L. Dapporto

### A sunny spot: habitat management through vegetation cuts increases oviposition in abandoned fields in an endemic Mediterranean butterfly

*Insect Conserv. Divers.*, 14 (5) (2021), pp. 582-596, [10.1111/icad.12489 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Colom et al., 2021](#) P. Colom, A. Traveset, D. Carreras, C. Stefanescu

### Spatio-temporal responses of butterflies to global warming on a Mediterranean island over two decades

*Ecol. Entomol.*, 46 (2) (2021), pp. 262-272, [10.1111/een.12958 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Colom et al., 2024](#) P. Colom, A. Traveset, M.R. Shaw, C. Stefanescu

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

*J. Biogeogr.*, 51 (3) (2024), pp. 499-510, [10.1111/jbi.14764 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Comay et al., 2021](#) O. Comay, O. Ben Yehuda, R. Schwartz-Tzachor, D. Benyamini, I. Pe'er, I. Ktalav, G. Pe'er

### Environmental controls on butterfly occurrence and species richness in Israel: The importance of temperature over rainfall

*Ecol. Evol.*, 11 (17) (2021), pp. 12035-12050, [10.1002/ece3.7969 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Combourieu-Nebout et al., 2015](#) N. Combourieu-Nebout, A. Bertini, E. Russo-Ermolli, O. Peyron, S. Klotz, V. Montade, S. Fauquette, J. Allen, F. Fusco, S. Goring, B. Huntley, S. Joannin, V. Lebreton, D. Magri, E. Martinetto, R. Orain, L. Sadori

### Climate changes in the central Mediterranean and Italian vegetation dynamics since the Pliocene

*Rev. Palaeobot. Palynol.*, 218 (2015), pp. 127-147, [10.1016/j.revpalbo.2015.03.001 ↗](#)

 [View PDF](#) [View article](#) [View in Scopus ↗](#) [Google Scholar ↗](#)

[Cos et al., 2022](#) J. Cos, F. Doblas-Reyes, M. Jury, R. Marcos, P.A. Bretonnière, M. Samsó

### The Mediterranean climate change hotspot in the CMIP5 and CMIP6 projections

*Earth Syst. Dyn.*, 13 (1) (2022), pp. 321-340, [10.5194/esd-13-321-2022 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

**Dapporto et al., 2017** L. Dapporto, A. Cini, M. Menchetti, R. Vodă, S. Bonelli, L.P. Casacci, V. Dincă, S. Scalercio, J.C. Hinojosa, H. Biermann, L. Forbicioni, U. Mazzantini, L. Venturi, F. Zanichelli, E. Balletto, T.G. Shreeve, R.L.H. Dennis, R. Vila

## Rise and fall of island butterfly diversity: understanding genetic differentiation and extinction in a highly diverse archipelago

Divers. Distrib., 23 (10) (2017), pp. 1169-1181, [10.1111/ddi.12610 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

**Dennis et al., 2003** R.L.H. Dennis, T.G. Shreeve, H. Van Dyck

## Towards a Functional Resource-Based Concept for Habitat: A Butterfly Biology Viewpoint

Nordic Society Oikos, 102 (2) (2003), pp. 417-426

[View in Scopus ↗](#) [Google Scholar ↗](#)

**Devictor et al., 2012** V. Devictor, C. Van Swaay, T. Brereton, L. Brotons, D. Chamberlain, J. Heliölä, S. Herrando, R. Julliard, M. Kuussaari, Å. Lindström, J. Reif, D.B. Roy, O. Schweiger, J. Settele, C. Stefanescu, A. Van Strien, C. Van Turnhout, Z. Vermouzek, M. WallisDeVries, F. Jiguet

## Differences in the climatic debts of birds and butterflies at a continental scale

Nat. Clim. Chang., 2 (2) (2012), pp. 121-124, [10.1038/nclimate1347 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

**Dincă et al., 2021** V. Dincă, L. Dapporto, P. Somervuo, R. Vodă, S. Cuvelier, M. Gascoigne-Pees, P. Huemer, M. Mutanen, P.D.N. Hebert, R. Vila

## High resolution DNA barcode library for European butterflies reveals continental patterns of mitochondrial genetic diversity

Commun. Biol., 4 (1) (2021), pp. 1-11, [10.1038/s42003-021-01834-7 ↗](#)

[Google Scholar ↗](#)

**Drobinski et al., 2020** P. Drobinski, N. Da Silva, S. Bastin, S. Mailler, C. Muller, B. Ahrens, O.B. Christensen, P. Lionello

## How warmer and drier will the Mediterranean region be at the end of the twenty-first century?

Reg. Environ. Chang., 20 (3) (2020), [10.1007/s10113-020-01659-w ↗](#)

[Google Scholar ↗](#)

**Elsaid et al., 2020** K. Elsaid, M. Kamil, E.T. Sayed, M.A. Abdelkareem, T. Wilberforce, A. Olabi

## Environmental impact of desalination technologies: A review



Sci. Total Environ., 748 (2020), Article 141528, [10.1016/j.scitotenv.2020.141528](https://doi.org/10.1016/j.scitotenv.2020.141528) ↗



[View PDF](#) [View article](#) [View in Scopus](#) ↗ [Google Scholar](#) ↗

[Fader et al., 2020](#) Fader, M., Giupponi, C., Burak, S., Dakhlaoui, H., Koutroulis, A., Lange, M. A., Llasat, M. C., Sanz-cobeña, A. 2020. *First Mediterranean Assessment Report – Chapter 3.1: Resources – Water*. <https://doi.org/10.5281/zenodo.7101074>.

[Google Scholar](#) ↗

[Fartmann et al., 2013](#) T. Fartmann, C. Müller, D. Poniowski

### Effects of coppicing on butterfly communities of woodlands

Biol. Conserv., 159 (2013), pp. 396-404, [10.1016/j.biocon.2012.11.024](https://doi.org/10.1016/j.biocon.2012.11.024) ↗



[View PDF](#) [View article](#) [View in Scopus](#) ↗ [Google Scholar](#) ↗

[Fileccia et al., 2015](#) V. Fileccia, S. Santorsola, S. Arpaia, B. Manachini

### Seasonal patterns in butterfly abundance and species diversity in five characteristic habitats in sites of community importance in Sicily (Italy)

Bull. Insectol., 68 (1) (2015), pp. 91-102

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Gil-Tapetado et al., 2023](#) D. Gil-Tapetado, C.D. Soria, J.F. Gómez, J.M. Sesma, F.J. Cabrero-Sañudo

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

Ecol. Entomol., 48 (1) (2023), pp. 40-54, [10.1111/een.13200](https://doi.org/10.1111/een.13200) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Goded et al., 2024](#) M. Goded, G. Ursul, A. Baz, R.J. Wilson

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

J. Insect Conserv., 1–15 (2024), [10.1007/s10841-024-00561-8](https://doi.org/10.1007/s10841-024-00561-8) ↗

[Google Scholar](#) ↗

[Graser et al., 2023](#) A. Graser, M. Kelling, R. Pabst, M. Schulz, N. Hölzel, J. Kamp

### Habitat quality, not patch isolation, drives distribution and abundance of two light-demanding butterflies in fragmented coppice landscapes

J. Insect Conserv., 27 (5) (2023), pp. 743-758, [10.1007/s10841-023-00494-8](https://doi.org/10.1007/s10841-023-00494-8) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Gutiérrez and Wilson, 2014](#) D. Gutiérrez, R.J. Wilson

### Climate conditions and resource availability drive return elevational migrations in a single-brooded insect

Oecologia, 175 (3) (2014), pp. 861-873, [10.1007/s00442-014-2952-4](https://doi.org/10.1007/s00442-014-2952-4) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Halsch et al., 2021](#) 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. *Proc. Natl. Acad. Sci. U. S. A.*, 118(2), 1–9. <https://doi.org/10.1073/PNAS.2002543117>.

[Google Scholar](#) ↗

[Harvey et al., 2023](#) J.A. Harvey, K. Tougeron, R. Gols, R. Heinen, M. Abarca, P.K. Abram, Y. Basset, M. Berg, C. Boggs, J. Brodeur, P. Cardoso, J.G. de Boer, G.R. De Snoo, C. Deacon, J.E. Dell, N. Desneux, M.E. Dillon, G.A. Duffy, L.A. Dyer, S.L. Chown

**Scientists' warning on climate change and insects**

*Ecol. Monogr.*, 93 (1) (2023), pp. 1-37, [10.1002/ecm.1553](https://doi.org/10.1002/ecm.1553) ↗

[Google Scholar](#) ↗

[Hawkins and Porter, 2003](#) B.A. Hawkins, E.E. Porter

**Water-energy balance and the geographic pattern of species richness of western Palearctic butterflies**

*Ecol. Entomol.*, 28 (6) (2003), pp. 678-686, [10.1111/j.1365-2311.2003.00551.x](https://doi.org/10.1111/j.1365-2311.2003.00551.x) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Hayes et al., 2023](#) M.P. Hayes, E. Ashe-Jepson, G.E. Hitchcock, A.J. Bladon, E.C. Turner

**Heatwave predicts a shady future for insects: impacts of an extreme weather event on a chalk grassland in Bedfordshire**

UK (2023), pp. 1-19, [10.21203/rs.3.rs-3462943/v1](https://doi.org/10.21203/rs.3.rs-3462943/v1) ↗

[Google Scholar](#) ↗

[Illán et al., 2012](#) G.J. Illán, D. Gutiérrez, S.B. Díez, R.J. Wilson

**Elevational trends in butterfly phenology: Implications for species responses to climate change**

*Ecol. Entomol.*, 37 (2) (2012), pp. 134-144, [10.1111/j.1365-2311.2012.01345.x](https://doi.org/10.1111/j.1365-2311.2012.01345.x) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Italian MAB National Committee, 2019](#) Italian MAB National Committee. 2019. *Italian MAB UNESCO Biosphere Reserves. A rising network.*

[Google Scholar](#) ↗

[Jamil et al., 2013](#) T. Jamil, W.A. Ozinga, M. Kleyer, C.J.F. Ter Braak

**Selecting traits that explain species-environment relationships: A generalized linear mixed model approach**

J. Veg. Sci., 24 (6) (2013), pp. 988-1000, [10.1111/j.1654-1103.2012.12036.x](https://doi.org/10.1111/j.1654-1103.2012.12036.x) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Kaal et al., 2011](#) J. Kaal, Y. Carrión Marco, E. Asouti, M. Martín Seijo, A. Martínez Cortizas, M. Costa Casáis, F. Criado Boado

**Long-term deforestation in NW Spain: Linking the Holocene fire history to vegetation change and human activities**

Quat. Sci. Rev., 30 (1–2) (2011), pp. 161-175, [10.1016/j.quascirev.2010.10.006](https://doi.org/10.1016/j.quascirev.2010.10.006) ↗



[View PDF](#) [View article](#) [View in Scopus](#) ↗ [Google Scholar](#) ↗

[Kerner et al., 2023](#) J.M. Kerner, J. Krauss, F. Maihoff, L. Bofinger, A. Classen

**Alpine butterflies want to fly high: Species and communities shift upwards faster than their host plants**

Ecology, 104 (1) (2023), pp. 1-17, [10.1002/ecy.3848](https://doi.org/10.1002/ecy.3848) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Koppen, 1936](#) W. Koppen

**Das geographische System de Klimate**

Handbuch Der Klimatologie (1936)

[Google Scholar](#) ↗

[Lee et al., 2020](#) M.S. Lee, J. Comas, C. Stefanescu, R. Albajes

**The Catalan butterfly monitoring scheme has the capacity to detect effects of modifying agricultural practices**

Ecosphere, 11 (1) (2020), [10.1002/ecs2.3004](https://doi.org/10.1002/ecs2.3004) ↗

[Google Scholar](#) ↗

[Legendre et al., 1997](#) P. Legendre, R.G. Galzin, M.L. Harmelin-Vivien

**Relating behavior to habitat: Solutions to the fourth-corner problem**

Ecology, 78 (2) (1997), pp. 547-562, [10.2307/2266029](https://doi.org/10.2307/2266029) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Lenth, 2022](#) Lenth, R. 2022. emmeans: Estimated marginal means, aka least-squares means.

R package version 1.7. 2.

[Google Scholar](#) ↗

[Luppi et al., 2018](#) M. Luppi, O. Dondina, V. Orioli, L. Bani

**Local and landscape drivers of butterfly richness and abundance in a human-dominated area**

Agric. Ecosyst. Environ., 254 (2018), pp. 138-148, [10.1016/j.agee.2017.11.020](https://doi.org/10.1016/j.agee.2017.11.020) ↗

[View PDF](#)[View article](#)[View in Scopus ↗](#)[Google Scholar ↗](#)

[Mattas et al., 2023](#) K. Mattas, E. Raptou, A. Alayidi, G. Yener, G. Baourakis

## Assessing the interlinkage between biodiversity and diet through the Mediterranean diet case

In: *Advances in Nutrition*, 14 (3) (2023), pp. 570-582, [10.1016/j.advnut.2023.03.011 ↗](#)

[View PDF](#)[View article](#)[View in Scopus ↗](#)[Google Scholar ↗](#)

[McCain and Garfinkel, 2021](#) C.M. McCain, C.F. Garfinkel

## Climate change and elevational range shifts in insects

*Curr. Opin. Insect Sci.*, 47 (2021), pp. 111-118, [10.1016/j.cois.2021.06.003 ↗](#)

[View PDF](#)[View article](#)[View in Scopus ↗](#)[Google Scholar ↗](#)

[Melero et al., 2016](#) Y. Melero, C. Stefanescu, J. Pino

## General declines in Mediterranean butterflies over the last two decades are modulated by species traits

*Biol. Conserv.*, 201 (2016), pp. 336-342, [10.1016/j.biocon.2016.07.029 ↗](#)

[View PDF](#)[View article](#)[View in Scopus ↗](#)[Google Scholar ↗](#)

[Middleton-Welling et al., 2020](#) J. Middleton-Welling, L. Dapporto, E. García-Barros, M. Wiemers, P.

Nowicki, E. Plazio, S. Bonelli, M. Zaccagno, M. Šašić, J. Liparova, O. Schweiger, A. Harpke, M. Musche, J. Settele, R. Schmucki, T. Shreeve

## A new comprehensive trait database of European and Maghreb butterflies, Papilionoidea

*Sci. Data*, 7 (1) (2020), [10.1038/s41597-020-00697-7 ↗](#)

[Google Scholar ↗](#)

[Molleman, 2010](#) F. Molleman

## Puddling: From natural history to understanding how it affects fitness

*Entomol. Exp. Appl.*, 134 (2) (2010), pp. 107-113, [10.1111/j.1570-7458.2009.00938.x ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Mora et al., 2023](#) A. Mora, A. Wilby, R. Menéndez

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

*Insect Conserv. Divers.*, 16 (6) (2023), pp. 838-852, [10.1111/icad.12676 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Moretti et al., 2017](#) M. Moretti, A.T.C. Dias, F. de Bello, F. Altermatt, S.L. Chown, F.M. Azcárate, J.R.

Bell, B. Fournier, M. Hedde, J. Hortal, S. Ibanez, E. Öckinger, J.P. Sousa, J. Ellers, M.P. Berg

## Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits

Funct. Ecol., 31 (3) (2017), pp. 558-567, [10.1111/1365-2435.12776](https://doi.org/10.1111/1365-2435.12776) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Myers et al., 2000](#) N. Myers, R.A. Mittermeyer, C.G. Mittermeyer, G.A.B. Da Fonseca, J. Kent

## Biodiversity hotspots for conservation priorities

Nature, 403 (6772) (2000), pp. 853-858, [10.1038/35002501](https://doi.org/10.1038/35002501) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Nardi, 1984](#) E. Nardi

## The genus «*Aristolochia*» L. (Aristolochiaceae) in Italy

Webbia, 38 (1) (1984), pp. 221-300

[Crossref](#) ↗ [View in Scopus](#) ↗ [Google Scholar](#) ↗

[Parmesan, 2007](#) C. Parmesan

## Influences of species, latitudes and methodologies on estimates of phenological response to global warming

Glob. Chang. Biol., 13 (9) (2007), pp. 1860-1872, [10.1111/j.1365-2486.2007.01404.x](https://doi.org/10.1111/j.1365-2486.2007.01404.x) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Parmesan et al., 1999](#) C. Parmesan, N. Ryrholm, C. Stefanescu, J.K. Hill, C.D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W.J. Tennent, J.A. Thomas, M. Warren

## Poleward shifts in geographical ranges of butterfly species associated with regional warming

Nature, 399 (6736) (1999), pp. 579-583, [10.1038/21181](https://doi.org/10.1038/21181) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Pe'er et al., 2011](#) G. Pe'er, C. van Maanen, A. Turbé, Y.G. Matsinos, S. Kark

## Butterfly diversity at the ecotone between agricultural and semi-natural habitats across a climatic gradient. Divers

Distrib., 17 (6) (2011), pp. 1186-1197, [10.1111/j.1472-4642.2011.00795.x](https://doi.org/10.1111/j.1472-4642.2011.00795.x) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Platania et al., 2020](#) L. Platania, R. Vodă, V. Dincă, G. Talavera, R. Vila, L. Dapporto

## Integrative analyses on Western Palearctic Lasiommata reveal a mosaic of nascent butterfly species

J. Zool. Syst. Evol. Res., 58 (4) (2020), pp. 809-822, [10.1111/jzs.12356](https://doi.org/10.1111/jzs.12356) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Pollard and Yates, 1993](#) E. Pollard, T.J. Yates

## Monitoring Butterflies for Ecology and Conservation: the British Butterfly Monitoring Scheme

Springer Science & Business Media (1993)

[Google Scholar ↗](#)

[Pöyry et al., 2009](#) J. Pöyry, M. Luoto, R.K. Heikkinen, M. Kuussaari, K. Saarinen

## Species traits explain recent range shifts of Finnish butterflies

Glob. Chang. Biol., 15 (3) (2009), pp. 732-743, [10.1111/j.1365-2486.2008.01789.x ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Proesmans et al., 2019](#) W. Proesmans, D. Bonte, G. Smagghe, I. Meeus, G. Decocq, F. Spicher, A. Kolb, I. Lemke, M. Diekmann, H.H. Bruun, M. Wulf, S. Van Den Berge, K. Verheyen

## Small forest patches as pollinator habitat: oases in an agricultural desert?

Landsc. Ecol., 34 (3) (2019), pp. 487-501, [10.1007/s10980-019-00782-2 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Roberts et al., 2011](#) N. Roberts, D. Brayshaw, C. Kuzucuoğlu, R. Perez, L. Sadori

## The mid-Holocene climatic transition in the Mediterranean: Causes and consequences

Holocene, 21 (1) (2011), pp. 3-13, [10.1177/0959683610388058 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

[Rödder et al., 2021](#) D. Rödder, T. Schmitt, P. Gros, W. Ulrich, J.C. Habel

## Climate change drives mountain butterflies towards the summits

Sci. Rep., 11 (1) (2021), [10.1038/s41598-021-93826-0 ↗](#)

[Google Scholar ↗](#)

[Rolo and Moreno, 2019](#) V. Rolo, G. Moreno

## Shrub encroachment and climate change increase the exposure to drought of Mediterranean wood-pastures

Sci. Total Environ., 660 (2019), pp. 550-558, [10.1016/j.scitotenv.2019.01.029 ↗](#)

 [View PDF](#) [View article](#) [View in Scopus ↗](#) [Google Scholar ↗](#)

[Romo et al., 2023](#) H. Romo, E. García-Barros, R.J. Wilson, R.G. Mateo, M.L. Munguira

## Modelling the scope to conserve an endemic-rich mountain butterfly taxon in a changing climate

Insect Conserv. Divers., 16 (4) (2023), pp. 451-467, [10.1111/icad.12636 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)



[Sánchez-Dávila et al., 2023](#) J. Sánchez-Dávila, A. Traveset, P. Colom  
Effects of food availability on butterfly diversity and network specialization across altitudinal levels in a Mediterranean landscape  
Biodivers. Conserv., 239–256 (2023), [10.1007/s10531-023-02745-1](https://doi.org/10.1007/s10531-023-02745-1) ↗  
[Google Scholar](#) ↗

[Scali, 1971](#) V. Scali  
Imaginal diapause and gonadal maturation of *Maniola jurtina* (Lepidoptera: Satyridae) from Tuscany  
J. Anim. Ecol., 40 (2) (1971), pp. 467-472  
[Crossref](#) ↗ [Google Scholar](#) ↗

[Schlegel, 2022](#) J. Schlegel  
Butterflies benefit from forest edge improvements in Western European lowland forests, irrespective of adjacent meadows' use intensity  
For. Ecol. Manage., 521 (May) (2022), Article 120413, [10.1016/j.foreco.2022.120413](https://doi.org/10.1016/j.foreco.2022.120413) ↗  
 [View PDF](#) [View article](#) [View in Scopus](#) ↗ [Google Scholar](#) ↗

[Schuurman et al., 2022](#) G.W. Schuurman, D.N. Cole, A.E. Cravens, S. Covington, S.D. Crausbay, C.H. Hoffman, D.J. Lawrence, D.R. Magness, J.M. Morton, E.A. Nelson, R. O'Malley  
Navigating ecological transformation: Resist-accept-direct as a path to a new resource management paradigm  
Bioscience, 72 (1) (2022), pp. 16-29, [10.1093/biosci/biab067](https://doi.org/10.1093/biosci/biab067) ↗  
[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Schweiger et al., 2014](#) O. Schweiger, A. Harpke, M. Wiemers, J. Settele  
Climber: Climatic niche characteristics of the butterflies in Europe  
ZooKeys, 367 (2014), pp. 65-84, [10.3897/zookeys.367.6185](https://doi.org/10.3897/zookeys.367.6185) ↗  
[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Sekar, 2012](#) S. Sekar  
A meta-analysis of the traits affecting dispersal ability in butterflies: Can wingspan be used as a proxy?  
J. Anim. Ecol., 81 (1) (2012), pp. 174-184, [10.1111/j.1365-2656.2011.01909.x](https://doi.org/10.1111/j.1365-2656.2011.01909.x) ↗  
[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Settele et al., 2008](#) J. Settele, O. Kudrna, A. Harpke, I. Kühn, V.C. Swaay  
Climatic risk atlas of European butterflies (2008)  
[Google Scholar](#) ↗

[Sevilleja et al., 2019](#) C.G. Sevilleja, C.A.M. van Swaay, N. Bourn, S. Collins, J. Settele, M.S. Warren, I. Wynhoff, D.B. Roy  
**Butterfly transect counts: manual to monitor butterflies**  
*Report VS2019* (2019)  
[Google Scholar ↗](#)

[Sistri et al., 2022](#) G. Sistri, M. Menchetti, L. Santini, L. Pasquali, S. Sapienti, A. Cini, L. Platania, E. Balletto, F. Barbero, S. Bonelli, L.P. Casacci, V. Dincă, R. Vila, C. Mantoni, S. Fattorini, L. Dapporto  
**The isolated *Erebia pandrose* Apennine population is genetically unique and endangered by climate change**  
*Insect Conserv. Divers.*, 15 (1) (2022), pp. 136-148, [10.1111/icad.12538 ↗](#)  
[View in Scopus ↗](#) [Google Scholar ↗](#)

[Slancarova et al., 2016](#) J. Slancarova, A. Bartonova, M. Zapletal, M. Kotilinek, Z.F. Fric, N. Micevski, V. Kati, M. Konvicka  
**Life history traits reflect changes in mediterranean butterfly communities due to forest encroachment**  
*PLoS One*, 11 (3) (2016), pp. 1-18, [10.1371/journal.pone.0152026 ↗](#)  
[Google Scholar ↗](#)

[Socolar et al., 2016](#) J.B. Socolar, J.J. Gilroy, W.E. Kunin, D.P. Edwards  
**How should beta-diversity inform biodiversity conservation?**  
*Trends Ecol. Evol.*, 31 (1) (2016), pp. 67-80, [10.1016/j.tree.2015.11.005 ↗](#)  
 [View PDF](#) [View article](#) [View in Scopus ↗](#) [Google Scholar ↗](#)

[Stange and Ayres, 2010](#) E.E. Stange, M.P. Ayres  
**Climate Change Impacts: Insects**  
*Encyclopedia of Life Sciences*, 1–7 (2010), [10.1002/9780470015902.a0022555 ↗](#)  
[Google Scholar ↗](#)

[Stefanescu et al., 2004](#) C. Stefanescu, S. Herrando, F. Páramo  
**Butterfly species richness in the north-west Mediterranean Basin: The role of natural and human-induced factors**  
*J. Biogeogr.*, 31 (6) (2004), pp. 905-915, [10.1111/j.1365-2699.2004.01088.x ↗](#)  
[View in Scopus ↗](#) [Google Scholar ↗](#)

[Stefanescu et al., 2011](#) C. Stefanescu, J. Carnicer, J. Peñuelas  
**Determinants of species richness in generalist and specialist Mediterranean butterflies: The negative synergistic forces of climate and habitat change**

Ecography, 34 (3) (2011), pp. 353-363, [10.1111/j.1600-0587.2010.06264.x](https://doi.org/10.1111/j.1600-0587.2010.06264.x) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Steffen et al., 2018](#) W. Steffen, J. Rockström, K. Richardson, T.M. Lenton, C. Folke, D. Liverman, C.P. Summerhayes, A.D. Barnosky, S.E. Cornell, M. Crucifix, J.F. Donges, I. Fetzer, S.J. Lade, M. Scheffer, R. Winkelmann, H.J. Schellnhuber

### Trajectories of the earth system in the anthropocene

Proc. Natl. Acad. Sci. U. S. A., 115 (33) (2018), pp. 8252-8259, [10.1073/pnas.1810141115](https://doi.org/10.1073/pnas.1810141115) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Stoppa, 1996](#) F. Stoppa

### The San Venanzo maar and tuff ring, Umbria, Italy: Eruptive behaviour of a carbonatite-melilitite volcano

Bull. Volcanol., 57 (7) (1996), pp. 563-577, [10.1007/bf00304440](https://doi.org/10.1007/bf00304440) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[Stoppa, 2014](#) Stoppa, F. 2014. *Geological map of the San Venanzo volcano (Central Italy): Explanatory notes. January 1995.*

[Google Scholar](#) ↗

[Sunde et al., 2023](#) J. Sunde, M. Franzén, P.E. Betzholtz, Y. Francioli, L.B. Pettersson, J. Pöyry, N. Ryrholm, A. Forsman

### Century-long butterfly range expansions in northern Europe depend on climate, land use and species traits

Commun. Biol., 6 (1) (2023), pp. 1-14, [10.1038/s42003-023-04967-z](https://doi.org/10.1038/s42003-023-04967-z) ↗

[Google Scholar](#) ↗

[Ubach et al., 2020](#) A. Ubach, F. Páramo, C. Gutiérrez, C. Stefanescu

### Vegetation encroachment drives changes in the composition of butterfly assemblages and species loss in Mediterranean ecosystems

Insect Conserv. Divers., 13 (2) (2020), pp. 151-161, [10.1111/icad.12397](https://doi.org/10.1111/icad.12397) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[van Swaay et al., 2006](#) C.A.M. van Swaay, M. Warren, G. Loïs

### Biotope use and trends of European butterflies

J. Insect Conserv., 10 (2) (2006), pp. 189-209, [10.1007/s10841-006-6293-4](https://doi.org/10.1007/s10841-006-6293-4) ↗

[View in Scopus](#) ↗ [Google Scholar](#) ↗

[van Swaay et al., 2008](#) C.A.M. van Swaay, P. Nowicki, J. Settele, A. Van Strien

### Butterfly monitoring in Europe: Methods, applications and perspectives

Biodivers. Conserv., 17 (14) (2008), pp. 3455-3469, [10.1007/s10531-008-9491-4](https://doi.org/10.1007/s10531-008-9491-4) ↗

[View in Scopus ↗](#) [Google Scholar ↗](#)

van Swaay and Warren, 2006 C.A.M. van Swaay, M.S. Warren

## Prime Butterfly Areas of Europe: An initial selection of priority sites for conservation

J. Insect Conserv., 10 (1) (2006), pp. 5-11, [10.1007/s10841-005-7548-1 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

Warren et al., 2021 M.S. Warren, D. Maes, C.A.M. van Swaay, P. Goffart, H. van Dyck, N.A.D. Bourn, I. Wynhoff, D. Hoare, S. Ellis

## The decline of butterflies in Europe: Problems, significance, and possible solutions

Proc. Natl. Acad. Sci. U. S. A., 118 (2) (2021), pp. 1-10, [10.1073/PNAS.2002551117 ↗](#)

[Google Scholar ↗](#)

Weiss et al., 2021 M. Weiss, P. Kozel, M. Zapletal, D. Hauck, J. Prochazka, J. Benes, L. Cizek, P. Sebek

## The effect of coppicing on insect biodiversity. Small-scale mosaics of successional stages drive community turnover

For. Ecol. Manage., 483 (2021), Article 118774, [10.1016/j.foreco.2020.118774 ↗](#)



[View PDF](#)

[View article](#)

[View in Scopus ↗](#)

[Google Scholar ↗](#)

Whitelaw et al., 2014 P.A. Whitelaw, B.E.M. King, D. Tolkach

## Protected areas, conservation and tourism - financing the sustainable dream

J. Sustain. Tour., 22 (4) (2014), pp. 584-603, [10.1080/09669582.2013.873445 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

Wiklund et al., 1983 C. Wiklund, A. Persson, P.O. Wickman

## Larval aestivation and direct development as alternative strategies in the speckled wood butterfly, *Pararge aegeria*, Sweden

Ecol. Entomol., 8 (2) (1983), pp. 233-238, [10.1111/j.1365-2311.1983.tb00503.x ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

Wilson et al., 2007 R.J. Wilson, D. Gutiérrez, J. Gutiérrez, V.J. Monserrat

## An elevational shift in butterfly species richness and composition accompanying recent climate change

Glob. Chang. Biol., 13 (9) (2007), pp. 1873-1887, [10.1111/j.1365-2486.2007.01418.x ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

Wood and Wood, 2015 Wood, S., Wood, M. S. 2015. Package 'mgcv.' *R Package Version*, 1(29), 729.

[Google Scholar ↗](#)

Zhan et al., 2015 A. Zhan, L. Zhang, Z. Xia, P. Ni, W. Xiong, Y. Chen, G. Douglas Haffner, H.J. MacIsaac

## Water diversions facilitate spread of non-native species

Biol. Invasions, 17 (11) (2015), pp. 3073-3080, [10.1007/s10530-015-0940-1 ↗](#)

[View in Scopus ↗](#) [Google Scholar ↗](#)

Zografou et al., 2014 K. Zografou, V. Kati, A. Grill, R.J. Wilson, E. Tzirkalli, L.N. Pamperis, J.M. Halley

## Signals of climate change in butterfly communities in a Mediterranean protected area

PLoS One, 9 (1) (2014), pp. 1-9, [10.1371/journal.pone.0087245 ↗](#)

[Google Scholar ↗](#)

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### Cited by (0)

- 1 These two authors equally contributed to the work.

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