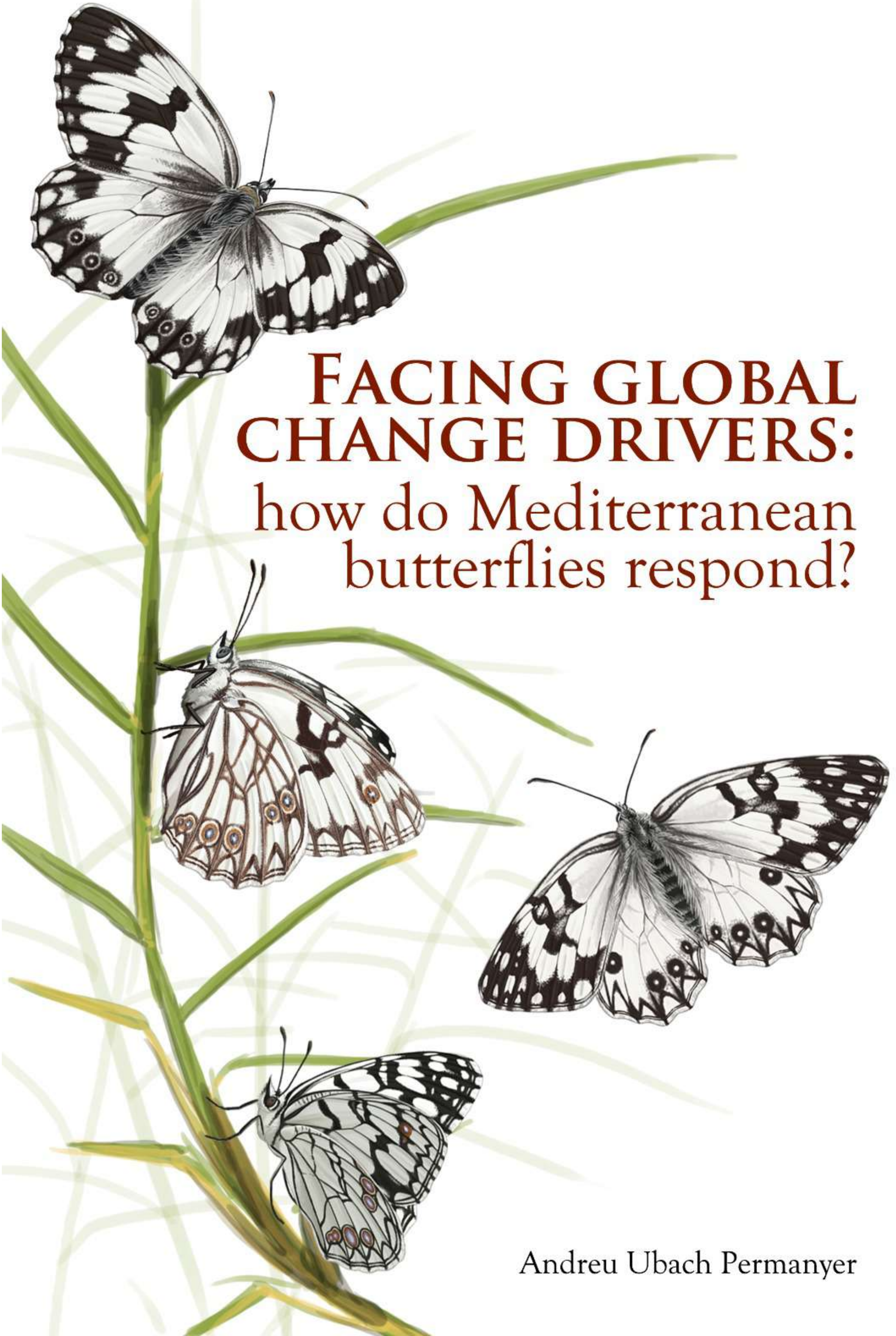
Facing global change divers: how do Mediterranean butterflies respond?

Andreu Ubach Permanyer



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TESI DOCTORAL

Museu de Ciències Naturals de Granollers (MCNG)

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The cover was designed and drawn by Martí Franch.

We should preserve every scrap of biodiversity as priceless while we learn to use it and come to understand what it means to humanity.

E. O. Wilson

People often ask, "What is the single most important environmental population problem facing the world today?" A flip answer would be, "The single most important problem is our misguided focus on identifying the single most important problem!

Jared Diamond, Collapse: How Societies Choose to Fail or Succeed

Agraïments

Agraïments generals:

És imprescindible començar els agraïments d'aquesta tesi per totes les persones voluntàries que aporten dades al projecte del CBMS. Penso que no els conec personalment a tots, però que des que m'he ficat a l'equip de coordinació és gràcies a les seves ganes i voluntat de col·laborar comptant papallones que cada vegada he anat coneixent més el nostre entorn. Penso que totes elles dediquen molt de temps a conèixer l'entorn que els rodeja i que aposten per realitzar un itinerari BMS perquè els apassiona veure com aquest entorn es transforma cada dia. Així, vull sentir que l'interès que posen és retornat i per això s'ha de remarcar que la coordinació dels projectes de ciència ciutadana té un sentit quan les dades retornen i serveixen perquè a cadascun dels llocs on es recopilen s'hi puguin fer coses.

Agraïr aleshores a totes les persones amb qui estem creant un equip per a l'estudi de les papallones al Museu de Ciències Naturals de Granollers i la seva esfera. Al Constantí, que va parir aquest projecte. El Quim i el Ferran que han coordinat parts cabdals perquè pugui tirar endavant. Als companys amb qui desenvolupoem projectes com la Clàudia, el Pau, l'Antonio, el Víctor... I també esmentar les persones amb qui hem trobat els darrers anys la passió naturalista per les papallones i que ens porta a cercar racons i trobar tresors amagats dins la natura, com les d'Osona (Martí, Jordi, Irene, Guillem) o el Juli. Amb tots ells estem engegant projectes que fan confluir la feina dels científics amb la dels gestors.

En el marc del Museu agrair a l'ambient generat que ha acompanyat tot el procés d'aquesta tesi. A totes les persones de l'equip de ratpenats, de micromamífers..., al Toni i el Carles per portar el barco a flote... a l'ambient creat que ens fa venir ganes d'anar cada dia al Museu a treballar i veure'ns les cares, comptant que aquesta tesi s'ha realitzat en mig d'una pandèmia que ens aïllava, i hem trobat els espais de trobada i comunitat a través del joc i el treball d'equip al propi Museu, amb les manetes d'un futbolí.

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Abstract

The current context of global change is causing many threats to biodiversity worldwide, and the profound and rapid transformations of the environment have led to a severe insect decline. Because of their sensitivity to landscape and climate agents, butterflies have become an ideal bioindicator group to reveal how global change drivers impact at the local and regional scales. Moreover, butterfly monitoring schemes (BMS) that use a common and standard methodology have spread through most of Europe in recent decades, allowing to record with unprecedented detail year-to-year population changes and species trends. However, many open questions remain about how natural and anthropogenic processes affect butterfly populations and how their responses differ between climatic regions. Here I made use of the Catalan BMS data to explore how natural processes such as weather and vegetation encroachment affect butterfly populations, and how butterfly communities have changed during the last decades as a result of global change. I explored how these responses are mediated through life-history traits, and how do they vary across different climatic regions. I also studied the factors shaping species richness and abundance of plants and herbivorous insects (butterflies and grasshoppers) in the Pyrenees (which harbour most of butterfly diversity in the continent), with a particular interest on the impact of cattle grazing on subalpine grasslands. To do so, I designed an experiment combining grazed control plots with enclosure plots where grazing was excluded. The climatic study identified a general positive effect of spring rainfall on butterfly populations occurring in the Mediterranean region, and of winter rainfall (i.e. snowy winters) in the Alpine region. I also found a strong negative effect of mild winters on butterfly populations. In the second study I developed an index to measure a species preference for closed vs open habitats. I found that the vast majority of the species are strongly associated with open habitats, and describe a widespread pattern of butterfly communities to become dominated by species preferring closed habitats as a result of a general phenomenon of vegetation encroachment. The Pyrenean study quantified the role of both abiotic and biotic factors on plants and herbivorous insects, and provided evidence of the effects of livestock exclusion on ecosystems during a short period of two years. In my last chapter, I unraveled how butterfly assemblages have responded to climatic and habitat drivers by using several ecological indicators. Long term monitoring data indicates how in mountain regions butterfly communities are changing towards more thermophilous and generalist species, but still act as a biodiversity reservoir, as population trends there are not so negative. I conclude

that Mediterranean butterflies respond differently across climatic regions, and that a combination of both climatic and landscape factors must be considered to explain butterfly population responses.

Sinopsi

L'actual context de canvi global està causant moltes amenaces a la biodiversitat a tot el món, i les ràpides transformacions del medi ambient han conduit cap a un sever declivi dels insectes. Donada la seva sensibilitat als agents climàtics i paisatgístics, les papallones diürnes s'han convertit en un grup bioindicador ideal per l'estudi de com els motors de canvi global actuen a escala local i regional. A més a més, l'ús de programes de seguiment de papallones BMS que usen una metodologia comuna i estàndard s'ha escampat els darrers anys per la major part d'Europa, permetent enregistrar canvis poblacionals any a any així com tendències de les espècies amb un detall sense precedents. Malgrat tot, encara hi ha moltes preguntes obertes respecte com els processos naturals i antròpics afecten les poblacions de papallones i com les seves respostes difereixen entre regions climàtiques. Aquí he fet ús de les dades del BMS català per explorar com els processos naturals tals com la meteorologia i el tancament de la vegetació afecten les papallones, i com les comunitats de papallones han canviat durant les darreres dècades com a resultat del canvi global. He explorat com aquestes respostes estan mediades a través dels trets de la seva història vital, i com varien entre regions climàtiques. També he estudiat els factors que donen forma a la riquesa i abundància d'espècies de plantes i insectes herbívibors (papallones i ortòpters) als Pirineus (que resguarden la major part de la diversitat de papallones del continent), amb un interès particular a l'impacte de l'avaluació dels efectes de la pastura a prats subalpins. Per a fer-ho, he dissenyat un experiment que combina parcel·les pasturades control amb parcel·les on la pastura s'ha exclòs. L' estudi climàtic ha identificat un efecte general positiu de la pluja primaveral a la regió mediterrània, i la neu hivernal a la regió alpina. També he trobat un fort efecte negatiu dels hiverns càlids a les poblacions de papallones. En el segon estudi he desenvolupat un index per mesurar la preferència d'espècies per hàbitats oberts o tancats. He trobat que la preferència de la majoria d'espècies és per ambients oberts, i he descrit un patró general en les comunitats de papallones que es troben cada vegada més dominades per espècies que prefereixen hàbitats tancats com a resultat d'un procés de tancament de la vegetació. L'estudi als Pirineus ha quantificat el rol dels factors abiòtics com biòtics les plantes i insectes herbívors, i he proveït evidències dels efectes de l'exclusió de la pastura en un termini curt. He desentranyat com les comunitats de papallones han respòs a mototors climàtics i d'hàbitat amb l'ús de diferents indicadors ecològics. Les sèries temporals llargues indiquen com a les regions muntanyoses les comunitats de papallones estan canviant cap a espècies més termòfiles i generalistes, però que aquestes encara actuen com un reservori ja que les tendències poblacionals no hi són tan negatives. Conlcloc que les papallones mediterrànies estan tenint respostes

diferents segons la regió climàtica estudiada i que la reva resposta poblacional s’explica per la combinació de factors climàtics i paisatgístics.

Contents

List of figures

List of tables

1.General Introduction

1.General Introduction

1.1 Studying biodiversity changes with butterflies as bioindicators

1.1.1 Monitoring with bioindicators

Biodiversity is facing many threats in the context of global change during the last decades (WWF, 2020), and faunal and floristic populations are suffering apparent changes because of the strong anthropogenic pressure and the profound and rapid transformations of the environment worldwide. To understand these changes it is very important to pinpoint their direction and to identify the drivers and trends that affect the different species. Robust methods for measuring current trends of wild faunal populations are needed, and monitoring programs aimed at recording population changes over time have become indispensable tools for biodiversity conservation (Magurran et al., 2010). Monitoring can be used to obtain data of the abundance of an organism (or group of organisms) over time and, therefore, to know what its population fluctuations are in a certain area (Yoccoz et al., 2001) and relate them to its requirements (Gerhardt, 2002; Thomas, 2005). Usage of bioindicator groups is useful to diagnose of the state of natural systems and allows natural heritage managers to assess the suitability of the measures taken and their impact on biodiversity (Torre et al., 2021).

Butterflies have become an ideal bioindicator group due to several reasons. First, they are extraordinarily sensitive to climate and respond markedly (with phenological changes, abundance, and geographic distribution) to phenomena such as global warming and variations in thermo- and rainfall regimes (Parmesan, 2006). Second, they show a great sensitivity with respect to the composition and structure of the vegetation: in their larval stage they depend exclusively on a small number of host plants and if these plants disappear or become scarce, butterfly populations begin rapid declines (Balmer and Erhardt, 2000). For example, a change in landscape management can radically alter the conditions of a meadow and the butterfly fauna that accompanies it (Stefanescu et al., 2009). Third, an important part of the species are sedentary and are severely affected by the phenomenon of habitat fragmentation (Hanski, 1994, Thomas et al., 2001). The connection between nearby populations decreases rapidly if barriers are created or favorable habitat disappears, and this progressive isolation leads, sometimes in a short time, to local extinctions with a relatively high frequency (Polus et al., 2007). Fourth, they play a key role in ecosystems, both as primary consumers (herbivores) and pollinators (Stefanescu et al., 2018), as well as a source of food for many secondary consumers (predators and parasitoids). Therefore, everything that affects them also does, in return, to many other organisms (van Nouhuys & Hanski, I, 2005). Finally, their great aesthetic value and the relative ease with which they can be identified have made them a very popular group, with a cultural function (Clark et al., 2014). Many naturalists observe them regularly and are able to recognize the species that live in the areas where they focus their activities, something very difficult with other groups of invertebrates.

1.1.2 Butterfly Monitoring Schemes in Europe: a long term project

Butterfly monitoring programs started in the United Kingdom in 1976 (Pollard & Yates, 1994), where a simple but robust methodology was developed, standardized and applied within the so-called UK Butterfly Monitoring Scheme (UK-BMS). The BMS methodology consists of visual counts of adult butterflies along fixed transect routes, with some differences depending on the country such as the span of the sampling period (e.g. March-September in Catalonia, April-September in the UK) and the frequency of transect counts (e.g. weekly in Catalonia, but every two weeks in Spain). The BMS has thereafter become a common methodology all through Europe, to the point that 23 countries were running BMS projects in 2022. All these schemes are coordinated at the continental scale within the European BMS program (https://butterfly-monitoring.net/). In Catalonia a BMS started in 1994 and consists of a monitoring project which collects data on the abundance of butterfly populations annually in a network of over 200 stations spread throughout the Catalan geography, the country of

Andorra and also the Balearic Islands (www.catalanbms.org). The project is coordinated from the Natural Sciences Museum of Granollers through an agreement with the Department d'Acció Climàtica i Agenda Rural of the 'Generalitat de Catalunya'.

This data base offers a unique opportunity to explore how butterfly population changes relate to different environmental factors. The use of a common methodology allows to carry out integrative analyses all over the continent (Van Swaay et al., 2008, Schmucki et al., 2016) and has turned the BMS into a leading monitoring program worldwide. Work relating Lepidopteran communities to different agents, such as climate change, habitat fragmentation or the degradation and humanization of natural environment is regularly published using BMS data (e.g. Stefanescu et al., 2003; Devictor et al., 2012; Van Swaay et al., 2019). Likewise, the simplicity of BMS methodology has led to the development of numerous specific projects involving transect counts which are not part of the global network but use the Pollard walk methodology to obtain data on the abundance and phenology of butterfly populations (Gupta et al., 2019, Stefanescu et al., 2022). Moreover, in comparison to other methodologies, Pollard walks have been seen to report significantly higher species diversity than Malaise traps and more species richness than citizen science portals (Prudic et al., 2018). For all these reasons, Pollard walk counts to monitor butterflies will form part of the standard methodology that has been designed for the future European pollinator monitoring scheme project (https://www.ufz.de/spring-pollination/index.php?en=49053) and even becoming an important part of global multi-species indicators such as the Living Planet Index (WWF, 2020).

1.1.3 Specific and community approaches in the study of butterfly populations

Superimposed to population trends, butterflies (as insects with short life-cycles and high reproduction rates) show year-to-year population changes influenced by weather (Roy et al., 2001), with both rapid growth under favourable weather conditions (Kerr et al., 2019) or population crashes under severe and extreme events (Palmer et al., 2017). When controlling for this variability caused by weather and climatic events, researchers focus on trends over time and try to unravel their causes. Monitoring programs allow exploring how butterfly populations have undergone long-term changes that are running parallel to climate and landscape changes (Stefanescu, 2021, Fig. 1.1). While each species responds uniquely to environmental conditions according to its own lifecycle and specific preferences (Radchuk et al., 2013), community approaches are useful for a more comprehensive assessment of the impact of global change at the ecosystem level (Julliard et al. 2006; Devictor et al. 2012). During the last decades, butterfly assemblages are experiencing profound changes in composition in many places with colonization and extinction events according to the habitat requirements of the species and their original distributions (González-Megías et al., 2008). A common recorded pattern is the disappearance of specialist species, which leads to ecosystems being dominated by generalist species (Thomas, 2016).

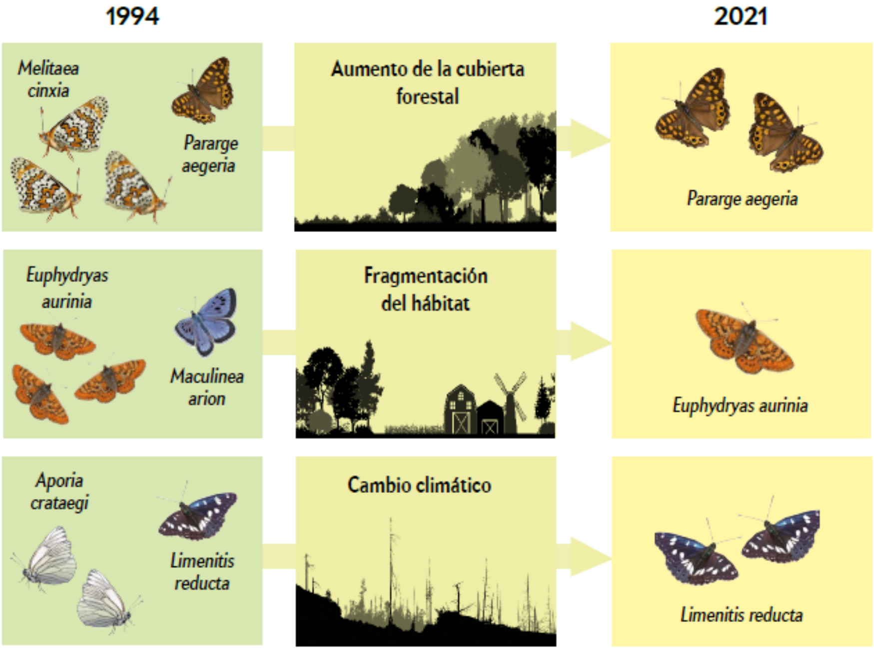


Fig 1.1. Long-term projects reveal changes in butterfly assemblages over the years and the drivers causing them. From "Stefanescu, C. 2021. El declive de las mariposas mediterráneas. *Investigación y Ciencia*, 40-47." Aumento de la cubierta forestal – Vegetation encroachment;

Fragmentación del hábitat – Habitat fragmentation; Cambio climático – Climate change.

1.2 The status of butterfly populations over the last decades, with a focus on the Mediterranean region

1.2.1 Butterfly trends and their status of conservation

In general terms a decline in insect biomass and diversity has been occurring during the last decades (Hallmann et al, 2017; Sánchez-Bayo and Wyckhus, 2019), becoming a crucial part of the anthropogenic mass extinction in the 21st century (Kolbert, 2014; Goulson, 2021). Butterflies are part of this so-called *Insectaggedon* with generalized declines worldwide (Forister et al., 2011; Warren et al., 2021; Nakamura et al., 2011). In the European continent, butterflies are facing diverse threats and as a result, many species are declining both at the local and the regional scales. Warren et al. (2021) placed three main factors causing this decline: habitat loss and degradation, chemical pollution, and climate change. According to the IUCN criteria, 9 % of butterfly species are threatened and 10% are considered 'near threatened' at the European level (Van Swaay et al., 2011), 5 % are threatened at the Mediterranean level (Numa et al, 2016) and 24% at the Catalan level (Vila et al., 2018). Regional declines are seen in many European countries (Warren et al., 2021), particularly in those that have been most intensively studied, such as the Netherlands (80% of the species in decline: Van Strien et al., 2019) and the United Kingdom (50% of the species). Moreover, in both countries an important number of species have become regionally extinct (20% in NL, 8% in UK). For the Mediterranean region, the first red list assessment for Italy placed the threatened species at 6.3%, but the majority of butterfly species were considered stable (Bonelli et al., 2018).

In North-East Iberia, Melero and others (2016) showed a negative trend in 70% of 66 common butterfly species using data from the CBMS. However, the most recent CBMS report (www.catalanbms.org) using data up to 2021 suggests that this percentage may have even increased recently. Indeed, in 78% of 113 species for which a temporal trend was calculated, the trend was negative. Although these numbers refer to only ~56% of the 201 species composing the Catalan fauna, the species for which insufficient data are available are mostly rare specialists that may have undergone severe declines in many cases (Ubach & Stefanescu, 2022; Stefanescu et al., in prep.). Interestingly enough, however, a closer analysis reveals that there is substantial variation in population trends according to the studied region. Thus, in the Mediterranean mesic region of Catalonia up to 41% of the species show significant declines, while in the subalpine-alpine region (which corresponds entirely to mountain areas) this number is reduced to only 16% (Chapter 4).

1.2.2. Mountains as reservoirs for butterfly diversity

Mountains are biodiversity reservoirs in many regions of the planet (Barrio et al., 2013; Körner et al., 2007) and they often constitute hotspots with high interest in conservation (Körner & Spehn, 2020). For example, in Europe, the highest butterfly species richness's is found in mountains, including the greatest proportion of endemic and threatened species (Van Swaay et al., 2011). This trend also applies to the Mediterranean zones (Vila et al., 2018; Bonelli et al., 2018). This amount of biodiversity is the result of historical processes of speciation (Schmitt et al., 2016) and, currently, from the combination of several abiotic and biotic factors (Stefanescu et al., 2011a). Amongst the abiotic factors, the high heterogeneity that is typically found in mountains for climate, soil, hill shade, slope or the orientation strongly contributes to the diversification of butterfly communities (Gutiérrez, 2009). The most important biotic factors shaping butterfly communities in mountains are related to anthropic activities, especially traditional grazing with cattle, sheep and horses (Pöyry et al., 2005; Bussan, 2022).

Both climatic and anthropogenic factors have effects on species composition but topoclimatic ones may dominate in regions with pronounced elevational gradients (Gutiérrez et al., 2010a; 2010b), placing climate change as a key driver for species distributions. Distribution shifts in elevation have been ocurring during the recent decades in Mediterranean mountains, with uphill movements of comparable butterfly communities (Wilson et al., 2007). Rödder et al. (2021) pointed that in the Alps mobile and generalist species with a broad ecological amplitude are tending to move uphill more than specialist and sedentary species. This changes have been occurring in parallel to plant altitudinal shifts, with species substitution occurring at alpine communities (Bonelli et al., 2021), and an overall increase in the abundance of some widespread lowland and thermophilous species (Zografou et al., 2014). However, other works pinpoint a failure in colonization by lowland species and thus estimating a net decline in species richness at some altitudes (Wilson et al., 2007).

In terms of a conservation strategy, this elevational shift places challenges in defining protected areas as climate change threatens mountain specialists in countries where many endangered species are occurring at mountain ranges (Bonelli et al., 2018), and it aims at the need for maintaining cooled or moist habitats which may support species associated with cooler conditions (Zografou et al., 2014). Indeed, recently various protective measures are being applied to promote active preservation to species not only threatened by climatic reasons but to habitat loss as well (Ubach & Figueroa, 2021; Ubach & Stefanescu, 2022), with measures such as habitat patch clearing and enhancing of larval host plants (Nakonieczny et al., 2007).

1.3 Major drivers of butterfly responses to global change

1.3.1 Climate and weather as drivers of population changes

Butterflies have long figured as a model group for understanding the impact of weather and climate change on insect populations (Pollard, 1988; Parmesan et al. 1999; Devictor et al. 2012; Hill et al., 2021). Climate change is a major force driving biodiversity changes globally but with different rates of intensity and velocity. In Europe, it has driven changes in species distributions with shifts towards higher latitudes (Parmesan et al., 1999), and altitudes (Wilson et al., 2007; Rödder et al., 2021). Shifts, however, have mostly occurred in common and mobile species. On the other hand, in most cases specialist species are unable to track these changes and undergo severe declines

(Warren et al., 2001). Some species may alter their habitat associations to exploit favourable microclimates, although these behavioural changes are unlikely to buffer species from impacts of climate change in a regional context (Suggitt et al., 2012). In the Mediterranean basin, there is some evidence that precipitation and aridity are better descriptors of butterfly population trends than temperature, and species having the lowest Species Precipitation Index values are the ones that have more negative trends (Herrando et al., 2019).

Climate change is to an increase in the frequency and severity of different climatic events (Jentsch et al., 2007), including extreme episodes that strongly affect butterfly population fluctuations (Oliver et al., 2015). Extreme droughts have been described as drivers of extinction of butterfly populations for a long time (Ehrlich et al., 1980), with recent work clearly demonstrating their important effects on meta-population structures (van Bergen et al., 2020). Responses to these events not only occur at the specific level (Palmer et al., 2017) but have also been described as causing reorganizations at the community level (Palma et al., 2017).

To fully understand how climate change affects butterfly populations, it seems essential to focus on species' life cycles because this provides information about when a species will be particularly vulnerable to certain climatic events and weather regimes (Pollard et al., 1988; Roy et al., 2001; WallisdeVries et al., 2011, Chapter1). For instance, warm winters have negative effects in larval survival of several species overwintering in the larval stage, because it increases metabolic activity and causes reserve depletion (Radchuk et al., 2013; Abarca et al., 2019; Klockmann & Fischer, 2019). In some species, plastic phenotypic traits such as body mass or wing size act as biomarkers of population vulnerability to extreme thermal conditions. This information can be used to infer the microhabitat buffering capacity at different sites where populations of the species occur (Carnicer et al., 2019).

Butterfly phenology is also prone to respond to climate change. Adult emergence is advanced in warm years in many species (Gutiérrez & Wilson, 2021), with species flying earlier in the season showing the greatest sensitivity to annual (temporal) variation in temperature (Colom et al. 2021). This is actually more complex when taking into account the critical period of phenological sensitivity, as the date of emergence of many species strongly depends on the temperatures experienced in certain months that may have shown particular temporal trends. For instance, while the average temperature has increased during the recent years in Catalonia, it has decreased in February, March and May at many sites, leading to phenological delays of a good number of species even if there has been a general warming trend at the site (Colom et al., 2022). The interspecific variability in the phenological response and its relationship with population trends reveals the importance of species plasticity to adapt to the observed changes. Actually, the capacity of species to combine range and phenology shifts is a winner strategy for many Lepidoptera (Hällfors et al., 2021) and those not responding are suffering severe declines (Colom et al., 2022).

1.3.2 Landscape as a driver of population changes

1.3.2.1 Vegetation encroachment and fragmentation

Landscape changes affect biodiversity at different levels and habitat loss and degradation is currently considered as the most severe cause of general butterfly declines in Europe (Warren et al., 2021). The strong association between butterflies and open habitats such as grasslands and meadows, places these amongst the most valuable habitats in the temperate region (van Swaay et al., 2006, Chapter 2). During the last decades, very important amounts of natural meadows have been lost in Europe, leading to important declines in grassland butterflies (van Swaay et al., 2019). In the Mediterranean basin, successional development of grasslands and open formations to scrub forest in the Southern Balkans has been identified as the main cause of a general recorded change in the community composition towards an increase of European or Euro-siberian species and a decrease of Mediterranean endemics (Slarancova et al., 2016). As described in other systems, habitat encroachment reduces dispersal among populations as it increases fragmentation, and causes population decoupling, which in turns leads to greater risk of local extinction (Roland & Matter, 2007, Matter et al., 2020).

Abandonment of traditional practices leading to vegetation encroachment has often been described as the cause of decline in species preferring open environments in the Mediterranean region (Krauss et al. 2010; Herrando et al., 2015), involving changes in biodiversity and communities of different groups of organisms. Abandonment of semi-natural pastures causes a vegetation succession and thus loss of specialized grassland species. Although butterfly species richness may even increase at the community level during the first years of vegetation encroachment (Pöyry et al., 2006; Öckinger et al., 2006), extinction of grassland specialists usually occurs very rapidly (e.g. Stefanescu et al., 2009). Indeed, in contrast to plants, extinction debt is minimal in butterfly grassland specialists (Krauss et al., 2010; but see Sang et al., 2010, showing the opposite for species requiring large habitat areas).

1.3.2.2 Management: intensification and traditional practices

Major changes in agricultural habitats have occurred in Europe with the disappearance of traditional practices during the first half of the 20th century and the establishment of large-scale and intensive farming (Warren et al., 2021). Agricultural intensification has played an important role both for landscape changes and direct pollution effects (Raven & Wagner, 2021), and has negative impacts on butterfly species richness and abundance. Specialist species are usually absent in grassland plots embedded in the agricultural matrix instead of those surrounded by extensively used and unsprayed crop fields (Habel et al., 2019). A well-studied issue concerning intensification is the effect of nitrogen deposition, which causes microclimate and vegetation changes (WallisDeVries et al., 2006), reducing the amount of bare ground where some species breed (Klop et al., 2015).

On the other hand, appropriate management of butterfly habitats is a requirement for reversing the negative impacts caused by landscape changes. Extensive grazing and rotational mowing appear to be the most suitable practices to imitate traditional grassland uses that benefit many butterfly species (Buvová et al., 2015). The role of grazing in maintaining meadow biodiversity is crucial for landscape heterogeneity (Rook & Tallowin, 2003) and has shaped montane and subalpine grasslands over millennia (García-Ruiz et al., 2021). Butterflies respond in different ways to pastoral management practices (Pöyry et al., 2005; Bussan, 2022, Chapter 3), and rural abandonment in many mountain regions is affecting negatively specialist species (Zografou et al., 2014; Mora et al., 2022). However, as a counterbalance, overgrazing is harmful by cattle trampling on butterfly hostplants, as long as direct consumption of leaves of hostplants and flowers affects nectar abundance (Munguira et al., 2017). Allowing different grazing intensities or using rotational grazing enhances survival of species suffering from continuously high intensity grazing (Poÿry et al., 2004) and innovative biodiversity friendly types of management have been proposed to enhance species richness and abundance of flower-visiting insects (Enri et al, 2017). Other approaches such as rewilding measures applied in natural ecosystems with mammals placed to mimic ecosystem functions of wild cattle also affect butterfly communities (Garrido et al., 2022). Besides livestock, other practices such as meadow haying are seen to be better for praire-specialist butterflies than management with controlled fires (Swengel, 1996). Nonetheless, a meta-analysis concluded that fire itself has no significant positive or negative effects on butterfly biodiversity (Mason Jr. et al., 2021). Apart from traditional practices, active management has also proven to be efficient for butterfly conservation, with many successful interventions that have favored butterflies and moths all over the world (Bladon et al., 2022).

2. Objectives and thesis structure

2.1 Objectives

Given this framework, we believe that studying butterfly population responses to environmental factors can help to understand how the different drivers of global change interact and influence our country's biodiversity and, at the same, can help to provide guidelines for landscape management. I present here the main objectives of this thesis with their specific objectives, as long as their following hypotheses:

Objective 1. To assess how weather events affect butterfly population fluctuations in a bioregional context.

1.1 To assess the climatic factors that affect the growth rate of butterfly species and how they vary according to climatic regions.
1.2 To identify which life-cycle stages are most sensitive to climate.
1.3 To quantify population crashes and explosions and how they are related to life-history traits and to extreme climatic events.

We hypothesize that weather conditions have contrasting effects on butterfly species depending on their life cycles, and that more negative effects will be noted in populations in the Mediterranean climatic zone given the more serious declines recorded in this area in recent years. We predict that larval and adult stages are the most sensitive, and that precipitation will have contrasting effects in both stages, with a positive impact on larvae, which will benefit from vegetation growth. But we predict a negative impact on adults due to a reduction in their potential flying time, with an eventual reduction in realised fecundity. We also hypothesize that the climatic events that most critically affect population growth may have a magnifying effect when they become climatic extremes, provoking in these situations population crashes and explosions.

Objective 2. To assess the effects of vegetation encroachment on butterfly communities using a landscape indicator as a management tool.

2.1 To explore how species perform depending on the degree of vegetation encroachment and on their preferences for open or closed habitats.
2.2 To test if the negative trend of species preferring open habitats is leading to the extinction of the populations.

We hypothesize that species performance at local scale depends on the degree of vegetation encroachment and on their preferences for open or closed habitats. We first hypothesize that butterfly species can be ordered along an axis of habitat preference from closed to open vegetation. Secondly, we hypothesize that, at the local scale, population trends of a given species will be partly explained by the relationship between changes in vegetation and the species preference for open or closed habitats. We predict that species with a strong preference for open habitats (e.g. grasslands) will show population declines at sites showing a phenomenon of vegetation encroachment, and the contrary for species preferring forest habitats.

We also hypothesize that, at the regional scale, the phenomenon of vegetation encroachment is leading to a higher frequency of extinction of populations of species that select open habitats.

Objective 3. To experimentally evaluate the effects of grazing on biodiversity with an exclusion experiment in a Pyrenean valley.

3.1 To compare the relative weight of abiotic and biotic factors influencing species richness and abundance of three taxa belonging to two trophic levels (plants, butterflies and grasshoppers) along a mountain altitudinal gradient.

3.2 To understand how the management of livestock grazing affects biodiversity both in the medium-term (over two years) and in the short-term (within the year) in mountain pastures.

We expect to find lower species richness and abundance at the higher sites in the studied altitudinal gradient (1300-2000 m). We also hypothesize a bottom-up effect, so hence the patterns in plant communities influence the patterns recorded in the two studied insect groups. We expect medium-term effects to be detected at the end of our 2-yr experimental study due to grazing exclusion, with changes in the proportion or composition of plant communities that will in turn affect butterfly and grasshopper communities. As for the short-term, we hypothesize that grazing has implications on nectar availability over the season that may result in different butterfly responses in grazed vs non-grazed experimental plots.

Objective 4. To evaluate changes in butterfly communities along bioclimatic regions based on climatic and landscape indicators.

4.1 To explore the level of coincidence in population trends of common butterflies in the northeast of the Iberian Peninsula over the past two-three decades by distinguishing three regions with well-differentiated climates.

4.2 To relate population trends to the habitat and climatic niches of the species.

4.3 To identify the most important trends in upland areas for a few model butterfly species that have been constantly monitored over periods of at least 14 years.

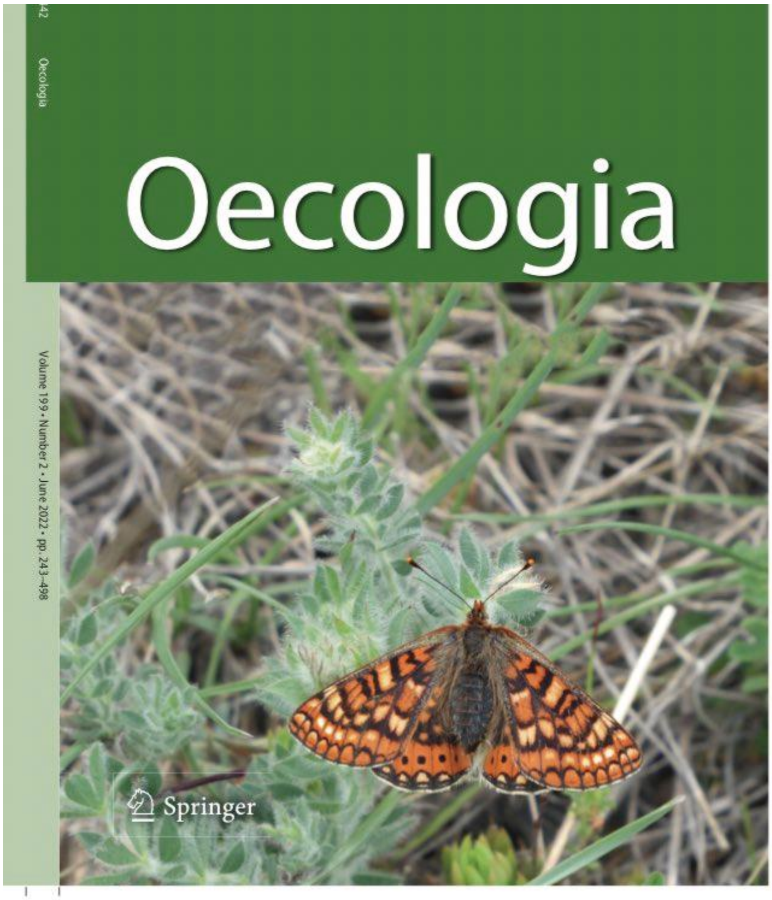
We hypothesize that butterfly population trends in the alpine region will be more positive than in two (humid and arid) Mediterranean regions. We hypothesize that both climatic and habitat factors are shaping butterfly communities with a combination of factors acting at local scales. We also hypothesize that butterfly communities are changing towards concurrent directions: communities (1) increasingly dominated by due to the decline of habitat specialists; (2) increasingly dominated by species preferring forest habitats due to open habitat specialists; and (3) increasingly dominated by more thermophilic species due to upward shifts of lowland generalist butterflies.

2.2 Structure of the thesis

Chapter 1. In the first chapter, we examine how weather events affect butterfly populations in a bioregional context. Previous studies have found the precise weather events influencing butterfly population growth and here we establish a framework to identify specific drivers and the general patterns affecting Mediterranean species. We used a citizen-science database of Mediterranean butterflies that consists of long-term population data (28 years) on 78 butterfly species from 146 sites in the Mediterranean mesic and alpine climate regions. We obtained climatic data from 93 meteorological stations operating during the same period near the butterfly sites. We studied how seasonal precipitation and temperature affect population growth and the magnitude of the year-to-year changes while taking into account the effects of density dependence. Climate change will lead to a higher frequency of extreme weather events (Rahmstorf & Coumou, 2011), and each year a number of species show population explosions while others show sharp population declines or cracks (as defined by Palmer et al., 2017). We aim to understand population responses to extreme climatic events and how these are influenced by the ecological characteristics of the species.

This chapter has been published in *Oecologia*, featured in the cover journal, and has the following reference:

> Ubach, A., Páramo, F., Prohom, M. & Stefanescu, C. (2022). Weather and butterfly responses: a framework for understanding population dynamics in terms of species' life-cycles and extreme climatic events. Oecologia. https://doi.org/10.1007/s00442-022-05188-7



Chapter 2. In the second chapter, we aim to quantify the response of butterfly assemblages to vegetation encroachment in NE Spain. This phenomenon, caused by land abandonment and loss of grazing is leading to forest cover greatly expanding in detrimental of semi-natural grasslands, areas of cultivation and pasture mosaics. To do so, we make use of an extensive citizen science program, the Catalan Butterfly Monitorng Scheme, and adapt an index developed by Suggitt et al. (2012) to set the preference of 147 butterfly species for open or closed habitats. We afterwards explore the relationship between the species preference for open or closed habitats and local trends taking into account vegetation changes recorded at the study sites. We show that this relationship is reflected in progressive changes in the butterfly communities, with a clear negative impact on species showing preference for open habitats (Herrando et al., 2015).

This chapter has been published in *Insect Conservation and Diversity* and has the following reference:

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

Chapter 3. In the third chapter, we quantify the importance of the main biotic and abiotic factors shaping the biodiversity gradient in a Pyrenean valley, by focusing on plant, butterfly and grasshopper communities inhabiting montane and subalpine grasslands. We follow an experimental approach to study the effects of livestock activity, consisting of a herd of about 300 cows that historically have been grazing over the valley. We intend to document the biodiversity associated with the meadows of the valley, to describe how it is affected by grazing and other environmental variables such as topography (Rook & Tallowin, 2003; Koch et al., 2015). We used here information of vascular plants and two groups of herbivorous insect, butterflies and grasshoppers. We aim to explain how grazing affects the biodiversity of our studied taxa and thus identify the best management options in order to sustain biodiversity. This experimental approach was carried out with an exclusion experiment and a selection of 10 plots to prevent the access of cattle.

This chapter correspond to a manuscript in preparation, aimed to be submitted for publication by late 2022.

Chapter 4. In the last chapter, we use statistical tools to quantitatively estimate changes in butterfly populations and relate them to habitat and climatic indicators. We use the CBMS citizen science program data to study butterfly responses in the long term and over broad spatial scales. In this work, we use the methodology developed by Schmucki et al. (2016) to calculate trends for 100 species from three climatic regions: subalpine-alpine, mesic Mediterranean and arid Mediterranean. We compare interregional trends for a number of common species, and we study the relationship between these trends and species' ecological characteristics. A community approach was also used to identify common responses in a number of long-term monitored sites to several drivers of global change.

This chapter has been published in *Ecosistemas* and has the following reference:

> Ubach, A., Páramo, F., & Stefanescu, C. (2021). Heterogeneidad en las respuestas demográficas asociadas al gradiente altitudinal: el caso de las mariposas en el noreste ibérico. *Ecosistemas*, *30*(1), 2148-2148. https://doi.org/10.7818/ECOS.2148

3.Director’s Report

Com a director de la tesi doctoral titulada “Facing global change drivers: how do Mediterranean butterflies respond?” realitzada per Andreu Ubach Permanyer, presento el següent informe sobre la contribució del doctorand en les publicacions en coautoria que composen la tesi:

Capítol 1.

Ubach, A., Páramo, F., Prohom, M. & Stefanescu, C. (2022). Weather and butterfly responses: a framework for understanding population dynamics in terms of species’ life-cycles and extreme climatic events. *Oecologia*. https://doi.org/10.1007/s00442-022-05188-7

Contribució del doctorand: Participació en el disseny del treball, treball de camp, anàlisi de les dades i participació en la redacció del manuscrit.

Dades de la revista: *Oecologia* apareix al Journal Citation Reports (JRC) de 2022 amb un índex d’impacte de 3.298. Q1 dins de l’àrea “Ecology, Evolution and Systematics”.

Capítol 2.

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

Contribució del doctorand: Participació en el disseny del treball, treball de camp, anàlisi de les dades i redacció del manuscrit.

Dades de la revista: *Insect Conservation and Diversity* apareix al Journal Citation Reports (JRC) de 2022 amb un índex d’impacte de 4.26. Q1 dins de l’àrea “Ecology, Evolution and Systematics”.

Capítol 3.

Ubach, A., Guardiola, M., Oliver, X., Lockwood, M., Artola, J. & Stefanescu, C. (en prep.). Spatial gradients and grazing effects on plants and insect herbivores in Pyrenean subalpine grasslands.

Contribució del doctorand: Participació en el disseny del treball, treball de camp, anàlisi de les dades i redacció del manuscrit.

Capítol 4.

Ubach, A., Páramo, F. & Stefanescu, C. (2021). Heterogeneidad en las respuestas demográficas asociadas al gradiente altitudinal: el caso de las mariposas en el noreste ibérico. *Ecosistemas*, *30*(1), 2148-2148. https://doi.org/10.7818/ECOS.2148

Contribució del doctorand: Participació en el disseny del treball, treball de camp, anàlisi de les dades i participació en la redacció del manuscrit.

Dades de la revista: *Ecosistemas* apareix al Journal Citation Reports (JRC) de 2022 amb un índex d'impacte de 1.5. Q4 dins de l'àrea "Ecology".

Barcelona, a 29 de setembre de 2022

firma del director/a

Dr. Constantí Stefanescu (director de la Tesi)
Museu de Ciències Naturals de Granollers

4. Chapter 1: Weather and butterfly responses: a framework for understanding population dynamics in terms of species' life-cycles and extreme climatic events

Ubach, A., Páramo, F., Prohom, M. & Stefanescu, C. (2022). Weather and butterfly responses: a framework for understanding population dynamics in terms of species' life-cycles and extreme climatic events. Oecologia. https://doi.org/10.1007/s00442-022-05188-7

Chapter 1: Weather and butterfly responses: a framework for understanding population dynamics in terms of species' life-cycles and extreme climatic events

Andreu Ubach, Ferran Páramo, Marc Prohom, and Constantí Stefanescu

4.1 Abstract

Understanding population responses to environmental conditions is key in the current context of climate change and the extreme climatic events that are threatening biodiversity in an unprecedented way. In this work we provide a framework for understanding butterfly population responses to weather and extreme climatic seasons by taking into account topographic heterogeneity, species' life-cycles and density-dependent processes. We used a citizen-science database of Mediterranean butterflies that contains long-term population data (28 years) on 78 butterfly species from 146 sites in the Mediterranean mesic and alpine climate regions. Climatic data were obtained from 93 meteorological stations operating during this period near the butterfly sites. We studied how seasonal precipitation and temperature affect population growth while taking into account the effects of density dependence. Our results reveal (i) the beneficial effects of winter and spring precipitation for butterfly populations, which are most evident in the Mediterranean region and in univoltine species, and mainly affect the larval stage; (ii) a general negative effect of summer rain in the previous year, which affects the adult stage; and (iii) a consistent negative effect of mild autumns and winters on population growth. In addition, density dependence played a major role in the population dynamics of most species, except for those with long-term negative population trends. Our analyses also provide compelling evidence that both extreme population levels in previous years and extreme climatic seasons in the current year provoke population crashes and explosions, especially in the Mediterranean mesic region.

Key words: Mediterranean butterflies, weather, extreme climatic seasons, density dependence, population responses

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Authors' contributions: AU and CS conceived the study. AU led the analyses, with assistance by the other authors. CS wrote the MS with the assistance of AU. All authors contributed to the data collection, and all have commented on and approved the final version.

4.2 Introduction

Under a context of global change, the responses of biological populations to future environmental conditions may become the key for species survival in many ecosystems (Lawson et al., 2015). However, although consistent recent negative trends have been identified for many taxa (e.g. terrestrial insects: Sánchez-Bayo and Wyckhus, 2019; Wagner, 2020), the contribution of the main drivers of global change to such declines is still the subject of debate. Climate change, in particular, is regarded as one of the main threats to biodiversity (Bellard et al., 2012), although for a number of species in cold environments it does in fact create new opportunities for population increases and range expansions (e.g. Menéndez et al., 2008; Pöyry et al. 2009). Rapid changes associated with climate change are expected in species such as insects with short life-cycles and high reproduction rates, whose populations can grow rapidly under favourable weather conditions (Kerr et al., 2019). However, in this type of species, unpredictable changes may also provoke sudden increases in mortality rates leading to population collapses and even extinctions (McLaughlin et al. 2002). This possibility is all the more likely given the current scenario of climate change provoked by the increase in extreme climatic events (ECEs) (Jentsch et al., 2007; Seneviratne et al., 2014).

For many decades, butterflies have figured as a model group for understanding the impact of weather and climate change on insect populations (Pollard, 1988; Parmesan et al. 1999; Devictor et al. 2012). Various studies have shown how year-to-year population changes are influenced by weather (Roy et al., 2001; Boggs and Inouye, 2012) and also how ECEs can lead to population crashes and/or explosions (Palmer et al., 2017; McDermott et al., 2017). Extreme drought events, for instance, have been linked to unusual population declines and an increase in the extinction risk in metapopulations (Oliver et al., 2015; Johansson et al., 2020; van Bergen et al., 2020). On the other hand, rapid growth rates make fast recoveries more likely, even after population crashes, thereby minimising the long-term effects of climatic extremes on population trends (Ehrlich et al., 1980; Palmer et al., 2017). The magnifying effects of ECEs on population growth and population size are well illustrated by nonlinear responses to abrupt changes in climate drivers, not only in insects and other short-lived organisms but even in long-lived tree species (Bestelmeyer et al., 2011; Cavin et al., 2013).

Another aspect to bear in mind when studying the responses of butterfly populations to climate is that its effects will vary greatly depending on the life stage it acts upon (Radchuk et al., 2013). Thus, for example, high temperatures may be detrimental during the overwintering period but beneficial during the adult flight period (WallisDeVries et al., 2011; McDermott et al., 2017). Therefore, the impact of climate change in a particular region (e.g. a warming trend in the winter period) will vary according to species' phenology and life histories.

However important weather is, there is compelling evidence that other factors linked to density dependence are equally important as drivers of butterfly population dynamics (Dempster, 1983; Rothery et al., 1997; Dooley et al., 2013). Indeed, density dependence has been identified as a key factor in the population dynamics of many butterfly species, ranging from sedentary species forming classical metapopulations to long-distance migrants, with highly contrasting life histories (Nowicki et al., 2009; Marini & Zalucki, 2017). A recent study focusing on a dozen common European butterfly species concluded that they were all uniformly sensitive to density dependence, which usually has a greater effect than climate near the centre of a species' range (Mills et al., 2017).

This framework for understanding the dynamics of butterfly populations is more complicated in topographically heterogeneous regions where small-scale climatic differences may be associated with dissimilarities in population responses within species. Catalonia (NE Spain) is a good example of such a complex scenario. Albeit relatively small in size (33,055 km^2), this region embraces a great diversity of climates and landscapes, ranging from arid Mediterranean zones and humid deciduous forests to Alpine mountains. Long-term butterfly monitoring data indicates that populations in arid areas are subjected to more negative trends than populations in cold and humid areas, a difference that could be related to the fact that drought episodes have a more severe impact on the former group (Herrando et al., 2019; Ubach et al., 2021). However, this possibility has not been formally tested and remains speculative.

In this work, we model the population responses of Catalan butterflies to climate, taking into account density dependence, the phenological differences between species, and the heterogeneity of the responses in the two climatic regions. Specifically, our aims were (i) to assess the climatic factors that affect the growth rate of butterfly species and how they vary according to climatic regions; (ii) to identify which life-cycle stages are most sensitive to climate; and (iii) to quantify population crashes and explosions and how they are related to life-history traits and to extreme climatic events. We hypothesized that weather conditions will have contrasting effects on butterfly species depending on their life-cycles, and that more negative effects will be noted in populations in the Mediterranean climatic zone given the more serious declines recorded in this area in recent years. We also hypothesized that larval and adult stages will probably be the most sensitive, and that precipitation will have contrasting effects in both stages, with a positive impact on larvae, which will benefit from vegetation growth, but a negative impact on adults due to a reduction in their potential activities. Finally, we hypothesized that the climatic events that most critically affect population growth may have a magnifying effect when they become climatic extremes and provoke population crashes and explosions.

4.3 Materials and methods

4.3.1 Recording sites and butterfly data

We used data from the Catalan Butterfly Monitoring Scheme (CBMS; www.catalanbms.org), a citizen-science project with a network of sites for recording butterfly abundance that has been operating in north-east Spain, Andorra and the Balearic Islands since 1994. At each recording site, weekly counts are made along a fixed route from March to September, under the standard weather conditions favourable for butterfly activity (Pollard & Yates, 1994).

The relative abundance of butterfly species each season was estimated from GAM models fitted to the weekly counts within a given climatic region, following the method described by Schmucki et al. (2016) and using the *rbms* package in R (Schmucki et al., 2021).

We used data from a total of 146 recording sites (average of years per site: 9.5, range: 1–27) (Fig. 4.1). Sites were classified as belonging to one of two climatic regions (cf. Metzger et al., 2013) based on average accumulation values for growing degree-days over the flight season (DGG21) calculated for the 15-yr period 1994–2009: 1) alpine climate region (ACR), 24 mountain sites (> 1000 m a.s.l.) and 2) Mediterranean mesic climatic region (MMCR), 122 sites. We worked with a subset of 78 butterfly species flying at more than 10 sites in at least eight years, but excluded the regular migrants *Vanessa cardui*, *V. atalanta*, *Pieris* *brassicae, Lampides boeticus* and *Leptotes pirithous*. The species and the number of populations in each climatic region are listed in Suppl. Table 4.1

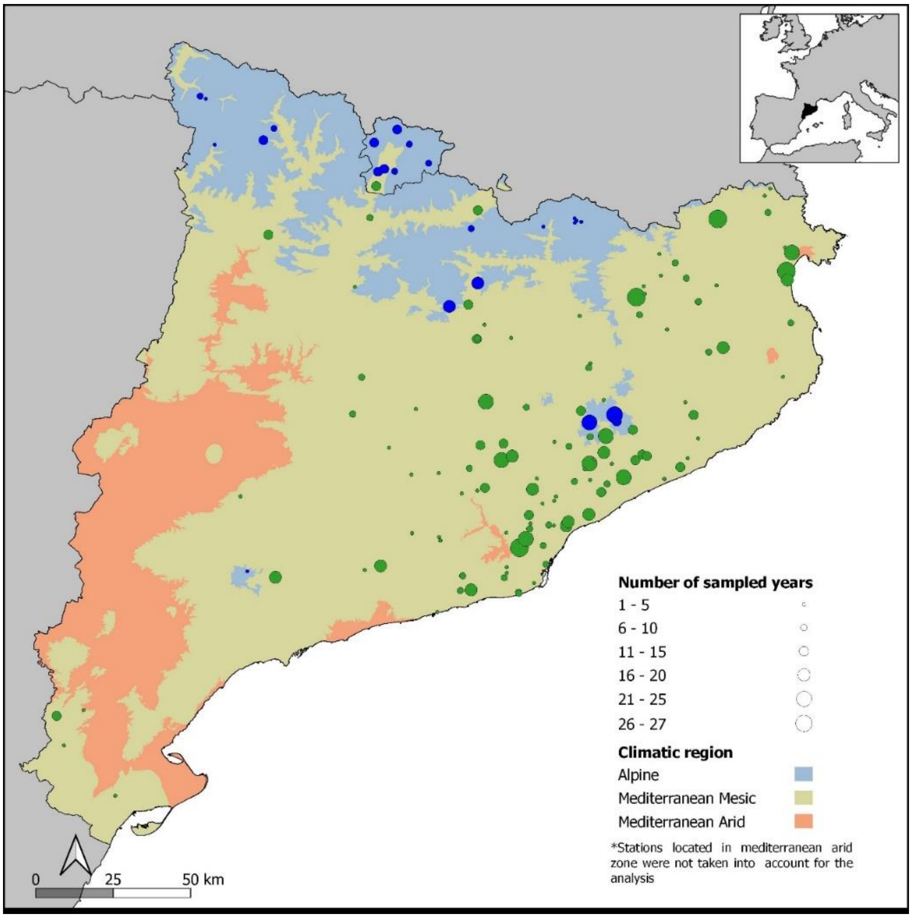

Figure 4.1 Map of the study region. The 146 monitored transects are represented with dots whose size is proportional to the number of sampling years. The 122 sites in the Mediterranean mesic climatic region are shown in green, while the 24 locations in the alpine climate region are shown in blue. No sampling sites within the Mediterranean arid climatic region were used in this study.

4.3.2 Climate data

Weather variables were calculated based on data from a network of 93 Authomatic Weather Stations (AWS) located near the butterfly transects. Each AWS was assigned either to the Mediterranean mesic or alpine climate region, and average values of weather variables were calculated at regional climatic level (ACR=15 meteorological stations, MMCR= 78 stations). Climatic data were provided by Meterorological Service of Catalonia (SMC, https://www.meteo.cat/) and Institut d'Estudis Andorrans (IEA, https://www.iea.ad/).

Within each region and year, we calculated separately the mean of daily minimum and maximum temperatures and the accumulated rainfall for each of the four climatic seasons (winter (WI): December–February; spring (SP): March–May; summer (SU): June–August; autumn (AU): September–November). In addition, the standard precipitation index (SPI), based on the probability of precipitation during the study period, was calculated for each climatic season:

$$SPI_i = \frac{X_i - Xm}{\sigma}$$

where *Xi* is the observed precipitation in a particular climatic season, *Xm* the mean precipitation value for a particular AWS, and σ the standard deviation of the time series from that station. SPI data were taken from locations in a 5x5-km grid for north-east Spain. For each butterfly recording site we assigned the SPI value of the grid square to which the station belonged, and then averaged the SPI values for each climatic region.

For the 16 weather variables per region (maximum and minimum temperature, total rainfall, and SPI for each climatic season), Pearson correlation tests were performed to remove highly correlated variables (Pearson's $|r| > 0.7$). We excluded the variable that had the greatest collinearity with other variables in all pair-wise comparisons, and retained 6–7 variables for each climatic region (Table 4.1). For the selected variables, we also included a lag effect from the previous year to account for effects on the developmental stages, so the final dataset included 11 weather variables for the ACR and 13 for the MMCR. As the annual indices of butterfly abundances are calculated from adult counts in the spring and summer of the current year, the weather variables used as predictors encompassed a time period from 'spring lag 1' (i.e. spring of the previous year) to the current summer. For a correct interpretation of the effect of weather variables on population growth (see below), caution is needed: a positive estimate coefficient for a *minimum temperature* variable means that population growth was positively affected by *warmer* or *milder* seasons.

Table 4.1 Climatic predictors included in the models after removing highly correlated variables (P>0.7) for both climatic regions (alpine, Mediterranean mesic). "i-1" corresponds to the weather variables from the previous year (lag 1).

Weather variable	Alpine	Med. mesic
Spring min. temperatures (i-1)		X
Spring SPI (i-1)		X
Summer min. temperatures (i-1)	X	X
Summer SPI (i-1)	X	X
Autumn max. temperatures (i-1)	X	
Autumn min. temperatures (i-1)	X	X
Autumn SPI (i-1)	X	X
Winter max. temperatures		X
Winter min. temperatures	X	X
Winter SPI	X	X
Spring min. temperatures	X	X
Spring SPI	X	X
Summer min. temperatures	X	X
Summer SPI	X	X

4.3.3 Specific models of population growth

For each species and climatic region we built models to associate the year-to-year change in the regional abundance index with the weather conditions in each of the different seasons (i.e. spring, summer, autumn and winter). The model structure followed Mills et al. (2017):

$$y_t = x_{t-1} + W_{1t} + \cdots + W_{nt-1}$$

where, y_t is the population growth rate calculated as the difference between the log-transformed annual indices in year 't' and year '(t-1)' assuming a Gaussian distribution, x_{t-1} the log annual abundance index in the previous year accounting for the density-dependence effect, and 'W_n' the weather variables included in the model, which include those acting in both the current and the previous years (i.e. a 1-year lag effect). All variables were scaled prior to any analyses. Species flying during the spring season had variables with a lag effect including the previous spring and summer, while those flying during the summer had a lag effect only up to the previous summer.

General linear models (GLMs) assuming a Gaussian distribution were built with the *lme4* package in R (Bates et al., 2015). Model selection from all possible combinations was based on the Akaike Information Criterion (AIC), with models that differed by < 2 points from the lowest AIC (ΔAIC < 2) considered as the top-ranked models. The effect of each significant variable was weighted as the average of the effects in all top-ranked models. These analyses were carried out with R Studio (R core Team, 2021), using the *MuMin* package (Barton & Barton, 2015). After this analysis, we used a Chi-square test to examine whether or not the strength of the density dependency effect (categorized as a binary variable, i.e. as significant or non-significant density dependence) was associated with population trends (classified, according to the *rbms* package, in four categories: decreasing, increasing, stable and uncertain).

4.3.4 Multispecies models for growth rate

After identifying the climatic factors that significantly affect each species, we carried out a second analysis combining data for all species to test whether or not some life-cycle stages are more sensitive than others to climate, and whether or not this sensitivity differs according to their voltinism (i.e. univoltine vs. multivoltine species) and between climatic regions. Prior to this analysis, we awarded each species a score based on which stage of their life-cycles the significant climatic factors acted upon predominantly (according to our previous findings; see Suppl. Table 4.2 for a complete phenological summary of all species considered).

We built two linear mixed models (GLMMs, with Satterthwaite's method for t-tests), one considering weather variables relating to temperature and the other weather variables relating to rainfall. In these models, the response variable was the average of the estimated coefficients of significant temperature/rainfall predictors in all top ranked specific models of population growth. The number of significant weather predictors for calculating this average varied between species in the range 1–8 (mean 2.1 predictors/species). Three independent categorical variables were used as predictors: (1) the life cycle stage on which the weather variable was acting: adult (A), pupa (P), larva (L), egg (E) and previous-year adults (A-1); (2) voltinism (univoltine vs. multivoltine); and (3) climatic region (ACR vs. MMCR). We also included the two interaction terms 'life cycle stage:voltinism' and 'life cycle stage:climatic region'. 'Species' was entered as a random factor. Four species that fly in highly overlapping generations (*Pararge aegeria*, *Colias crocea*, *Issoria lathonia* and *Cacyreus marshalli*) were excluded from the analysis because it was not possible to associate a critical life-cycle stage in these species to the significant weather variables that had been selected in the previous analysis.

4.3.5 Extreme population changes and their relationship with extreme climate seasons

The second part of our work was aimed at assessing whether or not extreme population changes in butterflies (i.e. population crashes and explosions) were related to extreme climatic seasons. To identify extreme events, both in the butterfly and climate data series, we followed the approach used by Leys et al. (2013), who recommend the use of absolute deviations (MAD, i.e. the median absolute deviation) instead of quartiles to detect outliers, as per the equation:

$$\left\{\frac{|x_i - median(x)|}{MAD}\right\} > 2$$

For the butterfly data, x_i is a species' year-to-year change index in year i, and x is the whole time series of species with year-to-year changes in their annual indices. We calculated extreme events separately for each butterfly species and classified them as either crashes (C) or explosions (E). We repeated the process with the annual index values to detect years with extreme abundances, which we classified as either extremely high abundance (Abu+) or extremely low abundance (Abu-). We then repeated the same process for each weather variable in each climatic region to define extreme climatic seasons (ECSs), with x_i being the climatic values at year i and x the whole time series for the region (ACR= 26 years (1995–2020), MMCR=27 years (1994–2020)). Note here that extreme events (ECEs) correspond to extreme climatic seasons (e.g. the whole spring period) and not to events such as heatwaves or cold snaps lasting just a few days.

We first used a three-way ANOVA to determine the proportion of population extremes that depended on two particular life-history traits (voltinism and overwintering stage) and on climatic region. The analysis included the interactions 'climatic region:hibernation stage' and 'climatic region:voltinism'. We performed different analyses for population crashes and explosions, and carried out a Post-Hoc Tukey test for pair-wise comparisons. Four species that hibernate in more than one life-cycle stage (*Pararge aegeria*, *Colias crocea*, *Issoria lathonia* and *Cacyreus marshalli*) were excluded from the analyses.

We also investigated whether or not population extremes of different species were synchronised in particular 'consensus years' (*sensu* Palmer et al. (2017)). We used one-tailed exact binomial tests with observed frequencies of crashes and explosions to identify years in which more species experienced population extremes than expected by chance.

Lastly, we investigated whether or not there was an association between population extremes and ECEs for those weather variables that, according to our initial analysis, significantly affected species' population growth (e.g. if the growth rate was affected by winter SPI, we asked whether or not an extreme population change occurred in the years with extreme winter SPI). We built GLMMs with a binary response variable (i.e. the occurrence or absence of a population extreme, either a crash or an explosion in separated models) and used both climatic and density-dependent predictors also structured as binary variables (Zuur et al., 2009). The climatic predictor tested whether or not the years when ECEs occurred were linked to population extremes. The two density-dependence terms (extremely high abundance (Abu+) and extremely low abundance (Abu-)) were used to test whether or not population extremes were linked to extreme population levels in the previous year (i.e. we asked whether or not population crashes followed years with extreme population abundance, and whether or not population explosions followed years in which the species was extremely rare). These models were fitted separately for the ACR and MMCR climatic regions and for univoltine and multivoltine species (four models in total), with the identity of species used as a random factor.

4.4 Results

4.4.1 Specific models of population growth

Our models identified density dependence (DD) as the most ubiquitous predictor for population growth (61 out of 78 species, 78.2%) – in all cases with a negative effect – and revealed a variety of responses to seasonal rainfall and temperature in most species (64 out of 78 species, 82.1%, Table 4.2, Suppl. Table 4.1). Six species were not affected by either climatic or density-dependent factors; five species in ACR and seven species in MMCR were significantly affected by DD but not by climatic factors.

Table 4.2 Number of species showing significant responses to weather variables in each climatic region. '+' indicates a positive effect on population growth, '-' indicates a negative effect or population decline. SPI: Standard Precipitation Index, DD: Density Dependence. 'i-1' corresponds to the weather variable from the previous year (lag 1).

Region		**Alpine (31 spp.)**		**Med mesic (58 spp.)**	
Population growth		+	-	+	-
Density dependence		0	26	0	51
Precipitation	Spring (i-1) SPI	NA	NA	1	0
	Summer (i-1) SPI	0	4	1	20
	Autumn (i-1) SPI	4	1	4	8
	Winter SPI	7	0	8	2
	Spring SPI	1	7	13	7
	Summer SPI	1	1	5	3
Temperature	Spring (i-1) min ºC	NA	NA	0	0
	Summer (i-1) min ºC	3	3	4	2
	Autumn (i-1) min ºC	0	2	1	7
	Autumn (i-1) max ºC	NA	NA	NA	NA
	Winter min ºC	0	4	3	6
	Winter max ºC	NA	NA	2	9
	Spring min ºC	2	2	9	2
	Summer min ºC	1	2	0	3

The importance of DD was similar in both climatic regions (significant relationships were recorded in 71% of the species in ACR and 67.1% in MMCR). Likewise, a similar proportion of species responded significantly to weather variables (69.4% of the species in ACR and 64.4% in MMCR). Species not affected by DD were mostly those whose populations were in decline in the study region (χ^2= 15.428, P=0.001).

Rainfall variables had contrasting effects depending on the species and climatic region (Table 4.2, Suppl. Table 4.1). *Maniola jurtina* was the species most affected by rainfall variables (with four significant SPI predictors corresponding to all four seasons in the current year), while as many as 15 species (19.2%) showed no significant relationship with rainfall. Focusing on climatic regions, the most important rainfall variables in ACR were winter SPI, with an overall positive effect of more humid and snowy winters (seven species responded positively and none negatively), and spring SPI, with an overall negative effect of rainy springs (seven species responded negatively and only one positively) (Table 1.2). In MMCR, spring SPI and the previous summer SPI were the predictors associated with the largest number of significant responses. Unlike ACR, spring SPI had a predominantly positive effect (13 species increasing compared to seven decreasing; Fig. 1.2). On the other hand, a rainy previous summer had a consistent negative effect (20 species decreasing compared to only one increasing).

Fewer species had significant relationships with temperature (Table 4.2). *Erynnis tages* was the species most affected by temperature variables (with five significant relationships), while 27 species (34.6%) had no significant relationships (Suppl. Table 4.1). Winter temperatures had the highest influence on population growth, with the negative effects of milder winters found for about 15% of the species in both ACR and MMCR (Fig. 1.2). Previous warm autumns also had consistent negative effects in both ACR and, especially, in MMCR (Table 4.2).

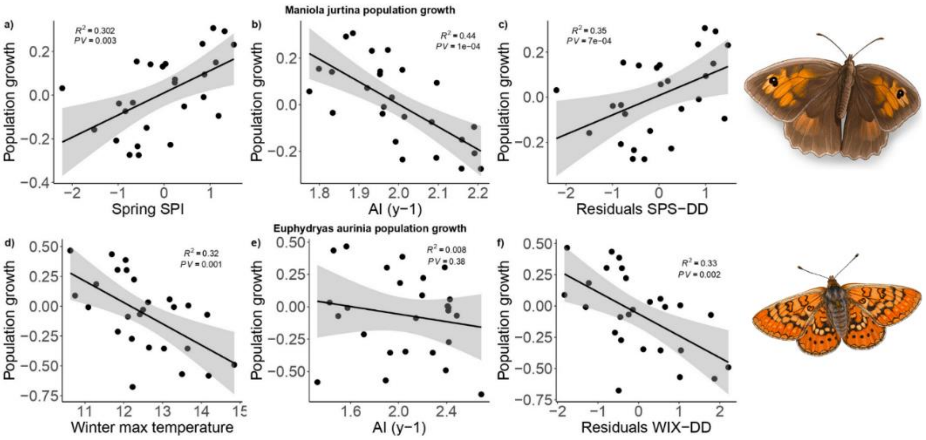

Figure 4.2 Examples of weather factors affecting the population growth of two univoltine species. The meadow brown butterfly (*Maniola jurtina*) (2a-c) shows a highly significant positive response to spring SPI (2a) and a highly significant negative response to population levels in the previous season (2b). The marsh fritillary (*Euphydryas aurinia*) (2d-f) shows a highly significant negative response to winter maximum temperatures (2d) and no density-dependence effect (2e). Panels c and f show these relationships after controlling for density dependence. The marsh fritillary is a declining species in the MMCR (Supp. Table 1.1).

4.4.2 Multispecies models for growth rate

The combined linear mixed-model performed for rainfall variables showed a significant difference between multivoltine and univoltine species, with the latter being more negatively influenced by rainfall variables (*P* = 0.003; Table 4.3). The model also showed a positive interaction between the larval stage and voltinism (*P* = 0.017), which indicates that in univoltine species rainfall acting on the larval stage had a disproportionately high positive effect on population growth rate compared to multivoltine species (Suppl. Fig. 4.1).

For temperature variables, we likewise detected a significant – albeit weaker – effect of voltinism, again with univoltine species having a generally more negative influence (*P* = 0.037; Table 4.3). We also found significant effects on two developmental stages, namely the adults of the previous season (*P* = 0.047) and, above all, the larval stage (*P* = 0.015), which were more negatively affected by higher temperatures than the other stages. Moreover, there was an interaction between the adults of the previous season and voltinism, with higher temperatures having a more negative effect on multivoltine than univoltine species (Suppl. Fig. 4.1).

Table 4.3 Results of the combined GLMM models for Precipitation and Temperature variables for all the studied species, with their estimates and P-values. A-1: Adults in the previous year, L: Larvae, P: Pupae, MMCR: Mediterranean mesic climatic region, AR: alpine climatic region. Significant values * : 0.01< *P* < 0.05; **: *P* < 0.01.

	Precipitation		**Temperature**	
	Estimate	P-value	Estimate	P-value
A-1 stage (ref. Adult)	-0.067	> 0.05	-0.190	0.047*
L stage (ref. Adult)	-0.010	> 0.05	-0.220	0.015*
P stage (ref. Adult)	0.046	> 0.05	-0.087	> 0.05
Univoltine (ref. Multivoltine)	-0.114	0.003**	-0.151	0.037*
MMCR (ref. AR)	-0.008	> 0.05	-0.078	> 0.05
A-1*Univoltine	0.029	> 0.05	0.207	0.035*
L*Univoltine	0.124	0.017*	0.125	> 0.05
P*Univoltine			0.011	> 0.05
A-1*MMCR	0.002	> 0.05	0.079	> 0.05
L*MMCR	-0.020	> 0.05	0.141	> 0.05
P*MMCR			0.077	> 0.05

4.4.3 Extreme population changes and their relationship with extreme climate seasons

We identified extreme population events in both climatic regions (Suppl. Fig. 4.2), which affected almost all the species included in the analysis (40 species in ACR (74%), 72 species in MMCR (84.7%)). The species experiencing the most severe population crashes in ACR were *Polyommatus icarus, Colias crocea* and *Boloria euphrosyne*, with four crashes over a period of 17, 22 and 15 years, respectively. In MMCR, *Colias crocea* and *Aporia crataegi* underwent six population crashes in 26 and 20 years, respectively, while *Lasiommata megera* and *Gonepteryx cleopatra* experienced five population crashes in a time series of 19 years each. A similar pattern was found for explosion events, with population explosions being recorded in 66.6% of the species in ACR and 85.9% in MMCR. The species experiencing most explosions were *Colias crocea* and *Melitaea phoebe* in ACR (four explosions in 22 and 15 years, respectively), and *Thymelicus acteon* in MMCR (six explosions in 23 years).

The proportion of years with population extremes depended on the climatic region and the hibernation stage but not on voltinism (Table 4.4). Relatively more species experienced population crashes in MMCR than in ACR (*P*= 0.047), while species overwintering in the larval stage had more population explosions than species overwintering in the egg stage (*P*=0.018). In MMCR we identified four consensus years. The only year with more explosions than expected by chance was 2002 (22, 30.9% of the species; *P*=0.001). Moreover, this same year was the only one in which no crashes were recorded (Suppl. Fig. 4.2). The other three consensus years had more crashes than expected randomly (2004: 18, 24.2% of species, *P* =0.02; 2012: 15, 17.1%, *P* =0.04; 2019: 20, 22.2%, *P* =0.04; Suppl. Fig. 4.2).

Table 4.4 Results of the three-way ANOVA showing separately the relationship of population crashes and explosions with two life-history traits (voltinism and hibernation stage) and with the climatic region.

		Df	**Sum Sq**	**Mean Sq**	**F-value**	**Pr(>F)**
Crashes	Region (MMCR-ACR)	1	0.041	0.041	4.034	0.047*
	Voltinism (U-M)	1	0.019	0.019	1.908	> 0.05
	Hibernation (L-A-O-P)	3	0.036	0.012	1.186	> 0.05
	Region*Voltinism	1	0.016	0.016	1.626	> 0.05
	Region*Hibernation	3	0.005	0.002	0.151	> 0.05
Explosions	Region (MMCR-ACR)	1	0.003	0.003	0.554	> 0.05
	Voltinism (U-M)	1	0.000	0.000	0.02	> 0.05
	Hibernation (L-A-O-P)	3	0.054	0.018	3.475	0.018*
	Region*Voltinism	1	0.009	0.009	1.804	> 0.05
	Region*Hibernation	3	0.018	0.006	1.149	> 0.05

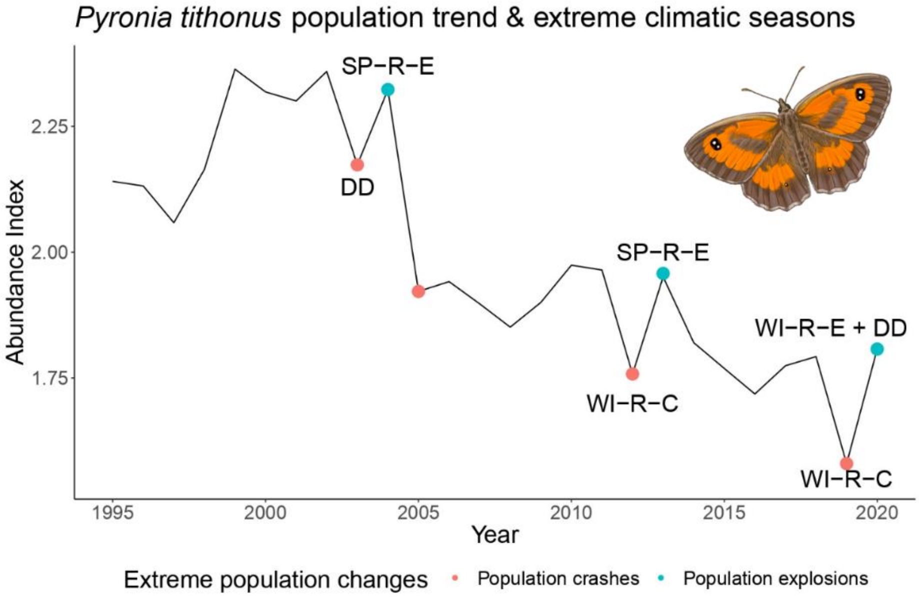

Figure 4.3 Population fluctuations of the gatekeeper butterfly (*Pyronia tithonus*) in the MMCR, showing four population crashes (red dots) and three population explosions (blue dots). Six out of seven population extremes can be accounted for by extreme climatic events and extreme population levels in the previous year (i.e. density dependence). Population growth in this species is mostly affected by winter rain and spring rain, both with a positive effect. All three population explosions and two population crashes occurred in seasons when these weather predictors reached extreme values in the same direction as expected. One population crash occurred the year after an abundance explosion. SP-R-E (Spring Rain Explosion), WI-R-E (Winter Rain Explosion), WI-R-C (Winter Rain Crash), DD (Density Dependence).

Similarly, extreme climatic seasons were found to occur almost every year. We identified 53 season extremes in ACR in a 22-yr time series (2.40 ECSs/ year), consisting of 13 rainfall crashes and 13 rainfall explosions, and 13 temperature crashes and 14 temperature explosions. In MMCR there were 59 ECSs in a 26-yr time series (2.25 ECSs/year), consisting of 20 temperature crashes and 14 temperature explosions, and six rainfall crashes and 19 rainfall explosions. Only four years had no ECSs of any type in MMCR.

The GLMMs gave consistent results for the effects of extreme population levels on population crashes and explosions (Table 4.5). Irrespective of the climatic region, crashes tended to occur following extremely high abundances the previous year (Abu+) and explosions following extremely low abundances in the previous year (Abu-), both in univoltine and multivoltine species (Table 4.5; Fig. 4.3).

Table 4.5 GLMMs testing the effects of extreme climatic events (ECS) and extreme high ('Abu+') or low abundances in the previous year ('Abu-') on population crashes and explosions in two climatic regions.

		Alpine climate region		**Med. mesic region**	
Univoltine		Estimate	Pr(>|z|) value	Estimate	Pr(>|z|) value
Crash	Abu+	1.569	0.004**	1.819	2.10E-06**
	Abu-	-2.88	> 0.05	-1.205	>0.05
	ECS	2.50	> 0.05	1.709	8.48E-10**
Explosion	Abu+	-0.636	> 0.05	-15.144	> 0.05
	Abu-	1.567	0.002**	1.402	4.02E-05**
	ECS	0.748	> 0.05	0.480	> 0.05
Multivoltine		Estimate	Pr(>|z|) value	Estimate	Pr(>|z|) value
Crash	Abu+	1.706	0.004**	2.250	4.77E-12**
	Abu-	0.114	> 0.05	-17.086	> 0.05
	ECS	0.729	> 0.05	0.762	0.015*
Explosion	Abu+	-17.683	0.997	-1.231	0.0926.
	Abu-	2.504	6.51E-07**	2.023	4.24E-12**
	ECS	0.612	> 0.05	0.465	> 0.05

The relationship between population extremes and the ECSs, on the other hand, differed according to the climatic regions and, to a lesser extent, to voltinism. In MMCR – but not in ACR – population crashes occurred in association with ECSs for the same weather variables that negatively affected population growth (Table 4.5). For population explosions, only marginally significant associations were found in univoltine species in ACR and in multivoltine species in MMCR (Table 4.5).

4.5 Discussion

4.5.1 Population growth and density dependence

In this study we explore which weather variables affect the population dynamics of Mediterranean butterflies, which developmental stages are the most sensitive to weather variables, and whether or not density-dependence factors also play a significant role in the population dynamics of these butterflies. We found that density dependence had a major effect on many species, including a ubiquitous negative effect on growth rate. Negative relationships correspond to classical population regulation theory (Royama, 1992), with high population levels the previous year provoking a variety of factors negatively affecting population growth such as the increase in the number of parasitoids and predators (Hassell, 1985). Although this effect was consistent both in MMCR and ACR, several species showed varying degrees of density dependence across the two climatic regions, indicating that the strength of density-dependent processes varies throughout a species' range (Dooley et al., 2013). For example, in *Aporia crataegi* significant density dependence was only detected in ACR, and in *Melanargia lachesis* only in MMCR. Interestingly, the least sensitive species were those with declining population trends in the study region (e.g. *Melanargia occitanica* and *Euphydryas aurinia*), suggesting that for these species the adverse effects of habitat degradation cannot be offset by density dependence processes.

4.5.2 Population growth and weather

Weather also represented a major driver of butterfly population dynamics, with more than 80% of species being affected by at least one weather variable. As in previous work (Herrando et al., 2019), we found a certain amount of evidence to suggest that precipitation is more important than temperature in Mediterranean butterflies (60% of significant relationships were associated with SPI, while 40% with thermal variables), and we found similar results in the alpine region (57% precipitation: 43% thermal).

Spring SPI, in particular, affected many species, with a dominant positive effect in MMCR but a consistent negative effect in ACR. In the Mediterranean climate, the rainfall pattern is characterised by two distinct peaks, one in spring and one in autumn, the first of which is essential for the growth of vegetation and, in turn, for the development of herbivorous insects (Yela & Herrera, 1993). In addition, spring rain largely determines nectar availability during the summer season, a crucial factor in explaining butterfly abundance (WallisDeVries et al., 2012). In our study, the few species that were negatively affected by spring SPI were those with a spring flight period and larval development in the previous season (e.g. *Pseudophilotes panoptes* and *Zerynthia rumina*). We believe that this is because both adult activity and detectability in these species are reduced in rainy springs. On the other hand, spring SPI in the alpine climate region was strongly associated with butterfly negative responses, possibly because the lengthening of the winter period with snow cover reduces larval and pupal survival and the subsequent number of adults.

Humid winters also showed frequent significant relationships with population growth, with positive effects both in ACR and MMCR. In the alpine climate region, such winters mean greater snow cover, which has repeatedly been shown to be beneficial for mountain butterfly species, both due to the direct effects on overwinter survival of immature stages and indirect effects on host plant and nectar resources (Boggs & Inouye, 2012; Nice et al., 2014; Roland et al., 2021). In the Mediterranean region, winter rainfall favours the growth of perennial plants and herbs later in the spring, with a predictably higher survival rates for species feeding on these resources at that time (e.g. *Satyrium esculi* feeding on evergreen oak leaves, and satyrines such as *Maniola jurtina*, *Pyronia cecilia* and *P. tithonus*, and skippers such as *Thymelicus acteon* and *T. sylvestris*, feeding on grasses).

In addition, regardless of the climatic region, we recorded consistent population declines after rainy summers. The same pattern has been noted in other studies (Pollard, 1988; Roy et al., 2001) and may be related to less adult activity and a consequent fall in potential fecundity, which will have repercussions the following year.

Temperature variables were also important in the MMCR, where the number of significant relationships was higher than in the ACR (0.83 and 0.61 significant relationships/species, respectively). Interestingly, mild autumns and winters had widespread negative effects in both regions, which concurs with experimental work providing clear evidence of a decrease in overwintering survival with rising temperatures during the diapausing period. Williams et al. (2012) identified an increase in metabolic consumption of overwintering larvae of *Erynnis propertius* under simulated high temperatures and suggested that longer warm autumns will have a negative impact on this butterfly by making its larvae more susceptible to an overwinter energy drain. Radchuk et al. (2013), Abarca et al. (2019) and Klockmann & Fischer (2019) also found that warm winters have negative effects on larval survival in *Boloria eunomia*, *Euphydryas phaeton* and *Lycaena tityrus*, respectively. Reserve depletion resulting from increased metabolic activity has been suggested as the main reason for increased mortality, although a larger incidence in diseases and fungal infections could also play a role (Radchuk et al., 2013). These examples can probably apply to many species overwintering as larvae and experiencing population declines following warm autumns and winters in our region (e.g. *Erynnis tages*, *Brintesia circe*, *Erebia meolans*, *Coenonympha arcania*, *Maniola jurtina*, *Satyrus actaea*, *Boloria dia*, *Euphydryas aurinia*, *Melitaea cinxia*, *M. didyma*, *M. phoebe* and *Aporia crataegi*).

Unlike winter and autumn, warm springs in the Mediterranean region had an overall positive effect on butterfly populations. Although this positive effect could be substantially lessened in the future if warm springs come to be associated with droughts (see above), a likely explanation for this effect is that a shortening of developmental times under high temperatures reduces the time of exposure to potential predators and parasitoids (e.g., Pollard, 1979). The fairly strong relationship we detected mirrors that found by earlier studies in the UK (Pollard, 1988; Roy et al., 2001), even though it occurs slightly earlier in the season due to the phenological advance in Mediterranean climates compared to Temperate Climate (TC) from Central Europe. A non-exclusive explanation is that warm springs favour adult activity and increase the detectability of butterflies flying in spring during transect counts.

On the other hand, our findings contrast with some of the relationships reported in previous studies in the TC region. Thus, the effect of rainfall on population growth was generally positive in the MMCR, where it is a scarce resource, but was negative in the TC region, where is not a limiting factor (Hawkins et al., 2003). Therefore, while butterfly populations benefitted from humid winters and springs in the MMCR, rainy winters had an opposite effect in the TC region (WallisDeVries et al., 2011) and it was dry years and, more precisely, dry summers that were associated with population increases in this region (Pollard, 1988; Roy et al., 2001). Quite predictably, temperature had positive effects during the period in which most species developed as immatures, that is, in spring in the MMCR but in summer in the TC (Pollard, 1988; Roy et al., 2001). Interestingly, and for the reasons already discussed, mild winters had consistent negative effects on population growth in both regions (WallisDeVries et al., 2011, and the current study), a worrying finding in the context of climate warming.

4.5.3 Climate sensitivity and life history

Our analyses revealed that larval and adult stages are the most sensitive to climate. This is not surprising since they correspond to the active part of the butterfly's life cycle (e.g. in which feeding, growth, mating and egg-laying take place) and both larvae and adults exhibit a wide range of thermoregulatory behaviour (Radchuck et al., 2013). On the other hand, the egg and pupal stages are concentrated in a much shorter time window and, when they overwinter, possess physiological adaptations that make them highly resistant to climate (Bauerfeind & Fischer, 2013).

In turn, our multispecies models allowed us to test whether or not the sensitivity to climate differed between climatic regions and the voltinism of species. Population growth was not explained by climatic region but was related to voltinism, with a higher frequency of negative effects recorded more frequently in univoltine species than in multivoltine ones both for temperature and rainfall variables. This finding is likely to be related to the poorer ability of single-generation species to recover in the same year from a negative climatic episode (Kerr et al., 2019). In addition, it suggests that univoltine species may suffer more severely under the current climate change scenario if it implies an increase in the frequency of the weather episodes we have identified as detrimental to population growth.

When the interaction between developmental stage and voltinism was taken into account, more complex patterns emerged. Thus, precipitation acting on the larval stage had disproportionately positive effects on univoltine species, while temperatures experienced by adults in the previous season had more negative effects on multivoltine species. We believe that these relationships highlight how important it is that single-brooded species synchronize their relatively short period of development with the right conditions for the growth of their host plants, and also the risk that multivoltine species accumulate harmful effects caused by high summer temperatures in successive generations, which will have negative consequences in the next season (Melero et al., 2016).

4.5.4 Extreme population changes and their relation with extreme climatic seasons

Extreme population changes occurred almost every year, with some species experiencing these changes more often than others. Moreover, these population events were more frequent in the Mediterranean than in the alpine climate region, although this difference only applied to population crashes. Consensus years (i.e. when more species than expected suffer extreme population changes) were similarly only detected in the Mediterranean region. Extreme climatic events were also recorded annually and there were only two years in MMCR when no ECSs were recorded.

Our data clearly show that density dependence is an important factor in population extremes as, regardless of region and voltinism, these extreme events were associated with abnormally high or low population levels in the previous season. Population collapses caused by the impact of parasitism, predation and disease are common among outbreaking forest Lepidoptera (Dwyer et al., 2004) but can also affect many other non-outbreaking species (Nowicki et al., 2009). Likewise, marked population increases recorded in a subsequent season after very low population levels suggest that a relaxation of density-dependent mortality factors occurs. While to some extent this might be expected, it is remarkable that density dependence alone can explain butterfly population extremes in many cases.

We also found an association between ECSs and population extremes, indicating magnified effects of climatic variables beyond some threshold that lead to abrupt shifts in population growth. The response, however, was not ubiquitous: population crashes were significantly related to climatic extremes but only in the Mediterranean region, which could partly explain the more negative butterfly trends there (Herrando et al., 2019; Ubach et al., 2021). This effect was clearly more strong in univoltine species than in multivoltine ones, which can be explained by the lower plasticity of the former in their responses to environmental stress (Forister et al., 2018). The absence of an association of ECSs and population crashes in the alpine region could be related, in part, to compensation mechanisms, such as the one suggested by Buckley and Kingsolver (2012) in their study of two alpine *Colias* species. These authors found that although extreme heat reduces egg viability, this negative effect is offset by an extension of the flight period under a warming climate. In contrast to population crashes, the evidence that climatic extremes provoke population explosions was weak in our data, even though under some circumstances this may occur. Indeed, the single consensus year when more population explosions than expected were recorded coincided with an extremely humid spring, which favoured the growth of vegetation and an abnormally high success of species that overwintered as larvae and concentrated their development in spring. No similar response was observed in the alpine climate region, where water is not such a limiting factor as it is in the Mediterranean region (Hawkins et al., 2003).

4.6 Conclusions

In this study we provide evidence of weather-dependent population dynamics of butterflies in the Mediterranean basin and identify the most important climatic variables driving population growth in two climatic regions. Amongst the clearest relationships, we highlight the importance of spring rainfall in the MMCR, where it has a clear positive effect given that water availability is a limiting resource. We also identify a general negative effect of mild winters on butterfly populations, both in the MMCR and the ACR. Both relationships are worrying in the context of climatic warming, as drier springs and warmer winters are expected to be more frequent and intense in the Mediterranean basin in the next decades, according to the majority of climate change scenarios. Another relevant conclusion from our work is the strong effect of density-dependent processes in the vast majority of the studied butterfly populations. This effect even accounts for a large fraction of the recorded extreme population changes (crashes and explosions). Extreme climatic events were related to population crashes and rarely to population explosions in the MMCR, but no relationship was found in the ACR. Although our results help to understand the population dynamics of Mediterranean butterflies, longer time-series are still needed to reveal some other patterns that may remain hidden with current data. Especially important is the need to include data from populations occurring in the Mediterranean xeric climate region, where the effects of climate change will be particularly severe.

5. Chapter 2: Vegetation encroachment drives changes in the composition of butterfly assemblages and species loss in Mediterranean ecosystems

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Chapter 2 Vegetation encroachment drives changes in the composition of butterfly assemblages and species loss in Mediterranean ecosystems

Andreu Ubach, Ferran Páramo, Cèsar Gutiérrez and Constantí Stefanescu

5.1 Abstract

Land abandonment and loss of grazing have been amongst the primary drivers of landscape change in the Mediterranean basin in recent decades. As a consequence, forest cover has greatly expanded in detrimental of semi-natural grasslands, areas of cultivation and pasture mosaics. Although predictably important, the impact that this phenomenon has on biodiversity has remained largely unexplored, partly because of lack of appropriate data. Here we make use of an extensive citizen science program, the Catalan Butterfly Monitoring Scheme, to quantify the response of butterfly assemblages to vegetation encroachment in NE Spain. We first adapted an index to describe the preference of 147 butterfly species for open or closed habitats, and found a strong association of most species for open habitats. We developed a community index to record changes in 54 long-term monitored sites (10 years or more), where plant communities were also periodically monitored. Butterfly assemblages have undergone changes towards species preferring closed habitats in 72% of the studied sites, in parallel to a process of vegetation encroachment in the region. Community changes were linked to population trends, and could be locally predicted by the interaction of the preference of butterfly species for open or closed habitats and the magnitude of vegetation encroachment at each site. These changes were accompanied by frequent extinction events (4.53% of the studied populations), that were highly biased towards species preferring open habitats. Our study confirms and quantifies the threat that vegetation encroachment imposes on biodiversity in this highly diverse region.

Keywords

Butterfly monitoring, Butterfly assemblages, Species loss, Land abandonment, Vegetation encroachment, TAO index

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5.2 Introduction

Vegetation encroachment, i.e. the spread of woody plant species into open habitats (Van Auken, 2009; Ratajczak et al., 2012), is a phenomenon that is occurring worldwide in grasslands and savannahs. It is very common in developed countries and was one of the main mechanisms driving forest transition and land cover changes in the past century (MacDonald et al., 2000; Rudel et al., 2005; Gerard et al., 2010). Encroachment is caused by a loss of traditional practices (Van Auken, 2009) such as livestock husbandry and low-intensity cultivation but also by increasing atmospheric CO_2 levels, nitrogen deposition and fire suppression (Ratajczak et al., 2012). Most of these drivers are fully applicable to the Mediterranean basin, where a rich mosaic of semi-natural grasslands and areas of cultivation and pastures, maintained by anthropogenic and natural processes for thousands of years, has been greatly reduced in recent decades as forest cover increases (Falcucci et al., 2007; Blondel et al., 2010; Mairota et al., 2013).

Vegetation encroachment is a serious threat to biodiversity, as the preservation of many species is strongly dependent on the maintenance of open habitats (Balmer & Erhardt, 2000; WallisDeVries et al., 2007; Ratajczak et al., 2012). It has been shown to cause a decrease in plant diversity (Ratajczak et al., 2012), have an impact on vegetation composition, affect higher trophic levels (Pöyry et al., 2006) and at larger scales may even lead to habitat fragmentation in semi-natural grasslands (Schirmel et al., 2015). It is therefore not surprising that much of recent research on vegetation encroachment has been aimed practically at improving pastoral practices and management options and thus biodiversity conservation (Balmer & Erhardt, 2000; WallisDeVries et al., 2007; Rivest et al. 2011; Mairota et al., 2013). Likewise, many on-going efforts are being made to identify biological indicators that respond rapidly and visibly to the phenomenon of vegetation encroachment (e.g. Pöyry et al., 2006; Tocco et al., 2013; Schirmel et al., 2015).

Butterflies, in particular, are known to be an excellent group for investigating the loss of traditional pastures and the resulting effects of vegetation encroachment (Erhardt, 1985; Stefanescu et al., 2009; Krauss et al., 2010; Verdasca et al., 2012; Koch et al., 2015). Moreover, their key role as an indicator group (Thomas et al., 2004; Thomas, 2005) has prompted their use in recent decades in extensive ecological monitoring programmes (van Swaay et al. 2008), which have generated large datasets that can be used to explore wide-ranging responses to vegetation encroachment. Here, we make use of one such dataset, the Catalan Butterfly Monitoring Scheme (CBMS), to quantify the response of butterfly assemblages to this phenomenon in the north-west Mediterranean over the past three decades.

In a previous study, Herrando et al. (2015) developed indicators for the open-closed gradient preferences of butterfly and bird populations in the Mediterranean region. They studied species' habitat preferences and showed how species preferring closed habitats have experienced more positive trends in recent decades than those that positively select for open habitats. However, although multi-species indicators help us understand how environmental factors drive population trends, a community approach is needed for a more comprehensive assessment of the impact of global change at ecosystem level (Julliard et al., 2006; Devictor et al., 2012). The use of such an approach in this paper allows us to explore how butterfly assemblages have undergone changes in diversity and composition that are running parallel to the landscape changes closely linked to the abandonment of traditional agricultural practices. We also provide a tool that can be used by conservation managers to show how butterfly communities change rapidly as a response to vegetation encroachment and to illustrate the changes that take place in ecosystems at local scale.

Several recent studies have highlighted the on-going decline of flying insect biomass (Hallmann et al., 2017). In particular monitoring programs have shown negative trends of lepidoptera in European countries and indicators of this decline highlight its affectation at grassland habitats (Van Swaay et al., 2015). In northern Europe, changes in land use associated with intensive grazing and vegetation encroachment have been shown to cause extinctions and declines in butterfly populations (Nilsson et al., 2008). Herrando et al. (2015) conclude that butterfly species preferring open habitats have more negative trends than those preferring closed habitats and here we test whether or not this link is leading to the extinction of the populations of species in the Mediterranean that select open habitats. More generally, we explore how species perform depending on the degree of vegetation encroachment and on their preferences for open or closed habitats.

5.3 Materials and methods

5.3.1. Study area and butterfly data

The study was carried out in Catalonia, Andorra and Menorca (Balearic Islands), in the north-west Mediterranean basin, where butterflies are monitored by the Catalan Butterfly Monitoring (CBMS) (Fig. 5.1). The region is environmentally diverse with different orobiomes ranging from sea level to alpine mountains, embracing a wide range of habitats including Mediterranean steppes and deciduous forests. Currently, more than 64% of its surface area is covered by forests (Fletas et al., 2012) partially due to vegetation encroachment resulting from the abandonment of traditional land uses. According to González Guerrero et al. (2018), the surface area of forest in Catalonia increased at a rate of 3300 ha/year in 1987–2012, while the land devoted to agriculture declined at a rate of 6300 ha/year during the same period.

The CBMS started in 1994 and at the end of 2017 93 sites out of the 160 that have provided data were active (see details in www.catalanbms.org). Butterflies are monitored using the standardized methodology originally developed in the UK (i.e. Pollard walks), which has been adopted as a standard in similar schemes throughout Europe (Schmucki et al., 2016). At each location, weekly counts along fixed routes start on March 1 and finish on September 26, spanning a total of 30 weeks. Butterflies are counted in a 5x5-m area (2.5 m to each side and 5 m in front of the recorder) whenever weather conditions are good (Pollard and Yates, 1994). The transect route is divided into a variable number of sections, each one corresponding to a distinguishable habitat type.

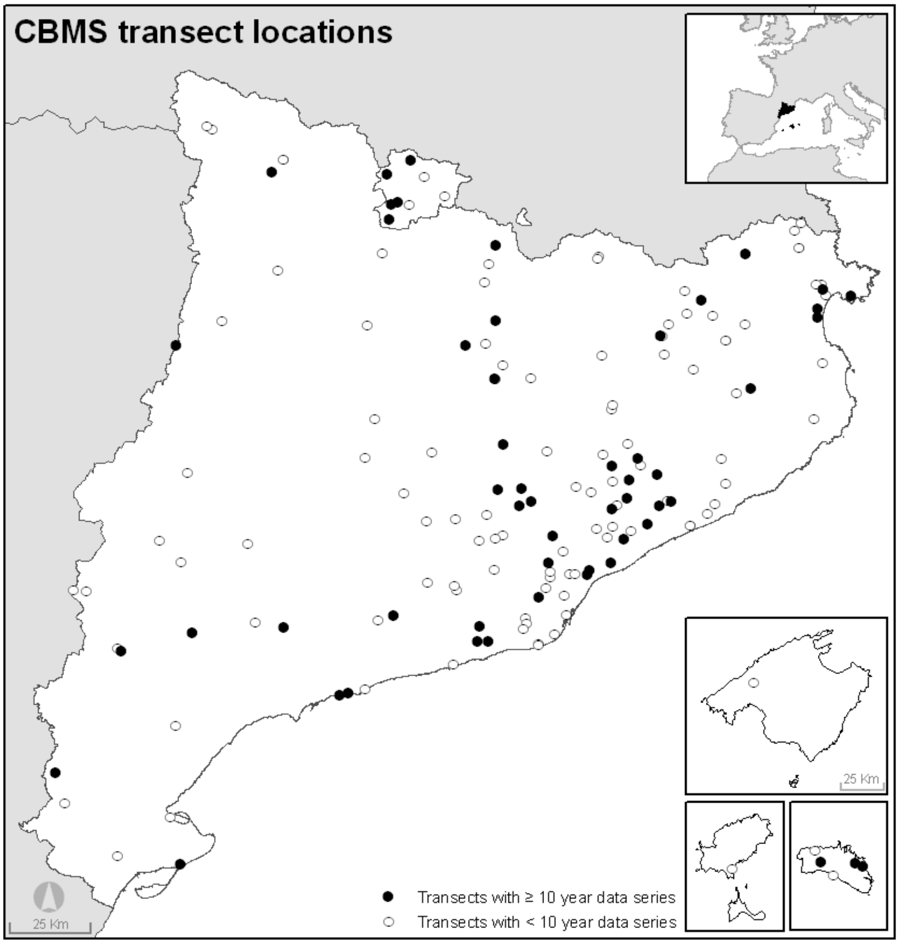

Figure 5.1 Map of the study region. The locations of the 54 long-monitored transects (≥ 10 years) in the CBMS network used for this study are represented by black dots. White dots represent the remaining 106 CBMS transects that existed up to 2017 and were used for calculating an index of preference along a gradient from closed to open habitats.

5.3.2 Species preferences for open/closed habitats

5.3.2.1 Vegetation characterization

A botanical characterization of the butterfly transects designed to monitor vegetation changes at the sites was repeated periodically by a botanist (CG). The first characterization of the older sites took place in 2000, after which subsequent characterizations were repeated every six years. Butterfly transects that joined the CBMS after 2000 were first characterized in the year they started to provide data and then at six-year intervals. Botanical characterizations were used both to derive a preference index of each butterfly species (i.e. open vs. closed habitats) and to record changes in the plant communities at individual sites during the butterfly recording period.

At each characterization, the cover of each plant community (defined according to the CORINE biotopes classification (Vigo et al., 2005)) was recorded at section level along the five-metre-wide butterfly walk. We established a binary classification for closed vs. open plant communities, assigning a value of -1 for closed communities and a value of +1 for open ones. All types of forest were categorized as closed and all grasslands as open, while shrubby communities were classified as either ‘closed’ or ‘open’ depending on the characteristic average height (see Suppl. Table 5.2 for details of each plant community). Subsequently, we calculated an average value for each section by multiplying the cover of each plant community by the assigned '-1' or '+1' value. Only sections with average values greater or equal to |0.1| were retained, as values very close to 0 (either positive or negative) represent a near equilibrium situation between open and closed habitats.

Butterfly data were associated to the nearest year of characterization and so between two botanical characterizations there were three years of data associated to the first and three years associated to the second. For transects that were active before the year 2000 we used butterfly data beginning in 1997 (three years before the first botanical characterization).

5.3.2.2 TAO species index

We used the formula in Suggitt et al. (2012) to calculate an index (TAO) of butterfly species’ preferences for open or closed habitats. This index allows us to order species along a gradient from -1 when they occur exclusively in closed (in Catalan: *TAncat*) habitats, to +1 when they occur exclusively in open (in Catalan: *Obert*) habitats. As in Suggitt *et al*. (2012), the TAO index was calculated for each species at transect level ('*i*') according to the formula:

$$\boldsymbol{I_{TAOi} = \frac{2\ x\ D_{open}}{D_{open} + D_{closed}} - 1}$$

where D_{open} is the mean density value (individuals/100 m) in open sections and D_{closed} is the mean density value in the closed sections .

The final TAO Index for each species (I_{TAO}) was thus the mean value of all the I_{TAOi} calculated for all transects in which a species appeared. We only used species with occurrences in a minimum of five transects, and for the calculation of the index we only used transects with both types of sections (i.e. closed and open; n=121); transects where a species could theoretically select either type of environments.

Given that species show slight preferences for more open or more closed habitats depending on the climatic conditions experienced by local populations (e.g. populations occurring in colder habitats tend to occupy more open habitats where microclimates are generally warmer; see Suggitt et al. (2012)), we assessed how the I_{TAO} varied between thermal regions in Catalonia by establishing four thermal regions using a 21 DDG threshold (i.e. number of hours per year over 21ºC). Climatic data was provided by the Servei de Meteorologia de Catalunya (www.meteo.cat) and was used to classify each of the 160 butterfly transects as belonging to one of these four climatic regions. We calculated I_{TAO} values separately for each species and thermal region and then performed a Spearman rank correlation test between thermal region pairs to assess how stable species' preferences are at country level.

5.3.3 Habitat changes and trends in butterfly assemblages

5.3.3.1 Vegetation encroachment

To assess vegetation changes at the monitored sites over time, we calculated the percentage of change occurring between the first and final botanical characterizations that was caused by vegetation encroachment. Depending on the duration of the sampling carried out at the site, changes in vegetation were assessed for periods spanning six years (two consecutive characterizations), 12 years (three characterizations), or 18 years (four characterizations).

For both the first and last characterization we calculated an average value of openness/closeness for the whole transect. This value was the sum of the product of the percentage of closed habitats in each section multiplied by -1, plus the product of the percentage of open habitats multiplied by +1. Thus, each section was assigned a value between -100 (totally closed) and 100 (totally open). A single value for each transect and characterization was then obtained by averaging the values of each section corrected for their length. A simple difference in the overall value between the two characterizations indicated the degree of encroachment of plant communities along a particular transect.

5.3.3.2 TAO community index

To study changes in butterfly communities over time, we assessed butterfly counts from a total of 54 sites with records from 1997–2017 with 10 years or more of data (mean = 14 years, range: 10–21 years) (Fig. 5.1). Three of these sites are situated on the island of Menorca, five in Andorra and the remaining ones in Catalonia (NE Spain).

We followed the rationale of Julliard et al. (2006) and Devictor et al. (2012) to develop a community index (TAOc) for each butterfly assemblage and year. The contribution of each species to the community index was weighted by the square root of its annual abundance to avoid biases resulting from large differences in population densities between species. The TAOc was thus obtained for each year of sampling for each butterfly transect. The slopes of linear models with TAOc as the dependent variable and year as the independent variable showed the trends of each butterfly community towards openness/closeness over time. Positive slopes corresponded to communities that tended to become dominated by open habitat species during the monitored period, while negative slopes tended to be dominated by closed habitat species.

We used generalized linear models (GLM) to relate the slopes summarising site changes in the TAOc to the degree of vegetation encroachment and several other predictors (see below). We hypothesised that butterfly communities will have negative TAOc slopes (i.e. a trend of the community is to become dominated by species preferring closed habitats) whenever (i) the vegetation of the site showed a degree of encroachment during the study period. In addition to vegetation encroachment, we included the following predictors: (ii) the Shannon diversity index of the CORINE habitat types at every itinerary at the initial time of the series, as we predicted that there would be a greater buffer effect (i.e. a greater stability of the butterfly community against vegetation encroachment) at sites with a wider range of resources and habitats; (iii) the initial TAOc value, as we believe that the structure of the community at the start of the monitoring period could influence the regression slopes; (iv) the time spanned since the start of monitoring since longer monitoring periods could be associated with greater community changes; (v) the thermal region to which the site belongs (a categorical variable, with four classes), as different rates of plant growth between regions could result in different rates of encroachment. We also added (vi) the interaction between vegetation encroachment and the thermal region.

We used a dredge function for a model selection approach based on the Akaike Information Criterion (AIC) to evaluate the strength of evidence for the relative influence of the predictors. The set of candidate models were derived from all combinations of predictors. Differences in AIC were used to rank the candidate models, using ΔAIC value <2 as a threshold for a model to be considered as receiving support. We then performed the five best models as individual GLMs. We also used a one way-ANOVA to test whether or not responses of the TAOc were similar for all four thermal regions considered and, as a comparison, we performed a similar analysis testing vegetation encroachment at each site. All the analyses were performed using Rstudio (R Core Team, 2018) with the *MuMin* package (Bartón, 2015) for the GLMs.

5.3.4 Species loss and population declines

To test whether or not vegetation encroachment could lead to population extinctions, we first identified all extinctions that had occurred in the 54 long-term monitored sites during the study period. We defined a local extinction as the absence of a species at the site during at least four years after a period with data of at least four years (see Pollard & Yates, 1992); thus, an eight-year series at least was needed to detect an extinction event. If a species recolonized the site after becoming extinct but then became extinct again, we counted that as two extinction events. We then calculated two TAO index values in each butterfly assemblage. The first one including all the species that have extinction events and thus no longer occur in a community, as a weighted mean value of the TAO index of these species. The other, the weighted mean value of the TAO index of the species that don’t present extinctions. We used a total of 2515 butterfly populations at the 54 sites with a minimum occurrence of half the total number of sampling years. We performed a paired t-test to test whether there were any differences between the mean TAO index for species showing extinction events and those that do not to show if species with a more positive TAO index are more likely to experience local extinction events.

In addition, we modelled population trends at site level (calculated as the slope of butterfly counts against years) as a function of species’ preferences for open or closed habitats, and the changes of plant communities at site level. A Generalized Linear Mixed Model (GLMM) was built, with trend slopes as the response variable (2484 butterfly populations with a calculated trend), the TAO index of each species, our measure of vegetation encroachment at the site where the species flies, and the interaction between the two variables as the three fixed factors, and ‘itinerary’ and ‘species’ as random factors.

5.4 Results

5.4.1 Species preferences for open/closed habitats

We obtained the I_{TAO} index for a total of 147 species of butterflies (Suppl. Table 5.1). The average number of sites used for calculating this index was 50; the maximum was 121 sites for clouded yellow (*Colias crocea*), large white *(Pieris brassicae*) and small white (*Pieris rapae*). The mean value (±SD) of the index was 0.408±0.566, with extreme values of -0.419 for speckled wood (*Pararge aegeria*), a species that prefers highly closed habitats (nº sites=117), and 1 for olive skipper (*Pyrgus serratulae*), which was only recorded in open habitats (nº sites=7). The mean value for I_{TAO} was highly positively skewed, indicating a strong association in most species with open habitats (Fig. 2). In total 91% of the species had positive values that according to our criteria correspond to open habitats.

Spearman correlations for the species indices between thermal regions were all positive and highly significant ($P << 0.01$ in nearly all pair-wise comparisons), the lowest ($P = 0.013$) correlation being between thermal region 1 (the coldest) and thermal region 4 (the warmest) (Suppl. Fig. 5.1). Thus, species showed great consistency in their preferences for open or closed habitats regardless of the climatic conditions experienced by populations.

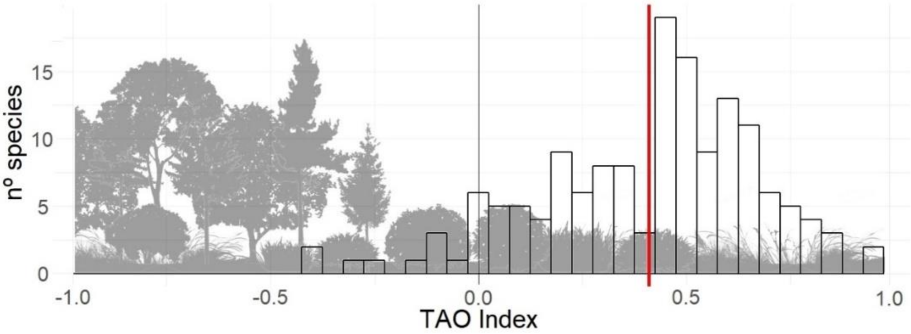

Figure 5.2 Distribution of the I_{TAO} values for all 147 species along a (-1, 1) axis. In all, 91% of the species values show positive values, thereby indicating very strong preferences for open habitats.

5.4.2 Habitat changes and trends in butterfly assemblages

Out of the 54 long-term monitored sites, in 41 (76%) there were changes towards greater vegetation encroachment. The overall increase in plant communities associated with closed habitats was in the range 0.1–31.7% between the first and final botanical characterizations. The 13 remaining sites changed in an opposite direction, moving towards a more open habitat (Fig. 3b). The TAOc values showed a similar pattern, with 39 butterfly communities (72%) becoming more dominated during the study period by species preferring closed habitats, and only 15 becoming more dominated by species preferring open habitats (Fig. 5.3a).

The five best models chosen with the AIC contain all the included variables except for the interaction between vegetation encroachment and thermal region (Table 5.1). Models 1 and 2 have delta<2 values and thus were selected as the best options out of all possible combinations. Vegetation encroachment had a significant relationship in all candidate models ($P<0.05$), with greater encroachment (more negative values) being related to more negative TAOc slopes (Table 5.2). In the first two selected models, it had a very severe effect ($P<0.01$). The Shannon index was also significant in all the models in which it was included, with a higher index being related to more positive TAOc slopes (i.e. a lesser response of the butterfly community to become dominated by species preferring closed habitats). Thermal region also had a significant response, with region 4 (the hottest) being associated with more negative trends. On the other hand, the initial TAOc number and the length of the monitoring series were not significant in the models in which they appeared.

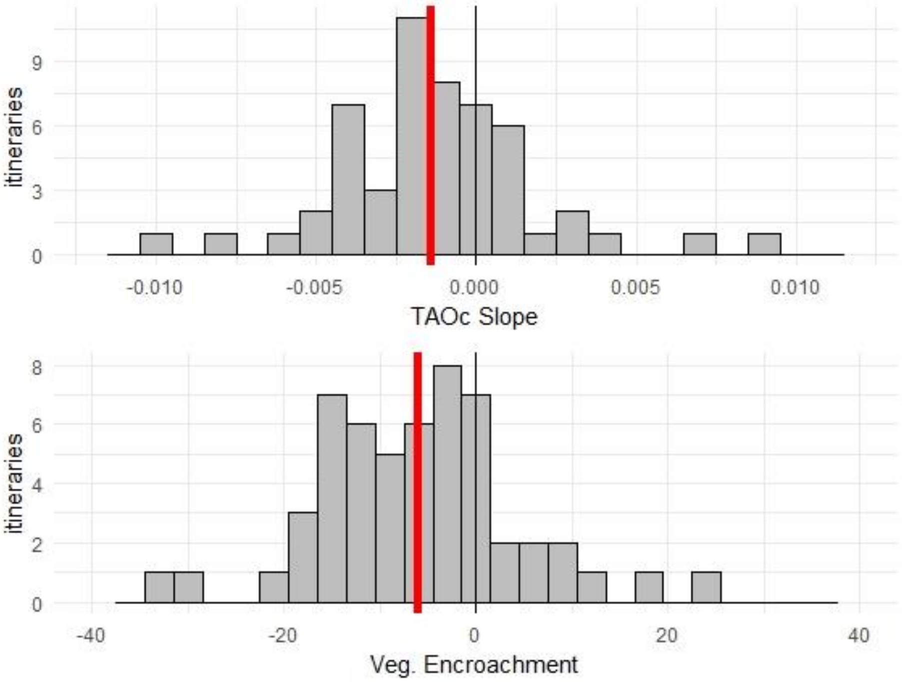

Figure 5.3 Histograms showing TAOc slopes for all the 54 studied butterfly assemblages (a) and vegetation encroachment at the same 54 sites (b). The red bar situates the mean value of both datasets. In all, 72% of the itineraries show a negative TAOc slope indicating change towards butterflies that prefer closed sites, while 76% of the itineraries showed negative values for vegetation encroachment, indicating greater afforestation.

Table 5.1 Model selection table of the best models according to the Akaike Information Criterion. Models 1 and 2 are the best fitted models as delta<2. VegEnc: vegetation encroachment; Shannon: Shannon index of vegetation diversity; ThReg: Thermal Region; TAOinitial: initial TAOc value; Timeseries: series length.

	Main effects	**Interaction**	**df**	**logLik**	**AICc**	**delta**	**weight**
Model1	VegEnc + Shannon + ThReg	-	7	240.323	-464.21	0	0.283
Model2	VegEnc + Shannon + TAOinitial +ThReg	-	8	241.484	-463.76	0.442	0.226
Model3	VegEnc + ThReg	-	6	237.843	-461.89	2.313	0.089
Model4	VegEnc + Shannon + Timeseries + ThReg	-	8	240.37	-461.54	2.669	0.074
Model5	VegEnc + Shannon + TAOinitial + Timeseries + ThReg	-	9	241.536	-460.98	3.231	0.056

Table 5.2 Results for the five best Generalized Linear Models (GLMs) with their estimate values and p-values. VegEnc: vegetation encroachment, Shannon: Shannon index of vegetation diversity; ThReg: Thermal Region; TAOinitial: initial TAOc value; Timeseries: series length.

	MODEL 1		**MODEL 2**		**MODEL 3**		**MODEL 4**		**MODEL 5**	
	Est	Pr(>|t|)	Est	Pr(>|t|)	Est	Pr(>|t|)	Est	Pr(>|t|)	Est	Pr(>|t|)
(Intercept)	-5E-03	0.02*	-9E-03	0.01*	-7E-04	0.46	-5E-03	0.06*	-9E-03	0.02*
VegEnc	1E-04	<0.01**	1E-04	<0.01**	1E-04	0.01*	1E-04	<0.01**	1E-04	<0.01**
Shannon	2E-03	0.03*	2E-03	0.01*			2E-03	0.04*	2E-03	0.02*
TAOinitial			9E-03	0.16					9E-03	0.16
Timeseries							3E-05	0.77	3E-05	0.77
Th Region2	7E-04	0.52	1E-03	0.34	9E-04	0.43	7E-04	0.57	1E-03	0.38
Th Region3	1E-04	0.89	6E-04	0.61	3E-04	0.78	1E-04	0.92	6E-04	0.63
Th Region4	-3E-03	0.01*	-3E-03	0.03*	-3E-03	0.05·	-3E-03	0.02*	-3E-03	0.03*

We observed significant differences between thermal regions (one-way ANOVA P=0.0219) for TAOc slopes, with more negative slopes in warmer regions (Fig. 5.4a). Vegetation encroachment also showed significant differences between regions (one way ANOVA P=0.0309). The pattern was similar to the TAOc, although the highest level of encroachment was not recorded in the warmest region but in thermal region 3 (Fig. 5.4b).

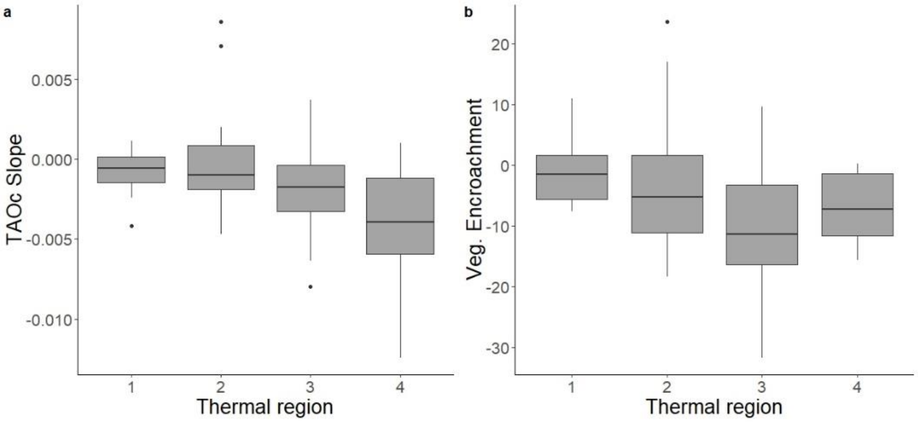

Figure 2.4 Boxplots for TAOc Slopes and Vegetation encroachment by Thermal region. Thermal regions numbering run from the coldest (1) to the warmest (4).

5.4.4 Species loss and population declines

A total of 126 extinction events occurred at 40 of the 54 studied sites; 15 sites had no recorded extinction events during the studied period. Extinction events were recorded in 5% of the populations that were monitored. Twelve extinction events were followed by colonization and so in 114 cases a population of a species was never again recorded at the site in question (4.53% of the studied populations). The mean TAO index value for extinct populations was 0.393±0.153, while the value for the remaining populations was 0.33±0.050 (Fig. 2.5). A paired t-test showed significant differences (t=2.4857, df=39, P=0.017) in the TAO index between species with extinction events and those with no extinction events, indicating that extinctions occurred more frequently in species preferring open habitats.

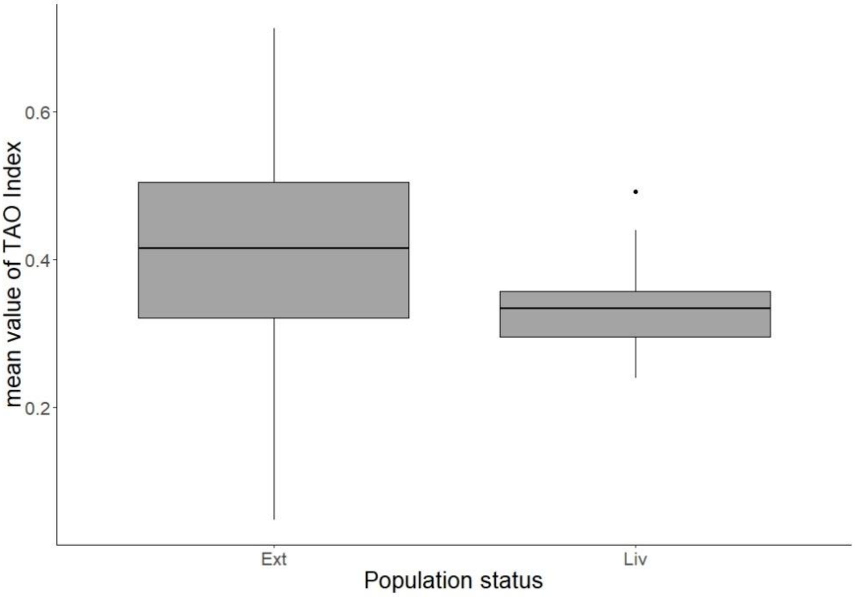

Figure 5.5 Boxplot showing the mean value of the TAO Index for all the extinct (Ext) and not extinct (Liv) species at each of the 54 studied sites.

The GLMM performed for the butterfly trends at itinerary level showed no direct relationship with the values of the TAO index (P=0.964) or vegetation encroachment (P=0.667). Nevertheless, there was a highly significant relationship with the interaction of these variables (estimate=1.37e-03, df=2390, t=4.646, P=3.57e-6). This indicates that species with higher TAOc indices had more negative trends when there was vegetation encroachment, while species with a negative TAO index tended to exhibit the opposite trend (Fig. 5.6). This difference is exemplified by two species with very different preferences for open or closed habitats, speckled wood (*Pararge aegeria*, I_{TAO}= -0.419, slope=-72.74, P=0.198) and mallow skipper (*Carcharodus alceae,* I_{TAO}=0.626, slope=114.12, P=0.009) (Fig. 2.6).

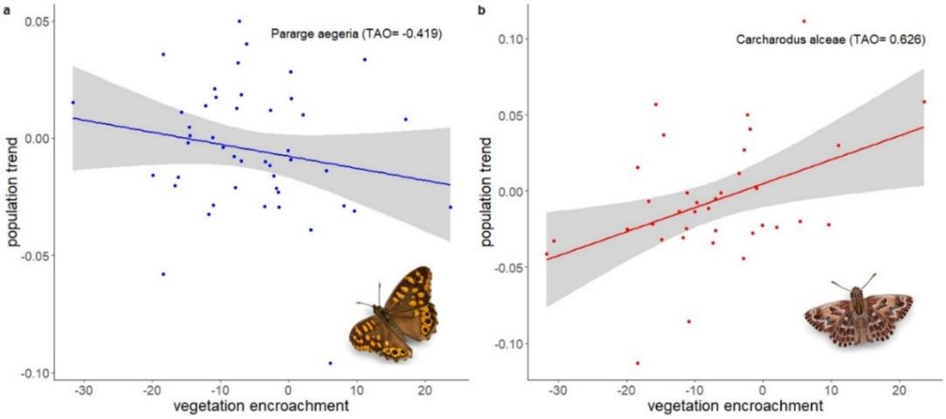

Figure 5.6 Population trends according to vegetation encroachment at site level of two species with very different TAO index values. Populations of speckled wood (*Pararge aegeria*, TAO= -0.419) tended to decline wherever the habitat became open (nº. sites = 46, R^2= 0.03, P= 0.198). Populations of mallow skipper (*Carcharodus alceae*, TAO= 0.626) declined strongly when there was habitat encroachment (nº. sites = 36, R^2=17.97, P= 0.009).

5.5 Discussion

5.5.1 Species preference for open/closed sites

In this work we used a large Mediterranean butterfly dataset to derive an index of preference for open/closed habitats for 147 species. We adapted the index from the original formula developed by Suggitt et al. (2012) to evaluate butterfly responses to year-to-year microclimatic variation in relation to habitat use. Our results show the strong preference of Catalan butterfly species for open habitats, with only a few species exclusively associated with forest habitats. Although this preference is widely recognised in temperate Europe (e.g. van Swaay et al., 2006), to our knowledge this is the first time that a precise measure based on population densities across plant communities has been provided for what is one of the continent's richest butterfly fauna.

Interestingly, we found consistent preferences in butterfly species across thermal regions, which in our study area range widely from very hot Mediterranean conditions in lowland south-western sites to cold climates in the high Pyrenean mountains. Thus, although butterfly species may compensate for differences in environmental temperature by shifting to more open or closed habitats with, respectively, warmer or cooler microclimates, as noted by Suggitt et al. (2012), thermal habitat sensitivity is in fact small. This means that species preferences remain fairly stable and that our general index values are applicable under different environmental conditions. Likewise, although values will vary with additional population data, changes will be small as current values are based on 25 years of data from more than 150 monitoring sites, which make them sufficiently robust to be used to explore changes in butterfly communities without the need for regular updates.

The highly skewed preference of the butterfly fauna towards open habitats indicates that this group of insects will respond very strongly to vegetation encroachment. Here, by analysing long-term data on the structure of over 50 butterfly communities, we tested this possibility in the north-west Mediterranean basin, a region where the increase in forest cover is one of the major changes that has taken place in the landscape in recent decades (Debussche et al., 1999; Blondel et al., 2010; Feranec et al., 2010; Gerard et al., 2010; Marull et al., 2015).

5.5.2 Habitat changes and trends in butterfly assemblages

More than 70% of our studied sites have experienced vegetation encroachment in the past two decades, which wholly confirms the importance of this phenomenon as part of landscape change in our region. Indeed, this was matched by a shift in 76% of the analysed butterfly communities towards domination over time by species preferring more closed habitats, as revealed by the community index (TAOc). Furthermore, the GLM models confirm that vegetation encroachment acted as the major factor in changes in the structure of butterfly communities.

It may be argued that the changes we recorded are not representative of major changes occurring at landscape level, as we only measured plant and butterfly communities along the transect routes (e.g. in a five-metre-wide band). However, in the last two decades, an increase in forest cover of 4% has also been recorded in buffer areas of 1 km surrounding a large number of our monitoring sites (Herrando et al., 2015), indicating that this phenomenon is very widespread and may be a primary driver of changes in biodiversity in our region. Our results thus complement those of Herrando et al. (2015), who found that an increase in forest cover was having an impact on both butterfly and bird populations, as revealed by a multi-species indicator based on monitoring data.

Changes in communities being dominated by closed-habitat-loving species were more marked in sites with less vegetation diversity (according to the Shannon diversity index). This may be because heterogeneous landscapes promote population stability offering greater ranges of resources and microclimates (Oliver et al., 2010). To a lesser extent, changes in the composition of butterfly communities were also affected by the thermal region, with the strongest changes occurring in the hottest regions (Fig. 5.4). This probably reflects the more severe encroachment processes occurring in Mediterranean habitats, which are linked, above all, to socioeconomic factors affecting agricultural abandonment that modify natural and cultural landscapes (Vidal-Macua et al., 2018). However, butterfly responses were qualitatively similar between regions, as shown by the non-significant interaction between thermal region and vegetation encroachment.

Contrary to our expectations, we found no relationship between the length of the time-series at each monitored site and the degree of butterfly community change. This result indicates that the response to encroachment is not time-dependent, probably because change in the community structure is very rapid once vegetation encroachment has begun (see also Stefanescu et al., 2009). Similarly, dung beetles have been shown to respond more quickly than vegetation to pastoral practices (Tocco et al., 2013). This important finding indicates that the main reason for such rapid responses are insects' short generation time coupled with their precise habitat requirements, which accords them great value as indicators of environmental change (e.g. Thomas et al., 2004; Krauss et al., 2010). We also found no relationship between the slope and the initial TAOc value, which highlights the role of vegetation encroachment as one of the ecological drivers that affects butterfly populations regardless of the initial composition of the community.

5.5.3 Species loss and population declines

A remarkable but worrying result was revealed by the analysis of extinction events. The finding that 4.53% of our monitored butterfly populations are already extinct is highly alarming. Extinct populations belonged to species with higher TAO values, which shows the threat that vegetation encroachment represents for open habitat species. Habitat loss is the major cause of species extinctions (Tilman et al., 1994) and it has been shown that the extinction risk in Mediterranean butterflies strongly decreases with suitable habitat availability (Fernández-Chacón et al., 2014). To date, butterfly population declines have been assessed using climatic and ecological factors; however, more work is needed to understand the mechanisms whereby declines are leading to extinction events at local and regional scales. In our region, lowland populations of some species have been shown to be more vulnerable towards extreme climatic events (i.e. summer drought) (Carnicer et al., 2019). We also found that vegetation encroachment was more important in warmer areas and so affects butterfly assemblages in typical Mediterranean habitats more severely. Therefore both climatic and landscape changes interact to ensure that butterfly species from Mediterranean habitats exhibit more negative trends (Herrando et al., 2019). All in all, our results indicate that most species in our region cannot cope with global change, which leads to mismatches affecting the overall butterfly assemblage (e.g. Devictor et al., 2012).

We believe that the TAO index and our community approach provide a very useful tool for local managers aiming to promote biodiversity conservation, even more so considering the indicator role of butterflies in insect communities (Thomas et al., 2004). Insect conservation is known to be important for saving endangered species and guaranteeing ecosystem processes at different scales (Kim, 1993), and the protection of open landscape diversity has often been described as an important aim (Lindborg et al., 2008). Reintroduction of traditional grazing and farming would help revert this problem (MacDonald et al., 2000; Verdú et al., 2000; WallisDeVries et al., 2007; Stefanescu et al., 2009, 2011; Tomaselli et al., 2013).

6. Chapter 3: Spatial gradients and grazing effects on plants and insect herbivores in Pyrenean subalpine grasslands

Chapter 3. Spatial gradients and grazing effects on plants and insect herbivores in Pyrenean subalpine grasslands

Andreu Ubach, Moisès Guardiola, Xavier Oliver, Mike Lockwood, Jordi Artola and Constantí Stefanescu

6.1 Abstract

Mountains harbour a disproportionate amount of biodiversity that is explained by both biotic and abiotic factors. Understanding the ultimate factors that shape these gradients including the interaction between trophic levels is important to highlight management practices that may help maintain biodiversity. Here we report an experiment carried out in a Pyrenean valley where a transhumant cattle herd grazes every year subalpine grasslands in a 700m altitudinal range (1300 – 2000 m). We measured species richness and abundance of plants and two groups of herbivorous insects (butterflies and grasshoppers) in 20 plots, and then we established 10 exclusion plots to study the effect of grazing. Our results show that there were differences among the relative weight of abiotic and biotic factors that shape biodiversity gradients. Overall, the elevation gradient strongly affected plant, butterfly and grasshopper richness, as well as insect abundances. The main predictor of butterfly richness was plant richness (bottom-up effect), while the slope played a very important role for grasshoppers. Livestock exclusion had a negative effect on plant richness through rapid growth of grass species but there were almost no changes in insect community composition after two years. A sub-set of plots within a narrow altitudinal range showed some differences in the short-term (within the season) for butterflies. In grazed plots, richness and abundance increased over the summer and exceeded those of non-grazed plots, indicating that mid-intensity grazing through traditional transhumance management system can help maintain butterfly biodiversity in subalpine grasslands.

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6.2 Introduction

Mountains are known to harbour biodiversity in a disproportionate way in many regions of the planet (Barrio et al., 2013; Körner et al., 2007) and they often constitute hotspots with high interest for conservation (Körner & Spehn, 2020). In European mountains, the drivers shaping this amount of biodiversity are a combination of abiotic factors (related to sharp gradients in elevation, climate, soil composition, hill shade, slope or orientation) (Ojeda et al., 2000; Moeslund et al., 2013) and biotic factors (species interactions, including anthropic activities like extensive livestock grazing and agricultural practices) (Payne et al., 2017). Understanding how these drivers interact is therefore crucial to establish beneficial management practices for the conservation of biodiversity. Amongst the abiotic drivers, the elevation gradient and underlying factors have been shown to associate with various biodiversity patterns (Rahbeck 1995; Körner, 2004; McCain & Grytnes, 2010). All these gradients create microhabitats resulting in differences of species richness at small spatial scales (Kleckova et al., 2014).

Biotic factors include bottom-up and top-down effects between functional groups as well as anthropic activities, and may explain even a larger proportion of species composition variance than abiotic factors (Rudmann-Maurer et al., 2008; Koch et al., 2015). Livestock grazing, in particular, has shaped temperate grasslands in mountain regions, with both positive and negative effects on wildlife depending on management and site factors, and with contrasting effects depending on the trophic level and the studied group (Filazzola et al., 2020). A recent review showed that grazing causes similar abundance and diversity responses on plant communities and insects depending directly on plants, such as pollinators and folivorous insects (Filazzola et al., 2020).

Human activity has reduced plant biodiversity in lowlands due to anthropic disturbance of natural habitats (Nogués-Bravo et al., 2008), and grazing can modify vegetation dramatically by altering its spatial heterogeneity and influencing ecosystem processes and biodiversity (Bullock et al., 2001, Collins et al., 2002). In mountain productive habitats, livestock may have a general positive effect on local plant species richness, but this depends on the species pool and the heterogeneity and the spatial configuration of sites (Austrheim & Eriksson, 2001). On the other hand, the lack of herbivory provokes vegetation encroachment at the expense of pastures and, ultimately, an increase in the forest cover and a general loss of plant diversity (Krauss et al., 2010).

The effects of biotic and abiotic factors on plants can propagate through the food webs and impact strongly on other levels such as herbivorous insects, such as butterflies or grasshoppers. Butterflies establish narrow relationships with specific plants which they use during the larval feeding phase and respond to differences in pastoral management practices (Pöyry et al., 2005; Bussan, 2022). In addition, specialist species are being negatively affected by rural abandonment in many mountain regions (Krauss et al. 2010; Stefanescu et al., 2011; Zografou et al., 2014; Mora et al., 2022). Grasshoppers represent a characteristic group of herbivorous insects in mountains, and have been used as an ideal subject for analysing demographic responses to pasture management given their importance in grassland ecosystems (Samways, 2005; Fartmann et al., 2012), though small-scale habitat heterogeneity has also been identified as one of the main drivers of this taxon richness in subalpine pastures (Löffler & Fartmann, 2017). Recently, Fumy et al. (2020) showed that low-intensity pastures affected by abandonment provokes the homogenization of species assemblages. Generally, all these various processes have led to a unimodal distribution pattern of plant biodiversity in elevation in European mountains (Bruun et al. 2006; Fontana et al. 2020; Ninot & Ferré, 2008). Many studies also reported butterfly richness following an unimodal pattern similar to that for plants, with higher richness at medium altitudes (Stefanescu et al., 2011, Gutiérrez et al., 1995; Fontana et al., 2020) as well as for grasshoppers (Sirin et al., 2010; Azil & Benzehra, 2020).

In this work, we aimed to understand which are the biodiversity drivers of plants, butterflies and grasshoppers in subalpine grasslands of a Pyrenean valley chosen as a case study. Although these three taxa have been studied in the Pyrenees for a long time, no work has simultaneously assessed how their assemblages covary in this mountain range. Thus, our first objective was to compare the relative importance of abiotic and biotic factors influencing species richness and abundance of plants, butterflies and grasshoppers. We hypothesize that elevation plays a major role in understanding spatial dynamics of communities in all three taxa. Given the well-established unimodal pattern of species richness in mountains, we expected to find lower species richness and abundance at the higher sites. We also hypothesize a bottom-up effect, so hence the patterns in plant communities should influence the patterns recorded in the two studied insect groups. Though commonly managed with cattle during the summer season, subalpine Pyrenean grasslands are experiencing a rapid process of vegetation encroachment in many areas, mainly as a result of abandonment of traditional practices (Améztegui et al., 2010, Muñoz-Ulecia et al., 2021) while certain areas may present high livestock concentrations and become overgrazed (Komac et al., 2014). To better assess the impact of this process on our studied taxa, we also designed a grazing exclusion experiment. Our second objective was therefore to understand how the management of livestock affects biodiversity both in the medium-term (over two years) and in the short-term (within the year). We expect medium-term effects to be detected at the end of our 2-yr study in grazing exclusion plots, with changes in the proportion or composition of plant communities that will in turn affect butterfly and grasshopper communities. Moreover, we hypothesize that short-term grazing effects on butterflies are also likely to be detected within the sample season, as grazing could reduce nectar and host plant resources and cause a temporal decrease in butterfly populations.

6.3 Materials and methods

6.3.1 Study site, cattle management and exclusion treatment

The study site, ‘Catllar Valley’, is located within the Capçaleres del riu Ter i Freser Natural Park (Natura 2000 network), in the East Pyrenees of Catalonia (NE Iberian Peninsula). The valley has an extension of 1,100 ha and is located between 1,200 and 2,680 m.a.s.l. Mean annual precipitation was 1,123 mm and average temperature was 9.9 ºC during our study period (data taken from a local meteorological station located at 1,450 m inside the study area). The vegetation of the valley consists mainly of subalpine and alpine grasslands, shrublands and deciduous and coniferous woodland. The main management is transhumance grazing by a herd of approximately 220 cows. Every year, the herd arrives in the valley in early June, coming from lowland areas where cows spend most of the winter. Cows concentrate in subalpine grasslands (at elevations between 1,300-1,800 m) for about one month, and then move to alpine grasslands at the highest elevations (between 1,900-2,600 m) during the summer peak. In September, they return to subalpine grasslands and stay until the end of November or beginning of December, and then they leave again to lowlands with the first snowfalls.

We selected a set of 20 sites in the subalpine area dominated by mesophilic siliceous grasslands of the habitat montane and subalpine belts of the Pyrenees, dominated by *Agrostis* spp. and *Festuca* spp., corresponding to the habitat CORINE 35.122+ (Carreras et al., 2016), and at each one, established a square plot measuring 60x60 m (0,36 ha). Sampling plots were distributed along the valley, ranging from 1,330-2,030 m.a.s.l., and included differences on the slope, aspect and hill shade (Fig. 3.1). After a first base-line sampling in 2018, half of the plots were enclosed with electric wires the following years to exclude cattle grazing. Sampling was repeated in 2019 and 2020. The exclusion treatment was assembled every year before the arrival of the herd in spring, and disassembled in late autumn to avoid damage during the winter season in snowy conditions. During the first year, we accounted for grazing intensity by counting cow dungs inside the selected plots area. We distinguished between fresh dungs (i.e. from the current season) and dry dungs (from the previous year).

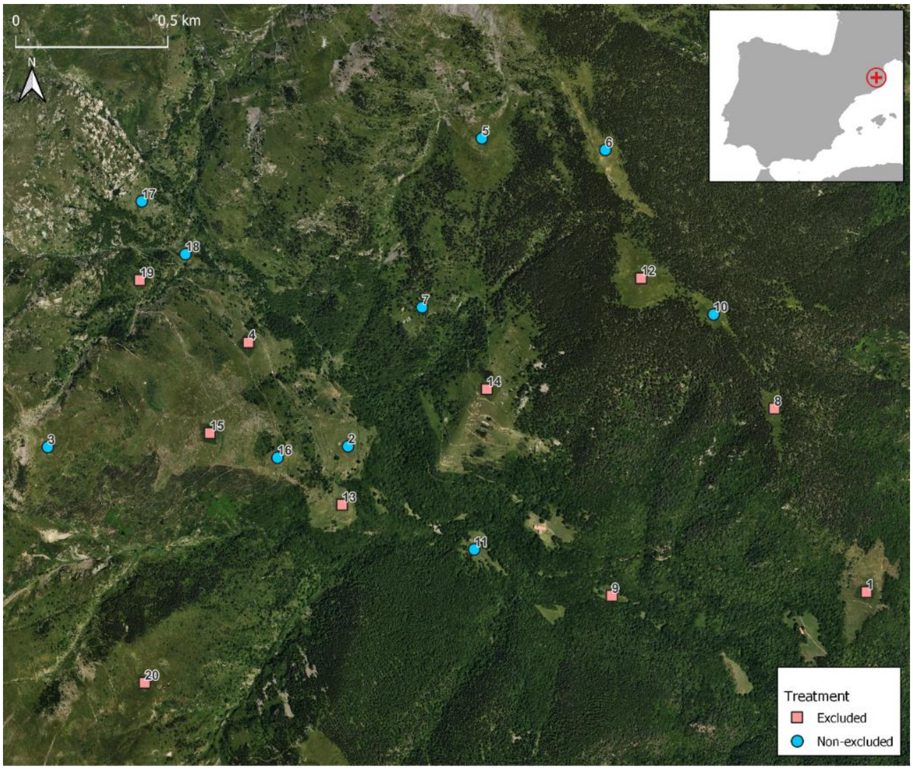

Figure 6.1. Map of the study area. Pink squares correspond to plots with the exclusion treatment and blue dots correspond to non-excluded plots.

6.3.2 Biodiversity measures

We sampled two trophic levels inside the selected plots: plants and two types of herbivorous insects, butterflies and grasshoppers. Butterflies are generally highly mobile insects and have evolved narrow relationships with some plant species which they use during the larval feeding phase. In contrast, many grasshoppers are generalist grass feeders and have less mobility. For plants, we established a 500-m transect in length and 50-m of width (25 m at both sides of the recording line), zigzagging inside the square plot. All vascular plant species were recorded during the flowering peak in mid-July. For butterflies we followed the original protocol of the Butterfly Monitoring Scheme (BMS) in the UK (Pollard & Yates, 1994), consisting in this case of fixed 500-m transect routes zigzagging inside the plots, similarly to those for plants. When suitable weather conditions occurred for butterfly activity, observers counted all individual butterflies detected along a fixed transect route within a 2,5 m distance on either side of the line transect and 5 m above and ahead of the observer. Plots were sampled three times each year to cover the phenology of the bulk of the butterfly species occurring in this mountain area (late May, early July and early August). For each species, an annual index of abundance was calculated as the sum of individuals recorded in the three annual counts. Grasshopper transects were standardized to a length of 160 m, and included two ‘V’ shaped walks inside the square plots. Transects were repeated two times each year, one in late August and the other in late September - early October. Grasshopper adults were detected visually within a 2 m distance on either side of the transect line. Grasshopper abundance was then referred to a density value (individuals/ha).

6.3.3 Factors determining patterns of species richness and abundance

We modelled biodiversity according to abiotic and biotic factors in the studied valley, building separate models for richness (plants, butterflies and grasshoppers) and abundance (butterflies and grasshoppers), as response variables. We built separate models for 2018 (before the exclusion treatment, BT) and 2019-2020 (after the exclusion treatment, AT), including ‘year’ as a fixed factor for this second subset of analyses. Abiotic factors included in the models were: elevation, slope, hill shade and aspect of each plot. Elevation was obtained from the topographic database at 1:5.000 scale of the Cartographical and Geological Catalan Institute (www.icgc.cat). Slope, hill shade and aspect were derived from the topographic database using QGIS 3.24 (QGIS.org, 2022). We also included three biotic factors. Firstly, the effect of grazing, which was measured in 2018 as the number of fresh dungs in the plot, and which was categorized as present or absent (i.e. fixed factor) according to the grazing exclusion treatments in 2019-2020. Secondly, the degree of shrub cover in a buffer area around each plot, using a percentage value of forest and scrubland and counting a 50-m radius from the centre of the plot. This percentage values were calculated from the Map of vegetation cover of Catalunya (Ibáñez & Burriel, 2010). The degree of habitat encroachment indicates a degree of patch isolation. Finally, we included plant richness to account for a bottom-up effect in the models of the two groups of herbivorous insects. Prior to the models, we built a Pearson correlation matrix for all the variables but none was excluded as all correlation values were < 0.7. All analyses were performed with R-4.1.0 (R Core Team, 2022).

Butterfly and plant richness, and butterfly abundance were modelled with GLMs with a Poisson distribution using the *lme4* package (Bates, 2011). Year was used as a fixed factor in the model of 2019 and 2020. Grasshopper richness and abundance were modelled with GLMs with a Gaussian distribution. All the predictor variables were rescaled prior to any analyses. We used a model selection approach with the *dredge* function of the *MuMin* package 1.43.17 (Bartón, 2015), in order to select the set of best models (i.e. those with ΔAICc<2). In the butterfly abundance models, we excluded the migratory butterfly *Vanessa cardui* from the analyses, as its abundance in a given season does not depend on the local management but on the build-up of source populations in N Africa (Hu et al., 2021). This species was extremely abundant in 2019, which greatly biased the composition of the butterfly communities in the studied plots that year.

6.3.4 Mid-term and short-term effects of grazing on butterflies

To investigate medium-term effects of grazing, we used a subset of 10 plots (5 per each exclusion treatment, excluded/non-excluded) distributed between 1,500 and 1,750 m. This selection was made to reduce environmental variability (e.g. altitude), which can obscure community responses to grazing. Here we have focused only on butterflies, as they are the only group for which we could measure intra- and inter-annual values of richness and abundance. We studied the changes between 2018 and 2020 with a two-way repeated measures ANOVA in order to determine the effects of the exclusion treatment and year on butterfly richness and abundance. We performed a Bonferroni correction for pairwise comparisons in cases where there were significant differences between years. To understand the short-term effects of management we compared the richness and abundance of butterfly populations in each selected plot in early July (i.e. when they were grazed by cattle) and in early August (i.e. three weeks after grazing had stopped, following movement of the herd to the highest altitudes in the valley) in the two years of the exclusion treatment (2019-2020). We tested whether butterfly richness and abundance were affected by the exclusion treatment (excluded or non-excluded) and time (July vs. August). We performed the analyses separately for 2019 and 2020.

6.4 Results

6.4.1 Patterns of species richness and abundance

During the three years of study, 396 vascular plants, 82 butterfly species and 36 grasshopper species were recorded in the 20 selected plots (see Suppl. Table 6.1, 6.2 & 6.3 for a complete list of the species). Plants had the highest accumulated and annual species richness, with means of 128.6 plant species/plot and 106.8 species/plot, respectively (Table 6.1). Butterflies and grasshoppers showed a much lower accumulated and annual richness per plot (36.5 and 20.9 species for butterflies, 16.5 and 10 species for grasshoppers, respectively). There was considerable variation in richness values among plots, especially for butterflies. Thus, butterfly annual richness was up to 11 times higher in the richest than in the poorest plot. Variation among individual plots was far lower for grasshoppers (about three times) and plants (about two times) (Table 6.1). There were also huge differences in abundance values, and in some plots we recorded about an order of magnitude more butterflies and grasshoppers than in others (Table 6.1). Fourteen plants appeared in all studied plots (*Achillea millefolium, Agrostis capillaris, Anthoxanthum odoratum, Cerastium fontanum, Dactylis glomerata, Festuca ovina, Galium verum, Lotus corniculatus, Plantago lanceolata, Poa supina, Ranunculus bulbosus, Trifolium pratense, Trifolium repens* and *Veronica arvensis*), but only twelve were very abundant in some plots (*Agrostis capillaris, Dactylis glomerata, Achillea millefolium, Plantago lanceolata, Holcus lanatus, Festuca nigrescens, Deschampsia flexuosa, Plantago media, Poa supina, Taraxacum dissectum, Trifolium pratense* and *Trisetum flavescens*). The most abundant butterfly species was *Melitaea parthenoides*, with 778 individuals counted in the three years, while single individuals were recorded in six species (*Carcharodus alceae, Pyronia tithonus, Apatura ilia, Euphydryas aurinia, Nymphalis polychloros* and *Satyrium w-album*). For grasshoppers, the most abundant species was *Chorthippus apricarius,* with 6983 individuals recorded, while singletons were detected in three species (*Chortippus montanus, Tetrix nutans* and *Tetrix undulata*).

Table 6.1. Mean richness and abundance values for each group studied, with the minimum and maximum values in parenthesis. Accumulated values correspond to all species found in each plot over the three-year study period, while annual values correspond to the average values per plot and year.

	Richness		**Abundance**
	Accumulated	Annual	Annual
Plants	128.6 (83-179)	106.8 (65-159)	
Butterflies	36.5 (19-50)	20.95 (3-35)	66.7 (3-239)
Grasshoppers	16.5 (6-24)	10 (5-15)	7320/ha (800-26604)

Our models identified various significant predictors that explain species richness and abundance (Table 6.2, Fig. 6.2). Among the abiotic predictors, elevation had a ubiquitous effect on species richness, with high altitudes having a lower richness for butterfly, plant and grasshoppers both before (BT, models for year 2018) and after the grazing exclusion treatment (AT, models for years 2019-2020). The slope played a significant role on plant and grasshopper richness, both BT and AT, with higher values at the steepest grasslands. Aspect played a significant role on plant richness BT and AT, with a higher richness in plots facing east and southeast, with an opposite effect for butterfly richness BT. Hill shade influenced butterfly richness only in the years AT, with higher values in sunnier plots. Accounting for biological factors, there was a positive effect of pasture intensity (i.e. more fresh dungs) on butterfly richness only in the years BT. The exclusion treatment only played a significant role on plant richness, which was higher in non-excluded (i.e. grazed) plots. There was a positive significant relationship between plant and butterfly richness BT and AT, meaning a bottom-up effect from plants to butterflies. This effect, on the other hand, did not exist for grasshoppers. Finally, we found a positive effect of the shrub cover percentage on butterfly richness in the AT years.

For abundance models, elevation was a significant driver for butterflies during the whole study (BT and AT), and for grasshoppers in the BT, with abundance decreasing at higher altitudes. Slope also had a regular negative effect on butterfly abundance, while aspect had a positive effect BT but a negative effect AT, also found in grasshoppers. Hill shade also played an important role on butterfly abundance in BT and AT, with lesser counts in shadier plots. The studied year was significant in AT models, as butterflies and grasshoppers were more abundant in 2019 than in 2020. Accounting for biological factors, shrub cover had a positive effect on butterfly abundance in the AT years, but a consistent negative effect for grasshoppers all through the study. Pasture intensity (measured as fresh dungs) favoured more abundant butterfly and grasshopper populations BT. Similar to butterfly richness, we also found a positive bottom-up effect of plant richness on butterfly abundance, but only BT, and no plant effect was found for grasshoppers. Overall, the elevation gradient strongly affected plant, butterfly and grasshopper richness, as well as butterfly and grasshopper abundances. Butterfly richness was mainly predicted by the elevation and plant richness, and for grasshoppers the slope played a very important part.

Table 6.2. Results for the models used to study the abiotic and biotic factors affecting plant, butterfly and grasshopper richness and abundance. Ex. Treatment: exclusion treatment. Pr(>|z|): P-value of the analysis. P: Plants, B: Butterflies, G: Grasshoppers.

		Before treatment (BT)			**After treatment (AT)**		
			Estimate	Pr(>|z|)		Estimate	Pr(>|z|)
Richness	P	Elevation	-0.091	**<0.001**	Elevation	-0.093	**<0.001**
		Slope	0.065	**0.020**	Slope	0.070	**<0.001**
		Aspect	-0.054	**0.036**	Aspect	-0.059	**<0.002**
		% shrub cover	0.060	**0.019**	% shrub cover	0.024	0.226
					Ex. Treatment - NE	0.104	**<0.002**
	B	Elevation	-0.261	**<0.001**	Elevation	-0.118	**<0.008**
		Aspect	0.210	**<0.001**	Hill shade	-0.161	**<0.001**
		Fresh dung count	0.167	**0.002**	% shrub cover	0.147	**<0.001**
					Slope	-0.040	0.393
		Plant richness	0.179	**0.005**	Plant richness	0.198	**<0.001**
	G	Elevation	-0.915	**0.044**	Elevation	-1.039	**0.047**
		Slope	1.214	**0.012**	Slope	1.103	**0.040**
					Hill shade	-0.851	0.072
					% shrub cover	-0.583	0.227
Abundance	B	Elevation	-0.419	**<0.001**	Elevation	-0.309	**<0.001**
		Slope	-0.178	**<0.001**	Slope	-0.060	**0.023**
		Aspect	0.208	**<0.001**	Aspect	-0.120	**<0.001**
		Hill shade	-0.194	**<0.001**	Hill shade	-0.320	**<0.001**
		Fresh dung count	0.333	**<0.001**	% shrub cover	0.239	**<0.001**
		Plant richness	0.365	**<0.001**	Year -2020	**-0.156**	**<0.001**
	G	Elevation	-3146.211	**<0.001**	Elevation	740.715	0.384
					Slope	1101.401	0.174
		Aspect	-872.761	0.152	Aspect	-1659.010	**0.042**
					Year - 2020	-3715.178	**0.002**
		Fresh dung count	1303.268	**0.025**	% shrub cover	-2683.480	**0.002**
		% shrub cover	-1419.116	**0.017**	Plant richness	1556.442	0.117

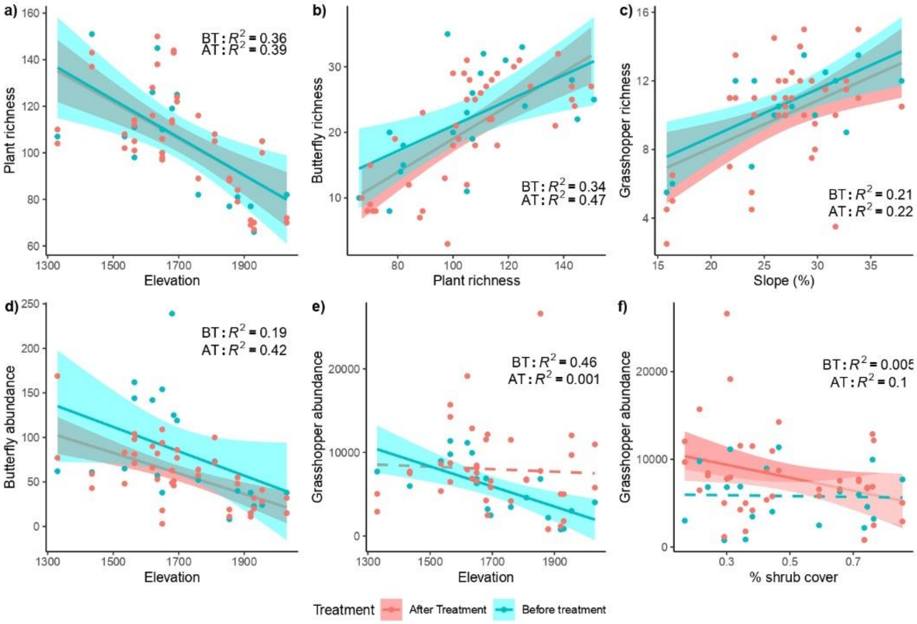

Figure 6.2. Main relationships observed in the models from Table 2. Panels a-c show the main predictor for richness of each taxa with a relationship between plants and elevation (a), butterflies and plant richness (b), and grasshoppers with the slope (c). Panels d-f show the most consistent predictors for insect abundances: elevation for butterflies (d) and grasshoppers BT (e), and shrub cover for grasshoppers AT (f).

6.4.2 Mid-term and short-term treatment effects on butterflies

A mid-term (2 year) grazing exclusion effect was found in butterflies, as butterfly communities decreased in richness in the exclusion treatment, after controlling for the elevation gradient (i.e. focusing on the subset of 10 plots; Fig. 6.3a, Suppl. Table 6.4). Butterfly abundance was not explained by treatment, but showed a decrease over years (Fig. 6.3b).

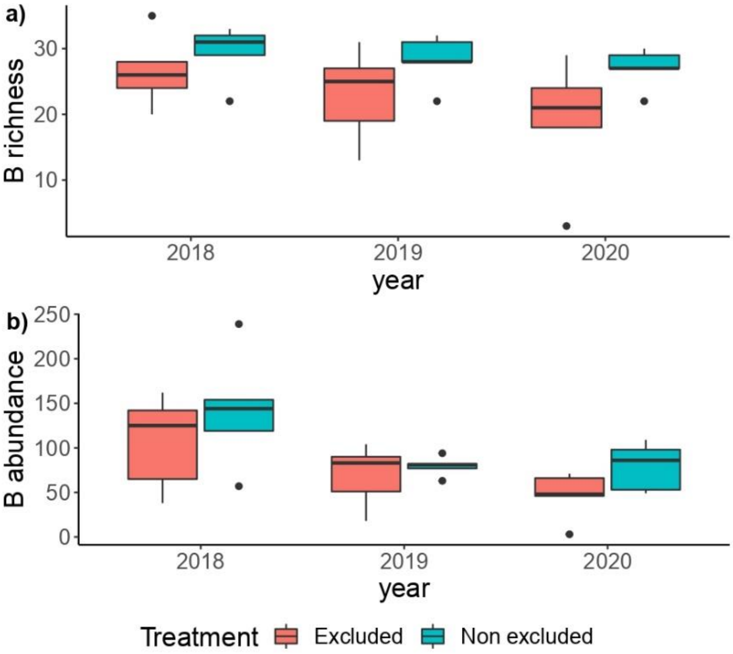

Figure 6.3 Boxplots showing mid-term significant relationships between butterfly (B) richness and abundance, and grazing exclusion treatment/years. Results are based on a selection of 10 plots located at a narrow altitudinal range, to control for the effect of altitudinal gradient on species richness and abundance.

A short-term (intra-annual) grazing exclusion treatment effect was also found in butterfly communities. Butterfly species richness increased in grazed plots between July and August, but this effect was not recorded in exclusion plots (Fig 6.4, a, b). A similar pattern was found for butterfly abundance, with greater values in August samples in grazed plots, but not in exclusion plots. These within-season different responses are seen in Fig. 6.4 as a weak interaction effect between month and treatment, resulting in only grazed plots having increasing values in late summer samples (Suppl. Table 6.6 & 6.7).

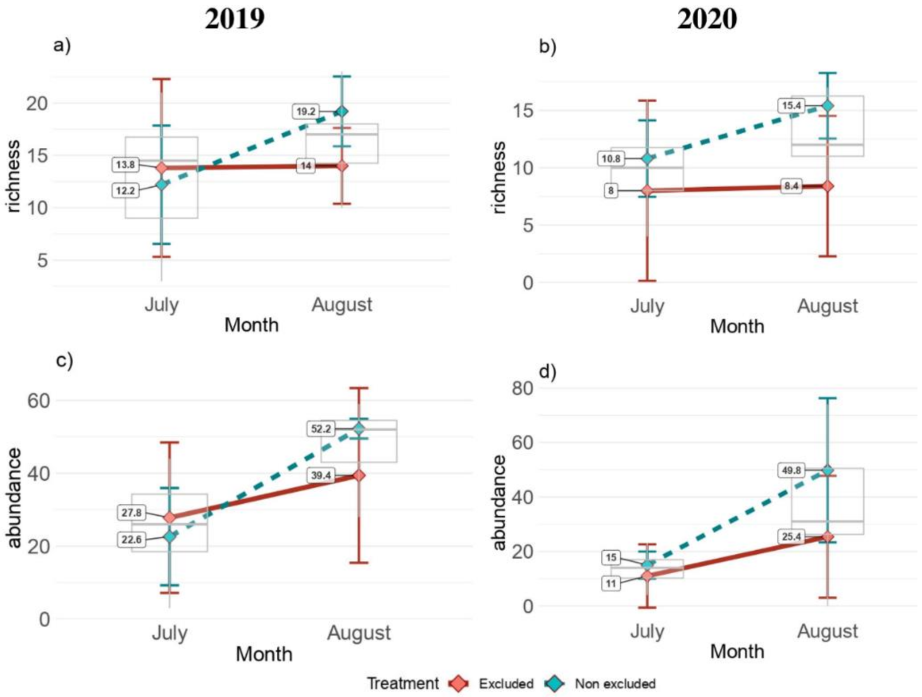

Figure 6.4. Interaction plots for butterfly richness (a, b) and abundance (c, d) for July and August samplings during 2019 (a, c) and 2020 (b, d), with red lines for exclusion plots and blue for grazed plots. Labelled numbers represent the mean value of each boxplot.

6.5 Discussion

6.5.1 Abiotic and biotic factors shaping species richness and abundance in a Pyrenean valley

Mountain biodiversity of plants and herbivorous insects in El Catllar valley is shaped by both abiotic and biotic factors, but their relative importance differed between our studied taxa. As a common response for all three groups we found the ubiquitous effect of the elevation gradient, both BT and AT, with species richness decreasing with altitude, supporting our first hypothesis. This agrees well with previous works that placed high altitudes in mountains with less richness in plants (Körner & Spehn, 2020), butterflies (Gutiérrez, 1997, Popović et al., 2021) and grasshoppers (Pitteloud et al., 2020, Fontana et al., 2020). When a complete altitudinal gradient, starting at sea level, is considered, a hump-shaped species richness relationship seems the commonest pattern, with highest richness at intermediate elevations. Again, examples include plants (Grau et al., 2012), butterflies (Gutiérrez & Menéndez, 1995; Stefanescu et al., 2011), grasshoppers (Sirin et al., 2010). Previous works within the Pyrenees mountains reveal higher richnesses between 800-1,200 m for plants (Grau et al., 2012) and 500-1,500 m for butterflies (Stefanescu et al., 2011). This altitudinal peak of species richness corresponds approximately to the lowest plots in our study system, which were located at 1,300-1,400 m.a.s.l. Therefore, it is in this broader spatial context that our results should be interpreted, with a linear decrease in species richness with altitude.

Butterfly abundance and richness were also negatively related to hill shade. We believe that shadier plots in this subalpine environment are associated with microclimates that may be too cold for some butterfly species, which generally figure among the insects with higher thermal needs (Heinrich, 2013). Although hill shade did not predict grasshopper abundance and richness, thermic constraints may still affect to some extent the distribution of grasshoppers within the valley, as evidenced by higher abundances at south-facing plots. Grasshoppers were also more diverse in steeper plots, a finding that is probably related to a major heterogeneity of grasslands in thin soils with sparse vegetation, including shrubs in less pastured areas. A subsequent analysis performed with the floristic data from the complete dataset showed a slight relationship between shrub abundance (calculated as the overall abundance of chamaephytes and phanerophytes at each plot) and the slope (P=0.089, Suppl. Fig. 6.1). Woody species are used as shelters by grasshoppers, which accounts for the importance of vegetation structure as a richness determinant in grasshopper communities (Löffler & Fartmann, 2017). Butterflies, on the other hand, are flying insects with higher mobility, and we suggest that other resource-based characteristics, such as nectar availability, are more important for the selection of habitat patches than the habitat structure related to slope.

In addition, we recorded a significant difference in grasshopper abundance between the two AT years, with a peak in 2019. This became a widespread pattern in almost all the plots, and we suggest that is related to a climatic bonanza for this group. Although we did not use climatic data for this analysis, it is well known that annual population growth for grasshoppers is related to variability in precipitation during the prior year growing season (Jonas et al., 2015).

Several biotic factors were also important in explaining richness and abundance of our studied taxa. Thus, we found strong evidence in favour of a bottom-up process relating butterfly species richness to plant species richness, as seen in other studies (Kruess et al., 2002; Joshi et al., 2008). Plant diversity means higher diversity of butterfly caterpillar host plants, given the high specialization in host plant use that is observed in many species as a result of co-evolutionary processes (Janz et al., 2006). More plant species also means an increase of nectar availability for butterfly adults over the season, thus favouring a greater variety of butterfly species visiting grassland habitats. Actually, the positive relationship between butterfly and plant richness found in our study is similar to that found by Carnicer et al. (2013) for the whole Catalan region, when comparing the diversity of plants and monophagous butterflies along the altitudinal gradient. Importantly, this connection between plants and butterflies has direct implications for conservation and management purposes, with measures enhancing floristic diversity also being beneficial for butterfly diversity (Scohier et al., 2013). Interestingly, this bottom-up explanation did not hold for grasshoppers' richness, which did not show any significant relationship with plants in our study. Most grasshoppers are described as oligophagous or polyphagous feeders (Joern, 1979) and some species are considered plastic grass feeders with no preferences in species diet composition (Franzke et al., 2010). Ibanez et al. (2013) showed in an experiment that grasshopper's niche breadth actually depends on the diversity of available plants and the generalization degree is not an intrinsic property of a given species, so richer grasslands do not necessarily mean more grasshopper species. In summary, our second hypothesis, that bottom-up processes should explain the diversity of herbivorous insects, is only confirmed for butterflies. The differences between the two herbivorous insect taxa seem to be related to their feeding ecology and to varying degrees of feeding specialization.

In addition to bottom-up relationships, we found other biotic factors shaping our studied taxa. For instance, percentage of shrub cover around the plots had positive effects on plant and butterfly communities, but negative effects on grasshopper assemblages. Thus, greater shrub cover around the plot was associated with more plant and butterfly species, and with more abundant butterfly populations. We suggest that this is possibly related to the higher fine-scale habitat heterogeneity (including different microclimates) associated with more diverse shrub-grassland ecotone conditions (Kleckova et al., 2014). On the other hand, we believe that the higher grasshopper abundances found in plots with less shrub cover is caused by the high numbers of a few generalist feeders that prefer extensive grassland (Pomares, 2002; Franzke et al., 2010) and avoid plots close to the forest.

Finally, and quite surprisingly, we only obtained evidence of grazing effects on plant richness, but neither on butterfly or grasshoppers richness and abundance. Thus, the grazing exclusion treatment did not have any significant effects on insect populations but resulted in higher plant richness in grazed vs non-grazed plots. We interpret these results in the framework of the competitive exclusion theory (Grime, 1973), which predicts a decline in plant diversity once dominant grasses (e.g. *Agrostis capillaris, Anthoxanthum odoratum, Dactylis glomerata, Festuca nigrescens, Festuca ovina, Phleum pratense, Poa supina, Trisetum flavescens*, etc., in our study system) take over excluded plots during the first years and outcompete forbs and other plants (see also Milligan et al., 2016). Large herbivores reduce the abundance of dominant or taller plant species in grasslands, thus increasing resource availability (e.g. light, nutrients, water) that favours the presence and abundance of rare species (Koerner et al., 2018). Moreover, Price et al. (2022) have recently demonstrated that herbivore exclusion in sites with a long history of grazing, such as Pyrenean grasslands, reduces plant richness. Large herbivore exclusion may result in highly variable outcomes during the first years of an exclusion treatment, with clear effects on plants but more complex relationships in herbivorous insects.

6.5.2 Mid-term and short-term treatment effects on butterflies

Butterflies experienced minor changes in our study in relation to the grazing treatment in the mid-term analysis, i.e. using the subset of 10 plots in the narrower altitudinal range of 1,500-1,700 m. Our results showed that showed that grazed plots were already slightly richer than non-grazed plots in 2018 (that is, in the year previous to the exclusion treatment). We would expect the differences to widen over the two years in the AT period whenever grazing actually benefits butterfly communities, but this did not occur. However, this may be explained by a time lag in butterfly responses, as found in other works that do not show significant changes during the first years after a management change (Öckinger et al., 2006).

A quick response was instead found when looking in more detail to the butterfly data within the sample season. In contrast to exclusion plots, which remained stable over the summer, we found some evidence that grazed plots had higher richness and abundance of butterflies during the August samples, indicating that an increase in both variables occurred in just a few weeks. This finding may be related to a change in habitat selection by butterflies due to parallel differences in resource availability in both kinds of plots. Exclusion plots became strongly dominated by grasses over the summer through competitive exclusion (see above), meaning that nectar availability declined in the August samples, making the plots less attractive for butterflies. On the other hand, non-exclusion plots had comparatively less flowers than exclusion plots in early summer due to the grazing impact, but as the herd moved to alpine grasslands in the summer peak grasslands could recover, and became more attractive to butterflies in August. In fact, it has been proposed that allowing flowering in grassland systems is key as a measure for pollinator conservation (Scohier et al., 2013), and in our Pyrenean valley this was achieved in subalpine pastures in summer thanks to the transhumance towards higher grasslands from July to September (see also Baena & Casas, 2010; Garcia-Ruiz et al., 2021). This reconciles the idea that traditional management systems should be optimized to allow flowering and seed set, acting as a sustainable impact through medium-intensity grazing that benefits biodiversity (Kruess et al., 2002).

6.5.3 Present and future of subalpine grasslands biodiversity in the Pyrenees

Our results represent a picture of the present (e.g. a decrease in species richness at increasing altitudes) but could change according to the predictions of climate change scenarios. There is compelling evidence in mountains that changes in community composition are occurring for plants (Gottfried et al., 2012), butterflies (Bonelli et al., 2021) and grasshoppers (Löffler et al., 2019). Climate change is pushing plants and butterfly species uphill (Wilson et al., 2007, Gottfried et al., 2012; Pauli et al., 2012; Rödder et al., 2021) but not all species are able to cope with this change. Plants present a thermophilization process in which the cold-adapted species decline but the warm-adapted species increase (Gottfried et al., 2012). For butterflies, only generalist and mobile species are able to track the velocity of changes (Devictor et al., 2012), and for grasshoppers, with more limited dispersal ability, most species do not change across different grassland types (Löffler et al., 2019). These predicted community changes could lead to changes in species interactions, especially in plant-insect food webs, decoupling climatic favourable ranges for plants and butterflies (Romo et al., 2014) or delayed responses in the structure of trophic networks (Guardiola et al., 2018).

Another important issue is that climate change could also imply management changes in terms of the transhumance schedule. Traditional management with transhumance herds has maintained montane and subalpine grasslands and its biodiversity through millennia (García-Ruiz et al., 2021), but the current climatic situation will require an adaptation to the effects these scenarios will have on grasslands. This will have in turn effects on plant and insect communities, through the possible changes in the grazing schedule. Phenological responses may then be key in terms of adaptation of species lifecycles to climatic conditions with a proper synchronization to find habitat resources (Colom et al., 2022)

Our study shows that extensive grazing is necessary to maintain plant and insect diversity, but also that transhumance schedule is a key factor to prevent overgrazing in subalpine grasslands and the recovery of plants and insect populations. Thus, the expected changes in plant and insect distributions and interactions due to climate change should be considered in future livestock management in order to maintain plant and insect biodiversity in Pyrenean grasslands.

7. Chapter 4: Heterogeneity in demographic responses associated with an altitudinal gradient: the case of butterflies in north-eastern Iberia

Ubach, A., Páramo, F., & Stefanescu, C. (2021). Heterogeneidad en las respuestas demográficas asociadas al gradiente altitudinal: el caso de las mariposas en el noreste ibérico. *Ecosistemas*, *30*(1), 2148-2148. https://doi.org/10.7818/ECOS.2148

Chapter 4: Heterogeneity in demographic responses associated with an altitudinal gradient: the case of butterflies in north-eastern Iberia

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7.1 Abstract

Heterogeneity in demographic responses associated with an altitudinal gradient: the case of butterflies in north-eastern Iberia. The impact of global change on biodiversity often has heterogeneous responses at a spatial scale. Citizen science programs such as the Catalan Butterfly Monitoring Scheme make it possible to study butterfly responses in the long term and over broad spatial scales, which helps understand how they are being affected by drivers of global change. In this work, a novel methodology and CBMS data were used to calculate trends for 100 species from three climatic regions: alpine, mesic Mediterranean and arid Mediterranean. An interregional comparison was made of trends occurring in a number of common species, and of the relationship between these trends and species' ecological characteristics. Changes in communities at a number of long-term monitored sites were also studied in the alpine region using several community indices. The results show that in the three regions the percentage of species in decline exceeds that of species on the increase. Nevertheless, these comparisons were performed using a largely generalist fraction of the fauna and probably underestimate the declines that certain rare species are experiencing. In common species, declines were more severe in the arid Mediterranean region than in the alpine region. In this latter region, no relationship between population trends and the ecological indices of the species were detected. Conversely, significant changes were found in certain community indices at local level, mainly due to the abandonment of grazing and the movement of thermophilic species towards higher altitudes.

Key words: butterflies, climate change, trends, indicators, climate regions.

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Authors' contributions

Andreu Ubach: Conceptualization, Data analysis, Writing. Ferran Páramo: Data analysis. Constantí Stefanescu: Conceptualization, Drafting, Supervision.

7.2 Introduction

There is an ever-increasing body of evidence that exposes the impact global change in all its multiple manifestations is having on biodiversity at a global scale (e.g. Dirzo et al., 2014; Wagner, 2020). However, the magnitude of this impact on natural communities varies considerably at a spatial level. For example, in the Northern Hemisphere, over the past two decades global warming has been comparatively more intense at higher latitudes and this has led to more marked phenological advances in these regions (Post et al., 2018). Climate change influences species' dynamics in different ways depending on whether the populations are at the centre or edge of their ranges. In general, populations located at the edges are more sensitive to climatic variations (Mills et al., 2017) and, relatively, trends tend to be more positive in populations at cold extremes than those at warm extremes, both latitudinally and altitudinally (Hampe and Petit, 2005; Wilson et al., 2005; Franco et al., 2006; Thomas, 2010).

At finer scales, changes in land use – the other major driver of global change – are generally more heterogeneous and generate mosaics in biodiversity responses. For example, problems derived from the destruction and fragmentation of habitats can be alleviated in parts of a territory by establishing appropriate protected areas. It has recently been shown that about 50% of bird species – above all, those with preferences for forest environments – have more positive population trends in and near areas designated as part of the European Natura 2000 network than in neighbouring but more distant unprotected areas (Pellissier et al., 2020). This same work, however, also shows that effects can vary strikingly according to the taxonomic group considered: unlike the case of birds, diurnal butterfly species were found to be very little affected by proximity to protected areas, a result that demonstrates the limitations of the current design of this network for this group of insects.

The ability to detect these heterogeneous responses to global change is often limited by a lack of data for a sufficient number of species at appropriate spatial and temporal scales. However, in recent decades, this problem has gradually been solved by the consolidation of biodiversity monitoring programs based on citizen science, which are now able to gather information on bioindicator groups over large areas (Pocock et al., 2018). Fortunately, in the Iberian area there are a number of well-established biodiversity monitoring programs, including monitoring schemes for birds (Martí and Del Moral, 1997; Herrando et al., 2008) and butterflies (Munguira et al., 2014). For this latter group, in particular, the Catalan Butterfly Monitoring Scheme has been documenting since the mid-1990s changes in butterfly communities in a large number of localities throughout Catalonia, Andorra and the Balearic Islands. These localities are located in very diverse environments subject to different anthropic pressures and contrasting climate regimes, and provide an optimal resource for addressing the heterogeneity of responses in biodiversity to global change at appropriate spatial and temporal scales.

Recently, to facilitate the comparison of butterfly trends at a European level using monitoring data, a methodology has been developed that significantly improves population estimates (Schmucki et al., 2016). The method produces phenological curves of species in regions of homogeneous climate based on the assumption that the populations of a species will have a similar phenology throughout a given climatic region. The standard phenological curve allows data not available from specific localities to be interpolated with much greater accuracy and thus produces much more reliable indices of abundance. Here, we use this methodology to explore the level of coincidence in the population trends of common diurnal butterflies in the northeast of the Iberian Peninsula over the past two-three decades by distinguishing three regions with well-differentiated climates, namely, alpine, mesic Mediterranean and arid Mediterranean regions. Based on recent results that suggest that the butterfly species that have suffered the most serious regressions in the northeast of the peninsula are those found in the most arid environments (Herrando et al., 2019), we hypothesized that, as a whole, the population trends in the alpine region will be more positive than in the two Mediterranean regions.

In a second analysis, we attempted to relate population trends to the ecological characteristics of each species. For this, we used four measures of species' ecological niches, two of which are related to the habitat preferences of adults, and two to the climatic niche of the species. Both types of measures have been identified as predictors of general trends by previous studies (Stefanescu et al., 2011b; Melero et al., 2016; Herrando et al., 2019; Ubach et al., 2020).

In addition to the population trends, long-term monitoring in fixed locations facilitates the exploration of the changes that occur at community level. For this, it is easy to calculate various community indices based on species' niche estimates, weighted according to their abundance, and so study which ecological aspects are most relevant to any recently observed changes (Devictor et al., 2012). In a third and final analysis, we focused on a few butterfly species in upland areas that have been constantly monitored over periods of at least 14 years in order to identify the most important trends taking place in their populations.

7.3 Materials and methods

7.3.1 Butterfly study and sampling area

Data from the Catalan Butterfly Monitoring Scheme (CBMS) monitoring program were used for this work. In this citizen science program, data of the abundance of butterfly populations is obtained through counts carried out along fixed transects. The sampling methodology is common to that of other similar programs in European countries and is based on the methodology originally developed in the United Kingdom (Pollard and Yates, 1994). Adult butterfly counts are carried out along itineraries, generally 1.5–2 km in length, in just a 5 x 5-m strip (2.5 m on both sides and 5 m in front of the counter) while walking at a steady pace. The itinerary is divided into a variable number of sections corresponding to different types of habitats. Ideally, samplings are repeated for 30 weeks, from the first week in March to the last in September, as long as the meteorological conditions are suitable and allow butterflies to fly.

The CBMS began in 1994 and by 2020 data had been obtained for 188 species of butterflies, from 185 itineraries or sampling stations distributed throughout Catalonia, Andorra and the Balearic Islands (Fig. 7.1). The time series vary according to the locality, with 40% of the stations now providing data for 10 years or more. For more information about the CBMS, visit http://www.catalanbms.org

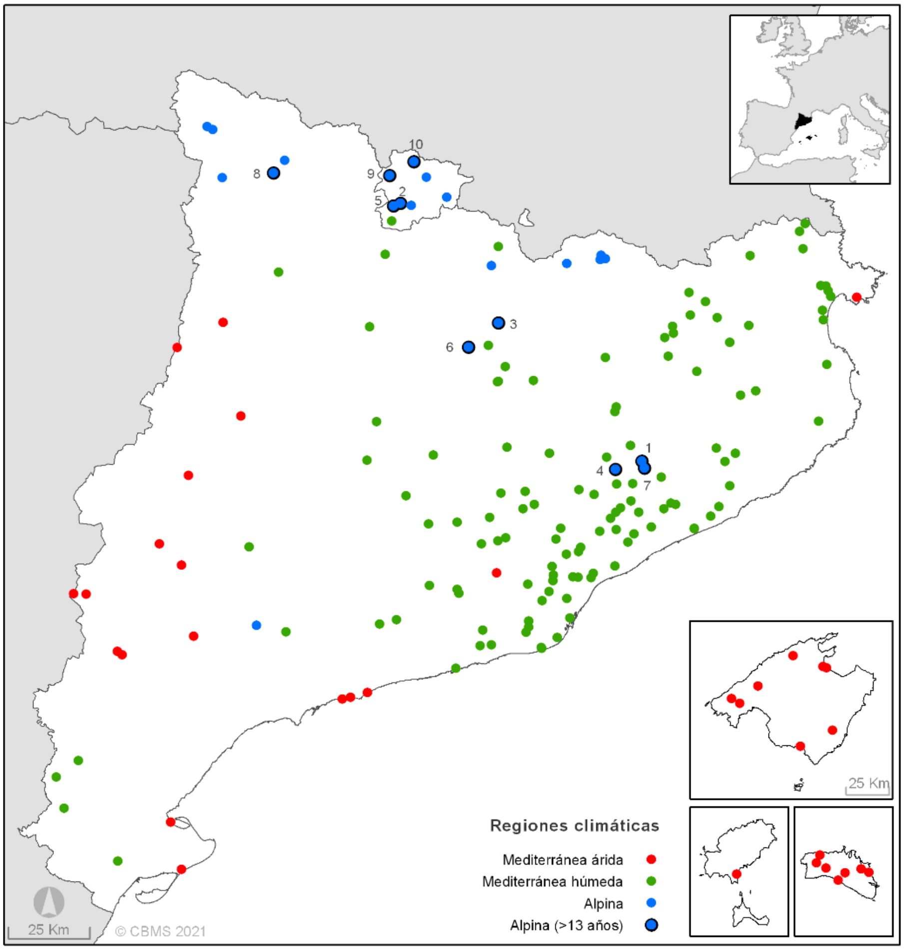

Figure 7.1 Map of the study region with all the itineraries walked in the CBMS network since the beginning of the project. The colour indicates the climatic region of each itinerary (blue: alpine, green: mesic Mediterranean, red: arid Mediterranean). The 10 itineraries in the alpine region with >13 years of data are marked and numbered.

7.3.2 Data analysis

7.3.2.1 Calculation of population trends

The annual population levels of the species were estimated using indices of abundance calculated from the sum of the counts performed on each itinerary. To estimate the counts of unsampled weeks, a flight curve was fitted using the counts from different itineraries in a climatic region determined by f a regional GAM (Schmucki et al., 2016). This method consists of fitting a general additive model to the counts of a species based on its phenology in the different itineraries within a particular climatic region. The resulting phenological curve, adapted according to the abundance of the species in each locality, allows us to estimate the abundance indices at local level. In a second phase, a GLM is used to generate a regional annual index by collapsing the local indices of the localities where there are viable populations of the species into a single value per year. The model corrects a bias – some routes have more data than others – and distributes the weight of local data according to the percentage of the phenological curve sampled in each locality. It also indirectly estimates the value of years that do not have enough data to meet the established threshold. Subsequently, a linear model is fitted to calculate the temporal trend of this annual index, adding 95% confidence intervals from a bootstrap method, which repeats the calculations up to 500 times with random subsamples of the data. The statistical package in R used to perform these calculations can be downloaded from Schmucki et al. (2019).

In the present work, three climatic regions were differentiated in which the regional GAM technique was applied. These regions were established using a threshold of 21DDG (number of hours per year in which a temperature of 21ºC is exceeded; data provided by the Catalan Meteorological Service) and correspond closely to those classified by Metzger et al. (2013) as the: (1) alpine region (≤ 0–150 DDG), (2) mesic Mediterranean region (between 150–400 DDG) and (3) arid Mediterranean region (≥ 400 DDG). The number of CBMS stations available for each regions is, respectively, 24, 123 and 33 (Fig. 7.1).

Minimum criteria were established to estimate the trend of a species in a region. The annual index of abundance was only calculated for species with data from a minimum of five populations with two or more positive counts (that is, the species has appeared in at least two weeks during the counting season). Furthermore, the time trend was only calculated for species with series of four or more annual indices. Using these criteria, it was possible to calculate the trends of 58 species in the alpine region, 89 in the mesic Mediterranean region and 21 in the arid Mediterranean region (Suppl. Table 7.1).

7.3.2.2 Comparison of trends between climatic regions

Linear mixed models (LMM) were used to check whether there were differences between regions in the values for population trends. In these models, the dependent variable is the magnitude of the population trend of a species (that is, the slope of the trend obtained with the linear model; see previous section), the region is a fixed factor, and the species a random factor. In this analysis, species with time series of a minimum of 10 years were selected. This criterion is much more conservative than the four years used to calculate population trends (see previous section) and therefore reduces the number of species that can be compared between regions. However, in this way the trends correspond to time segments that are sufficiently broad and representative of the situation over the past two decades. Comparisons were made of pairs of regions (three models in total). For the LMM models the *lme4* package in RStudio version 1.3.1. was used.

7.3.2.3 Population trends and ecological characteristics of species

To relate regional trends with the ecological characteristics of the species, four indicators of the ecological niche were used, two related to climate (STI and SPI) and two to habitat (SSI and TAO).

The STI (Species Temperature Index) corresponds to the mean annual temperature experienced by the species over its whole Iberian distribution (according to recent data from García-Barros et al. 2004). The SPI (Species Precipitation Index) is an equivalent index for accumulated annual precipitation. For more details on the calculation of these indices, see Herrando et al. (2019).

The TAO index places the preference of a species along a gradient running from closed environments (forest) to open environments (meadows). The index is calculated from data on the density of the species in the sections of the CBMS itineraries, previously classified as either ‘open’ or ‘closed’ depending on the dominant plant communities. The methodology for calculating this index, which is bounded between -1 (for a totally forest species) and +1 (for a species totally linked to open environments) is described in Ubach et al. (2020).

The SSI (Species Specialization Index) estimates the degree of specialization of a species with respect to the use of different types of habitat. It is calculated from the distribution of the density of adults in the sections of the CBMS itineraries, which are previously assigned to one of 19 habitat categories taken from an adaptation of the Corine classification to the plant communities of Catalonia (Carreras et al. 2015). The calculation of the index follows the formula described by Julliard et al. (2006), values being situated between 0 (for a totally generalist species with no preferences) to unlimited positive values (although with the CBMS data, the maximum specialists never exceed a value of 4).

To relate the population trends to these indicators, linear models were built in each region, with the dependent variable the trend of the species in that region, and the predictors the four niche indices. Bivariate interactions between climatic and habitat variables were also included in the models. However, due to the high collinearity between the SPI and STI (-0.81 in the alpine region, -0.68 in the mesic Mediterranean region, and -0.47 in the arid Mediterranean region; Pearson's correlation), we chose to perform models using two habitat variables with only the STI or with only the SPI. Before modelling, the variables were scaled due to their different magnitude of values using the ‘scale’ function in R.

7.3.2.4 Community indicators

Ten itineraries in the alpine region with 14 or more years of monitoring were selected as a sample of the ecological trends that high-level communities have undergone over the past two decades. The same four ecological niche specific indicators (SSI, TAO, STI, SPI) were used to derive the corresponding community indicators. The community index of a specific year and place can be summarized as the sum of the specific indices multiplied by the relative abundance index of the species (calculated with the regional GAM), divided by the sum of all the abundances. According to the minimum criteria established, for a given year the species that appeared in only a single count were excluded from the community as they are considered to be only occasional. In these calculations, the relative abundances were transformed with a square root to minimize the differences in density that exist between the species. Analyses without this transformation, however, provide qualitatively similar results. Subsequently, the relative abundances were contrasted with a linear model if there were significant changes in the evolution of the community indices, which then represent the main factors of change at local level. This method has been widely used in previous studies to show, for example, how European butterfly and bird communities have become progressively dominated by more thermophilic (Devictor et al. 2012) or more generalist (Le Viol et al. 2012) species due to global change.

7.4 Results

Population trends (time series of four or more years) were calculated for a total of 105 species of butterflies, with the exact number varying greatly in terms of the region (Table 7.1). In the mesic Mediterranean region, with the greatest number of itineraries (Fig. 7.1), trends were estimated for 89 species with time series of generally more than 20 years. Due to the high lepidopterological diversity, in the alpine region trends were estimated for more than twice the number of species (58) than in the arid Mediterranean region (21), although the annual series are similar in both regions (approximately 15 years on average).

Table 7.1 General results of population trends for the three climatic regions, with the percentages of trend categories given by the *rBMS* software.

Climatic region	Alpine	Mesic Mediterranean	Arid Mediterranean
Nº species	58	89	21
Nº years	13.88±5.54	22.84±5.41	16.71±5.54
% declining species	22.41	31.46	28.57
% increasing species	3.45	2.24	14.29
% stable species	15.51	30.33	23.81
% uncertain species	58.63	35.95	33.33

Irrespective of the region, species with population regressions (significant negative trends) are much more frequent than species with increases (significant positive trends). Stable trends occupy an intermediate position. About a third of the trends are uncertain in the two Mediterranean regions, this number being notably higher in the alpine region (59%). This very high proportion is due to a still low number of itineraries combined with relatively short annual series in this region (Suppl. Table 4.1).

Comparison of trends between regions was limited to species with annual series of at least 10 years. Of these, the species that have most increased are speckled wood *Pararge aegeria* and Adonis blue *Lysandra bellargus* in the alpine region, Cleopatra *Gonepteryx cleopatra* and grey banded grayling *Brintesia circe* in the mesic Mediterranean region, and holly blue *Celastrina argiolus* in the arid Mediterranean region. Among those that have declined most noticeably are black satyr *Satyrus actaea* in the alpine region, black-veined white *Aporia crataegi*, marsh fritillary *Euphydryas aurinia*, black-eyed blue *Glaucopsyche melanops*, western marbled white *Melanargia occitanica* and dingy skipper *Erynnis tages* in the mesic Mediterranean region, and Bath white *Pontia daplidice*, green hairstreak *Callophrys rubi* and southern brown argus *Aricia cramera* in the arid Mediterranean region. Suppl. Table 4.1 shows the trends of all species calculated for each region with the multiplicative value of their annual rate of change.

The magnitude of the population trends does not differ significantly between the alpine and mesic Mediterranean region for the 35 species compared ($P = 0.66$) or between the mesic and arid Mediterranean regions for the 17 species compared ($P = 0.429$). On the contrary, trends are significantly more negative in the arid Mediterranean region than in the alpine region ($P = 0.002$), although this comparison is based on only 10 species.

The statistical models based on the specific indicators were performed separately with the STI and the SPI due to the high collinearity between them (Table 7.2). In the alpine region, none of the niche indices or their interactions have predictive power for the magnitude of the population trend. On the other hand, significant relationships were observed in the Mediterranean regions. In the mesic region, the TAO index is highly significant in the model that includes the SPI, indicating that species with the greatest preference for open environments have the most noteworthy negative trends. In this model, the interaction between TAO and SPI also indicates that the most positive trends were observed for the combination of species that prefer closed and relatively dry environments. Both in the model using the STI and the one using the SPI, significant effects of the interaction between the TAO and the habitat specialization index (SSI) appeared, which can be interpreted as a more strongly negative trend in the species that prefer open environments and are also clear habitat specialists.

Table 7.2 Results of the generalized linear models examining species indicators predicting the magnitude of population trends in all three climatic regions. SSI: species specialization index; TAO: species index for open-closed habitat preference; STI: species temperature index; SPI: species precipitation index. Two models were generated separately for STI and SPI given the high collinearity between these two variables.

	Alpine (58 spp.)		**M. mesic (89 spp.)**		**M. arid (21 spp.)**	
	Estimate	PV	Estimate	PV	Estimate	PV
MODELS WITH SPI						
SSI	0.334	0.169	-2.46e-1	0.38	-12.04	0.04**
TAO	-0.747	0.325	-9.68e-1	6.09e-5***	2.871	0.208
SPI	0.001	0.170	-3.39e-4	0.406	-0.009	0.077
SSI:TAO	0.107	0.351	3.36e-1	0.016*	2.39	0.012*
SSI:SPI	-0.001	0.064	7.66e-5	0.827	0.017	0.005**
TAO:SPI	0.001	0.362	9.14e-4	0.003**	-0.006	0.057
MODELS WITH STI						
SSI	0.089	0.713	-0.309	0.229	-39.16	0.001**
TAO	0.685	0.345	0.208	0.630	-13.95	0.001**
STI	0.021	0.531	0.006	0.802	-3.12	0.001***
SSI:TAO	0.059	0.619	0.356	0.007**	0.20	0.832
SSI:STI	-0.016	0.434	0.008	0.699	3.04	0.001**
TAO:STI	-0.057	0.298	-0.044	0.164	1.06	0.005**

Despite the few species, many significant factors appear in the models of the arid Mediterranean region. The specialist species (high SSI values) are those that show the most negative population trends, with both the STI and with the SPI. Furthermore, the SSI interacts with both climatic factors in their respective models, indicating that generalist species associated with a low rainfall index or a high thermal index have undergone greater population declines. Even so, care should be taken as for this region we do not have trend data from authentic specialists, the maximum SSI value being only 1.20 (for *Leptotes pirithous*), which constrains the interpretation of these results. The STI model points to other significant relationships with habitat and climatic indicators. Species with a preference for open environments and the most thermophilic species show more negative trends. In addition, significant interaction is observed between the TAO and STI indices, which indicates greater population declines in species associated with open spaces and those with lower thermal indices.

Community indices for the 10 itineraries monitored for 14–27 years in the alpine area show numerous significant trends (Table 7.3). The two most widespread relationships are the decrease in the TAOC index and the increase in the thermal index (CTI), both observed in 60% of the routes (Fig. 7.2). In the first case, the negative trend reflects a progressive dominance of species that prefer forest environments to the detriment of species typical of open environments (Fig. 7.2a), while in the second case there is a trend towards a greater predominance of the most thermophilic species (Fig. 7.2b). Furthermore, in 40% of the itineraries a significant change was also observed in the level of habitat specialization, which always tends towards a relative increase in the more generalist species (negative trend of the CSI). The CPI index shows only three significant relationships with opposite signs according to the itineraries.

Table 7.3 Changes in 10 mountain butterfly communities monitored for 14–27 years. Linear models were applied to different community indices (calculated from the corresponding species indices) and monitoring years for the specialization (CSI), open-closed (TAOC), temperature (CTI) and precipitation (CPI) indices. The directions of the arrows indicate the direction of the change, and the number of arrows corresponds to the significance level (↑: P < 0.05, ↑↑: P < 0.01, ↑↑↑: P < 0.001).

Transsect name	**Map**	**Elevation**	**Years**	**CSI**	**TAOC**	**CTI**	**CPI**
El Puig	1	1030	27	↓↓	↓↓↓	↑	
Rec del Solà	2	1103	14		↓↓	↑	
Nou de Berguedà	3	1124	18	↓↓	↓↓↓		↑↑
Pla de la Calma	4	1193	24	↓		↑↑	↓↓
Enclar	5	1208	15		↓		
Campllong	6	1288	18		↓↓↓	↑	
Turó de l'Home	7	1656	14			↑	
Sant Maurici	8	1702	17	↓	↓↓	↑	↓
Comapedrosa	9	1782	15				
Sorteny	10	1946	15				

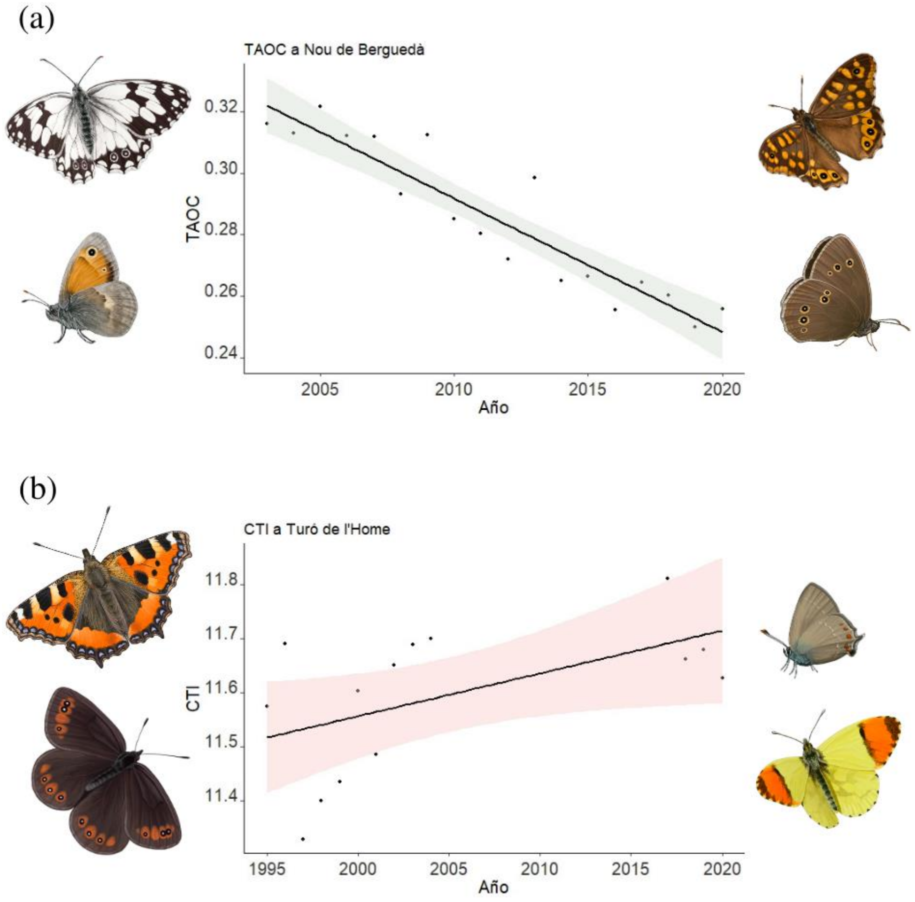

Figure 7.2 Community index trends in the two recent decades illustrating different drivers of global change. (a) Nou de Bergueda (1124 m), pre-Pyrenees: a significant TAOC decline and a progressive substitution of open space species (Iberian marbled white *Melanargia lachesis* (TAO=0.458) and small heath *Coenonympha pamphilus* (TAO=0.657)) by more forest-preferring species (ringlet *Aphantopus hyperanthus* (TAO=0.219) and speckled wood *Pararge aegeria* (TAO=-0.416)). (b) Turó de l'Home (1656 m), summit of the Montseny massif: an observed regression of montane species (small tortoiseshell *Aglais urticae* (STI=10.51) and piedmont ringlet *Erebia meolans* (STI=8.73)) and an increase in thermophilic species (false ilex hairstreak *Satyrium esculi* (STI=12.94) and Provence orange tip *Anthocharis euphenoides* (STI=11.88))

7.5 Discussion

In this work we used data from the CBMS monitoring program to check for differences in recent population trends in butterflies from three climatic regions in the northeast of the Iberian Peninsula. Based on the analytical tool proposed by the regional GAM and its implementation in a freely accessible statistical package (Schmucki et al., 2016; 2019), we were able to improve the estimates of the annual abundances at sampling locations and then calculate population trends adjusted to regions with homogeneous climatic conditions. This aspect represents a significant improvement over previous calculations in which trends were estimated for the entire northeast of the peninsula, without taking into account the possibility that specific trends vary in environments as different as high mountains or arid Mediterranean ecosystems. Nevertheless, this division into climate regions inevitably reduced the sample available in each region and, ultimately, reducing the number of trends that could be calculated.

The results coincide in general with previous estimates by showing a much higher percentage of species in decline than on the increase (Stefanescu et al., 2011b; Melero et al., 2016). This predominance of negative trends is a constant in recent studies evaluating the situation of insects and of butterflies in particular (Thomas, 2016; Sánchez-Bayo and Wickhuys, 2019; Wagner, 2019; Seibold et al., 2020), and is a clear example of the mostly negative impact of global change on this group. However, in our analysis, the relationship between declining and increasing species varied notably according to the climatic region. Thus, in the arid Mediterranean region twice as many species were detected to be in decline than on the increase, and this proportion increases up to six and 14 times more in the alpine and mesic Mediterranean region, respectively. In all likelihood, this disparity in values is largely an artifact related to sampling limitations. The mesic Mediterranean region, the most extensive and well populated of the three regions, has a higher concentration of CBMS itineraries. Thanks to this, population trends can be calculated for many more species than in the other two regions, including those of rarer and more specialized butterflies, which are precisely the ones that most quickly note the negative effects of global change and show more obvious regressive trends (e.g. Warren et al., 2001; Ekroos et al., 2010; Eskildsen et al., 2015; Habel et al., 2019). In the other two regions, the more limited number of itineraries means that trends can only be calculated for the more generalist, widely distributed species. This is an important aspect to take into account when evaluating the results provided by monitoring programs, especially when they are based on only a few sampling points; in these cases, it is very likely that they tend to underestimate the loss of biodiversity due to the bias towards the more general components of the studied group.

Despite these limitations, when the comparison of population trends is restricted to species shared between climatic regions with, furthermore, long annual series, interesting results are obtained that partially confirm our predictions. Specifically, a significant difference in trends is observed between the two most extreme regions, with those of the arid Mediterranean region being more negative than those of the alpine region. In a recent work with CBMS data, Herrando et al. (2019) found a general pattern according to which species with a preference for more arid environments have suffered more serious declines over the past two decades than those found in mesic environments. These authors speculate that the most likely reason for this is the negative impact of climate change (especially the increasing frequency of drought events) on the survival of immature stages of Lepidopterans inhabiting warmer drier areas. In the present analysis, this interspecific pattern is reinforced at intraspecific level, so that within a species the populations that occupy the most arid environments are also those that have experienced the clearest regressions. This situation, in fact, has already been highlighted for the green-veined white *Pieris napi* (Carnicer et al., 2019), although this species does not appear among those included in the comparison between the alpine and arid Mediterranean regions given its rarity in the latter. Our comparison is based on only 10 species, all of them very common (Suppl. Table 4.1) but, even so, the difference is very noticeable. The set of populations in the arid zone has a multiplicative rate of annual change of less than 1 (mean ± SD: 0.973 ± 0.025) denoting a decline, which contrasts with the trend of a slight increase in the alpine zone (1.004 ± 0.0232). These results agree with the work of Stefanescu et al. (2011a), who warned of a regression in generalist species in drier environments in the northeast of the peninsula due to a combination of global warming and agricultural intensification.

The success in identifying characteristics of the ecological niches of the species that explain the magnitude of the trends varied according to the climatic region. The indices used do not have predictive power in the alpine region but do in the Mediterranean regions, and give rise to apparent contradictions in cases with few species, all generalists, in the arid Mediterranean region. These indices reveal that the species associated with the most open environments, especially the more specialized ones, are suffering more pronounced declines. As we have pointed out on previous occasions, the abandonment of grazing in large areas of our geography is seriously affecting grassland specialists (Herrando et al., 2016), a process that is also being observed in other regions of southern Europe (Slancarova et al., 2016) and will ultimately entail local extinctions (Ubach et al., 2020). The models also indicate that changes related to land use interact with climate change and accelerate the decline in the populations that occupy Mediterranean ecosystems (see Stefanescu et al., 2011a; Herrando et al., 2019). The absence of significant relationships in the alpine region suggests, once again, that the negative impact of this set of factors on the butterfly fauna is less severe. However, this does not mean that these same factors are not also acting in mountain areas and the analysis of the changes at community level in 10 mountain localities monitored for periods of 1–2 decades shows unequivocally how community composition is changing in relation to the processes of global change.

By working with whole communities it is possible to use information from all species, including those that are not common enough to be used to estimate population trends. In this sense, the aggregated calculations make it possible to detect patterns in the alpine zone that were not reflected in the previous analysis such as the consequences of the abandonment of grazing and the advance of thermophilic species towards higher altitudes. For example, the TAO index trend towards more negative values in more than half of the cases studied shows the relative increase of species associated with forest and scrub to the detriment of typical meadow species. This is a generalised trend in the northeast of the peninsula and, as we have already commented, is a consequence of the abandonment of extensive grazing and a progressive increase in forest mass, well documented by Cervera et al. (2019). These authors also identify altitude as a factor that favours the speed of this process, since this rural exodus has been most intense and rapid in mountain areas. The Campllong and Nou de Berguedà itineraries, located in the pre-Pyrenees, are excellent examples of this problem (Fig. 2a). In these environments, there are numerous species typical of open ecosystems such as Iberian marbled white *Melanargia lachesis*, chestnut heath *Coenonympha glycerion*, small heath *C. pamphilus* and silver-studded blue *Plebejus argus* that are in local decline, The increasing species are typically forest ones, including speckled wood *Pararge aegeria*, white admiral *Limenitis Camilla*, comma *Polygonia c-album* and ringlet *Aphantopus hyperantus*.

Global warming is also acting as an engine of change in mountain butterfly communities, as has been shown by several studies based on our data. In the Iberian Peninsula, the movement of more thermophilic species to higher altitudes has been studied and documented in the Sierra de Guadarrama for over four decades using various methods including the calculation of the CTI (Wilson et al., 2005; 2007; Nieto-Sánchez et al., 2015). In the eastern Mediterranean, Zografou et al. (2014) have found CTI increased in butterfly aggregates for a shorter period of 15 years in a mountainous area of Greece at a moderate altitude (maximum of 650 m). In the present work, six of the 10 aggregates of selected species have experienced CTI increases over the past 14–27 years, which are associated with the increasing success of thermophilic species in mountain areas. An obvious example is provided by the Montseny massif, which at 1,706 m a.s.l. stands out as the highest point in the Catalan pre-coastal mountains, and is where various species from Mediterranean environments are colonizing the upper parts of the massif to the detriment of those with a preference for colder environments (see also Peñuelas et al., 2007). CBMS data shows how butterflies such as dark green fritillary *Speyeria aglaja*, purple-shot copper *Lycaena alciphron* and Mazarine blue *Cyaniris semiargus* – all typical upland species – are in decline at El Puig (1030 m a.s.l.), while Piedmont ringlet *Erebia meolans* and small tortoiseshell *Aglais urticae*, which maintain small populations on the summit of this massif, have significantly decreased in the Turó de l'Home itinerary (1,656 m a.s.l.). On this peak, up to three new species have been recorded in the past three years, all originating from lower mountain areas (grey banded grayling *Brintesia circe*, southern white admiral *Limenitis reducta* and Spanish gatekeeper *Pyronia bathseba*). In addition, Mediterranean species such as Provence orange tip *Anthocharis euphenoides* and false ilex hairstreak *Satyrium esculi* are stable or increasing in these locations. Our results contrast with those of Devictor et al. (2012), who did not detect any overall decrease in CTI in the CBMS data. However, in these authors' study, routes located above 1000 m a.s.l. were ruled out, a factor that could have affected their findings. Furthermore, in the 10 years since that study, additional changes to the CTI may well have occurred.

In short, in this study we provide evidence that the negative changes that butterflies are undergoing in the mountains of the northeast of the Iberian Peninsula in relation to global change are currently less severe than those occurring in arid Mediterranean environments. However, the comparisons between climatic regions are mainly based on the most generalist fraction of the butterfly fauna, which may underestimate the declines that many rare species are experiencing. In fact, the foreseeable effects of climate and landscape change on mountain butterfly communities become much clearer when trends in various community indices are analyzed for the past two decades.

8.General Discussion

8.General Discussion

This thesis explores how different drivers of global change affect butterfly species and communities. I explore separately how natural processes such as weather (Chapter 1) and vegetation encroachment (Chapter 2) affect species and their populations, and how ecological indicators of global change associated to butterfly species and assemblages are related to these drivers and have changed during the last decades in our region (Chapter 4). I provide overall information of the impacts all these drivers have in different climatic regions in the North-East of the Iberian Peninsula (Chapters 1,2,4). I also investigate the factors shaping mountain biodiversity using an experimental, multi-taxa approach in a study system located in subalpine grasslands in a Pyrenean valley (Chapter 3). The experimental design allowed me to assess the effects on biodiversity of a direct anthropogenic activity such as livestock management.

8.1 How weather events affect butterfly population dynamics in a bioregional context

To adress to objective 1 (see section "2.1 Objectives" of the thesis), in Chapter 1 I present the results from an analysis that identifies which are the main weather events affecting the majority of butterfly species in our region, and provides insights into the mechanisms underlying population fluctuations related to weather.

As a specific answer to objectives 1.1 ("to assess the climatic factors that affect the growth rate of butterfly species and how they vary according to climatic regions") and 1.2 ("to identify which life-cycle stages are most sensitive to climate"), we consider the effects of precipitation and thermal regimes for different groups of species and moments of the year. We found beneficial effects of winter and spring precipitation for butterfly populations, which are most evident in the Mediterranean region and in univoltine species, and mainly affect the larval stage, supporting our working hypothesis. In the Mediterranean region, spring rain is essential for the growth of vegetation and, in turn, for the development of herbivorous insects (Yela & Herrera, 1993). In the Alpine region, humid winters means greater snow cover, which has repeatedly been shown to be benefit mountain butterfly species, through both direct effects on overwinter survival of immature stages, and indirect effects on host plant and nectar resources (Boggs & Inouye, 2012; Nice et al., 2014; Roland et al., 2021). Also, we found a general negative effect of summer rain in the previous year, which affects the adult stage and may be related to less adult activity and a consequent fall in realised fecundity and will have repercussions the following year. For thermal variables, we found a consistent negative effect of mild autumns and winters on population growth which concurs with experimental work providing evidence that rising temperatures during the diapausing period causes a decrease in overwintering survival in many butterfly species (Williams et al., 2012). Increased metabolic activity causes reserve depletion and has been suggested as the main reason for increased winter mortality in diapausing larvae (e.g. Radchuk et al., 2013).

To respond to objective 1.3 ("to quantify population crashes and explosions and how they are related to life-history traits and to extreme climatic events"), we assessed and quantified population crashes and explosions and showed a relationship with extreme climatic seasons (ECSs), thus supporting our hypothesis. Population crashes were significantly related to climatic extremes but only in the Mediterranean region, which could partly explain the more negative butterfly trends recently been recorded in this region (Herrando et al., 2019; Chapter 4). The absence of an association of ECSs and population crashes in the alpine region could be related, in part, to compensation mechanisms, as negative effects such as reduction in egg viability under abnormally hot weather may be offset by an extension of the flight period of adult butterflies and a corresponding increase of realised fecundity (Buckley and Kingsolver, 2012).

In addition, we found that density dependence factors had a major negative effect on the growth rate of many species, as corresponded to classical population regulation theory (Royama, 1992). But, interestingly, several species showed varying degrees of density dependence across the two climatic regions, indicating that the strength of density-dependent processes varies throughout a species' range (Dooley et al., 2013). Our analyses also provide compelling evidence that extreme population levels in previous years provoke population crashes and explosions. Population collapses caused by the impact of parasitism, predation and disease are common in outbreaking forest Lepidoptera (Dwyer et al., 2004) but can also affect many other non-outbreaking species (Nowicki et al., 2009). Likewise, marked population increases recorded in a subsequent season after very low population levels suggest that a relaxation of density-dependent mortality factors occurs.

8.2 The effects of vegetation encroachment on butterfly communities using a landscape indicator as a management tool

Objective 2 is mainly addressed with the results obtained in Chapter 2. Here I show a strong association of most species for open habitats, and quantify its strength through the adaptation of an index developed by Suggitt et al. (2012).

The index (TAO) is used to describe the preference of 147 butterfly species for open or closed habitats. Although a general preference for open habitats is widely recognised in temperate European butterflies (e.g. van Swaay *et al*., 2006), to our knowledge this is the first time that a precise measure based on variation in population densities in different plant communities has been provided for what is one of the continent's richest butterfly faunas.

To specifically assess objective 2.1 ("to explore how species perform depending on the degree of vegetation encroachment and on their preferences for open or closed habitats"), we developed a community index (TAOc) to record changes in 54 long-term monitored sites (10 years or more), where plant communities were also periodically monitored. We found that butterfly assemblages have undergone changes towards an increasing dominance of species preferring closed habitats in 72% of the studied sites, in parallel to a process of vegetation encroachment, supporting our first hypothesis of the chapter. Our results can be extrapolated to large areas of the Mediterranean basin, where the increase in forest cover is one of the major changes in the landscape in recent decades (Feranec *et al*., 2010; Gerard *et al*., 2010, Brotons et al, 2020). Our results thus complement those of Herrando *et al*. (2015), who found that an increase in forest cover was impacting on both butterfly and bird populations, as revealed by a multi-species indicator based on monitoring data. Our results also show that butterfly responses to this driver are qualitatively similar between climatic regions, as shown by the non-significant interaction between region and vegetation encroachment. There was also no relationship between the slope and the initial TAOc value, which highlights the role of vegetation encroachment as one of the ecological drivers that affects butterfly populations regardless of the initial composition of the community.

To address objective 2.2 ("to test if the negative trend of species preferring open habitats is leading to the extinction of the populations"), we linked local population trends to the preference of species for open and closed habitats and the local vegetation encroachment, supporting our second hypothesis. These changes were accompanied by frequent extinction events, which were highly biased towards species preferring open habitats. Habitat loss is the major cause of species extinctions (Tilman *et al*., 1994) and it has been shown that the extinction risk in Mediterranean butterflies strongly decreases with suitable habitat availability (Fernández-Chacón *et al*., 2014). Our study confirms and quantifies the threat that vegetation encroachment imposes on biodiversity in this highly diverse region.

8.3 Factors shaping biodiversity in a Pyrenean valley: a multi-taxa and experimental approach

I addressed Objective 3 in the third chapter of this thesis, where we studied the gradients shaping biodiversity of mountain butterflies in a three-year experiment with an exclusion treatment to prevent grazing from cattle.

To address specifically objective 3.1 ("to compare the relative weight of abiotic and biotic factors influencing species richness and abundance of three taxa belonging to two trophic levels (plants, butterflies and grasshoppers) along a mountain altitudinal gradient") we sampled plants and two herbivorous insect groups in 20 plots and related their richness and abundance to the mountain's gradients. Biodiversity in El Catllar valley is shaped by both abiotic and biotic factors, but their relative importance differed between our studied taxa. We found the ubiquitous effect of the elevation gradient for all three groups, with species richness decreasing with altitude, supporting our first hypothesis. This agrees well with previous works that placed high altitudes in mountains with less richness in plants (Körner & Spehn, 2020), butterflies (Gutiérrez, 1997, Popović et al., 2021) and grasshoppers (Pitteloud et al., 2020, Fontana et al., 2020). Other abiotic factors found to be important include hill-shade for butterflies, or the slope for grasshoppers. Several biotic factors had important roles in explaining richness and abundance of our studied taxa. We found strong evidence in favour of a bottom-up process that related butterfly species richness to plant species richness, as seen in other studies (Kruess et al., 2002; Joshi et al., 2008).

To respond to objective 3.2 ("to understand how the management of livestock grazing affects biodiversity both in the medium-term (over two years) and in the short-term (within the year) in mountain pastures") we evaluated the effects of the livestock exclusion treatment in our experiment. We only obtained evidence of grazing effects on plant richness with the full set of plots; the absence of a detectable response by butterflies and grasshoppers may be attributed to a temporal lag effect as seen in other works (Öckinger et al., 2006). We interpret these results in the framework of the competitive exclusion theory (Grime, 1973), which predicts a decline in plant diversity once dominant grasses take over exclusion plots and outcompete other plants.

However, a subset of plots with a narrow altitudinal range (1500-1700 m) revealed short-term treatment effects for butterflies as we could measure intra- an inter annual effects. In contrast to exclusion plots, which remained stable over the summer, we found some evidence that grazed plots had higher richness and abundance of butterflies during the August samples, indicating that an increase in both variables occurred in just a few weeks, a change related to habitat selection by butterflies due to parallel differences in resource availability in both kinds of plots. Allowing flowering in grassland systems is key as a measure for pollinator conservation (Scohier et al., 2013), and in our Pyrenean valley this was achieved in subalpine pastures in summer thanks to the transhumance towards higher grasslands from July to September (see also Baena & Casas, 2010; Garcia-Ruiz et al., 2021). This reconciles the idea that traditional management systems should be optimized to allow flowering and seed set, acting as a sustainable impact through medium-intensity grazing that benefits biodiversity (Kruess et al., 200.

8.4 Changes in butterfly communities based on climatic and landscape indicators in different bioclimatic regions

I explored this objective mainly in Chapter 4, where we studied species regional trends and changes in butterfly communities in 3 bioclimatic regions using long-term data.

To address the objective 4.1 (“to explore the level of coincidence in population trends of common butterflies in the northeast of the Iberian Peninsula over the past two-three decades by distinguishing three regions with well-differentiated climates”), we analysed the population trends of all butterfly species that met certain criteria to reliably calculate representative trends for our region. Our results show that the number of species declining exceeds that of species increasing. This coincides with previous results obtained with different methods (Stefanescu et al. 2011, Melero et al. 2016). All analyses to date have used a largely generalist fraction of the butterfly fauna and, actually, probably underestimate the general decline of butterfly fauna by ignoring some rare and threatened species, which are precisely the ones that most quickly respond to global change and show more obvious regressive trends (e.g. Warren et al.

2001; Ekroos et al. 2010; Eskildsen et al. 2015; Habel et al. 2019). In our study, this bias is minimised to some extent in the Mediterranean mesic region, the most extensive and populated of all three regions, where the higher concentration of BMS itineraries means that population trends can be calculated for many more species, including rarer and more specialized butterflies, than in the other two regions. On the other hand, the more limited number of itineraries in the other two regions means that trends can only be calculated for the more generalist and widely distributed species. However, by using a small subset of common species we could compare trends between regions, and found declines being more severe in the arid Mediterranean region than in the alpine region, supporting our first hypotheis of this chapter. This suggests that climate in the arid region contributes to the more negative trends, especially given the results presented in chapters 1 and 2.

To assess objectives 4.2 ("to relate population trends to the habitat and climatic niches of the species") and 4.3 ("to identify the most important trends in upland areas for a few model butterfly species that have been constantly monitored over periods of at least 14 years"), a more detailed analysis was carried out for the alpine region, showing no relationship between population trends and the ecological indices of the species considered. Conversely, significant changes were found in certain community indices at the local level, as for example an increasing dominance of forest-loving and thermophilic species, which clearly reflect the effects of the abandonment of grazing and the movement of Mediterranean species towards higher altitudes. This partially supports our second hypothesis, as we found a clear effect of changes in community composition in terms of preferences for open and closed habitats, decline of habitat specialists and increase of the community temperature index, but in a local perspective.

8.5 Changes in butterfly populations at short and long time scales

Our results pinpoint several drivers affecting butterfly abundance through different processes acting at different time scales. Studies using short-term data (Chapter 3) and long-term monitoring programs (Chapter 1, 2 & 4) are both needed to better understand species responses to natural and anthropic drivers in the modern world.

First, we need to understand the year-to-year population changes in response to weather (Chapter 1). This knowledge is crucial to tease apart population fluctuations from population trends that arise from responses to more regular and long-lasting changes in environmental conditions. It is also essential to understand how extreme weather events affect butterfly populations in our region, and to predict the impact of climate change on the butterfly fauna. Second, it is important to combine short and long-term butterfly data in combination with measures of habitat changes over time to understand how landscape modification will affect the butterfly fauna in the current scenario of global change. In this context, we have explored the impact of one of the most prevalent drivers in our country, namely vegetation encroachment, using data from more than two decades of butterfly monitoring at a large number of sites (Chapter 2), but also data from a short-term experiment carried out in a Pyrenean valley (Chapter 3).

Following a community approach, in this thesis I also present various community indices that are informative of how butterfly assemblages are responding to the impact of climate and landscape changes, both at the local and regional scales (Chapter 4). The widespread pattern of a negative trend of the TAO community index in local assemblages reveals the generalized phenomenon of forest and shrub encroachment in our country, to the detriment of grassland species (Chapters 2 & 4). This ecological indicator was originally developed for use as a management tool, for example in protected areas that aim to promote biodiversity. Indeed, since chapter 2 was published the TAO community index has become part of the essential information given to managers of the natural heritage of Catalonia's natural parks, as included in different reports (MCNG-DIBA, 2019; 2020; Stefanescu & Ubach, 2022), and has also been used in more recent butterfly ecological studies in the Iberian Peninsula (Mingarro et al., 2021; Mora at al., 2022).

It is also important to note that the approach followed in Chapter 3 points to the need to develop integrative studies to explore how anthropogenic impacts affect biodiversity across different levels. Only by following this approach will it be revealed what measures can be recommended in order to preserve biodiversity from an ecosystem perspective.

Finally, as global warming is acting as a prevailing driver of change worldwide, scientific results obtained in terms of management practices to benefit butterfly populations have to be taken cautiously. Inevitable changes will occur under the new environmental conditions, according to the current climatic predictions and scenarios. Our results show that climate change is pushing butterfly species uphill towards the summits (Chapter 4), similarly to other works (Rödder et al., 2021, Bonelli et al., 2021), though it is only generalist and mobile species that are able to track the velocity of the changes. In the Iberian Peninsula, the movement of more thermophilic species to higher altitudes presents challenges in understanding to what extent mountains will become a biodiversity reservoir for Mediterranean butterflies.

9.Conclusions

9.Conclusions

- Population dynamics of Mediterranean butterflies is weather-dependent, and several climatic variables are among the most important factors driving population growth of most species, with differences according to climatic regions.
- Spring rainfall in the Mediterranean Mesic Climate Region (MMCR) has a clear positive effect on population growth, given that water availability is a limiting resource during the critical growth period of most species. Mild winters have a general negative effect on butterfly populations, both in the MMCR and the Alpine Climate Region (ACR). Both relationships are worrying in the context of climatic warming, with increasingly drier springs and warmer winters.
- The strong effect of density-dependent processes in the vast majority of the studied butterfly populations accounts for a large fraction of the recorded extreme population changes (crashes and explosions).
- Extreme climatic events are related to population crashes and rarely to population explosions in the MMCR, but no relationships were found in in the ACR.
- The preference of butterfly species along a continuous open-closed habitat gradient has been calculated for the first time with an index built on quantitative data. The index shows a strong association of most species for open habitats.
- Butterfly assemblages have undergone changes in the last three decades in relation to habitat encroachment, showing a significant tendency to be dominated by species that prefer closed habitats.
- Local population trends are predicted by the interaction of the preference of butterfly species for open or closed habitats and the magnitude of vegetation encroachment at each site.
- Frequent extinction events of butterfly populations are highly biased towards species preferring open habitats. The quantification of the phenomenon emphasizes the threat that vegetation encroachment imposes on biodiversity.
- The open-closed habitat indicator has proved to be a useful tool for local managers aiming to promote biodiversity conservation, even more considering the indicator role of butterflies in insect communities.
- Plants and herbivorous insects of subalpine grasslands show differences in the relative weight of abiotic and biotic factors affecting their richness and abundance. The elevation gradient affects

ubiquitously all these taxa, with less species at higher altitudes, but other factors such as the slope and vegetation structure were important for grasshoppers, and plant richness for butterflies (via a s accounting as a bottom-up effect).

- Livestock exclusion had a slight negative effect on plant richness but there were almost no changes in insect community composition after two years.
- However, medium-intensity grazing through traditional transhumance management system can help maintain butterfly biodiversity in sub-alpine grasslands, as we observe that in grazed plots, richness and abundance increased over the summer and exceeded those of non-grazed plots.
- The negative changes that butterflies are undergoing in the mountains of the northeast of the Iberian Peninsula in relation to global change are currently less severe than those occurring in arid Mediterranean environments.
- Comparisons between climatic regions are mainly based on the most generalist fraction of the butterfly fauna, which may underestimate the declines that many rare species are experiencing.
- Global change drivers that affect mountain butterfly communities include the abandonment of grazing and climate warming, leading to an increase of forest dwelling species and the movement of thermophilic species towards higher altitudes.

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Appendices

A. Chapter 4 Supporting information

Supplementary Table 4.1 Results of GLMs showing the weather variables significantly associated with population growth in the 78 studied butterfly species, in two climatic regions (alpine region - ACR; and Mediterranean mesic region - MMCR). Density-dependence effects (DD) are highlighted in green, temperature climate variables in pink, and precipitation climate variables in light blue. '+' and '-' correspond to significant positive and negative effects, respectively, of a predictor of population growth. 'Vol' refers to voltinism (M- multivoltine, U-univoltine). 'Pop.trend' is a classification of species' long-term trends in the study region as: U-Uncertain, S-Stable, D-Decline, I-Increase. 'Hib. stage' indicates the overwintering strategy of each species (A-Adult, P-Pupa, L-Larva, E-Egg, NO-more than one strategy). 'Nº sites' corresponds to the number of sites in which a species was monitored. Species names follow the taxonomy given by Wiemers et al., 2020.

			Temperature (minimum(m) and maximum(M))							**Standard Precipitation Index**									
Species	**CR**	**DD**	**SPm(i-1)**	**SUm(i-1)**	**AUm**	**WIm**	**WIM**	**SPm**	**SUm**	**SP (i-1)**	**SU (i-1)**	**AU**	**WI**	**SP**	**SU**	**Vol**	**Pop. trend**	**Hib. stage**	**Nº sites**
Aglais io	ACR	-		-									+			M	U	A	22
	MMCR	-									+					M	S	A	72
Aglais urticae	ACR	-										+				M	U	A	23
Anthocharis cardamines	ACR	-			-			+								U	S	P	24
	MMCR	-								+						U	S	P	90
Anthocharis euphenoides	MMCR	-			-											U	D	P	54
Apatura ilia	MMCR															M	U	L	
Aporia crataegi	MMCR	-					-	+			-					U	D	L	63
	ACR								-		-					U	D	L	23
Argynnis addipe	ACR	-														U	U	E	18
Speyeria aglaja	ACR	-									-	-		-		U	U	E	24
Argynnis paphia	MMCR	-				-						-				U	S	E	83
	ACR	-				-										U	U	E	21
Aricia agestis	MMCR															M	D	L	
Aricia cramera	MMCR	-				+					-		-			M	S	L	76

Species	CR	DD	SPm(i-1)	SUm(i-1)	AUm	WIm	WIM	SPm	SUm	SP (i-1)	SU (i-1)	AU	WI	SP	SU	Vol	Pop. trend	Hib. stage	Nº sites
Boloria dia	MMCR	-				-										M	U	L	58
Boloria euphrosyne	ACR	-												-		U	U	L	16
Brintesia circe	MMCR	-				-					-			+	-	U	U	L	110
Brintesia circe	ACR	-														U	U	L	16
Cacyreus marshalli	MMCR	-			-							+		-	+	M	D	NO	63
Callophrys rubi	MMCR	-														U	D	P	102
Carcharodus alceae	MMCR	-													+	M	S	L	111
Celastrina argiolus	MMCR	-				+	+									M	S	P	117
Coenonympha arcania	ACR	-		+		-		+								U	S	L	65
Coenonympha dorus	MMCR															U	D	L	
Coenonympha pamphilus	MMCR	-		+				+	-			-				M	D	L	102
Colias crocea	MMCR	-				+								+		M	S	P	
Erebia meolans	ACR			-	-							+	+			U	U	L	22
Erebia neoridas	ACR	-														U	U	L	17
Erynnis tages	MMCR				-	-	-	+	-					-		M	D	L	48
Euchloe crameri	MMCR	-		-							-					M	U	P	99
Euphydryas aurinia	MMCR						-									U	D	L	68
Glaucopsyche alexis	MMCR	-		-				-	-				+			U	U	P	64
Glaucopsyche melanops	MMCR						-	+				-				U	D	P	63
Gonepteryx cleopatra	MMCR	-						+			-			+		U	I	A	114
Gonepteryx rhamni	MMCR	-				-						-	-	+		U	S	A	106
	ACR	-											+			U		A	24
Hipparchia fagi	MMCR	-									-					U	U	L	58
Hipparchia fidia	MMCR	-												-		U	D	L	70
Hipparchia semele	MMCR	-									-					U	U	L	49
Hipparchia statilinus	MMCR	-														U	U	L	82
Iphiclides feisthamelii	MMCR	-						+			-			-		M	D	P	115
	ACR	-												-		M	S	P	17
Issoria lathonia	ACR	-									-	+	+			M	S	NO	24
	MMCR	-									-					M	S	NO	78
Lasiommata megera	ACR	-		+											-	M	U	L	24
	MMCR	-									-					M	S	L	120
Leptidea sinapis	MMCR	-													+	M	D	P	106

Species	CR	DD	SPm(i-1)	SUm(i-1)	AUm	WIm	WIM	SPm	SUm	SP (i-1)	SU (i-1)	AU	WI	SP	SU	Vol	Pop. trend	Hib. stage	Nº sites
	ACR	-												-		U	D	P	22
Libythea celtis	MMCR	-												+		U	U	A	86
Limenitis reducta	MMCR	-									-					M	D	L	99
Lycaena phlaeas	MMCR	-													+	M	S	L	117
Lysandra bellargus	ACR	-		-				-				+	+			M	I	L	22
	MMCR	-														M	U	L	57
Lysandra coridon	ACR													-		U	U	E	22
Lysandra hispana	MMCR	-											+			M	S	E	53
Maniola jurtina	MMCR	-		+	-	-	-				-	+	+	+		U	S	L	116
	ACR	-												+		U	U	L	24
Melanargia lachesis	MMCR				-						-				-	U	D	L	111
	ACR	-									-					U	U	L	20
Melanargia occitanica	MMCR																D	L	
Melitaea cinxia	MMCR	-			-		-				-	-		-		U	U	L	47
	ACR	-				-							+			U	U	L	20
Melitaea deione	MMCR	-			-			+								M	U	L	63
Melitaea didyma	MMCR	-					-							+		M	S	L	77
Melitaea phoebe	MMCR	-				+	-	+				-				M	U	L	86
	ACR	-							-							U	U	L	19
Favonius quercus	MMCR	-												+		U	U	P	67
Nymphalis antiopa	MMCR										-					U	D	A	36
Nymphalis polychloros	MMCR															U	D	A	
Ochlodes sylvanus	MMCR													+		M	U	L	87
Papilio machaon	MMCR	-						+			-					M	D	P	119
Pararge aegeria	MMCR	-				+		+	-							M	S	L	
Pieris napi	ACR	-							+							M	U	P	23
	MMCR	-		+												M	S	P	120
Pieris rapae	MMCR	-									-			+		M	S	P	120
	ACR	-														M	S	P	24
Plebejus argus	MMCR	-														M	U	E	42
Polygonia c-album	MMCR	-													+	M	S	A	92
	ACR	-														M	U	A	23
Polyommatus icarus	ACR													-		M	S	L	24
	MMCR	-														M	S	L	120

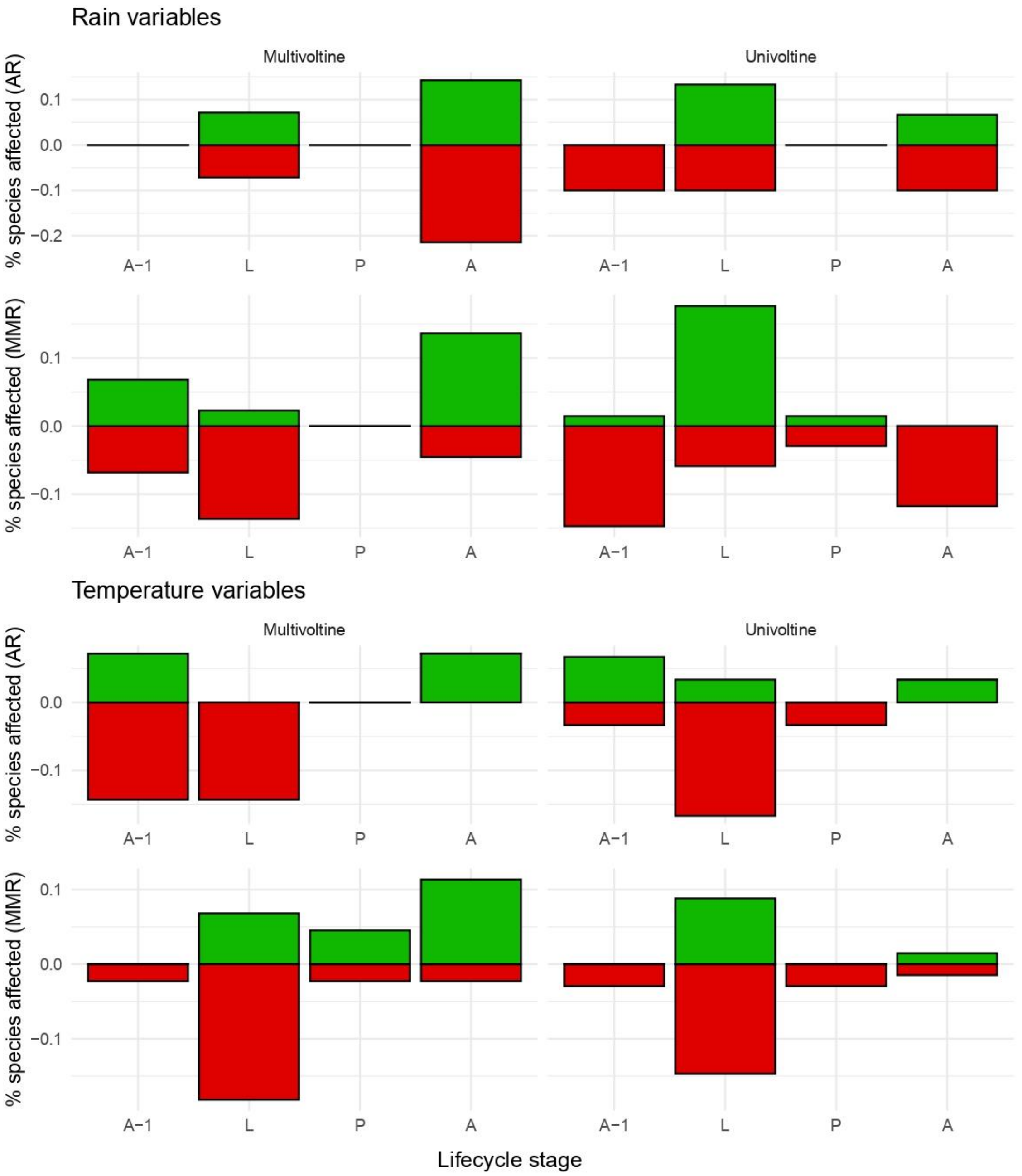
Species	**CR**	**DD**	**SPm(i-1)**	**SUm(i-1)**	**AUm**	**WIm**	**WIM**	**SPm**	**SUm**	**SP (i-1)**	**SU (i-1)**	**AU**	**WI**	**SP**	**SU**	**Vol**	**Pop. trend**	**Hib. stage**	**Nº sites**
Pontia daplidice	MMCR	-														M	D	NO	17
Pseudophilotes panoptes	MMCR	-										-		-		U	D	P	75
Pyrgus malvoides	MMCR	-					-									M	U	P	74
Pyronia bathseba	MMCR	-									-					U	D	L	96
Pyronia cecilia	MMCR						+					+	+	+	-	U	U	L	102
Pyronia tithonus	MMCR	-											+	+		U	D	L	81
	ACR	-													+	U	U	L	17
Satyrium esculi	MMCR	-										+	+	+		U	U	L	108
	ACR	-						-								U	U	L	11
Satyrium spini	MMCR															U	U	L	
Satyrus actaea	ACR			+		-								-		U	D	L	14
Spialia sertorius	MMCR	-														M	U	L	77
Thymelicus acteon	MMCR	-		+	+						-		+			U	S	L	104
Thymelicus sylvestris	MMCR	-						-			-		+	+		U	U	L	55
	ACR												+			U	U	L	22
Tomares ballus	MMCR															U	U	P	
Zerynthia rumina	MMCR	-										-		-		U	U	P	29

Supplementary Table 4.2 Life-cycle stages of the 78 studied species during a full year cycle (A-Adult, P-Pupae, L-Larvae, E-Egg) used in the multispecies GLMM. Life-history data was based on García-Barros et al. (2013) and Vila et al. (2018). For each combination of species and climatic region, the climatic variables (those related to temperature (TºC) and precipitation (SPI)) with significant effects on population growth, the season in which they occur (SU-summer, AU-autumn, WI-winter, SP-spring), and the stage upon which they predominantly act (A: Adult in the current year, A-1: Adult in the previous year, L: Larva) are indicated. 'Estimate' gives the estimated coefficient in the GLMs testing for the effects of weather variables on population growth. Note that summer variables in the current year were always assigned to the adult stage, following the simple criterium that data from the previous summer were assigned to adults (A-1), i.e. the reference point of the previous generation.

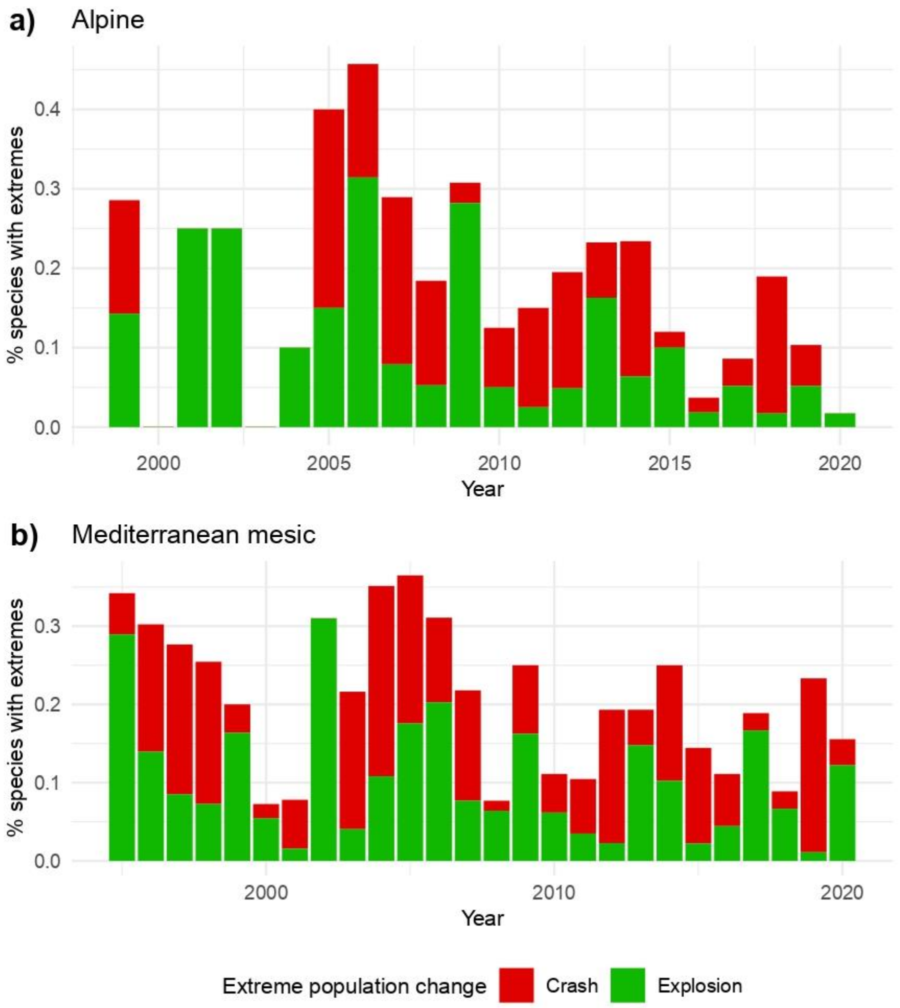
Family	Species	Voltinism	SU-1	AU-1	WI	SP	SU	Region	Climatic Variable	Stage affected	Estimate
HESPERIDAE	***Carcharodus alceae***	Multivoltine	A	L	L	A	A	MMCR	SPI-SU	A	0.067
	Erynnis tages	Multivoltine	A	L	L	A	A	MMCR	TºC-AU	L	-0.069
								MMCR	TºC-SP	A	0.114
								MMCR	SPI-SP	A	-0.083
								MMCR	TºC-SU	A	-0.097
								MMCR	TºC-WI	L	-0.087
								MMCR	TºC-WI	L	-0.079
	Ochlodes sylvanus	Multivoltine	A	L	L	A	A	MMCR	SPI-SP	L	0.093
	Pyrgus malvoides	Multivoltine	A	L	L	A	A	MMCR	TºC-WI	L	-0.05
	Thymelicus acteon	Univoltine	A	L	L	L	A	MMCR	SPI-WI	L	0.079
								MMCR	SPI-SU	A-1	-0.059
								MMCR	TºC-WI	L	0.077
								MMCR	TºC-SU	A-1	0.056
	Thymelicus sylvestris	Univoltine	A	L	L	L	A	ACR	SPI-WI	L	0.08
								MMCR	TºC-WI	L	-0.093
								MMCR	SPI-SU	A-1	-0.102
								MMCR	SPI-WI	L	0.104
								MMCR	SPI-WI	L	0.082
LYCAENIDAE	***Aricia cramera***	Multivoltine	A	L	L	A	A	MMCR	TºC-WI	L	0.174
								MMCR	SPI-SU	A-1	-0.128
								MMCR	SPI-WI	L	-0.155
	Celastrina argiolus	Multivoltine	A	P	P	A	A	MMCR	TºC-WI	P	0.083
								MMCR	TºC-WI	P	0.078
	Glaucopsyche alexis	Univoltine	P	P	P	L/A	P	MMCR	SPI-WI	P	0.218
								MMCR	TºC-WI	P	-0.15
								MMCR	TºC-SP	A	-0.201
	Lycaena phlaeas	Multivoltine	A	L	L	A	A	MMCR	SPI-SP	A	0.055
	Favonius quercus	Univoltine	A	E	E	L	A	MMCR	SPI-SP	L	0.179
	Lysandra bellargus	Multivoltine	A	L	L	A	A	ACR	SPI-AU	L	0.214
								ACR	SPI-WI	L	0.158
								ACR	TºC-SU	A-1	-0.118
								ACR	TºC-SP	L	-0.15
	Lysandra coridon	Univoltine	A	E	E	L	A	ACR	SPI-SP	L	-0.133
	Lysandra hispana	Multivoltine	A	E	E	L	A	MMCR	SPI-WI	E	0.042
	Polyommatus icarus	Multivoltine	A	L	L	L	A	ACR	SPI-SP	A	-0.081
	Pseudopilotes panoptes	Univoltine	P	P	P	L/A	P	MMCR	SPI-WI	P	-0.107
								MMCR	SPI-SP	A	-0.084
	Satyrium esculi	Univoltine	A	E	E	L	A	ACR	TºC-SP	L	-0.379
								MMCR	SPI-SP	L	0.158
								MMCR	SPI-AU	E	0.098
								MMCR	SPI-WI	E	0.11
NYMPHALIDAE	***Speyeria aglaja***	Univoltine	A	L	L	L	A	ACR	TºC-SP	L	-0.113
								ACR	SPI-SU	A-1	-0.089
								ACR	SPI-AU	L	-0.086
	Argynnis paphia	Univoltine	A	L	L	L	A	ACR	TºC-WI	L	-0.081
								MMCR	TºC-WI	L	-0.08
								MMCR	SPI-AU	L	-0.06
	Aglais urticae	Multivoltine	L	A	A	A	L	ACR	SPI-AU	A	0.131
	Boloria dia	Multivoltine	A	L	L	A	A	MMCR	TºC-WI	L	-0.106
	Boloria euphrosyne	Univoltine	A	L	L	L	A	ACR	SPI-SP	L	-0.109
	Euphydryas aurinia	Univoltine	L	L	L	A	L	MMCR	TºC-WI	L	-0.21
	Aglais io	Multivoltine	L	A	A	A	L	ACR	TºC-SU	A-1	-0.106
								ACR	SPI-WI	A	0.124
								MMCR	SPI-SU	A-1	0.102
	Limenitis reducta	Multivoltine	A	L	L	A	A	MMCR	SPI-SU	A-1	-0.09
	Libythea celtis	Univoltine	A	A	A	L	A	MMCR	SPI-SP	L	0.133
	Melitaea cinxia	Univoltine	A	L	L	L	A	ACR	TºC-WI	L	-0.14
								ACR	SPI-WI	L	0.228
								MMCR	TºC-AU	L	-0.137

								MMCR	TºC-WI	L	-0.135
								MMCR	SPI-AU	L	-0.131
								MMCR	SPI-SU	A-1	-0.156
								MMCR	SPI-SP	L	-0.14
	Melitaea deione	Multivoltine	A	L	L	A	A	MMCR	TºC-AU	L	-0.079
								MMCR	TºC-SP	A	0.115
	Melitaea didyma	Multivoltine	A	L	L	A	A	MMCR	TºC-WI	L	-0.044
								MMCR	SPI-SP	A	0.05
	Melitaea phoebe	Univoltine	A	L	L	A	A	ACR	TºC-SP	L	-0.224
								MMCR	TºC-WI	L	-0.094
								MMCR	TºC-WI	L	0.047
								MMCR	TºC-SP	A	-0.072
								MMCR	SPI-AU	L	-0.045
	Nymphalis antiopa	Univoltine	A	A	A	L	A	MMCR	SPI-SU	A-1	-0.208
	Polygonia c-album	Multivoltine	A	A	A	L/A	A	MMCR	SPI-SU	A	0.059
	Brintesia circe	Univoltine	A	L	L	L	A	MMCR	TºC-WI	L	-0.088
								MMCR	SPI-SU	A-1	-0.107
								MMCR	SPI-SU	A	-0.052
								MMCR	SPI-SP	L	0.043
	Coenonympha arcania	Univoltine	A	L	L	L	A	ACR	TºC-WI	L	-0.043
								ACR	TºC-SP	L	0.041
								ACR	TºC-SU	A-1	0.032
	Coenonympha pamphilus	Multivoltine	A	L	L	L	A	MMCR	TºC-SP	L	0.067
								MMCR	SPI-AU	L	-0.06
								MMCR	TºC-SU	A	0.073
								MMCR	TºC-SU	A-1	-0.047
	Erebia meolans	Univoltine	A	L	L	L	A	ACR	TºC-SU	A-1	-0.142
								ACR	TºC-AU	L	-0.09
								ACR	SPI-AU	L	0.115
								ACR	SPI-WI	L	0.114
	Hipparchia fagi	Univoltine	A	L	L	L	A	MMCR	SPI-SU	A-1	-0.145
	Hipparchia fidia	Univoltine	A	L	L	L	A	MMCR	SPI-SP	L	-0.097
	Hipparchia semele	Univoltine	A	L	L	L	A	MMCR	SPI-SU	A-1	-0.108
	Lasiommata megera	Multivoltine	A	L	L	A	A	ACR	TºC-SU	A-1	0.079
								ACR	SPI-SU	A	-0.06
								MMCR	SPI-SU	A-1	-0.065
	Maniola jurtina	Univoltine	A	L	L	L	A	ACR	SPI-SP	L	0.147
								MMCR	TºC-AU	L	-0.033
								MMCR	TºC-SU	A-1	0.035
								MMCR	SPI-SU	A-1	-0.064
								MMCR	SPI-SP	L	0.064
								MMCR	TºC-WI	L	-0.04
								MMCR	TºC-WI	L	-0.035
								MMCR	SPI-AU	L	0.047
								MMCR	SPI-WI	L	0.032
	Melanargia lachesis	Univoltine	A	L	L	L	A	ACR	SPI-SU	A-1	-0.092
								MMCR	TºC-AU	L	-0.049
								MMCR	SPI-SU	A-1	-0.074
								MMCR	SPI-SU	A	-0.047
	Pyronia bathseba	Univoltine	A	L	L	L	A	MMCR	SPI-SU	A-1	-0.084
	Pyronia cecilia	Univoltine	A	L	L	L	A	MMCR	TºC-WI	L	0.071
								MMCR	SPI-AU	L	0.097
								MMCR	SPI-SU	A	-0.112
								MMCR	SPI-WI	L	0.114
								MMCR	SPI-SP	L	0.051
	Pyronia tithonus	Univoltine	A	L	L	L	A	ACR	SPI-SU	A	0.125
								MMCR	SPI-WI	L	0.072
								MMCR	SPI-SP	L	0.062
	Satyrus actaea	Univoltine	A	L	L	L	A	ACR	TºC-SU	A-1	0.14
								ACR	TºC-WI	L	-0.159
								ACR	SPI-SP	L	-0.241
PAPILIONIDAE	***Iphiclides feisthamelii***	Multivoltine	A	P	P	L/A	A	ACR	SPI-SP	L	-0.101
								MMCR	TºC-SP	A	0.041
								MMCR	SPI-SU	A-1	-0.079
								MMCR	SPI-SP	A	-0.068
	Papilio machaon	Multivoltine	A	P	P	A	A	MMCR	TºC-SP	A	0.06
								MMCR	SPI-SU	A-1	-0.071
	Zerynthia rumina	Univoltine	P	P	P	A	P	MMCR	SPI-SP	A	-0.103
								MMCR	SPI-AU	P	-0.128
PIERIDAE	***Anthocharis cardamines***	Univoltine	P	P	P	A	P	ACR	TºC-AU	P	-0.063
								ACR	TºC-SP	A	0.057
								MMCR	SPI-SP	A-1	0.065
	Aporia crataegi	Univoltine	A	L	L	L	A	ACR	SPI-SU	A-1	-0.12
								ACR	TºC-SU	A	-0.09
								MMCR	TºC-WI	L	-0.149
								MMCR	TºC-SP	L	0.116
								MMCR	SPI-SU	A-1	-0.144

Anthocharis euphenoides	Univoltine	P	P	P	L/A	P	MMCR	TºC-AU	P	-0.075
Euchloe crameri	Multivoltine	A	P	P	A	A	MMCR	TºC-SU	A-1	-0.128
							MMCR	SPI-SU	A-1	0.096
Gonepteryx cleopatra	Univoltine	A	A	A	L	A	MMCR	TºC-SP	L	0.061
							MMCR	SPI-SU	A-1	-0.071
							MMCR	SPI-SP	L	0.041
Gonepteryx rhamni	Univoltine	A	A	A	L	A	ACR	SPI-WI	A	0.046
							MMCR	TºC-WI	A	-0.065
							MMCR	SPI-AU	A	-0.056
							MMCR	SPI-WI	A	-0.059
							MMCR	SPI-SP	L	0.051
Leptidea sinapis	Univoltine	A	P	P	A	A	ACR	SPI-SP	L	-0.067
							MMCR	SPI-SU	A	0.092
Pieris napi	Multivoltine	A	P	P	A	A	ACR	TºC-SU	A	0.084
							MMCR	TºC-SU	A-1	0.069
Pieris rapae	Multivoltine	A	P	P	A	A	MMCR	SPI-SU	A-1	-0.071
							MMCR	SPI-SP	A	0.063



Supp. Figure 4.1 Histogram showing the percentage of species affected by rain and temperature variables either positively (green) or negatively (red) according to their life-cycle stage (A-1: adults of the previous generation, L: Larvae, P: Pupae, A: adult of the current year). Data are presented separately according to the climatic region (MMCR: Mediterranean mesic region, aR: alpine climate region) and voltinism.



Supp. Figure 4.2 Percentage of species showing extreme population changes (Crashes - red, Explosions - green) each year in the studied time series in (a) the alpine climate region and (b) the Mediterranean mesic climate region.

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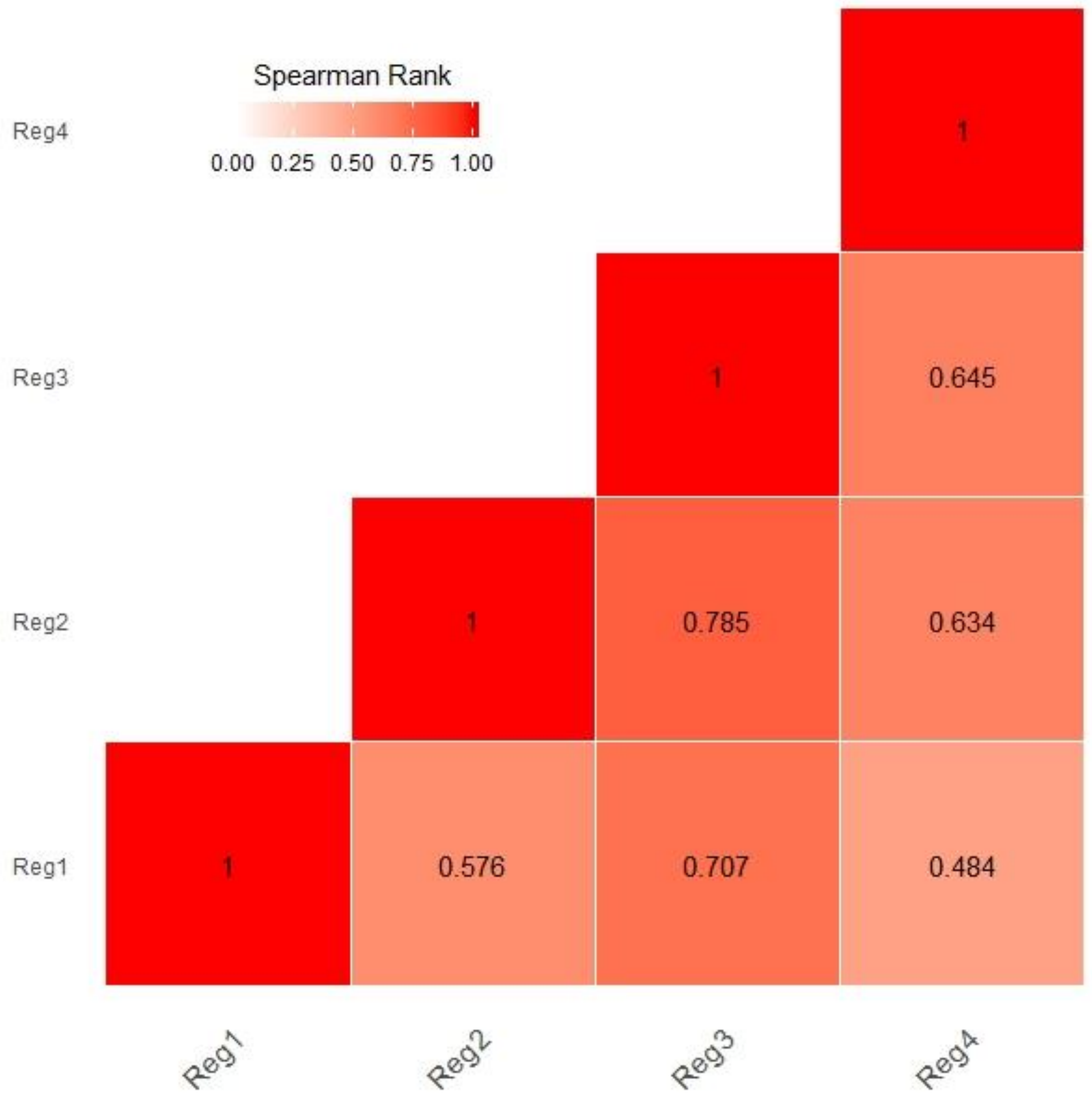
B. Chapter 5 Supporting Information

Supplementary table 5.1. List of all the I_{TAO} for the 147 studied species, ordered from the lowest to the highest value. Nitins refers to the number of itineraries where a species occurred. I_{TAO} desvest is the standard deviation of the TAO index.

IDesp	**Family**	**Nitins**	**I_{TAO}**	**I_{TAO} desvest**
Pararge aegeria	Nymphalidae	117	-0.419	0.432
Iolana debilitata	Lycaenidae	5	-0.389	0.820
Neozephyrus quercus	Lycaenidae	59	-0.291	0.603
Araschnia levana	Nymphalidae	14	-0.267	0.712
Limenitis camilla	Nymphalidae	45	-0.141	0.722
Leptidea sinapis	Pieridae	102	-0.099	0.459
Thecla betulae	Lycaenidae	15	-0.096	0.866
Polyommatus damon	Lycaenidae	5	-0.087	1.010
Polygonia c-album	Nymphalidae	85	-0.046	0.615
Anthocharis cardamines	Pieridae	87	-0.027	0.558
Nymphalis antiopa	Nymphalidae	42	-0.016	0.618
Pyronia bathseba	Nymphalidae	86	-0.007	0.414
Hipparchia fagi	Nymphalidae	43	0.003	0.695
Apatura ilia	Nymphalidae	42	0.025	0.825
Argynnis paphia	Nymphalidae	83	0.044	0.594
Coenonympha arcania	Nymphalidae	66	0.047	0.544
Nymphalis polychloros	Nymphalidae	71	0.049	0.706
Pieris napi	Pieridae	87	0.050	0.624
Celastrina argiolus	Lycaenidae	113	0.058	0.581
Gonepteryx rhamni	Pieridae	87	0.070	0.473
Limenitis reducta	Nymphalidae	92	0.083	0.616
Pieris mannii	Pieridae	87	0.109	0.719
Hipparchia alcyone	Nymphalidae	19	0.111	0.624
Anthocharis euphenoides	Pieridae	87	0.115	0.728
Lasiommata megera	Nymphalidae	120	0.116	0.430
Vanessa atalanta	Nymphalidae	118	0.134	0.484
Carcharodus lavatherae	Hesperidae	25	0.145	0.918
Gonepteryx cleopatra	Pieridae	87	0.161	0.463
Erebia meolans	Nymphalidae	18	0.164	0.672
Libythea celtis	Libytheidae	70	0.170	0.703
Brenthis daphne	Nymphalidae	32	0.185	0.720
Hipparchia fidia	Nymphalidae	63	0.197	0.619
Hipparchia semele	Nymphalidae	45	0.200	0.683
Pyronia tithonus	Nymphalidae	79	0.206	0.626
Charaxes jasius	Nymphalidae	74	0.208	0.631
Aphantopus hyperantus	Nymphalidae	14	0.216	0.814
Lasiommata maera	Nymphalidae	34	0.225	0.607
Satyrium esculi	Lycaenidae	96	0.229	0.400
Pieris brassicae	Pieridae	87	0.244	0.390
Euphydryas aurinia	Nymphalidae	66	0.248	0.624
Ochlodes venatus	Hesperidae	78	0.255	0.597
Maniola jurtina	Nymphalidae	112	0.257	0.478
Aglais io	Nymphalidae	76	0.259	0.623

Cupido minimus	Lycaenidae	46	0.274	0.730
Cupido osiris	Lycaenidae	23	0.279	0.662
Pieris rapae	Pieridae	87	0.284	0.373
Laeosopis roboris	Lycaenidae	18	0.309	0.741
Erebia neoridas	Nymphalidae	14	0.310	0.689
Hipparchia statilinus	Nymphalidae	76	0.313	0.582
Cupido alcetas	Lycaenidae	31	0.316	0.693
Argynnis addipe	Nymphalidae	34	0.317	0.658
Callophrys avis	Lycaenidae	34	0.321	0.752
Euphydryas desfontainii	Nymphalidae	6	0.326	0.696
Argynnis aglaja	Nymphalidae	36	0.340	0.686
Coenonympha dorus	Nymphalidae	40	0.346	0.587
Polyommatus ripartii	Lycaenidae	14	0.347	0.771
Boloria euphrosyne	Nymphalidae	10	0.357	0.645
Satyrium ilicis	Lycaenidae	22	0.359	0.609
Callophrys rubi	Lycaenidae	106	0.369	0.549
Glaucopsyche alexis	Lycaenidae	61	0.390	0.685
Thymelicus acteon	Hesperidae	85	0.394	0.570
Hamearis lucina	Riodinidae	15	0.406	0.643
Thymelicus sylvestris	Hesperidae	56	0.416	0.584
Polyommatus hispana	Lycaenidae	41	0.430	0.536
Satyrium spini	Lycaenidae	31	0.438	0.712
Iphiclides feisthamelii	Papilionidae	105	0.441	0.463
Brintesia circe	Nymphalidae	92	0.442	0.496
Satyrium w-album	Lycaenidae	16	0.443	0.865
Aglais urticae	Nymphalidae	45	0.448	0.667
Melanargia lachesis	Nymphalidae	98	0.450	0.445
Erebia triaria	Nymphalidae	11	0.451	0.531
Melitaea nevadensis	Nymphalidae	18	0.452	0.609
Aporia crataegi	Pieridae	63	0.454	0.619
Zerynthia rumina	Papilionidae	30	0.454	0.540
Polyommatus escheri	Lycaenidae	54	0.457	0.602
Polyommatus coridon	Lycaenidae	23	0.460	0.587
Glaucopsyche melanops	Lycaenidae	58	0.462	0.647
Satyrium acaciae	Lycaenidae	28	0.464	0.655
Muschampia proto	Hesperidae	11	0.467	0.701
Issoria lathonia	Nymphalidae	78	0.475	0.521
Polyommatus semiargus	Lycaenidae	24	0.475	0.679
Pseudophilotes panoptes	Lycaenidae	69	0.475	0.692
Thymelicus lineola	Hesperidae	24	0.480	0.575
Hesperia comma	Hesperidae	39	0.480	0.608
Pyronia cecilia	Nymphalidae	91	0.491	0.457
Leptotes pirithous	Lycaenidae	109	0.496	0.535
Cacyreus marshalli	Lycaenidae	62	0.496	0.703
Lampides boeticus	Lycaenidae	113	0.499	0.540
Melitaea diamina	Nymphalidae	12	0.500	0.746
Aricia cramera	Lycaenidae	73	0.503	0.523
Melitaea deione	Nymphalidae	63	0.504	0.566
Arethusana arethusa	Nymphalidae	18	0.509	0.559
Lycaena phlaeas	Lycaenidae	117	0.517	0.489
Papilio machaon	Papilionidae	119	0.517	0.486
Boloria dia	Nymphalidae	59	0.535	0.508
Vanessa cardui	Nymphalidae	119	0.537	0.354

Spialia sertorius	Hesperidae	71	0.540	0.655
Melitaea cinxia	Nymphalidae	51	0.540	0.565
Aricia agestis	Lycaenidae	47	0.543	0.447
Gegenes nostrodamus	Hesperidae	20	0.544	0.738
Colias alfacariensis	Pieridae	87	0.545	0.542
Pyrgus malvoides	Hesperidae	66	0.553	0.498
Polyommatus amandus	Lycaenidae	17	0.557	0.671
Cupido argiades	Lycaenidae	33	0.573	0.592
Maculinea arion	Lycaenidae	15	0.577	0.543
Scolitantides orion	Lycaenidae	9	0.584	0.697
Pyrgus armoricanus	Hesperidae	26	0.587	0.595
Melitaea trivia	Nymphalidae	25	0.591	0.618
Polyommatus fulgens	Lycaenidae	11	0.595	0.603
Melitaea parthenoides	Nymphalidae	83	0.596	0.514
Colias crocea	Pieridae	121	0.598	0.337
Polyommatus icarus	Lycaenidae	115	0.600	0.396
Euchloe crameri	Pieridae	87	0.601	0.496
Melitaea parthenoides	Nymphalidae	30	0.604	0.652
Pontia daplidice	Pieridae	87	0.608	0.465
Danaus chrysippus	Daniaidae	7	0.610	0.550
Argynnis pandora	Nymphalidae	29	0.613	0.608
Polyommatus bellargus	Lycaenidae	54	0.613	0.435
Carcharodus alceae	Hesperidae	102	0.626	0.511
Erynnis tages	Hesperidae	47	0.631	0.455
Chazara briseis	Nymphalidae	7	0.637	0.805
Plebejus argus	Lycaenidae	40	0.639	0.571
Polyommatus thersites	Lycaenidae	47	0.645	0.493
Carcharodus flocciferus	Hesperidae	22	0.646	0.693
Coenonympha pamphilus	Nymphalidae	73	0.654	0.441
Polyommatus celina	Lycaenidae	5	0.658	0.183
Lycaena alciphron	Lycaenidae	17	0.659	0.439
Lycaena virgaureae	Lycaenidae	9	0.669	0.439
Coenonympha glycerion	Nymphalidae	6	0.682	0.450
Melitaea didyma	Nymphalidae	78	0.696	0.450
Melanargia occitánica	Nymphalidae	23	0.705	0.461
Satyrus actaea	Nymphalidae	25	0.706	0.482
Tomares ballus	Lycaenidae	36	0.712	0.512
Parnassius apollo	Papilionidae	9	0.734	0.339
Pyrgus alveus	Hesperidae	8	0.741	0.385
Carcharodus baeticus	Hesperidae	18	0.745	0.666
Polyommatus dorylas	Lycaenidae	10	0.764	0.594
Boloria selene	Nymphalidae	7	0.766	0.407
Pyrgus cirsii	Hesperidae	10	0.783	0.458
Pyrgus carthami	Hesperidae	5	0.801	0.446
Plebejus idas	Lycaenidae	6	0.829	0.219
Lycaena tityrus	Lycaenidae	10	0.852	0.339
Melanargia russiae	Nymphalidae	7	0.853	0.230
Polyommatus daphnis	Lycaenidae	7	0.864	0.197
Argynnis niobe	Nymphalidae	5	0.949	0.114
Brenthis ino	Nymphalidae	5	0.974	0.037
Pyrgus serratulae	Hesperidae	7	1.000	0.000



Suplementary figure 5.1 Correlation heatmap for the TAO Index calculated for different thermal regions. Values indicate Spearman's Rank correlation. All relations resulted in a positive significant relationship (reg1~reg2: p=6.1e-09; reg1~reg3: p=2.2e-16; reg1~reg4: p=0.013; reg2~reg3: p<2.2e-16; reg2~reg4: p=4.9e-05; reg3~reg4: p=3.36e-05).

Suppl. Table 5.2 CORINE biotope codes and habitat description in with their binary value for open (+1) or closed (-1) habitats (OPCL). The number of square meters of each habitat type in the first and last botanical characterizations of the 54 long term monitored sites are given in the “First” and “Last” columns, respectively.

CORINE code	First	Last	OPCL	Description
15.12	157.50	0.00	1	Halonitrophilous herbaceous communities with Frankenia pulverulenta, Salsola soda, Hordeum marinum...
15.51	222.11	554.92	-1	Juncus maritimus beds of coastal and inland long-inundated, brackish depressions
15.52	532.50	1323.64	1	Humid meadows of low vegetation dominated by Hordeum marinum, Carex divisa, Juncus gerardi... of brackish soils
15.53	1271.51	1337.17	1	Meadows dominated by fleshy (Plantago crassifolia…) or junciform-leaved plants (Schoenus nigricans, Juncus acutus...) of saline, sandy, rather dry soils
15.54	330.56	189.09	1	Salt meadows, with Aeluropus littoralis… of low, marshy interior depressions
15.571*	286.67	0.00	1	Artemisia gallica formations of brackish wetlands
15.572*	0.00	567.27	1	Elymus spp. Beds
15.612	429.55	316.59	1	Coastal shrubby formations of Arthrocnemum fruticosum of temporarily inundated salt marshes
15.613	66.11	565.00	1	Shrubby Arthrocnemum macrostachyum formations of inundable dry, clayey, highly saline soils
15.616	159.62	333.09	1	Coastal low shrubby formations of Atriplex portulacoides on inundable dry, clayey, highly saline soils
15.618*	159.62	0.00	1	Shrubby Inula crithmoides formations on rather dry brackish soils
15.721	0.00	126.00	1	Interior, halo-nitrophilous scrubs dominated by Salsola vermiculata, Artemisia herba-alba, Kochia prostrata, Atriplex halimus…
15.81	789.62	390.91	1	Limonium rich communities on saline soils subject to extreme summer drying
16.111*	928.25	1069.59	1	Supralittoral unvegetated sandy beaches
16.12	22.08	0.00	1	Sand beach annual communities, with Cakile maritima, Salsola kali, Euphorbia peplis, Atriplex tornabenei…of sands rich in nitrogenous organic matter
16.2112	63.08	229.17	1	Open communitie of Elymus farctus, Sporobolus pungens… of embryonic dunes
16.2122	154.58	216.82	1	Coastal white dunes, dominated, when vegetated, by marram grass (Ammophila arenaria)
16.223	63.08	82.00	1	Coastal fixed dunes, with Crucianella maritima, Ononis natrix subsp. ramosissima, Thymelaea hirsuta…
16.228	1273.50	0.00	1	Annual-herb communities, with Medicago littoralis, Vulpia fasciculata, Desmazeria marina... of deep sands in dry interdunal depressions of southern coasts
16.229	65.50	196.50	1	Brachypodium retusum grasslands and related annual-herb communities in coastal sands
16.28	611.58	0.00	1	Shrubby formations on fixed coastal dunes
18.16	315.38	0.00	1	Supralittoral rocks
18.223*	63.08	410.00	1	Central and southern coastal cliffs
22.22*	0.00	38.64	1	Unvegetated shingles of water bottoms or shores
23.211	47.73	52.50	1	Submerged Ruppia beds of brackish waters
24.142*	0.00	107.22	1	Upper and middle zones of rivers (Cyprinidae zone)

24.21	1925.27	424.91	1	Unvegetated river gravel Banks
24.43	96.50	0.00	1	Submerged, mesotrophic river vegetetion, with Potamogeton densus, Callitriche stagnalis...
24.53	2840.56	189.55	1	Nitrophilous grass communities of lowland alluvial and coastal mud banks
31.215	47.27	65.00	1	Montane low Vaccinium heaths of the Pyrenees (and the Cantabrian range)
31.2261*	1564.08	582.05	1	Pyrenean and northern Catalanidic Calluna heaths, often with Genista pilosa, Genista anglica… of the montane and subalpine levels
31.412	85.50	124.03	1	Upper Pyrenean low Vaccinium heaths
31.42	85.50	266.53	-1	Alpenrose heaths of acid soils in snowy localities of the subalpine and alpine zones
31.431	234.00	331.17	-1	Juniperus nana formations of the subalpine zone
31.8111	2111.97	1597.78	-1	Rainy montane mesophile blackthorn-bramble thickets, characteristic of mesohygrophile forest edges and substitution formations
31.8122	268.84	80.17	-1	Sub-Mediterranean dry montane blackthorn-bramble thickets
31.8127*	116.25	268.33	-1	Alluvial forest hygrophile and sub-nitrophilous elder formations, with Clematis vitalba, Rubus ulmifolius...
31.8414	3202.04	1511.92	-1	Acidophile, mesophile broom formations of rainy montane (and lowland) areas
31.863	1977.42	2673.44	-1	Sub-Mediterranean montane (and lowland) bracken fields
31.872	169.00	386.61	-1	Subalpine (and montane) shrubby clearing formations, with Sambucus racemosa, Salix caprea, Rubus idaeus...
31.881	76.50	266.45	-1	Common juniper colonization of montane grasslands
31.891	28091.15	27599.89	-1	Lowland (and montane) thickets with Rubus ulmifolius, Coriaria myrtifolia...
31.8C1*	679.40	234.58	-1	Montane meso-hygrophile hazel formations
31.8C2*	1075.86	1691.88	-1	Lowland (and submontane) hazel formations of ravines and deep valleys
31.8C3*	1512.03	1352.40	-1	Montane mesophile or mesoxerophile hazel formations
32.1121*	1723.25	1190.50	-1	Acidiphile holm oak (Quercus ilex) maquis of the lowlands and Mediterranean mountains
32.1131*	351.53	1647.58	-1	Calciphile holm oak (Quercus ilex) maquis of the lowlands and Mediterranean mountains
32.1134*	196.36	0.00	-1	Lowland and submontane calciphile Quercus rotundifolia maquis
32.123	50.00	0.00	-1	Lowland lentisc (Pistacia lentiscus) maquis
32.1311	0.00	97.22	-1	Maquis and garrigues organized around arborescent Juniperus oxycedrus of dry, rocky slopes and deforested areas
32.1321	0.00	185.63	-1	Juniperus phoenicea subsp. phoenicea formations occupying steep rocky slopes
32.1322	315.38	82.00	-1	Juniperus phoenicea subsp. turbinata formations of abrupt coastal shores
32.143	1579.10	1360.27	-1	Maquis and garrigues dotted by Aleppo pine (Pinus halepensis)
32.1B*	294.54	154.50	-1	Calcicolous strawberry tree (Arbutus unedo) formations of the lowlands and Mediterranean mountains
32.211	420.36	284.30	-1	Thermo-Mediterranean Oleo-lentisc garrigues
32.214	2478.54	5019.60	-1	Thermo-Mediterranean Pistacia lentiscus dominated garrigues
32.215	0.00	558.89	-1	Thermo-Mediterranean Calicotome spinosa dominated garrigues
32.2191	3087.82	5147.08	-1	Thermo-Mediterranean kermes oak garrigues
32.21C	0.00	109.55	1	Thermo-Mediterranean Osyris formations

32.21I	71.67	0.00	-1	Formations dominated by prostrate or low shrubby Juniperus phoenicea or J. oxycedrus, growing on warm maritime areas
32.23	435.05	153.19	1	Thermo-Mediterranean scrub or garrigues invaded and dominated by the high tussocks of Ampelodesmos mauritanica
32.24	0.00	209.25	-1	Thermo-Mediterranean garrigues dominated by palmetto (Chamaerops humilis)
32.2D*	2079.59	0.00	-1	Other thermo-Mediterranean garrigues
32.311	1347.92	1624.66	-1	Western Mediterranean strawberry tree (Arbutus unedo) formations and related silicicolous communities
32.321*	274.51	614.78	-1	Lowland (and montane) Erica scoparia heaths, established on deep, rather moist soils
32.322*	940.64	3038.97	-1	Erica arborea heaths of maritime territories, established on dry-soil slopes
32.341	1513.58	2524.14	1	Silicicolous Cistus monspeliensis formations of maritime zones
32.342	5658.64	2827.82	1	Silicicolous Cistus salviifolius formations of maritime zones
32.348	332.31	471.88	1	Silicicolous Cistus albidus formations of the lowlands
32.351	78.50	0.00	1	Lowland dry-soil Lavandula stoechas formations
32.36	7052.19	0.00	1	Lowland sparse, low silicicolous formations of Cistus, Erica…
32.374*	669.15	0.00	-1	Sarothamnus catalaunicus heaths of maritime, rainy zones of the Ruscinic and northern Catalanidic territories
32.375*	312.67	158.33	-1	Formations dominated by Calicotome spinosa of maritime zones
32.378*	343.13	310.81	-1	Silicicolous Anthyllis cytisoides lowland formations of slightly acid terrains
32.379*	290.45	0.00	-1	Ulex parviflorus), silicícolas, de las tierras mediterráneas marítimas Maritime heaths rich in other leguminous shrubs
32.41	1361.84	371.48	-1	Kermes oak garrigues with little or no thermo-Mediterranean plants
32.42	7364.27	8159.27	1	Lowland rosemary scrubs
32.431	1242.84	322.31	1	Calcicolous Cistus albidus formations of the lowlands
32.432	0.00	44.00	1	Thermo-Mediterranean Cistus clusii formations
32.433	205.00	459.27	1	Calcicolous Cistus salviifolius formations of the lowlands
32.45	0.00	125.51	-1	Low scrubs dominated by Juniperus oxycedrus
32.47	1844.25	2911.91	1	Very low, open scrubs dominated by Thymus spp., Satureja montana, Sideritis scordioides or other labiate shrubs (except Lavandula)
32.4811*	238.43	210.45	1	Lowland and montane Genista scorpius formations
32.4A2	493.33	201.92	1	Lowland and montane formations dominated by small-leaved Artemisia species
32.4A3	612.31	221.16	1	Lowland formations dominated by the invasive Inula viscosa of abandoned fields, watercourse beds, waste places…
32.4B + 32.2121	1666.67	843.33	1	Calciphile Erica multiflora formations of maritime zones
32.4C	261.84	203.83	1	Lowland Globularia alypum scrubs
32.4D	1685.63	1662.27	1	Formations dominated by small or dwarf shrubs of the genera Helianthemum (H. syriacum, H. hirtum…) or Fumana (F. ericoides, F. thymifolia...) of dry localities of the lowlands
32.4E	239.85	128.13	1	Low scrubs dominated by Lithospermum fruticosum of the lowlands
32.4G	422.73	86.36	-1	Lowland tall formations dominated by Bupleurum fruticosum, characteristic of holm-oak forest edges

32.4H + 32.274	151.08	265.03	-1	Mediterranean calcicolous scrubs dominated by Ulex parviflorus
32.4L*	44.00	0.00	1	Dry Mediterranean calcicolous scrubs with abundant or dominant Genista biflora colonies, mainly in inner territories
32.641*	5870.88	5035.53	-1	Montane (and Mediterranean) box formations
32.A	670.13	1037.41	-1	Formations of Spanish broom (Spartium junceum) in Mediterranean, mainly maritime, areas
34.32611*	12155.39	8618.32	1	Calcicolous mesophile grasslands, with Festuca nigrescens, Plantago media, Galium verum, Cirsium acaule... of the montane and subalpine zones of the Pyrenees and neighbouring areas
34.332G1*	762.78	637.86	1	Pyrenean xerophile calcareous grasslands, with Festuca ovina, Avenula iberica, Bromus erectus, Brachypodium phoenicoides, Seseli montanum, Teucrium pyrenaicum… of the montane belt
34.36	45833.80	32510.04	1	Dry grasslands usually dominated by Brachypodium phoenicoides, with Euphorbia serrata, Galium lucidum…on eutrophic, deep soils of the lowlands and low Mediterranean mountains
34.37*	810.15	537.75	1	Plantago albicans formations of clayey soils of the lowlands
34.41	6409.90	6248.84	1	Montane (and Mediterranean) hems of semi-dry oak woods and related communities, with Origanum vulgare, Geranium sanguineum, Tanacetum corymbosum, Oryzopsis paradoxa…
34.42	864.05	843.45	1	Montane mesophile hems of beech or ash woods and related communities, with Trifolium medium, Trifolium ochroleucon, Valeriana officinalis…
34.511	12687.50	5922.24	1	Calcicolous grasslands dominated by Brachypodium retusum and with many therophytes and geophytes, of the lowlands
34.5131	10282.90	10894.71	1	Western Mediterranean calciphile annual communities
34.6321*	1258.33	792.20	1	Open lowland formations dominated by Oryzopsis miliacea of abandoned fields, waste places…
34.6322*	407.59	398.13	1	Calcicolous dry grasslands dominated by feathergrass species (Stipa offneri, S. pennata, S. capillata), often rich in low shrubs and therophytes, of the lowlands (and the montane zone)
34.633	1775.51	3299.45	1	Thermo-Mediterranean formations dominated by Ampelodesmos mauritanica
34.634	548.07	704.41	1	Andropogonid dry grasslands colonizing sunny slopes of maritime zones
34.7133	916.36	1216.40	1	Xerohile calcicolous grasslands, often rich in chamaephytes, with Ononis striata, Anthyllis montana, Globularia cordifolia…of the montane (and subalpine) belt, mainly in the Prepyrenees
34.721	10384.02	11177.09	1	Calcicolous Aphyllanthes grasslands, often rich in chamaephytes, of Mediterranean areas and semi-dry montane belt
34.81	8549.69	4254.87	1	Subnitrophilous annual grasslands (or thistle formations), with Aegilops geniculata, Bromus rubens, Medicago rigidula, Carthamus lanatus… of the lowlands
35.122*	7795.63	9242.75	1	Anthoxanthum odoratum, Galium verum, Genistella sagittalis… of the montane and subalpine belts of the Pyrenees
35.21	1806.80	1618.58	1	Dwarf annual siliceous grasslands, with Aira caryophyllea, Vulpia myuros, Filago minima, Trifolium arvense… in particular of sandy soils, of the montane zone

35.31*	7353.26	5361.25	1	Siliceous grasslands rich in therophytes (Helianthemum guttatum, Tolpis barbata, Crassula tillaea, Silene gallica, Aira cupaniana), often with stonecrops (Sedum spp.) of the lowlands
35.32*	4244.60	6486.13	1	Silicicolous dry grasslands dominated by Brachypodium retusum, rich in therophytes, of the lowlands
35.81*	8408.37	6649.28	1	Montane silicicolous dry grasslands, with Agrostis capillaris, Seseli montanum, Festuca ovina, Dichanthium ischaemum… of the Pyrenees and the Montseny massif
36.311	580.00	516.53	1	Subalpine and lower alpìne mesophile mat-grasslands
36.3311	675.95	546.52	1	Silicicolous Festuca paniculata grasslands on rocky soils of steep, warm slopes of the subalpine level of the Pyrenees
37.242	0.00	58.71	1	Montane subnitrophilous swards of temporarly flooded, trampled soils
37.26*	0.00	107.22	-1	Northern and central Catalanidic tall herb formations with horsetails (Equisetum telmateia) and sedges (Carex pendula, C. remota) of ravines and marshy soils
37.311	473.67	172.63	1	Montane calcareous purple moorgrass meadows
37.312	0.00	42.50	1	Montane neutro-acidiphile purple moorgrass meadows
37.4	2978.55	839.29	1	Lowland (and montane) hygrophile rush and tall grass formations, with Scirpus holoschoenus
37.5	1842.73	912.49	1	Short grasslands of impermeable compact soils, wet and temporaly inundated, of the lowlands
37.71	206.16	0.00	-1	Subnitrophilous tall herb fringes and screens or veils lining watercourses
37.72	1006.45	343.75	1	Montane subnitrophilous shady woodland edge fringes
37.83	256.50	287.08	1	Subalpine meso-hygrophile tall herb communities of the Pyrenees and the Montseny massif
37.88	292.00	0.00	1	Alpine and subalpine nitrophilous communities of Chenopodium bonus-henricus, and related tall herb formations
37.89*	332.50	158.33	1	Subalpine tall herb communities with Trollius europaeus, Polygonum bistorta…
38.112	1174.49	2737.72	1	Mesophile regularly grazed grasslands dominated by Cynosurus cristatus
38.23	2971.28	5431.60	1	Montane and submontane hay meadows, with Arrhenatherum elatius
38.24*	9189.46	9846.63	1	Lowland hay meadows, usually with Gaudinia fragilis, in rainy areas
38.3	1373.50	1048.72	1	Meso-hygrophile hay meadows, mainly of upper montane and subalpine levels
41.172	0.00	76.11	-1	Eastern Pyrenees and Cévennes acidophilous beech forests
41.1751	0.00	88.85	-1	Sub-Mediterranean calcicolous beech forests, often with box
41.2A*	1248.23	76.11	-1	Mesohygrophile Quercus petraea forests of the Pyrenees and the northern Catalanidic mountains
41.33	1158.59	1867.70	-1	Ash forests of the Pyrenees and the northern Catalanidic mountains
41.7131*	1704.86	1365.46	-1	Calcicolous montane white oak woods, and other related communities
41.7132*	1200.45	1004.45	-1	Silicicolous montane white oak woods
41.714	1948.69	2663.29	-1	Silicicolous montane white oak woods
41.7713	170.32	424.01	-1	Calcicolous Quercus faginea woods of rather dry sub-Mediterranean mountains (and the lowlands)
41.9	713.08	623.33	-1	Montane and lowland chestnut woods
41.B332*	662.68	891.50	-1	Other Pyrenean and northern Catalanidic birch woods, often secondary or subclimax formations
41.D4	0.00	83.50	-1	Mesophile aspen stands, often lacking in a woody understory, occurring within the environment of the deciduous or evergreen broad-leaved forests

42.113	0.00	110.00	-1	Acidophilous inner Pyrenean fir forests
42.413	85.50	71.25	-1	Pyrenean alpenrose mountain pine forests
42.4241	234.00	86.67	-1	Xerophile mountain pine forests of siliceous Pyrenean adrets
42.43	110.00	162.78	-1	Mountain pine woods, or reforestations, lacking in a forestry understory
42.561	183.00	0.00	-1	Pyrenean calcicolous mesophile Scots pine forests
42.5921*	419.18	0.00	-1	Pyrenean calcicolous xerophile Scots pine forests
42.5922*	866.88	674.41	-1	Neutro-basophile and mesophile Scots pine forests of the Pyrenees and other northern areas
42.5A23*	0.00	191.76	-1	Calcicolous Scots pine forests of southern areas
42.5B11*	796.32	1086.90	-1	Acidophilous and xerophile Scots pine forests of montane and sub-montane belt
42.5E	1634.68	1613.52	-1	Scots pine woods, or reforestations, lacking in a forestry understory
42.5F*	590.91	590.91	-1	Scots pine woods with a Mediterranean shrub layer
42.637*	221.67	375.88	-1	Southern Mediterranean mountains Salzmann’s pine forests
42.67	1115.85	844.67	-1	Salzmann’s pine forests, or reforestation, lacking in a forestry understory
42.8217	213.33	212.38	-1	Catalonian mesogean pine forests, with an acidophilous shrub layer
42.827*	864.44	751.35	-1	Catalonian mesogean pine woods or reforestations lacking in a shrub layer
42.8315	4445.37	3542.42	-1	Catalonian stone pine forests
42.8412*	0.00	1633.49	-1	Aleppo pine forests with a shrubby Quercus coccifera layer
42.8413*	5272.81	6926.40	-1	Aleppo pine forests with a shrubby Quercus ilex or Q. rotundifolia layer
42.8414*	3641.23	2774.76	-1	Maritime Aleppo pine forests with a calcicolous scrub layer
42.8415*	355.77	624.60	-1	Inner Alepo pine forests with a calcicolous scrub layer
42.8416*	1265.61	0.00	-1	Lowland Aleppo pine forests with a siliceous shrub layer
42.8417*	2562.74	4535.71	-1	Aleppo pine forests lacking in a woody understory
42.B5*	0.00	122.50	-1	Other mixed coniferous Woods
44.122	46.22	264.35	-1	Lowland willow shrubby formations
44.124	337.00	0.00	-1	Montane willow shrubby formations
44.128*	274.44	451.53	-1	Catalanidic low forests of Salix atrocinerea, with Equisetum telmateia, Carex pendula… of ravines and other wett sites
44.316*	195.56	160.00	-1	Pyrenean and northern Catalanidic alder forests with Carex remota, growing close to water courses or on very wet soils
44.3431*	671.71	461.25	-1	Pyreneo-Catalonian alder galleries, with Circaea lutetiana
44.3432*	955.81	632.22	-1	Sub-montane and lowland alder galleries, with Lamium flexuosum
44.462*	199.44	303.23	-1	North Catalanidic mixed ash-elm-oak riparian forests
44.515*	96.50	0.00	-1	Lowland laurel or mixed laurel-alder galleries
44.6111*	34.44	373.18	-1	Lowland, and montane, poplar galleries, with Vinca difformis
44.612	183.22	473.18	-1	Poplar galleries, with Iris foetidissima
44.62	3093.19	4725.84	-1	Mediterranean riparian elm forests
44.637*	1067.57	4380.53	-1	Lowland Fraxinus angustifolia-dominated galleries

44.812	213.82	0.00	-1	Chaste tree formations
44.8131	467.50	731.26	-1	Tamarisk formations on slightly saline soils
45.2161*	2685.25	2081.77	-1	Cork-oak woods with a forestry understory
45.2162*	0.00	82.22	-1	Catalan cork-oak woodland with an acidophillous shrubby layer
45.3121*	10328.53	16822.36	-1	Catalano-Provençal lowland holm-oak forests
45.3122*	5603.98	8196.45	-1	Lowland and sub-Montane forests of mixed holm-oak and deciduous oaks
45.3123*	5324.73	6146.20	-1	Lowland forests of mixed holm-oak and pines
45.3131*	4098.21	5115.40	-1	Siliceous montane holm-oak forests
45.3132*	1630.87	2412.76	-1	Calcicolous montane holm-oak forests
45.3133*	1536.82	525.00	-1	Montane mixed holm-oak and pines forests
45.3411	123.89	792.32	-1	Continental Quercus rotundifolia Woodland
45.3415*	2088.66	2827.62	-1	Montane Quercus rotundifolia Woodland
45.3416*	1013.15	253.94	-1	Quercus rotundifolia woodland, with deciduous oaks (Quercus faginea, Q. pubescens...)
45.3417*	502.15	436.36	-1	Quercus rotundifolia woodland, with pines
53.1	482.96	0.00	-1	Reed beds
53.111	0.00	249.55	-1	Flooded Phragmites beds
53.112	2269.56	3564.05	-1	Reed beds dry for a large part of the year
53.18*	0.00	186.50	1	Lowland water-fringe communities with Iris pseudacorus, Polygonum salicifolium...
53.2192	0.00	138.00	1	Formations dominated by Carex cuprina of water-fringe and humid sites
53.62	932.00	0.00	-1	Provence cane beds along water courses
54.111	0.00	42.50	1	Soft water bryophyte springs
54.4241*	0.00	59.44	1	Pyrenean black sedge acidic fens
54.4242*	127.50	127.50	1	Pyrenean acidic fens with black sedge and sphagnums
54.452	297.50	212.50	1	Pyrenean deergrass acidic fens
61.12	1701.14	1470.05	1	Montane siliceous screes, with Epilobium collinum, Galeopsis spp…
61.32	970.34	1438.93	1	Mediterranean low mountains screes
61.371*	159.14	379.66	1	Pyrenean fern-dominated chaotic, boulder fields of siliceous high mountains
61.51*	2818.08	2053.23	1	Calcareous, mainly marly or gipsaceous, badlands, nacked or poorly vegetated
61.52*	305.14	696.42	1	Siliceous, clayey or gritty, badlands, nacked or poorly vegetated
62.1111	0.00	491.67	1	Mediterranean calcareous and dolomitic cliffs, with chasmophytic vegetation
62.1115	0.00	85.00	1	Mediterranean, shaded calcareous cliffs, with mostly comophytic bryophytes and ferns
62.1C*	158.75	0.00	1	Shaded calcareous cliffs, with mostly comophytic bryophytes and ferns, of the montane level and Mediterranean mountains
62.26	196.11	86.36	1	Siliceous cliffs, with Antirrhinum asarina… of the montane level (and cool lowlands
62.28	1046.95	1288.56	1	Mediterranean siliceous, warm and dry cliffs, with Cheilanthes tinaei

62.2B*	149.00	300.00	1	Mediterranean, shaded siliceous cliffs, with mostly comophytic bryophytes and ferns
62.31* + 36.2p	905.23	270.75	1	Siliceous rocky outcrops of the montane and subalpine levels, colonized by stonecrops (Sedum spp.) and houseleaks (Sempervivum spp.)
62.32*	6732.87	6366.31	1	Limestone and conglomeratic rocky outcrops of the Pyrenees and the Catalanidic mountains, colonized by Erodium spp., Arenaria aggregata, Allium senescens…
62.41	693.17	1268.55	1	Limestone inland cliffs, colonized by communities of lichens
62.42	348.25	597.78	1	Siliceous inland cliffs, colonized by communities of lichens
62.7*	1174.37	2635.78	1	Rocks and walls colonized by subnitrophilous communities
81.1	0.00	183.33	1	Dry or mesophile intensive pastures
82.11	675.00	0.00	1	Cereal and other crops grown on large, unbroken surfaces
82.12	1642.50	0.00	1	Intensive cultivation of vegetables, flowers…, usually in alternating strips of different crops
82.31*	95.00	2549.42	1	Irrigated or wet extensive cultivation
82.32*	7828.54	8105.35	1	Lowland dry extensive cultivation
82.33*	433.38	1362.00	1	Mountain dry extensive cultivation
82.41	0.00	262.27	1	Rice fields
83.11	147.50	747.32	1	Olive groves
83.14	1410.06	629.32	1	Almond groves
83.15	564.97	666.13	-1	High-stem orchards of apple, pear, peach and other Rosaceae
83.182*	1309.56	1011.68	1	Other high-stem orchards
83.212	0.00	1847.13	1	Intensive vineyards
83.3121	135.00	135.00	-1	Exotic cedar, douglas fir… plantations
83.3123	107.22	263.18	-1	Other exotic pine plantations
83.321	1399.96	252.22	-1	Poplar plantations
83.324	270.45	47.00	-1	Locust tree plantations
83.3251*	1238.55	1323.27	-1	Oriental plane and other broad-leaved tree plantations on wet soils
83.3252*	423.33	636.89	-1	Other broad-leaved tree plantations
84.11*	82.22	61.67	-1	Evergreen tree lines
84.2	321.59	320.63	-1	Hedgerows
85.3	1800.14	1890.70	1	Gardens
86.1	0.00	170.00	1	Towns
86.2	316.67	199.50	1	Villages
86.43	503.08	1019.13	1	Railroad switch yards and other open spaces
87.1	3303.79	2174.56	1	Fallow fields
87.21*	42963.59	41629.34	1	Lowland ruderal communities
87.22*	442.84	1079.59	1	Mountain ruderal communities

87.61*	0.00	65.00	-1	Groves and bushes of alien species
89.22	0.00	743.75	1	Ditches and small Canals
90.1	0.00	447.67	-1	Forest areas strongly clear-cut

C. Chapter 6 Supporting Information

Supplementary table 6.1. List of all vascular plants recorded within the 20 plots studied in Catllar valley, with 1 for presence and 0 for absence.

Taxon	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20	Nº
Achillea millefolium	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Aconitum anthora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	3
Aconitum napellus	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	1	1	1	9
Aconitum vulparia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	2
Agrimonia eupatoria	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Agrostis capillaris	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Agrostis rupestris	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	4
Alchemilla alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	3
Alchemilla cf. fissa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Alchemilla hybrida subsp. flabellata	0	1	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	13
Alchemilla vulgaris	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Alnus glutinosa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Androsace carnea subsp. carnea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anemone hepatica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
Angelica sylvestris	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Antennaria dioica	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	3
Anthoxanthum odoratum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Anthyllis vulneraria	1	1	1	0	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	1	12
Antirrhinum asarina	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Aquilegia vulgaris	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Arabis alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Arabis brassica	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	5
Arabis ciliata	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	1	1	0	9
Arabis glabra	1	0	0	1	0	0	0	1	1	0	0	0	1	0	1	0	1	1	1	0	9
Arabis hirsuta	1	1	1	0	0	0	1	1	1	0	0	0	1	1	1	0	1	1	1	0	12

Arabis turrita	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
Arctium minus	0	1	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	1	0	12
Arenaria serpyllifolia	1	1	1	1	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	13
Armeria alliacea	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	11
Arnica montana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
Arrhenatherum elatius	1	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	6
Artemisia vulgaris	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
Asplenium septentrionale	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2
Asplenium viride	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Aster alpinus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
Astrantia major	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2
Athyrium filix-femina	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Avenula pratensis	0	0	1	1	0	1	1	1	0	1	1	1	0	0	1	1	1	1	1	1	14
Barbarea intermedia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Bellardiochloa violacea	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Betula pendula	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	5
Biscutella laevigata	1	1	1	1	0	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	13
Botrychium lunaria	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	3
Brachypodium sylvaticum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Briza media	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	17
Bromus hordeaceus	1	1	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	16
Bromus sterilis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Bryonia cretica subsp. dioica	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Bupleurum ranunculoides	0	0	1	1	1	1	1	1	0	1	0	1	0	0	1	1	1	1	1	1	14
Calluna vulgaris	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	1	5
Caltha palustris	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Campanula glomerata	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	3
Campanula persicifolia	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
Campanula rapunculoides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Campanula scheuchzeri	0	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	17
Campanula trachelium	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Capsella bursa-pastoris	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20

Cardamine impatiens	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2
Cardamine pratensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Cardamine raphanifolia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Carduus carlinoides	0	1	1	0	1	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	15
Carduus crispus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Carex caryophyllea	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	19
Carex cuprina	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Carex echinata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Carex frigida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Carex muricata	1	1	0	0	1	0	1	0	1	0	1	0	1	1	0	0	1	0	0	0	9
Carex ovalis	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	0	6
Carex pallescens	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2
Carex umbrosa	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	5
Carlina acanthifolia	1	1	1	1	0	1	1	0	0	1	1	0	1	1	1	0	1	1	1	0	14
Carlina acaulis	0	1	1	1	1	1	1	1	0	1	0	1	0	1	1	0	0	1	1	1	14
Carum carvi	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	18
Centaurea jacea	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	16
Cerastium alpinum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cerastium arvense	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	19
Cerastium fontanum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Chaerophyllum aureum	1	1	1	1	0	0	1	0	1	0	1	0	1	1	1	0	0	1	1	0	12
Chaerophyllum hirsutum	1	1	1	1	0	0	1	0	1	0	1	0	1	1	1	0	0	1	1	0	12
Chamaespartium sagittale	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	19
Chenopodium album	0	0	1	1	0	0	1	1	0	0	0	0	1	1	1	0	1	1	1	0	10
Chenopodium bonus-henricus	0	1	1	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	16
Chrysosplenium oppositifolium	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Cirsium acaule	0	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	1	1	0	1	11
Cirsium eriophorum	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	19
Cirsium palustre	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Cirsium rivulare	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Coincya cheiranthos	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
Conopodium majus	1	1	0	1	1	0	1	1	1	0	1	0	1	1	1	0	1	0	0	0	12

Corylus avellana	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1	1	0	6
Crataegus monogyna	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Crepis capillaris	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	6
Crepis lampsanoides	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Crepis mollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Crepis pyrenaica	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Cruciata glabra	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	16
Cruciata laevipes	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	0	1	1	1	0	15
Cuscuta epithymum	1	1	1	1	0	0	1	0	0	1	0	1	1	1	1	1	1	1	1	0	14
Cuscuta europaea	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	16
Cynoglossum officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Cynosurus cristatus	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	1	0	8
Cystopteris fragilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Dactylis glomerata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Dactylorhiza elata subsp. sesquipedalis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Dactylorhiza maculata	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	1	6
Dactylorhiza sp.	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Danthonia decumbens	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	3
Daphne mezereum	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	4
Daucus carota	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	5
Deschampsia flexuosa	0	0	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	15
Dianthus deltoides	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	19
Dianthus hyssopifolius	1	1	1	1	0	0	1	1	0	0	1	0	1	1	1	1	1	1	1	1	15
Digitalis lutea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Draba nemorosa	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Dryopteris filix-mas	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	3
Echium vulgare	1	1	0	1	0	0	1	1	1	0	1	0	1	1	1	0	1	1	1	0	13
Epilobium alsinifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Epilobium montanum	0	0	0	1	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	0	10
Epilobium palustre	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Equisetum arvense	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Erigeron annuus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2

Eryngium bourgatii	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	16
Erysimum grandiflorum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Euphrasia hirtella	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	17
Euphrasia salisburgensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Euphrasia stricta	1	0	0	1	1	1	0	1	0	1	0	1	1	1	0	1	1	1	1	1	14
Fallopia dumetorum	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	3
Festuca arundinacea	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Festuca gautieri	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	5
Festuca heterophylla	1	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	8
Festuca nigrescens	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	19
Festuca ovina	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Festuca pratensis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Festuca rivularis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Filipendula ulmaria	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Fragaria vesca	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	4
Fraxinus excelsior	0	0	1	1	0	0	1	1	1	1	1	0	1	0	1	0	1	1	1	0	12
Galeopsis tetrahit	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	16
Galium aparine	0	1	1	1	0	0	1	1	1	0	1	0	1	1	1	0	0	1	0	0	11
Galium maritimum	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Galium pumilum	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	19
Galium verum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Genista balansae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	2
Genista pilosa	0	0	1	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	1	1	11
Gentiana acaulis	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	1	0	1	7
Gentiana campestris	0	0	0	0	0	1	0	1	0	1	1	1	1	1	0	1	1	1	1	1	12
Gentiana lutea	1	1	1	1	0	0	1	1	0	0	1	0	0	1	1	1	0	1	1	1	13
Gentiana verna	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	1	6
Geranium columbinum	1	1	1	1	0	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	12
Geranium pratense	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2
Geranium pusillum	1	1	1	1	0	0	1	0	1	0	1	0	1	0	1	1	1	1	1	0	13
Geranium pyrenaicum	1	1	1	1	1	0	1	0	1	0	0	0	1	1	1	0	1	1	1	0	13
Geranium robertianum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1

Geranium sylvaticum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Geum urbanum	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	6
Glyceria fluitans	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Gymnadenia conopsea	1	1	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	9
Helianthemum nummularium	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	18
Helleborus foetidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
Helleborus viridis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	3
Heracleum sphondylium	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2
Hieracium breviscapum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hieracium lactucella	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	7
Hieracium pilosella	1	1	1	1	1	1	1	1	0	1	0	1	0	0	1	1	1	0	1	1	15
Hippocrepis comosa	0	1	1	0	0	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	9
Holcus lanatus	1	1	0	0	1	0	0	0	1	0	1	0	1	1	0	0	1	1	0	0	9
Holcus mollis	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	3
Hypericum maculatum	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	19
Hypochoeris maculata	1	1	0	1	0	0	1	0	1	0	1	0	1	1	1	0	1	1	1	0	12
Hypochoeris radicata	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	4
Ilex aquifolium	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Jasione crispa	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Jasione montana	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
Juncus articulatus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Juncus bufonius	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Juncus effusus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Juncus inflexus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Juncus trifidus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	3
Juniperus communis communis	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	2
Juniperus nana	0	1	1	1	0	1	1	1	0	1	0	1	0	1	1	1	1	0	1	1	14
Koeleria macrantha	0	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	1	0	1	1	12
Koeleria pyramidata	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	17
Lamium album	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Lapsana communis	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	5
Laserpitium latifolium	1	1	1	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	1	0	13

Lathyrus linifolius	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	3
Lathyrus pratensis	1	1	0	1	0	0	1	0	1	0	1	0	1	1	1	0	1	1	1	0	12
Leontodon autumnalis	1	0	1	1	0	0	1	0	1	0	1	0	1	1	1	0	1	1	0	0	11
Leontodon duboisii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Leontodon hispidus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Leucanthemum vulgare	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	1	1	0	8
Ligusticum lucidum	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lilium martagon	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	4
Linaria repens	0	1	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	6
Linum catharticum	1	1	0	1	0	0	1	0	1	0	1	0	1	1	1	0	1	1	1	0	12
Listera ovata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
Lolium perenne	0	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	0	15
Lonicera nigra	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Lotus corniculatus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Luzula campestris	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	18
Luzula multiflora	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Luzula spicata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Malva neglecta	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	7
Malva sylvestris	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Medicago lupulina	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	4
Medicago suffruticosa	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	4
Mentha longifolia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Minuartia laricifolia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	3
Moehringia trinervia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2
Molinia coerulea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Molopospermum peloponnesiacum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
Montia fontana	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Myosotis alpestris	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	6
Myosotis arvensis	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	0	0	1	0	1	8
Myosotis scorpioides subsp. tuxeniana	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Myosotis sylvatica subsp. teresiana	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	3
Nardus stricta	0	0	1	0	1	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	9

Nigritella austriaca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Nigritella gabasiana	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Odontites vernus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	3
Ononis spinosa	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	5
Orchis ustulata	1	1	0	0	0	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	8
Origanum vulgare	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	5
Orobanche alba	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2
Orobanche minor	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Orobanche purpurea	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Orobanche rapum-genistae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Orobanche reticulata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Oxalis acetosella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Parnassia palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Petrorhagia prolifera	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Phleum pratense	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	19
Phyteuma hemisphaericum	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	3
Phyteuma spicatum	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	3
Picris hieracioides	1	0	0	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	8
Pimpinella saxifraga	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	18
Pinus sylvestris	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Pinus uncinata	0	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	0	1	0	0	7
Plantago lanceolata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Plantago major	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	19
Plantago media	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	19
Plantago monosperma	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	1	0	1	0	1	8
Platanthera bifolia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Platanthera chlorantha	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	3
Poa alpina	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	18
Poa chaixii	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Poa nemoralis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	3
Poa supina	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Polygala alpestris	0	1	1	1	0	0	1	1	1	0	1	1	1	1	1	0	1	1	1	0	14

Polygonatum verticillatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Polygonum alpinum	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	7
Polygonum aviculare	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Polygonum bistorta	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	4
Polygonum convolvulus	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Polygonum persicaria	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2
Polygonum viviparum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Polypodium vulgare	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	4
Populus tremula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Potentilla crantzii	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3
Potentilla erecta	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Potentilla micrantha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Potentilla neumanniana	0	0	1	0	0	1	1	1	0	1	0	0	1	0	1	0	1	1	1	0	10
Potentilla pyrenaica	0	1	1	1	1	1	0	1	0	1	0	1	0	0	1	1	1	1	1	1	14
Potentilla reptans	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Primula elatior	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1	1	0	1	1	1	13
Primula veris subsp. columnae	0	1	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	0	0	6
Prunella grandiflora subsp. pyrenaica	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	17
Prunella vulgaris	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	4
Prunus avium	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Pteridium aquilinum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Pulsatilla alpina	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	4
Quercus petraea	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ranunculus acris subsp. friesianus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	4
Ranunculus bulbosus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Ranunculus montanus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2
Ranunculus repens	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2
Rhamnus alpina	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	5
Rhinanthus mediterraneus	1	1	1	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	15
Rosa sp.	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	18
Rubus idaeus	0	0	1	1	0	0	1	1	1	1	1	0	0	1	0	0	1	1	1	0	11
Rubus ulmifolius	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Rumex acetosa subsp. acetosa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Rumex acetosella subsp. acetosella	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	19
Rumex conglomeratus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Rumex longifolius	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	5
Rumex obtusifolius	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Rumex scutatus	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	5
Sagina procumbens	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Salix caprea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	3
Sanguisorba minor	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Saponaria officinalis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Sarothamnus scoparius	1	1	0	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	9
Satureja acinos	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	5
Satureja vulgaris	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	0	1	1	1	0	15
Saxifraga granulata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	3
Scabiosa columbaria	1	1	1	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	14
Scleranthus annuus subsp. polycarpos	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3
Scleranthus perennis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scrophularia alpestris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Scrophularia auriculata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Sedum album	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2
Sedum annuum	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	3
Sedum hirsutum	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2
Sedum rupestre	1	1	0	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1	1	0	12
Sedum telephium	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	4
Selinum pyrenaeum	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	4
Sempervivum tectorum	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	3
Senecio inaequidens	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	5
Senecio viscosus	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Serratula tinctoria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Seseli montanum	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sideritis hyssopifolia	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	7
Silene ciliata	0	0	0	1	0	1	0	1	0	1	0	0	0	0	1	1	0	1	1	1	9

Silene dioica	0	0	1	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	1	0	7
Silene nutans	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	0	1	1	1	0	16
Silene rupestris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2
Silene vulgaris	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	1	0	1	0	10
Sisymbrium officinale	0	0	1	1	0	0	1	1	1	0	1	0	0	1	1	0	1	1	1	0	11
Solidago virgaurea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Sorbus aria	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Sorbus aucuparia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Stachys officinalis	1	1	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	16
Stachys sylvatica	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2
Stellaria alsine	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Stellaria graminea	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	17
Stellaria media	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	19
Stellaria nemorum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Succisa pratensis	0	1	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	1	9
Taraxacum dissectum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	19
Taraxacum officinale	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	16
Teucrium scorodonia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Thalictrum aquilegifolium	1	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	8
Thesium alpinum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	3
Thlaspi alpestre subsp. brachypetalum	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Thymus serpyllum	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	18
Torilis japonica	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Tragopogon pratensis	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	10
Trifolium alpinum	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	0	0	1	6
Trifolium arvense	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2
Trifolium aureum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Trifolium campestre	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	4
Trifolium ochroleucon	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Trifolium pratense	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Trifolium repens	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Trisetum flavescens	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	1	1	0	15

Trollius europaeus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	1	6
Tussilago farfara	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Urtica dioica	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	19
Vaccinium myrtillus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2
Vaccinium uliginosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2
Valeriana montana tripteris	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Valeriana officinalis	0	0	1	1	0	0	1	1	0	0	1	0	0	0	1	1	0	1	1	1	10
Valerianella eriocarpa subsp. truncata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Veratrum album	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	0	1	1	1	0	8
Verbascum boerhavii	0	1	0	1	1	0	1	0	1	0	0	0	1	0	0	1	1	0	0	0	8
Verbascum lychnitis	1	1	0	1	1	0	1	1	0	0	0	0	1	0	0	1	1	0	0	0	9
Veronica arvensis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20
Veronica austriaca subsp. teucrium	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2
Veronica beccabunga	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2
Veronica chamaedrys	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	17
Veronica fruticulosa subsp. saxatilis	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3
Veronica officinalis	0	0	1	0	1	1	0	1	0	1	0	1	0	0	0	1	1	0	0	1	9
Veronica serpyllifolia subsp. humifusa	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3
Vicia hirsuta	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3
Vicia pyrenaica	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	4
Vicia sativa	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	1	0	7
Vicia sepium	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	1	0	6
Vincetoxicum hirundinaria	0	1	1	1	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1	1	11
Viola canina	0	0	1	1	0	0	1	0	0	0	1	0	0	0	1	1	0	1	1	1	9
Viola sylvestris	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Viola tricolor	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	0	17

Supplementary table 6.2 List of all butterflies and their abundances all over the three sampled years within the 20 plots studied in Catllar valley.

Taxon	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**	**P11**	**P12**	**P13**	**P14**	**P15**	**P16**	**P17**	**P18**	**P19**	**P20**	**Nº Plots**
Aglais io	3	1	0	1	1	2	0	1	9	0	1	0	1	1	2	0	0	0	1	1	13
Aglais urticae	3	2	11	9	11	9	10	11	2	16	1	11	6	1	15	26	6	4	6	3	20
Anthocharis cardamines	3	1	1	0	0	2	4	1	4	1	1	0	3	2	0	1	2	3	1	0	15
Anthocharis euphenoides	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	3	1	1	1	0	6
Apatura ilia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Apatura iris	0	4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	2
Aphantopus hyperantus	1	1	0	22	0	0	15	5	85	4	50	0	3	0	0	3	1	5	4	0	13
Aporia crataegi	14	1	0	0	0	0	1	3	3	1	1	0	1	0	0	0	0	2	0	0	9
Argynnis paphia	1	0	0	0	0	0	0	0	19	0	3	0	1	0	0	0	0	0	0	0	4
Aricia agestis	1	5	1	6	0	0	2	1	2	0	1	0	1	0	4	3	3	3	1	0	14
Boloria dia	1	0	1	3	1	0	3	7	2	1	1	0	2	0	1	2	5	4	6	0	15
Boloria euphrosyne	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	6
Boloria selene	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	1	2	0	3
Callophrys rubi	0	3	0	3	0	0	1	0	0	0	0	0	2	0	0	0	1	0	1	0	6
Carcharodus alceae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Carcharodus flocciferus	0	2	1	1	0	0	1	0	0	0	1	0	2	0	2	2	0	0	1	0	9
Carcharodus lavatherae	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Coenonympha arcania	9	2	2	8	0	0	9	16	36	2	6	0	10	2	2	13	1	9	9	0	16
Coenonympha glycerion	0	3	0	5	2	0	15	5	0	3	1	0	3	2	2	3	2	12	1	6	15
Coenonympha pamphilus	7	13	2	10	1	0	13	2	2	5	1	1	12	4	4	13	7	6	12	0	18
Colias alfacariensis	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	3	3	1	0	0	7
Colias crocea	11	15	3	4	6	4	7	4	2	4	5	4	14	5	7	7	8	6	5	1	20
Cupido alcetas	0	0	1	0	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	3
Cupido minimus	0	1	3	4	0	1	2	0	0	0	0	0	3	0	0	0	1	0	2	0	8
Cyaniris semiargus	1	2	0	0	0	0	1	0	0	0	0	0	2	0	0	2	1	1	0	0	7
Erebia euryale	0	0	0	0	0	4	0	2	0	6	0	1	0	0	0	0	0	0	0	0	4
Erebia meolans	0	15	6	6	7	3	8	41	0	10	0	4	0	1	1	4	3	5	2	0	15
Erebia rondoui	0	0	3	0	2	8	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
Erebia triaria	0	0	0	6	0	0	1	0	0	0	0	0	0	0	0	2	5	7	5	0	6
Euchloe simplonia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Euphydryas aurinia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Fabricianna addipe	1	0	0	0	0	0	0	0	2	0	6	0	0	0	0	0	0	0	0	0	3

Gonepteryx cleopatra	1	1	0	2	4	1	1	1	0	0	2	0	2	1	0	0	0	0	1	0	11
Gonepteryx rhamni	0	1	1	0	2	2	3	1	5	0	4	1	1	0	0	1	1	1	1	1	15
Hamearis lucina	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
Hesperia comma	0	1	0	0	1	4	0	0	2	1	1	0	1	0	1	1	17	4	0	0	11
Issoria lathonia	2	3	6	1	1	14	1	47	4	51	0	30	3	1	5	12	2	4	1	2	19
Lampides boeticus	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	4
Lasiommata maera	1	0	0	0	1	5	1	1	0	1	0	1	0	0	0	0	6	1	2	1	11
Lasiommata megera	0	0	0	0	0	4	0	6	0	1	0	0	0	0	1	0	0	0	0	0	4
Limenitis camilla	0	0	0	0	0	0	0	0	5	0	2	0	0	0	0	0	0	0	0	0	2
Lycaena alciphron	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2	0	4
Lycaena hippothoe	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	6	0	3
Lycaena phlaeas	8	2	1	0	1	0	1	4	2	2	3	0	5	0	4	4	1	0	1	0	14
Lycaena tityrus	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	1	0	0	3
Lycaena virgaureae	0	1	2	11	1	0	4	12	18	6	6	1	7	1	0	2	3	12	7	3	17
Lysandra bellargus	0	7	0	4	0	0	10	0	2	0	2	2	8	0	1	5	6	8	2	0	12
Lysandra coridon	1	5	5	4	2	1	5	1	1	0	4	1	1	0	1	3	5	1	5	0	17
Maniola jurtina	39	63	0	11	0	0	12	4	10	4	4	0	75	3	28	46	16	15	10	0	15
Melanargia lachesis	12	0	0	0	1	0	3	3	1	0	0	0	0	1	0	1	0	0	1	0	8
Melitaea cinxia	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	1	0	4
Melitaea deione	1	2	0	0	0	0	1	0	10	0	3	0	5	0	1	0	1	0	1	0	9
Melitaea diamina	0	5	0	6	0	0	0	0	1	0	3	0	3	0	0	5	0	3	0	1	8
Melitaea didyma	6	8	0	3	1	0	15	2	3	0	3	1	9	2	2	14	2	7	8	0	16
Melitaea nevadensis	1	4	0	6	0	1	8	2	6	0	2	0	4	0	1	4	2	5	0	0	13
Melitaea parthenoides	16	75	10	94	6	1	72	8	0	4	0	2	52	9	19	90	198	8	60	2	18
Melitaea phoebe	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2
Nymphalis antiopa	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
Nymphalis polychloros	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Ochlodes sylvanus	0	1	0	1	0	0	0	1	14	0	3	0	1	1	0	0	1	0	0	0	8
Papilio machaon	0	1	0	0	0	2	1	0	0	0	0	0	2	0	0	0	0	0	0	1	5
Pararge aegeria	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	5
Parnassius apollo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2
Pieris brassicae	2	3	3	1	1	4	2	2	0	0	2	3	7	1	6	4	2	0	1	0	16
Pieris napi	0	1	0	1	0	0	1	2	11	1	7	0	1	0	0	0	2	6	7	0	11
Pieris rapae	3	17	7	7	2	1	8	3	3	5	1	2	6	2	14	15	9	15	3	1	20
Plebejus argus	10	1	0	0	0	0	1	0	0	0	2	0	4	0	0	1	0	0	0	0	6

Polygonia c-album	1	3	0	1	0	0	1	12	14	1	4	0	4	0	0	0	3	0	2	1	12
Polyommatus dorylas	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	3
Polyommatus escheri	4	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	0	6
Polyommatus icarus	13	5	1	0	0	0	4	0	1	4	2	0	13	1	0	3	1	2	1	0	13
Pyrgus alveus	0	6	0	6	0	0	3	1	0	0	1	0	2	2	6	2	4	3	6	0	12
Pyrgus cirsii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	1
Pyrgus serratulae	2	2	11	6	2	9	5	2	0	1	0	2	4	2	18	4	4	3	8	2	18
Pyronia tithonus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Satyrium w-album	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Speyeria aglaja	0	12	7	14	1	0	5	9	2	4	1	0	16	1	6	15	4	7	11	9	17
Spialia sertorius	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	3
Thymelicus lineola	2	4	0	3	0	0	1	1	0	0	0	1	1	0	0	6	0	0	0	0	8
Thymelicus sylvestris	10	5	0	7	0	0	4	4	4	1	0	0	5	0	0	11	2	5	3	0	12
Vanessa atalanta	0	7	0	6	3	0	5	13	10	1	5	3	10	8	6	12	2	3	5	1	17
Vanessa cardui	20	19	9	19	12	27	3	14	3	9	1	8	33	7	17	14	6	4	3	5	20

Supplementary table 6.3 List of all grashoppers and their abundances all over the three sampled years within the 20 plots studied in Catllar valley.

Taxon	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**	**P11**	**P12**	**P13**	**P14**	**P15**	**P16**	**P17**	**P18**	**P19**	**P20**	**Nº**
Antaxius hispanicus	0	0	4	1	0	6	2	1	2	1	0	0	0	0	0	0	0	16	0	2	9
Arcyptera fusca	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	1
Chortippus apricarius	194	690	412	507	233	352	336	338	360	129	176	29	283	561	456	388	206	307	188	838	20
Chortippus biguttulus	22	37	5	2	4	15	25	36	10	17	6	8	7	24	18	17	1	59	21	27	20
Chortippus gr binonatus	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chortippus bin. saulcyi	44	79	56	49	5	20	55	30	57	23	22	12	40	115	62	17	43	82	42	131	20
Chortippus brunneus/jacobsi	26	27	16	8	1	23	4	11	2	0	5	0	26	15	31	14	3	23	24	18	18
Chortippus dorsatus	96	311	23	135	0	0	9	76	3	0	42	0	315	9	321	0	2	0	9	84	14
Chortippus montanus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Chortippus parallelus	163	653	106	413	46	285	425	571	272	83	330	16	277	509	335	117	214	286	134	165	20
Chortippus vagans	5	6	3	8	0	0	27	0	8	0	0	0	23	14	16	18	0	0	3	0	11
Cophopodisma pyrenaea	0	1	4	0	0	9	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4
Decticus verrucivorus	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	4
Epiphigger epiphigger	7	4	3	4	0	0	0	0	3	0	1	0	2	8	1	0	0	3	6	0	11

Gryllus campestris	12	8	1	0	0	0	2	6	3	0	3	0	1	4	1	1	1	4	7	0	14
Metrioptera bicolor	5	3	0	1	0	0	0	0	0	0	0	0	9	10	7	0	10	0	18	0	8
Metriopptera saussuriana	0	2	1	0	0	0	0	0	0	0	0	0	3	1	1	0	6	0	6	9	8
Nemobius sylvestris	0	0	0	0	0	0	1	7	0	0	6	0	0	0	1	0	3	0	6	0	6
Oedipoda caerulescens	3	0	2	0	1	14	2	2	0	1	0	0	0	1	0	0	0	1	0	1	10
Omocestus antigai	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	19	2
Omocestus haemorrhoidalis	211	253	354	0	112	241	197	299	176	139	48	23	173	202	105	149	140	138	62	251	19
Omocestus rufipes	1	0	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	1	0	3
Parapleurus alliaceus	14	21	0	0	0	0	10	1	3	0	56	0	3	4	1	0	0	0	184	0	10
Pholidoptera griseoapterus	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	11	0	3
Platycleis albopunctata	35	15	9	8	1	3	7	31	5	2	3	0	20	83	23	4	18	15	9	13	19
Psophus stridulus	0	11	14	6	0	0	3	8	7	0	0	0	9	0	7	6	0	0	1	1	11
Stauroderus scalaris	3	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	3	0	0	3
Stridulus nigromaculatus	0	5	121	0	27	121	52	21	30	15	1	3	0	2	36	69	56	13	0	62	16
Stridulus lineatus	90	119	106	61	3	10	116	116	42	23	0	0	137	160	31	26	34	116	19	79	18
Stethophyma grossum	0	0	0	0	0	0	0	0	0	0	64	0	0	0	0	0	0	0	0	0	1
Tetrix depressa	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	2
Tetrix nutans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Tetrix subulata	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	2	0	3
Terix undulata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Tettigonia cantans	7	5	1	10	0	1	5	1	3	0	37	0	10	5	4	0	15	0	19	2	15
Tettigonia viridissima	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	3

Supplementary Table 6.4 Results of two-way ANOVAs with repeated measures performed separately for PR (Plant richness), BR (Butterfly richness), GR (Grasshopper richness), BA (Butterfly abundance) and GA (Grasshopper abundance). P: specifies the p-value, ges: the generalized effect size (amount of variability due to the within-subjects factor).

	Effect	DFn	DFd	F	p	ges
BR	Treatment	1	24	5.784	**0.024***	0.194
	Year	2	24	1.695	0.205	0.124
	Treatment:Year	2	24	0.459	0.637	0.037
BA	Treatment	1	24	3.132	0.089	0.115
	Year	2	24	6.534	**0.005***	0.353
	Treatment:Year	2	24	0.298	0.745	0.024

Supplementary Table 6.5. Results for the effect of time at each level of treatment for the two-way ANOVA performed for mid-term effects. P: specifies the p-value, ges: the generalized effect size (amount of variability due to the within-subjects factor), Padj: the adjusted p-value after the Bonferroni correction for pairwise comparisons, with significant values when the three time points are different between them.

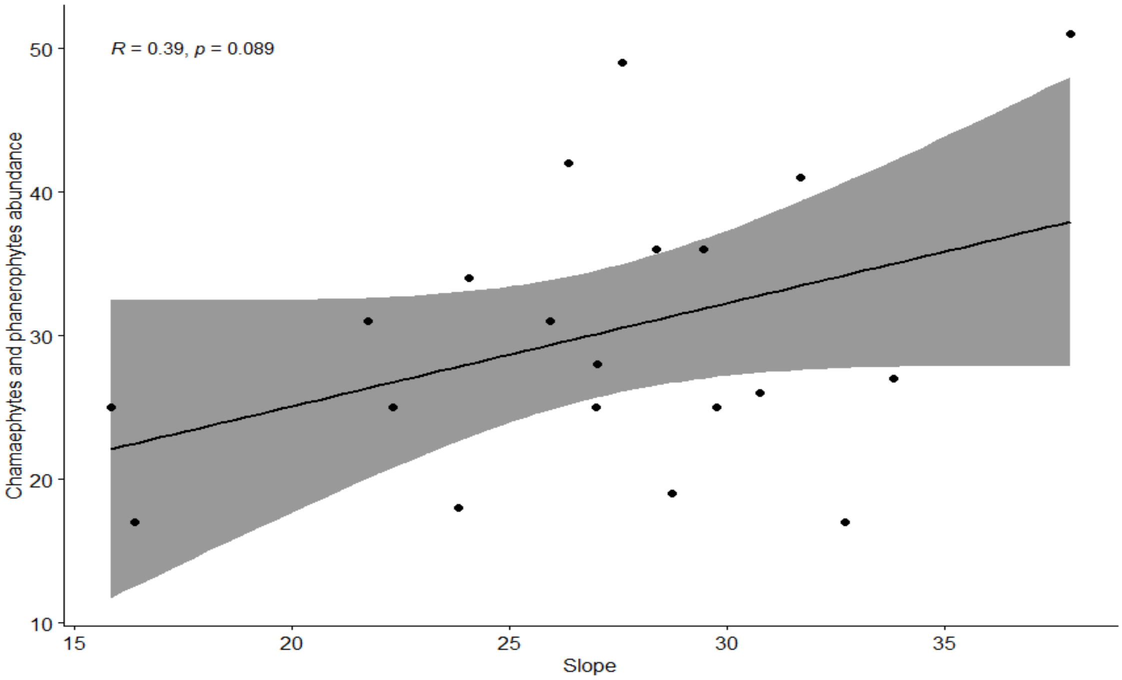
	Treatment	**Effect**	**DFn**	**DFd**	**F**	**p**	**ges**	**p.adj**
BR	EXCLUDED	year	2	8	3.508	0.081	0.169	0.162
	NON-EXCLUDED	year	2	8	0.529	0.609	0.076	1
BA	EXCLUDED	year	2	8	10.842	**0.005***	0.326	**0.01***
	NON-EXCLUDED	year	2	8	3.678	0.074	0.393	0.148

Supplementary Table 6.6 Results for the two-way ANOVA with repeated measures on butterfly species richness (R) and abundance (A) with the effect of time at each level of treatment.

	Effect	**DFn**	**DFd**	**F**	**p**	**ges**
2019-R	Treatment	1	16	0.78	0.39	0.046
	Month	1	16	3.119	0.096	0.163
	Treatment:Month	1	16	2.782	0.115	0.148
2019-A	Treatment	1	16	0.376	0.548	0.023
	Month	1	16	11.044	**0.004***	0.408
	Treatment:Month	1	16	2.108	0.166	0.116
2020-R	Treatment	1	16	6.253	**0.024***	0.281
	Month	1	16	1.628	0.22	0.092
	Treatment:Month	1	16	1.148	0.3	0.067
2020-A	Treatment	1	16	4.572	**0.048***	0.222
	Month	1	16	13.722	**0.002***	0.462
	Treatment:Month	1	16	2.359	0.144	0.129

Supplementary Table 6.7 Results for the effect of time at each level of treatment for the two-way ANOVA performed for short-term effects for butterflies. P: specifies the p-value, ges: the generalized effect size (amount of variability due to the within-subjects factor), Padj: the adjusted p-value after the Bonferroni correction for pairwise comparisons, with significant values when the three time points are different between them.

		Treatment	**Effect**	**DFn**	**DFd**	**F**	**P**
2019	Richness	EXCLUDED	Month	1	4	0.012	0.918
		NON-EXCLUDED	Month	1	4	5.904	0.072
	Abundance	EXCLUDED	Month	1	4	9.179	**0.039***
		NON-EXCLUDED	Month	1	4	36.115	**0.004****
2020	Richness	EXCLUDED	Month	1	4	0.049	0.836
		NON-EXCLUDED	Month	1	4	18.241	**0.013***
	Abundance	EXCLUDED	Month	1	4	2.964	0.16
		NON-EXCLUDED	Month	1	4	16.269	**0.016***



Supplementary Figure 6.1. Relationship between the slope of the 20 studied plots and the abundance of chamaephytes and phanerophytes.

D. Chapter 7 Supporting Information

Supplementary table 4.1 Species trends calculated in each climatic region. It is indicated for each species the available time series and the multiplicative rate of annual change. Several categories are indicated in the population trend, according to the classification provided by the rBMS software.

	Alpine region			Mediterranean humid region			Mediterranean arid region		
Species	**Years**	**% change**	**Trend**	**Years**	**% change**	**Trend**	**Years**	**% change**	**Trend**
Aglais io	15	1.009	Uncertain	26	1.003	Stable			
Aglais urticae	18	0.971	Uncertain						
Anthocharis cardamines	15	0.994	Stable	27	1.002	Stable			
Anthocharis euphenoides				24	0.969	Moderate regression			
Apatura ilia				15	0.954	Uncertain			
Aphantopus hyperanthus	5	0.835	Strong regression						
Aporia crataegi	22	0.960	Moderate regression	21	0.897	Strong regression			
Araschnia levana				7	0.532	Strong regression			
Argynnis adippe	15	0.965	Uncertain						
Argynnis aglaja	18	0.973	Uncertain						
Argynnis paphia	18	0.945	Uncertain	27	1.007	Stable			
Aricia agestis	17	0.960	Uncertain	21	0.963	Moderate regression			

Aricia cramera				24	0.982	Stable	18	0.931	Moderate regression
Boloria dia	18	0.971	Uncertain	26	1.025	Uncertain			
Boloria euphrosyne	15	0.972	Uncertain						
Brenthis daphne				11	0.835	Strong regression			
Brintesia circe	17	1.000	Uncertain	27	1.016	Moderate increase			
Cacyreus marshalli				24	0.942	Moderate regression			
Callophrys rubi	15	1.039	Uncertain	27	0.952	Moderate regression	19	0.947	Moderate regression
Carcharodus alceae				27	0.999	Stable			
Celastrina argiolus	4	0.696	Strong regression	27	0.990	Stable	15	1.136	Moderate increase
Charaxes jasius				27	0.992	Stable			
Coenonympha arcania	17	1.002	Stable	27	0.956	Uncertain			
Coenonympha dorus				21	0.964	Moderate regression			
Coenonympha pamphilus	18	0.942	Moderate regression	27	0.966	Moderate regression	5	1.233	Incremento fuerte
Colias alfacariensis	6	1.070	Uncertain	21	0.954	Uncertain			
Colias croceus	22	0.992	Stable	27	1.005	Stable	20	0.964	Uncertain
Cupido argiades				13	0.981	Moderate regression			
Cupido minimus	7	0.908	Moderate regression	10	0.829	Strong regression			
Cupido osiris				11	0.912	Strong regression			
Cyaniris semiargus	7	0.908	Uncertain						
Erebia meolans	15	0.974	Uncertain						
Erebia neoridas	14	0.972	Uncertain						
Erynnis tages				21	0.901	Strong regression			
Euchloe crameri				27	1.023	Uncertain			
Euphydryas aurinia				27	0.906	Strong regression			

Glaucopsyche alexis				21	0.931	Uncertain			
Glaucopsyche melanops				24	0.879	Strong regression			
Gonepteryx cleopatra	4	0.694	Strong regression	27	1.047	Moderate increase	20	0.978	Uncertain
Gonepteryx rhamni	22	0.990	Stable	27	1.016	Stable			
Hipparchia fagi				20	1.016	Uncertain			
Hipparchia fidia				24	0.964	Moderate regression	4	0.802	Uncertain
Hipparchia hermione	5	0.875	Strong regression						
Hipparchia semele				20	1.023	Uncertain			
Hipparchia statilinus				26	0.953	Uncertain			
Iphiclides feisthamelii	17	0.990	Stable	27	0.982	Moderate regression			
Issoria lathonia	22	1.000	Stable	27	1.010	Stable			
Lampides boeticus	6	0.942	Uncertain	27	0.979	Stable			
Lasiommata maera	5	0.875	Strong regression						
Lasiommata megera	22	0.989	Uncertain	27	1.002	Stable	20	0.953	Moderate regression
Leptidea sinapis	17	0.980	Moderate regression	27	0.963	Moderate regression			
Leptotes pirithous				27	1.008	Stable	6	1.973	Incremento fuerte
Libythea celtis				21	1.042	Uncertain			
Limenitis camilla				15	0.975	Uncertain			
Limenitis reducta				27	0.978	Moderate regression			
Lycaena phlaeas	9	0.985	Uncertain	27	0.983	Stable	17	0.923	Uncertain
Lycaena tityrus	7	0.848	Moderate regression						
Lycaena virgaureae	8	1.026	Uncertain						
Lysandra bellargus	15	1.074	Moderate increase	24	1.027	Uncertain			
Lysandra coridon	15	0.974	Uncertain	13	0.964	Uncertain			
Maniola jurtina	17	1.019	Uncertain	27	1.008	Stable	18	0.984	Uncertain

Melanargia lachesis	22	1.003	Uncertain	27	0.948	Moderate regression			
Melanargia occitanica				21	0.877	Strong regression			
Melitaea cinxia	14	0.986	Uncertain	20	0.950	Uncertain			
Melitaea deione				25	0.984	Uncertain			
Melitaea didyma	12	0.938	Moderate regression	26	1.013	Stable			
Melitaea parthenoides	4	0.868	Uncertain						
Melitaea phoebe	15	0.897	Uncertain	24	0.968	Uncertain			
Melitaea trivia				11	1.103	Uncertain			
Neozephyrus quercus				25	1.048	Uncertain			
Nymphalis antiopa				20	0.930	Moderate regression			
Nymphalis polychloros				19	0.944	Uncertain			
Ochlodes sylvanus	11	0.981	Uncertain	27	0.969	Uncertain			
Papilio machaon	5	0.992	Uncertain	27	0.977	Moderate regression	20	1.012	Stable
Pararge aegeria	18	1.031	Moderate increase	27	0.993	Stable	20	1.009	Stable
Pieris napi	15	1.056	Uncertain	27	0.984	Stable			
Pieris rapae	17	0.993	Stable	27	1.013	Stable	20	0.990	Stable
Piers brassicae	22	1.017	Uncertain	27	0.989	Stable	20	1.006	Stable
Plebejus argus				21	1.093	Uncertain			
Polyogonia c-album	15	1.002	Uncertain	27	1.000	Stable			
Polyommatus celina							9	1.100	Uncertain
Polyommatus escheri				21	0.941	Moderate regression			
Polyommatus hispana				24	0.984	Stable			
Polyommatus icarus	17	0.992	Stable	27	0.987	Stable	20	0.956	Moderate regression
Polyommatus thersites				20	0.945	Moderate regression			

Pontia daplidice				27	0.983	Stable	20	0.973	Moderate regression
Pseudophilotes panoptes				24	0.964	Uncertain			
Pyrgus armoricanus				11	1.098	Uncertain			
Pyrgus malvoides				26	1.005	Uncertain			
Pyronia bathseba				27	0.985	Stable			
Pyronia cecilia				27	0.934	Moderate regression	20	0.958	Uncertain
Pyronia tithonus	15	0.973	Uncertain	27	0.948	Moderate regression			
Satyrium acaciae	7	0.908	Uncertain	12	0.972	Uncertain			
Satyrium esculi	14	0.944	Uncertain	27	1.022	Uncertain			
Satyrium ilicis				10	1.032	Uncertain			
Satyrium spini				15	0.977	Uncertain			
Satyrus actaea	15	0.898	Strong regression						
Spialia sertorius				20	0.992	Uncertain			
Thymelicus acteon	7	0.936	Moderate regression	27	0.990	Stable			
Thymelicus lineola	15	0.976	Uncertain						
Thymelicus sylvestris				19	0.965	Uncertain			
Tomares ballus				15	0.973	Uncertain			
Vanessa atalanta	15	1.005	Stable	27	0.990	Stable	20	0.985	Stable
Vanessa cardui	21	0.961	Uncertain	27	0.974	Moderate regression	20	0.936	Moderate regression
Zerynthia rumina				20	0.976	Uncertain			

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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Weather and butterfly responses: a framework for understanding population dynamics in terms of species' life-cycles and extreme climatic events

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Abstract

Understanding population responses to environmental conditions is key in the current context of climate change and the extreme climatic events that are threatening biodiversity in an unprecedented way. In this work, we provide a framework for understanding butterfly population responses to weather and extreme climatic seasons by taking into account topographic heterogeneity, species' life-cycles and density-dependent processes. We used a citizen-science database of Mediterranean butterflies that contains long-term population data (28 years) on 78 butterfly species from 146 sites in the Mediterranean mesic and alpine climate regions. Climatic data were obtained from 93 meteorological stations operating during this period near the butterfly sites. We studied how seasonal precipitation and temperature affect population growth while taking into account the effects of density dependence. Our results reveal (i) the beneficial effects of winter and spring precipitation for butterfly populations, which are most evident in the Mediterranean region and in univoltine species, and mainly affect the larval stage; (ii) a general negative effect of summer rain in the previous year, which affects the adult stage; and (iii) a consistent negative effect of mild autumns and winters on population growth. In addition, density dependence played a major role in the population dynamics of most species, except for those with long-term negative population trends. Our analyses also provide compelling evidence that both extreme population levels in previous years and extreme climatic seasons in the current year provoke population crashes and explosions, especially in the Mediterranean mesic region.

Keywords Mediterranean butterflies · Weather · Extreme climatic seasons · Density dependence · Population responses

Introduction

Under a context of global change, the responses of biological populations to future environmental conditions may become the key for species survival in many ecosystems (Lawson et al. 2015). However, although consistent recent negative trends have been identified for many taxa (e.g., terrestrial insects: Sánchez-Bayo and Wyckhus 2019; Wagner 2020), the contribution of the main drivers of global change to such declines is still the subject of debate. Climate change, in particular, is regarded as one of the main threats to biodiversity (Bellard et al. 2012), although for a number of species in cold environments it does in fact create new opportunities for population increases and range expansions (e.g., Menéndez et al. 2008; Pöyry et al. 2009). Rapid changes associated with climate change are expected in species such as insects with short life-cycles and high reproduction rates, whose populations can grow rapidly under favourable weather conditions (Kerr et al. 2019). However, in this type of species, unpredictable changes may also provoke sudden increases in mortality rates leading to population collapses and even extinctions (McLaughlin et al. 2002). This possibility is all the more likely given the current scenario of climate change provoked by the increase in extreme climatic events (ECEs) (Jentsch et al. 2007; Seneviratne et al. 2014).

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For many decades, butterflies have figured as a model group for understanding the impact of weather and climate change on insect populations (Pollard 1988; Parmesan et al. 1999; Devictor et al. 2012). Various studies have shown how year-to-year population changes are influenced by weather (Roy et al. 2001; Boggs and Inouye 2012) and also how ECEs can lead to population crashes and/or explosions (Palmer et al. 2017; McDermott Long et al. 2017). Extreme drought events, for instance, have been linked to unusual population declines and an increase in the extinction risk in metapopulations (Oliver et al. 2015; Johansson et al. 2020; van Bergen et al. 2020). On the other hand, rapid growth rates make fast recoveries more likely, even after population crashes, thereby minimising the long-term effects of climatic extremes on population trends (Ehrlich et al. 1980; Palmer et al. 2017). The magnifying effects of ECEs on population growth and population size are well illustrated by nonlinear responses to abrupt changes in climate drivers, not only in insects and other short-lived organisms but even in long-lived tree species (Bestelmeyer et al. 2011; Cavin et al. 2013).

Another aspect to bear in mind when studying the responses of butterfly populations to climate is that its effects will vary greatly depending on the life stage it acts upon (Radchuk et al. 2013). Thus, for example, high temperatures may be detrimental during the overwintering period but beneficial during the adult flight period (WallisDeVries et al. 2011; McDermott Long et al. 2017). Therefore, the impact of climate change in a particular region (e.g., a warming trend in the winter period) will vary according to species' phenology and life histories.

However important weather is, there is compelling evidence that other factors linked to density dependence are equally important as drivers of butterfly population dynamics (Dempster 1983; Rothery et al. 1997; Dooley et al. 2013). Indeed, density dependence has been identified as a key factor in the population dynamics of many butterfly species, ranging from sedentary species forming classical metapopulations to long-distance migrants, with highly contrasting life histories (Nowicki et al. 2009; Marini and Zalucki 2017). A recent study focusing on a dozen common European butterfly species concluded that they were all uniformly sensitive to density dependence, which usually has a greater effect than climate near the centre of a species' range (Mills et al. 2017).

This framework for understanding the dynamics of butterfly populations is more complicated in topographically heterogeneous regions where small-scale climatic differences may be associated with dissimilarities in population responses within species. Catalonia (NE Spain) is a good example of such a complex scenario. Albeit relatively small in size (33,055 km^2), this region embraces a great diversity of climates and landscapes, ranging from arid Mediterranean zones and humid deciduous forests to Alpine mountains. Long-term butterfly monitoring data indicate that populations in arid areas are subjected to more negative trends than populations in cold and humid areas, a difference that could be related to the fact that drought episodes have a more severe impact on the former group (Herrando et al. 2019; Ubach et al. 2021). However, this possibility has not been formally tested and remains speculative.

In this work, we model the population responses of Catalan butterflies to climate, taking into account density dependence, the phenological differences between species, and the heterogeneity of the responses in the two climatic regions. Specifically, our aims were (i) to assess the climatic factors that affect the growth rate of butterfly species and how they vary according to climatic regions; (ii) to identify which life-cycle stages are most sensitive to climate; and (iii) to quantify population crashes and explosions and how they are related to life-history traits and to extreme climatic events. We hypothesized that weather conditions will have contrasting effects on butterfly species depending on their life-cycles, and that more negative effects will be noted in populations in the Mediterranean climatic zone given the more serious declines recorded in this area in recent years. We also hypothesized that larval and adult stages will probably be the most sensitive, and that precipitation will have contrasting effects in both stages, with a positive impact on larvae, which will benefit from vegetation growth, but a negative impact on adults due to a reduction in their potential activities. Finally, we hypothesized that the climatic events that most critically affect population growth may have a magnifying effect when they become climatic extremes and provoke population crashes and explosions.

Materials and methods

Recording sites and butterfly data

We used data from the Catalan Butterfly Monitoring Scheme (CBMS; www.catalanbms.org), a citizen-science project with a network of sites for recording butterfly abundance that has been operating in north-east Spain, Andorra and the Balearic Islands since 1994. At each recording site, weekly counts are made along a fixed route from March to September, under the standard weather conditions favourable for butterfly activity (Pollard and Yates 1994).

The relative abundance of butterfly species each season was estimated from GAM models fitted to the weekly counts within a given climatic region, following the method described by Schmucki et al. (2016) and using the *rbms* package in R (Schmucki et al. 2021).

We used data from a total of 146 recording sites (average of years per site: 9.5, range: 1–27) (Fig. 1). Sites were

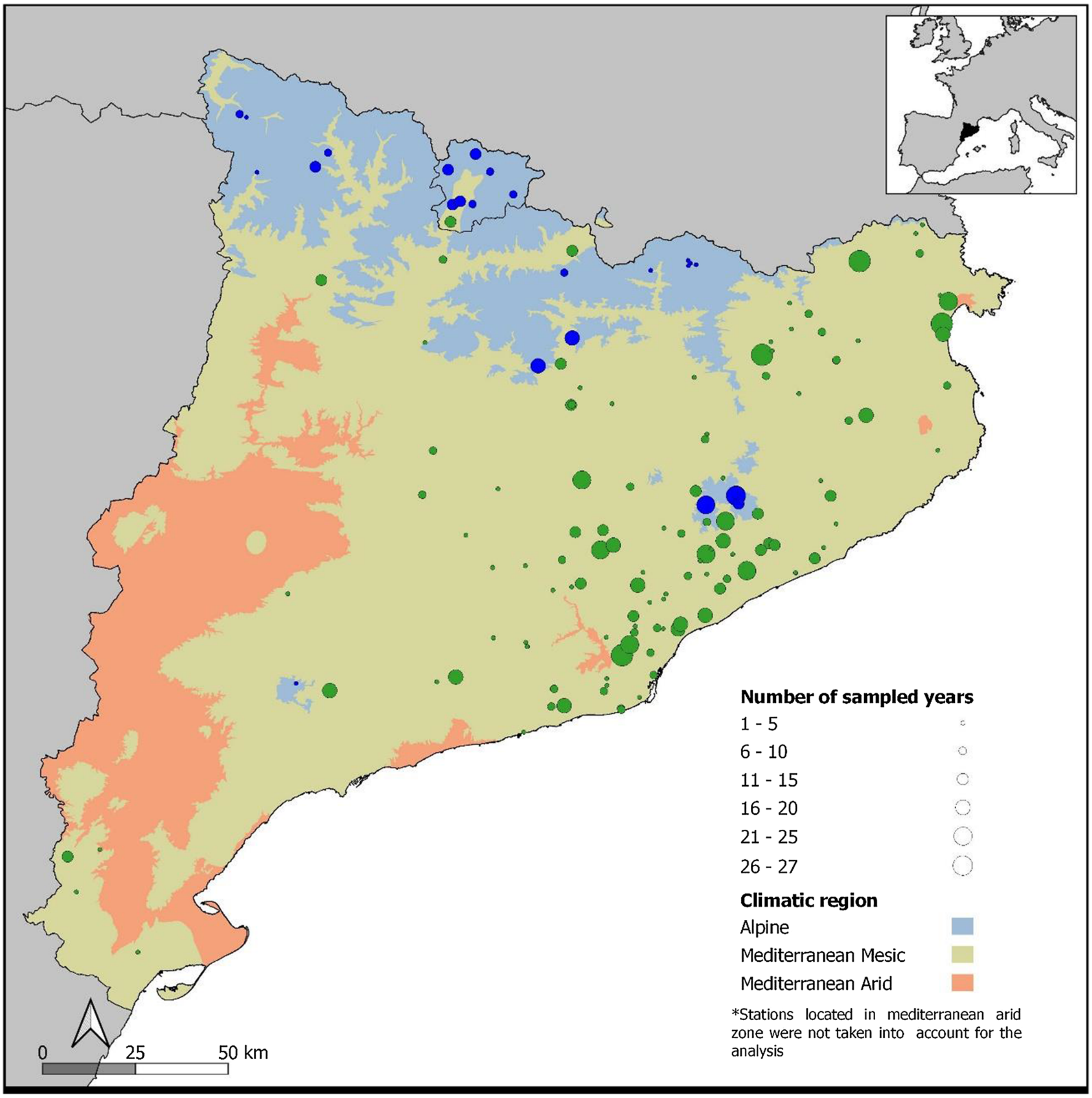

Fig. 1 Map of the study region. The 146 monitored transects are represented with dots whose size is proportional to the number of sampling years. The 122 sites in the Mediterranean mesic climatic region are shown in green, while the 24 locations in the alpine climate region are shown in blue. No sampling sites within the Mediterranean arid climatic region were used in this study

classified as belonging to one of two climatic regions (cf. Metzger et al. 2013) based on average accumulation values for growing degree-days over the flight season (DGG21) calculated for the 15-year period 1994–2009: (1) alpine climate region (ACR), 24 mountain sites (> 1000 m a.s.l.) and (2) Mediterranean mesic climatic region (MMCR), 122 sites. We worked with a subset of 78 butterfly species flying at more than 10 sites in at least 8 years, but excluded the regular migrants *Vanessa cardui, V. atalanta, Pieris brassicae, Lampides boeticus* and *Leptotes pirithous*. The species and the number of populations in each climatic region are listed in Suppl. Table 1.

Climate data

Weather variables were calculated based on data from a network of 93 Authomatic Weather Stations (AWS) located near the butterfly transects. Each AWS was assigned either to the Mediterranean mesic or alpine climate region, and average values of weather variables were calculated at regional climatic level (ACR = 15 meteorological stations, MMCR = 78 stations). Climatic data were provided by Meterorological Service of Catalonia (SMC, https://www.meteo.cat/) and Institut d'Estudis Andorrans (IEA, https://www.iea.ad/).

Within each region and year, we calculated separately the mean of daily minimum and maximum temperatures and the accumulated rainfall for each of the four climatic seasons (winter (WI): December–February; spring (SP): March–May; summer (SU): June–August; autumn (AU): September–November). In addition, the standard precipitation index (SPI), based on the probability of precipitation during the study period, was calculated for each climatic season:

$$\mathrm{SPI}_i = \frac{X_i - X_\mathrm{m}}{\sigma},$$

where X_i is the observed precipitation in a particular climatic season, X_m the mean precipitation value for a particular AWS, and σ the standard deviation of the time series from that station. SPI data were taken from locations in a 5 × 5-km grid for north-east Spain. For each butterfly recording site, we assigned the SPI value of the grid square to which the station belonged, and then averaged the SPI values for each climatic region.

For the 16 weather variables per region (maximum and minimum temperature, total rainfall, and SPI for each climatic season), Pearson correlation tests were performed to remove highly correlated variables (Pearson's $|r| > 0.7$). We excluded the variable that had the greatest collinearity with other variables in all pair-wise comparisons, and retained 6–7 variables for each climatic region (Table 1). For the selected variables, we also included a lag effect from the previous year to account for effects on the developmental stages, so the final dataset included 11 weather variables for the ACR and 13 for the MMCR. As the annual indices of butterfly abundances are calculated from adult counts in the spring and summer of the current year, the weather variables used as predictors encompassed a time period from 'spring lag 1' (i.e., spring of the previous year) to the current summer. For a correct interpretation of the effect of weather variables on population growth (see below), caution is needed: a positive estimate coefficient for a *minimum temperature* variable means that population growth was positively affected by *warmer* or *milder* seasons.

Table 1 Climatic predictors included in the models after removing highly correlated variables ($P > 0.7$) for both climatic regions (alpine, Mediterranean mesic)

Weather variable	Alpine	Med. mesic
Spring min. temperatures (i-1)		X
Spring SPI (i-1)		X
Summer min. temperatures (i-1)	X	X
Summer SPI (i-1)	X	X
Autumn max. temperatures (i-1)	X	
Autumn min. temperatures (i-1)	X	X
Autumn SPI (i-1)	X	X
Winter max. temperatures		X
Winter min. temperatures	X	X
Winter SPI	X	X
Spring min. temperatures	X	X
Spring SPI	X	X
Summer min. temperatures	X	X
Summer SPI	X	X

"i-1" corresponds to the weather variables from the previous year (lag 1)

Specific models of population growth

For each species and climatic region, we built models to associate the year-to-year change in the regional abundance index with the weather conditions in each of the different seasons (i.e., spring, summer, autumn and winter). The model structure followed Mills et al. (2017):

$$y_t = x_{t-1} + W_{1t} + \cdots + W_{nt-1},$$

where, y_t is the population growth rate calculated as the difference between the log-transformed annual indices in year 't' and year '$(t-1)$' assuming a Gaussian distribution, x_{t-1} the log annual abundance index in the previous year accounting for the density-dependence effect, and 'W_n' the weather variables included in the model, which include those acting in both the current and the previous years (i.e., a 1-year lag effect). All variables were scaled prior to any analyses. Species flying during the spring season had variables with a lag effect including the previous spring and summer, while those flying during the summer had a lag effect only up to the previous summer.

General linear models (GLMs) assuming a Gaussian distribution were built with the *lme4* package in R (Bates et al. 2015). Model selection from all possible combinations was based on the Akaike Information Criterion (AIC), with models that differed by < 2 points from the lowest AIC ($\Delta\mathrm{AIC} < 2$) considered as the top-ranked models. The effect of each significant variable was weighted as the average of the effects in all top-ranked models. These analyses were carried out with R Studio (R Core Team 2021), using the *MuMin* package (Barton and Barton 2015).

After this analysis, we used a Chi-square test to examine whether or not the strength of the density dependency effect (categorized as a binary variable, i.e., as significant or non-significant density dependence) was associated with population trends (classified, according to the *rbms* package, in four categories: decreasing, increasing, stable and uncertain).

Multispecies models for growth rate

After identifying the climatic factors that significantly affect each species, we carried out a second analysis combining data for all species to test whether or not some life-cycle stages are more sensitive than others to climate, and whether or not this sensitivity differs according to their voltinism (i.e., univoltine vs. multivoltine species) and between climatic regions. Prior to this analysis, we awarded each species a score based on which stage of their life-cycles the significant climatic factors acted upon predominantly (according to our previous findings; see Suppl. Table 2 for a complete phenological summary of all species considered).

We built two linear mixed models (GLMMs, with Satterthwaite's method for t-tests), one considering weather variables relating to temperature and the other weather variables relating to rainfall. In these models, the response variable was the average of the estimated coefficients of significant temperature/rainfall predictors in all top ranked specific models of population growth. The number of significant weather predictors for calculating this average varied between species in the range 1–8 (mean 2.1 predictors/species). Three independent categorical variables were used as predictors: (1) the life cycle stage on which the weather variable was acting: adult (A), pupa (P), larva (L), egg (E) and previous-year adults ($A-1$); (2) voltinism (univoltine vs. multivoltine); and (3) climatic region (ACR vs. MMCR). We also included the two interaction terms 'life cycle stage:voltinism' and 'life cycle stage:climatic region'. 'Species' was entered as a random factor. Four species that fly in highly overlapping generations (*Pararge aegeria, Colias crocea, Issoria lathonia* and *Cacyreus marshalli*) were excluded from the analysis because it was not possible to associate a critical life-cycle stage in these species to the significant weather variables that had been selected in the previous analysis.

Extreme population changes and their relationship with extreme climate seasons

The second part of our work was aimed at assessing whether or not extreme population changes in butterflies (i.e., population crashes and explosions) were related to extreme climatic seasons. To identify extreme events, both in the butterfly and climate data series, we followed the approach used by Leys et al. (2013), who recommend the use of absolute deviations (MAD, i.e., the median absolute deviation) instead of quartiles to detect outliers, as per the equation:

$$\left\{ \frac{\left| x_i - \text{median}(x) \right|}{\text{MAD}} \right\} > 2.$$

For the butterfly data, x_i is a species' year-to-year change index in year i, and x is the whole time series of species with year-to-year changes in their annual indices. We calculated extreme events separately for each butterfly species and classified them as either crashes (C) or explosions (E). We repeated the process with the annual index values to detect years with extreme abundances, which we classified as either extremely high abundance (Abu+) or extremely low abundance (Abu−). We then repeated the same process for each weather variable in each climatic region to define extreme climatic seasons (ECSs), with x_i being the climatic values at year i and x the whole time series for the region [ACR = 26 years (1995–2020), MMCR = 27 years (1994–2020)]. Note here that extreme events (ECEs) correspond to extreme climatic seasons (e.g., the whole spring period) and not to events such as heatwaves or cold snaps lasting just a few days.

We first used a three-way ANOVA to determine the proportion of population extremes that depended on two particular life-history traits (voltinism and overwintering stage) and on climatic region. The analysis included the interactions 'climatic region:hibernation stage' and 'climatic region:voltinism'. We performed different analyses for population crashes and explosions, and carried out a Post-Hoc Tukey test for pair-wise comparisons. Four species that hibernate in more than one life-cycle stage (*Pararge aegeria, Colias crocea, Issoria lathonia* and *Cacyreus marshalli*) were excluded from the analyses.

We also investigated whether or not population extremes of different species were synchronised in particular 'consensus years' (sensu Palmer et al. (2017)). We used one-tailed exact binomial tests with observed frequencies of crashes and explosions to identify years in which more species experienced population extremes than expected by chance.

Lastly, we investigated whether or not there was an association between population extremes and ECEs for those weather variables that, according to our initial analysis, significantly affected species' population growth (e.g., if the growth rate was affected by winter SPI, we asked whether or not an extreme population change occurred in the years with extreme winter SPI). We built GLMMs with a binary response variable (i.e., the occurrence or absence of a population extreme, either a crash or an explosion in separated models) and used both climatic and density-dependent predictors also structured as binary variables (Zuur et al. 2009). The climatic predictor tested whether or not the years when ECEs occurred were linked to population extremes. The two density-dependence terms (extremely high abundance (Abu+) and extremely low abundance (Abu−)) were used to test whether or not population extremes were linked to extreme population levels in the previous year (i.e., we asked whether or not population crashes followed years with extreme population abundance, and whether or not population explosions followed years in which the species was extremely rare). These models were fitted separately for the ACR and MMCR climatic regions and for univoltine and multivoltine species (four models in total), with the identity of species used as a random factor.

Results

Specific models of population growth

Our models identified density dependence (DD) as the most ubiquitous predictor for population growth (61 out of 78 species, 78.2%) – in all cases with a negative effect—and revealed a variety of responses to seasonal rainfall and temperature in most species (64 out of 78 species, 82.1%, Table 2, Suppl. Table 1). Six species were not affected by either climatic or density-dependent factors; five species in ACR and seven species in MMCR were significantly affected by DD but not by climatic factors.

The importance of DD was similar in both climatic regions (significant relationships were recorded in 71% of the species in ACR and 67.1% in MMCR). Likewise, a similar proportion of species responded significantly to weather variables (69.4% of the species in ACR and 64.4% in MMCR). Species not affected by DD were mostly those whose populations were in decline in the study region ($\chi^2 = 15.428$, $P = 0.001$).

Table 2 Number of species showing significant responses to weather variables in each climatic region

Region	Alpine (31 spp.)		Med mesic (58 spp.)	
Population growth	+	−	+	−
Density dependence	0	26	0	51
Precipitation				
Spring (i-1) SPI	NA	NA	1	0
Summer (i-1) SPI	0	4	1	20
Autumn (i-1) SPI	4	1	4	8
Winter SPI	7	0	8	2
Spring SPI	1	7	13	7
Summer SPI	1	1	5	3
Temperature				
Spring (i-1) min °C	NA	NA	0	0
Summer (i-1) min °C	3	3	4	2
Autumn (i-1) min °C	0	2	1	7
Autumn (i-1) max °C	NA	NA	NA	NA
Winter min °C	0	4	3	6
Winter max °C	NA	NA	2	9
Spring min °C	2	2	9	2
Summer min °C	1	2	0	3

'+' indicates a positive effect on population growth, '–' indicates a negative effect or population decline, *SPI* standard precipitation index, *DD* density dependence, 'i-1' corresponds to the weather variable from the previous year (lag 1)

Rainfall variables had contrasting effects depending on the species and climatic region (Table 2, Suppl. Table 1). *Maniola jurtina* was the species most affected by rainfall variables (with four significant SPI predictors corresponding to all four seasons in the current year), while as many as 15 species (19.2%) showed no significant relationship with rainfall. Focusing on climatic regions, the most important rainfall variables in ACR were winter SPI, with an overall positive effect of more humid and snowy winters (seven species responded positively and none negatively), and spring SPI, with an overall negative effect of rainy springs (seven species responded negatively and only one positively) (Table 2). In MMCR, spring SPI and the previous summer SPI were the predictors associated with the largest number of significant responses. Unlike ACR, spring SPI had a predominantly positive effect (13 species increasing compared to 7 decreasing; Fig. 2). On the other hand, a rainy previous summer had a consistent negative effect (20 species decreasing compared to only one increasing).

Fewer species had significant relationships with temperature (Table 2). *Erynnis tages* was the species most affected by temperature variables (with 5 significant relationships), while 27 species (34.6%) had no significant relationships (Suppl. Table 1). Winter temperatures had the highest influence on population growth, with the negative effects of milder winters found for about 15% of the species in both ACR and MMCR (Fig. 2). Previous warm autumns also had consistent negative effects in both ACR and, especially, in MMCR (Table 2).

Multispecies models for growth rate

The combined linear mixed-model performed for rainfall variables showed a significant difference between multivoltine and univoltine species, with the latter being more negatively influenced by rainfall variables ($P = 0.003$; Table 3). The model also showed a positive interaction between the larval stage and voltinism ($P = 0.017$), which indicates that in univoltine species rainfall acting on the larval stage had a disproportionately high positive effect on population growth rate compared to multivoltine species (Suppl. Figure 1).

For temperature variables, we likewise detected a significant—albeit weaker—effect of voltinism, again with univoltine species having a generally more negative influence ($P = 0.037$; Table 3). We also found significant effects on two developmental stages, namely the adults of the previous season ($P = 0.047$) and, above all, the larval stage ($P = 0.015$), which were more negatively affected by higher temperatures than the other stages. Moreover, there was an interaction between the adults of the previous season and voltinism,

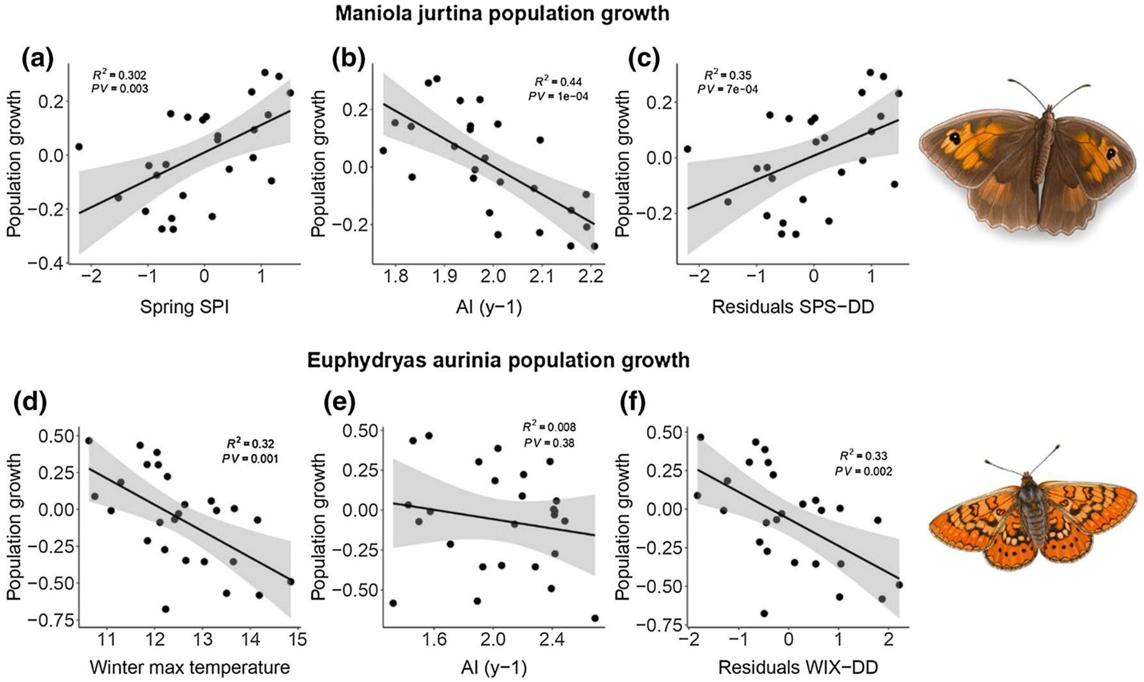

Fig. 2 Examples of weather factors affecting the population growth of two univoltine species. The meadow brown butterfly (*Maniola jurtina*) (**a**–**c**) shows a highly significant positive response to spring SPI (**a**) and a highly significant negative response to population levels in the previous season (**b**). The marsh fritillary (*Euphydryas aurinia*) (**d**–**f**) shows a highly significant negative response to winter maximum temperatures (**d**) and no density-dependence effect (**e**). Panels **c** and **f** show these relationships after controlling for density dependence. The marsh fritillary is a declining species in the MMCR (Supp. Table 1)

Table 3 Results of the combined GLMM models for Precipitation and temperature variables for all the studied species, with their estimates and *P* values

	Precipitation		Temperature	
	Estimate	*P* value	Estimate	*P* value
A-1 stage (ref. adult)	− 0.067	> 0.05	− 0.190	0.047*
L stage (ref. adult)	− 0.010	> 0.05	− 0.220	0.015*
P stage (ref. adult)	0.046	> 0.05	− 0.087	> 0.05
Univoltine (ref. multivoltine)	− 0.114	0.003**	− 0.151	0.037*
MMCR (ref. AR)	− 0.008	> 0.05	− 0.078	> 0.05
A-1 × univoltine	0.029	> 0.05	0.207	0.035*
L × univoltine	0.124	0.017*	0.125	> 0.05
P × univoltine			0.011	> 0.05
A-1 × MMCR	0.002	> 0.05	0.079	> 0.05
L × MMCR	− 0.020	> 0.05	0.141	> 0.05
P × MMCR			0.077	> 0.05

A-1 adults in the previous year, *L* larvae, *P* pupae, *MMCR* Mediterranean mesic climatic region, *AR* alpine climatic region. Significant values *: $0.01 < P < 0.05$; **: $P < 0.01$

with higher temperatures having a more negative effect on multivoltine than univoltine species (Suppl. Figure 1).

Extreme population changes and their relationship with extreme climate seasons

We identified extreme population events in both climatic regions (Suppl. Figure 2), which affected almost all the species included in the analysis (40 species in ACR (74%), 72 species in MMCR (84.7%)). The species experiencing the most severe population crashes in ACR were *Polyommatus icarus, Colias crocea* and *Boloria euphrosyne*, with four crashes over a period of 17, 22 and 15 years, respectively. In MMCR, *Colias crocea* and *Aporia crataegi* underwent six population crashes in 26 and 20 years, respectively, while *Lasiommata megera* and *Gonepteryx cleopatra* experienced five population crashes in a time series of 19 years each. A similar pattern was found for explosion events, with population explosions being recorded in 66.6% of the species in ACR and 85.9% in MMCR. The species experiencing most explosions were *Colias crocea* and *Melitaea phoebe* in ACR (four explosions in 22 and 15 years, respectively), and *Thymelicus acteon* in MMCR (six explosions in 23 years).

The proportion of years with population extremes depended on the climatic region and the hibernation stage but not on voltinism (Table 4). Relatively more species experienced population crashes in MMCR than in ACR ($P = 0.047$), while species overwintering in the larval stage

Table 4 Results of the three-way ANOVA showing separately the relationship of population crashes and explosions with two life-history traits (voltinism and hibernation stage) and with the climatic region

		Df	Sum Sq	Mean Sq	*F*-value	Pr(> *F*)
Crashes	Region (MMCR-ACR)	1	0.041	0.041	4.034	0.047*
	Voltinism (U-M)	1	0.019	0.019	1.908	> 0.05
	Hibernation (L-A-O-P)	3	0.036	0.012	1.186	> 0.05
	Region × voltinism	1	0.016	0.016	1.626	> 0.05
	Region × hibernation	3	0.005	0.002	0.151	> 0.05
Explosions	Region (MMCR-ACR)	1	0.003	0.003	0.554	> 0.05
	Voltinism (U-M)	1	0.000	0.000	0.02	> 0.05
	Hibernation (L-A-O-P)	3	0.054	0.018	3.475	0.018*
	Region × voltinism	1	0.009	0.009	1.804	> 0.05
	Region × hibernation	3	0.018	0.006	1.149	> 0.05

Significant values *: $0.01 < P < 0.05$; **: $P < 0.01$

had more population explosions than species overwintering in the egg stage ($P = 0.018$). In MMCR, we identified 4 consensus years. The only year with more explosions than expected by chance was 2002 (22, 30.9% of the species; $P = 0.001$). Moreover, this same year was the only one in which no crashes were recorded (Suppl. Figure 2). The other 3 consensus years had more crashes than expected randomly (2004: 18, 24.2% of species, $P = 0.02$; 2012: 15, 17.1%, $P = 0.04$; 2019: 20, 22.2%, $P = 0.04$; Suppl. Figure 2).

Similarly, extreme climatic seasons were found to occur almost every year. We identified 53 season extremes in ACR in a 22-year time series (2.40 ECSs/ year), consisting of 13 rainfall crashes and 13 rainfall explosions, and 13 temperature crashes and 14 temperature explosions. In MMCR there were 59 ECSs in a 26-year time series (2.25 ECSs/year), consisting of 20 temperature crashes and 14 temperature explosions, and 6 rainfall crashes and 19 rainfall explosions. Only 4 years had no ECSs of any type in MMCR.

The GLMMs gave consistent results for the effects of extreme population levels on population crashes and explosions (Table 5). Irrespective of the climatic region, crashes tended to occur following extremely high abundances the previous year (Abu+) and explosions following extremely low abundances in the previous year (Abu−), both in univoltine and multivoltine species (Table 5; Fig. 3).

The relationship between population extremes and the ECSs, on the other hand, differed according to the climatic regions and, to a lesser extent, to voltinism. In MMCR—but not in ACR—population crashes occurred in association with ECSs for the same weather variables that negatively affected population growth (Table 5). For population explosions, only marginally significant associations were found in univoltine species in ACR and in multivoltine species in MMCR (Table 5).

Table 5 GLMMs testing the effects of extreme climatic events (ECS) and extreme high (‘Abu+’) or low abundances in the previous year (‘Abu−’) on population crashes and explosions in two climatic regions

	Alpine climate region		Med. mesic region	
	Estimate	Pr(> |*z*|) value	Estimate	Pr(> |*z*|) value
Univoltine				
Crash				
Abu+	1.569	0.004**	1.819	2.10E−06**
Abu−	−2.88	> 0.05	−1.205	> 0.05
ECS	2.50	> 0.05	1.709	8.48E−10**
Explosion				
Abu+	−0.636	> 0.05	−15.144	> 0.05
Abu−	1.567	0.002**	1.402	4.02E−05**
ECS	0.748	> 0.05	0.480	> 0.05
Multivoltine				
Crash				
Abu+	1.706	0.004**	2.250	4.77E−12**
Abu−	0.114	> 0.05	−17.086	> 0.05
ECS	0.729	> 0.05	0.762	0.015*
Explosion				
Abu+	−17.683	0.997	−1.231	0.0926
Abu−	2.504	6.51E−07**	2.023	4.24E−12**
ECS	0.612	> 0.05	0.465	> 0.05

Significant values *: $0.01 < P < 0.05$; **: $P < 0.01$

Discussion

Population growth and density dependence

In this study, we explore which weather variables affect the population dynamics of Mediterranean butterflies, which developmental stages are the most sensitive to weather variables, and whether or not density-dependence factors also play a significant role in the population dynamics of these butterflies. We found that density dependence had a major

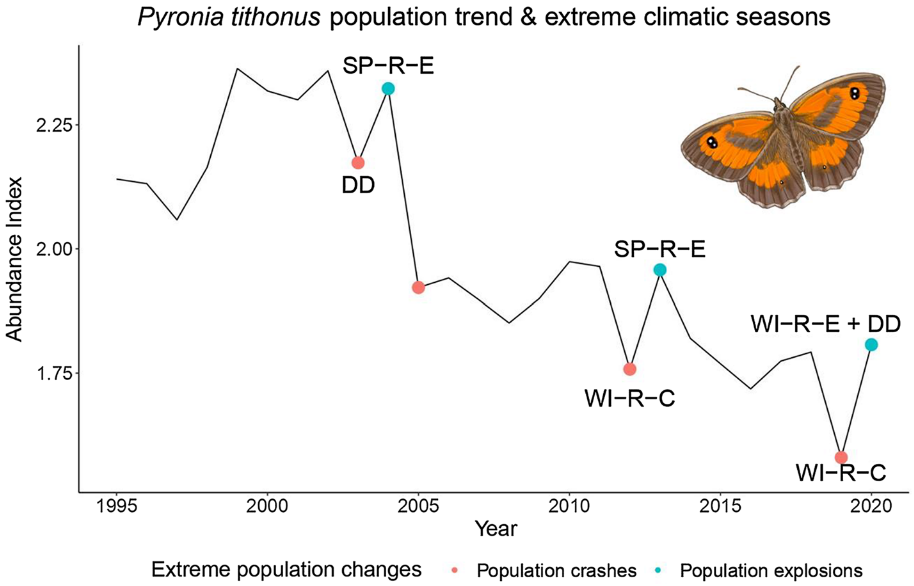

Fig. 3 Population fluctuations of the gatekeeper butterfly (*Pyronia tithonus*) in the MMCR, showing four population crashes (red dots) and three population explosions (blue dots). Six out of seven population extremes can be accounted for by extreme climatic events and extreme population levels in the previous year (i.e., density dependence). Population growth in this species is mostly affected by winter rain and spring rain, both with a positive effect. All three population explosions and two population crashes occurred in seasons when these weather predictors reached extreme values in the same direction as expected. One population crash occurred the year after an abundance explosion. SP-R-E (Spring Rain Explosion), WI-R-E (Winter Rain Explosion), WI-R–C (Winter Rain Crash), DD (Density Dependence)

effect on many species, including a ubiquitous negative effect on growth rate. Negative relationships correspond to classical population regulation theory (Royama 1992), with high population levels the previous year provoking a variety of factors negatively affecting population growth such as the increase in the number of parasitoids and predators (Hassell 1985). Although this effect was consistent both in MMCR and ACR, several species showed varying degrees of density dependence across the two climatic regions, indicating that the strength of density-dependent processes varies throughout a species' range (Dooley et al. 2013). For example, in *Aporia crataegi* significant density dependence was only detected in ACR, and in *Melanargia lachesis* only in MMCR. Interestingly, the least sensitive species were those with declining population trends in the study region (e.g., *Melanargia occitanica* and *Euphydryas aurinia*), suggesting that for these species the adverse effects of habitat degradation cannot be offset by density dependence processes.

Population growth and weather

Weather also represented a major driver of butterfly population dynamics, with more than 80% of species being affected by at least one weather variable. As in previous work (Herrando et al. 2019), we found a certain amount of evidence to suggest that precipitation is more important than temperature in Mediterranean butterflies (60% of significant relationships were associated with SPI, while 40% with thermal variables), and we found similar results in the alpine region (57% precipitation, 43% thermal).

Spring SPI, in particular, affected many species, with a dominant positive effect in MMCR but a consistent negative effect in ACR. In the Mediterranean climate, the rainfall pattern is characterised by two distinct peaks, one in spring and one in autumn, the first of which is essential for the growth of vegetation and, in turn, for the development of herbivorous insects (Yela and Herrera 1993). In addition, spring rain largely determines nectar availability during the summer season, a crucial factor in explaining butterfly abundance (WallisDeVries et al. 2012). In our study, the few species that were negatively affected by spring SPI were those with a spring flight period and larval development in the previous season (e.g., *Pseudophilotes panoptes* and *Zerynthia rumina*). We believe that this is because both adult activity and detectability in these species are reduced in rainy springs. On the other hand, spring SPI in the alpine climate region was strongly associated with butterfly negative responses, possibly because the lengthening of the winter period with snow cover reduces larval and pupal survival and the subsequent number of adults.

Humid winters also showed frequent significant relationships with population growth, with positive effects both in ACR and MMCR. In the alpine climate region, such winters mean greater snow cover, which has repeatedly been shown to be beneficial for mountain butterfly species, both due to the direct effects on overwinter survival of immature stages and indirect effects on host plant and nectar resources (Boggs and Inouye 2012; Nice et al. 2014; Roland et al. 2021). In the Mediterranean region, winter rainfall favours the growth of perennial plants and herbs later in the spring, with a predictably higher survival rates for species feeding on these resources at that time (e.g., *Satyrium esculi* feeding on evergreen oak leaves, and satyrines such as *Maniola jurtina*, *Pyronia cecilia* and *P. tithonus*, and skippers such as *Thymelicus acteon* and *T. sylvestris*, feeding on grasses).

In addition, regardless of the climatic region, we recorded consistent population declines after rainy summers. The same pattern has been noted in other studies (Pollard 1988; Roy et al. 2001) and may be related to less adult activity and a consequent fall in potential fecundity, which will have repercussions the following year.

Temperature variables were also important in the MMCR, where the number of significant relationships was higher than in the ACR (0.83 and 0.61 significant relationships/species, respectively). Interestingly, mild autumns and winters had widespread negative effects in both regions, which concurs with experimental work providing clear evidence of a decrease in overwintering survival with rising temperatures during the diapausing period. Williams et al. (2012) identified an increase in metabolic consumption of overwintering larvae of *Erynnis propertius* under simulated high temperatures and suggested that longer warm autumns will have a negative impact on this butterfly by making its larvae more susceptible to an overwinter energy drain. Radchuk et al. (2013), Abarca et al. (2019) and Klockmann and Fischer (2019) also found that warm winters have negative effects on larval survival in *Boloria eunomia*, *Euphydryas phaeton* and *Lycaena tityrus*, respectively. Reserve depletion resulting from increased metabolic activity has been suggested as the main reason for increased mortality, although a larger incidence in diseases and fungal infections could also play a role (Radchuk et al. 2013). These examples can probably apply to many species overwintering as larvae and experiencing population declines following warm autumns and winters in our region (e.g., *Erynnis tages*, *Brintesia circe*, *Erebia meolans*, *Coenonympha arcania*, *Maniola jurtina*, *Satyrus actaea*, *Boloria dia*, *Euphydryas aurinia*, *Melitaea cinxia*, *M. didyma*, *M. phoebe* and *Aporia crataegi*).

Unlike winter and autumn, warm springs in the Mediterranean region had an overall positive effect on butterfly populations. Although this positive effect could be substantially lessened in the future if warm springs come to be associated with droughts (see above), a likely explanation for this effect is that a shortening of developmental times under high temperatures reduces the time of exposure to potential predators and parasitoids (e.g., Pollard 1979). The fairly strong relationship we detected mirrors that found by earlier studies in the UK (Pollard 1988; Roy et al. 2001), even though it occurs slightly earlier in the season due to the phenological advance in Mediterranean climates compared to Temperate Climate (TC) from Central Europe. A non-exclusive explanation is that warm springs favour adult activity and increase the detectability of butterflies flying in spring during transect counts.

On the other hand, our findings contrast with some of the relationships reported in previous studies in the TC region. Thus, the effect of rainfall on population growth was generally positive in the MMCR, where it is a scarce resource, but was negative in the TC region, where is not a limiting factor (Hawkins et al. 2003). Therefore, while butterfly populations benefitted from humid winters and springs in the MMCR, rainy winters had an opposite effect in the TC region (WallisDeVries et al. 2011) and it was dry years and, more precisely, dry summers that were associated with population increases in this region (Pollard 1988; Roy et al. 2001). Quite predictably, temperature had positive effects during the period in which most species developed as immatures, that is, in spring in the MMCR but in summer in the TC (Pollard 1988; Roy et al. 2001). Interestingly, and for the reasons already discussed, mild winters had consistent negative effects on population growth in both regions (WallisDeVries et al. 2011, and the current study), a worrying finding in the context of climate warming.

Climate sensitivity and life history

Our analyses revealed that larval and adult stages are the most sensitive to climate. This is not surprising since they correspond to the active part of the butterfly's life cycle (e.g., in which feeding, growth, mating and egg-laying take place) and both larvae and adults exhibit a wide range of thermoregulatory behaviour (Radchuk et al. 2013). On the other hand, the egg and pupal stages are concentrated in a much shorter time window and, when they overwinter, possess physiological adaptations that make them highly resistant to climate (Bauerfeind and Fischer 2013).

In turn, our multispecies models allowed us to test whether or not the sensitivity to climate differed between climatic regions and the voltinism of species. Population growth was not explained by climatic region but was related to voltinism, with a higher frequency of negative effects recorded more frequently in univoltine species than in multivoltine ones both for temperature and rainfall variables. This finding is likely to be related to the poorer ability of single-generation species to recover in the same year from a negative climatic episode (Kerr et al. 2019). In addition, it suggests that univoltine species may suffer more severely under the current climate change scenario if it implies an increase in the frequency of the weather episodes we have identified as detrimental to population growth.

When the interaction between developmental stage and voltinism was taken into account, more complex patterns emerged. Thus, precipitation acting on the larval stage had disproportionately positive effects on univoltine species, while temperatures experienced by adults in the previous season had more negative effects on multivoltine species. We believe that these relationships highlight how important it is that single-brooded species synchronize their relatively short period of development with the right conditions for the growth of their host plants, and also the risk that multivoltine species accumulate harmful effects caused by high summer temperatures in successive generations, which will have negative consequences in the next season (Melero et al. 2016).

Extreme population changes and their relation with extreme climatic seasons

Extreme population changes occurred almost every year, with some species experiencing these changes more often than others. Moreover, these population events were more frequent in the Mediterranean than in the alpine climate region, although this difference only applied to population crashes. Consensus years (i.e., when more species than expected suffer extreme population changes) were similarly only detected in the Mediterranean region. Extreme climatic events were also recorded annually and there were only 2 years in MMCR when no ECSs were recorded.

Our data clearly show that density dependence is an important factor in population extremes as, regardless of region and voltinism, these extreme events were associated with abnormally high or low population levels in the previous season. Population collapses caused by the impact of parasitism, predation and disease are common among outbreaking forest Lepidoptera (Dwyer et al. 2004) but can also affect many other non-outbreaking species (Nowicki et al. 2009). Likewise, marked population increases recorded in a subsequent season after very low population levels suggest that a relaxation of density-dependent mortality factors occurs. While to some extent this might be expected, it is remarkable that density dependence alone can explain butterfly population extremes in many cases.

We also found an association between ECSs and population extremes, indicating magnified effects of climatic variables beyond some threshold that lead to abrupt shifts in population growth. The response, however, was not ubiquitous: population crashes were significantly related to climatic extremes but only in the Mediterranean region, which could partly explain the more negative butterfly trends there (Herrando et al. 2019; Ubach et al. 2021). This effect was clearly more strong in univoltine species than in multivoltine ones, which can be explained by the lower plasticity of the former in their responses to environmental stress (Forister et al. 2018). The absence of an association of ECSs and population crashes in the alpine region could be related, in part, to compensation mechanisms, such as the one suggested by Buckley and Kingsolver (2012) in their study of two alpine *Colias* species. These authors found that although extreme heat reduces egg viability, this negative effect is offset by an extension of the flight period under a warming climate. In contrast to population crashes, the evidence that climatic extremes provoke population explosions was weak in our data, even though under some circumstances this may occur. Indeed, the single consensus year when more population explosions than expected were recorded coincided with an extremely humid spring, which favoured the growth of vegetation and an abnormally high success of species that overwintered as larvae and concentrated their development in spring. No similar response was observed in the alpine climate region, where water is not such a limiting factor as it is in the Mediterranean region (Hawkins et al. 2003).

Conclusions

In this study, we provide evidence of weather-dependent population dynamics of butterflies in the Mediterranean basin and identify the most important climatic variables driving population growth in two climatic regions. Amongst the clearest relationships, we highlight the importance of spring rainfall in the MMCR, where it has a clear positive effect given that water availability is a limiting resource. We also identify a general negative effect of mild winters on butterfly populations, both in the MMCR and the ACR. Both relationships are worrying in the context of climatic warming, as drier springs and warmer winters are expected to be more frequent and intense in the Mediterranean basin in the next decades, according to the majority of climate change scenarios. Another relevant conclusion from our work is the strong effect of density-dependent processes in the vast majority of the studied butterfly populations. This effect even accounts for a large fraction of the recorded extreme population changes (crashes and explosions). Extreme climatic events were related to population crashes and rarely to population explosions in the MMCR, but no relationship was found in the ACR. Although our results help to understand the population dynamics of Mediterranean butterflies, longer time-series are still needed to reveal some other patterns that may remain hidden with current data. Especially important is the need to include data from populations occurring in the Mediterranean xeric climate region, where the effects of climate change will be particularly severe.

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Author contribution statement AU and CS conceived the study. AU led the analyses, with assistance by the other authors. CS wrote the MS with the assistance of AU. All authors contributed to the data collection, and all have commented on and approved the final version.

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Availability of data and material The data from this study will be made available on Dryad by the time of publication.

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Declarations

Conflict of interest The authors declare that they have no conflict of interests.

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

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Abstract. 1. Land abandonment and loss of grazing have been amongst the primary drivers of landscape change in the Mediterranean basin in the recent decades. As a consequence, forest cover has greatly expanded in detrimental of semi-natural grasslands, areas of cultivation and pasture mosaics. Although predictably important, the impact that this phenomenon has on biodiversity has remained largely unexplored, partly because of lack of appropriate data.

2. Here, we make use of an extensive citizen science program, the Catalan Butterfly Monitoring Scheme, to quantify the response of butterfly assemblages to vegetation encroachment in NE Spain. We first adapted an index to describe the preference of 147 butterfly species for open or closed habitats and found a strong association of most species for open habitats.

3. We developed a community index to record changes in 54 long-term monitored sites (10 years or more), where plant communities were also periodically monitored. Butterfly assemblages have undergone changes toward species preferring closed habitats in 72% of the studied sites, in parallel to a process of vegetation encroachment in the region.

4. Community changes were linked to population trends, and could be locally predicted by the interaction of the preference of butterfly species for open or closed habitats and the magnitude of vegetation encroachment at each site. These changes were accompanied by frequent extinction events (4.53% of the studied populations), that were highly biased toward species preferring open habitats. Our study confirms and quantifies the threat that vegetation encroachment imposes on biodiversity in this highly diverse region.

Key words. Butterfly assemblages, butterfly monitoring, land abandonment, species loss, TAO index, vegetation encroachment.

Introduction

Vegetation encroachment, that is, the spread of woody plant species into open habitats (van Auken 2009; Ratajczak et al. 2012), is a phenomenon that is occurring worldwide in grasslands and savannahs. It is very common in developed countries and was one of the main mechanisms driving forest transition and land cover changes in the past century (MacDonald et al. 2000; Rudel et al. 2005; Gerard et al. 2010). Encroachment is caused by a loss of traditional practices (van Auken 2009) such as livestock husbandry and low-intensity cultivation but also by increasing atmospheric CO_2 levels, nitrogen deposition, and fire suppression (Ratajczak et al. 2012). Most of these drivers are fully applicable to the Mediterranean basin, where a rich mosaic of semi-natural grasslands and areas of cultivation and pastures, maintained by anthropogenic and natural processes for thousands of years, has been greatly reduced in recent decades as forest cover increases (Falcucci et al. 2007; Blondel et al. 2010; Mairota et al. 2013).

Vegetation encroachment is a serious threat to biodiversity, as the preservation of many species is strongly dependent on the

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maintenance of open habitats (Balmer and Erhardt 2000; WallisDeVries et al. 2007; Ratajczak et al. 2012). It has been shown to cause a decrease in plant diversity (Ratajczak et al. 2012) have an impact on vegetation composition, affect higher trophic levels (Pöyry et al. 2006), and at larger scales may even lead to habitat fragmentation in seminatural grasslands (Schirmel et al. 2015). It is therefore not surprising that much of recent research on vegetation encroachment has been aimed practically at improving pastoral practices and management options and thus biodiversity conservation (Balmer and Erhardt 2000; WallisDeVries et al. 2007; Rivest et al. 2011; Mairota et al. 2013). Likewise, many on-going efforts are being made to identify biological indicators that respond rapidly and visibly to the phenomenon of vegetation encroachment (e.g. Pöyry et al. 2006; Tocco et al. 2013; Schirmel et al. 2015).

Butterflies, in particular, are known to be an excellent group for investigating the loss of traditional pastures and the resulting effects of vegetation encroachment (Erhardt 1985; Stefanescu et al. 2009; Krauss et al. 2010; Verdasca et al. 2012; Koch et al. 2015). Moreover, their key role as an indicator group (Thomas et al. 2004; Thomas 2005) has prompted their use in recent decades in extensive ecological monitoring programmes (van Swaay et al. 2008), which have generated large data sets that can be used to explore wide-ranging responses to vegetation encroachment. Here, we make use of one such data set, the Catalan Butterfly Monitoring Scheme (CBMS), to quantify the response of butterfly assemblages to this phenomenon in the north-west Mediterranean over the past three decades.

In a previous study, Herrando et al. (2015) developed indicators for the open-closed gradient preferences of butterfly and bird populations in the Mediterranean region. They studied species' habitat preferences and showed how species preferring closed habitats have experienced more positive trends in the recent decades than those that positively select for open habitats. However, although multi-species indicators help us understand how environmental factors drive population trends, a community approach is needed for a more comprehensive assessment of the impact of global change at ecosystem level (Julliard et al. 2006; Devictor et al. 2012). The use of such an approach in this article allows us to explore how butterfly assemblages have undergone changes in diversity and composition that are running parallel to the landscape changes closely linked to the abandonment of traditional agricultural practices. We also provide a tool that can be used by conservation managers to show how butterfly communities change rapidly as a response to vegetation encroachment and to illustrate the changes that take place in ecosystems at local scale.

Several recent studies have highlighted the on-going decline of flying insect biomass (Hallmann et al. 2017). In particular monitoring programs have shown negative trends of lepidoptera in European countries and indicators of this decline highlight its affectation at grassland habitats (van Swaay et al. 2015). In northern Europe, changes in land use associated with intensive grazing and vegetation encroachment have been shown to cause extinctions and declines in butterfly populations (Nilsson et al. 2008). Herrando et al. (2015) conclude that butterfly species preferring open habitats have more negative trends than those preferring closed habitats and here we test whether or not this link is leading to the extinction of the populations of species in the Mediterranean that select open habitats. More generally, we explore how species perform depending on the degree of vegetation encroachment and on their preferences for open or closed habitats.

Materials and methods

Study area and butterfly data

The study was carried out in Catalonia, Andorra, and Menorca (Balearic Islands), in the north-west Mediterranean basin, where butterflies are monitored by the Catalan Butterfly Monitoring (CBMS) (Fig. 1). The region is environmentally diverse with different orobiomes ranging from sea level to alpine mountains, embracing a wide range of habitats including Mediterranean steppes and deciduous forests. Currently, more than 64% of its surface area is covered by forests (Fletas et al. 2012) partially due to vegetation encroachment resulting from the abandonment of traditional land uses. According to González et al. (2018), the surface area of forest in Catalonia increased at a rate of 3300 ha/year in 1987–2012, while the land devoted to agriculture declined at a rate of 6300 ha/year during the same period.

The CBMS started in 1994 and at the end of 2017 93 sites out of the 160 that have provided data were active (see details in www.catalanbms.org). Butterflies are monitored using the standardised methodology originally developed in the United Kingdom (i.e. Pollard walks), which has been adopted as a standard in similar schemes throughout Europe (Schmucki et al. 2015). At each location, weekly counts along fixed routes start on March 1 and finish on September 26, spanning a total of 30 weeks. Butterflies are counted in a 5 × 5-m area (2.5 m to each side and 5 m in front of the recorder) whenever weather conditions are good (Pollard and Yates 1994). The transect route is divided into a variable number of sections, each one corresponding to a distinguishable habitat type.

Species preferences for open/closed habitats

Vegetation characterisation. A botanical characterisation of the butterfly transects designed to monitor vegetation changes at the sites was repeated periodically by a botanist (CG). The first characterisation of the older sites took place in 2000, after which subsequent characterizations were repeated every six years. Butterfly transects that joined the CBMS after 2000 were first characterised in the year they started to provide data and then at six-year intervals. Botanical characterizations were used both to derive a preference index of each butterfly species (i.e., open vs. closed habitats) and to record changes in the plant communities at individual sites during the butterfly recording period.

At each characterisation, the cover of each plant community (defined according to the CORINE biotopes classification (Vigo et al. 2005)) was recorded at section level along the five-metre-wide butterfly walk. We established a binary classification for closed versus open plant communities, assigning a value of −1 for closed communities and a value of +1 for open ones.

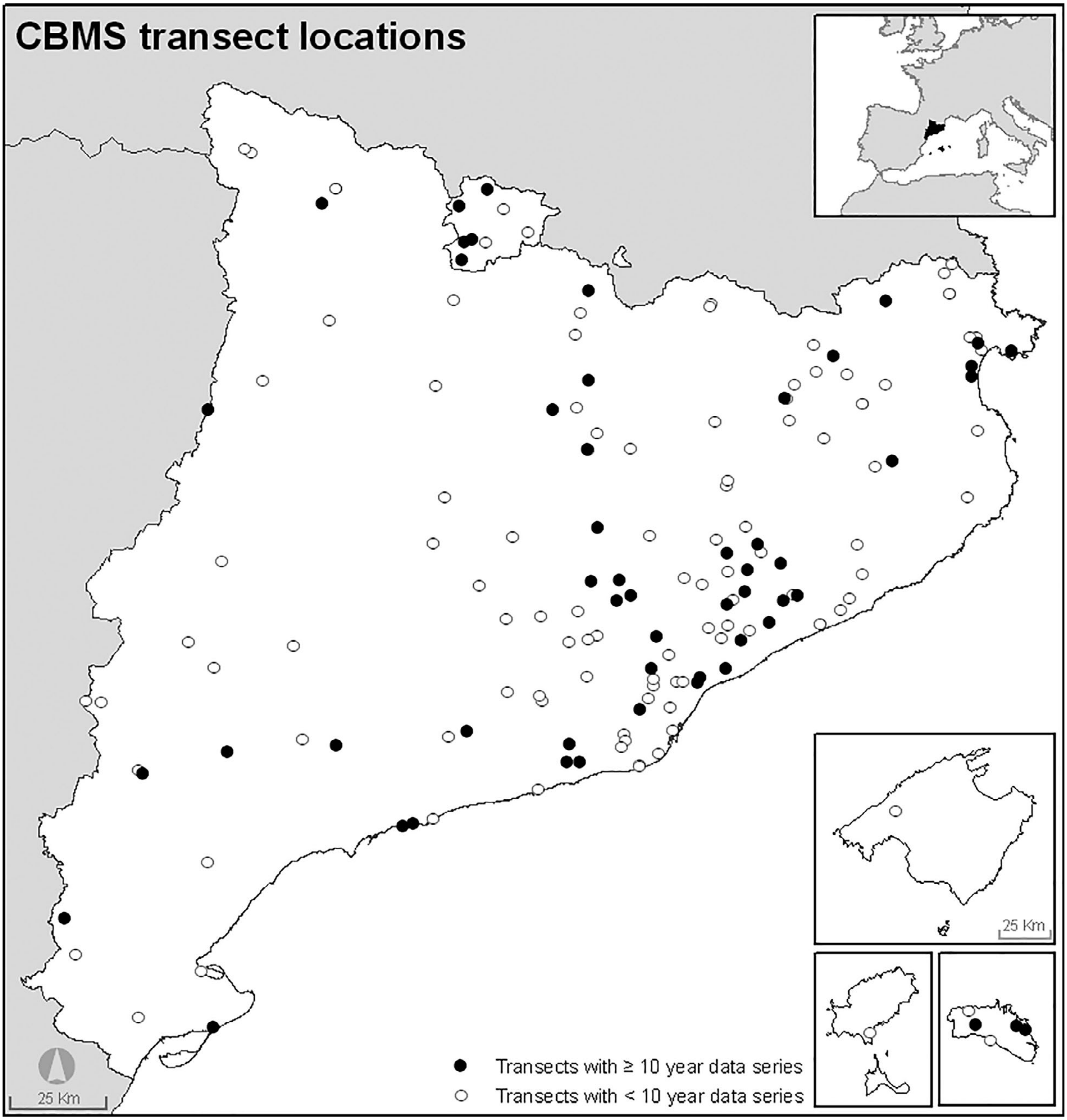

Fig. 1. Map of the study region. The locations of the 54 long-monitored transects (≥10 years) in the CBMS network used for this study are represented by black dots. White dots represent the remaining 106 CBMS transects that existed up to 2017 and were used for calculating an index of preference along a gradient from closed to open habitats.

All types of forest were categorised as closed and all grasslands as open, while shrubby communities were classified as either ‘closed’ or ‘open’ depending on the characteristic average height (see Table A2 for details of each plant community). Subsequently, we calculated an average value for each section by multiplying the cover of each plant community by the assigned ‘-1’ or ‘+1’ value. Only sections with average values greater or equal to |0.1| were retained, as values very close to 0 (either positive or negative) represent a near equilibrium situation between open and closed habitats.

Butterfly data were associated to the nearest year of characterisation and so between two botanical characterizations there were 3 years of data associated to the first and three years associated to the second. For transects that were active before the year

2000, we used butterfly data beginning in 1997 (three years before the first botanical characterisation).

TAO species index. We used the formula in Suggitt et al. (2012) to calculate an index (TAO) of butterfly species' preferences for open or closed habitats. This index allows us to order species along a gradient from −1 when they occur exclusively in closed (in Catalan: *TAncat*) habitats, to +1 when they occur exclusively in open (in Catalan: *Obert*) habitats. As in Suggitt et al. (2012), the TAO index was calculated for each species at transect level ('*i*') according to the formula:

$$I_{TAOi} = \frac{2 \times \boldsymbol{D}_{\mathbf{open}}}{\boldsymbol{D}_{\mathbf{open}} + \boldsymbol{D}_{\mathbf{closed}}} - \mathbf{1}$$

where D_{open} is the mean density value (individuals/100 m) in open sections and D_{closed} is the mean density value in the closed sections.

The final TAO index for each species (I_{TAO}) was thus the mean value of all the I_{TAOi} calculated for all transects in which a species appeared. We only used species with occurrences in a minimum of five transects, and for the calculation of the index, we only used transects with both types of sections (i.e. closed and open; $n = 121$); transects where a species could theoretically select either type of environments.

Given that species show slight preferences for more open or more closed habitats depending on the climatic conditions experienced by local populations (e.g., populations occurring in colder habitats tend to occupy more open habitats where microclimates are generally warmer; see Suggitt et al. (2012)), we assessed how the I_{TAO} varied between thermal regions in Catalonia by establishing four thermal regions using a 21 DDG threshold (i.e., number of hours per year over 21 °C). Climatic data were provided by the Servei de Meteorologia de Catalunya (www.meteo.cat) and was used to classify each of the 160 butterfly transects as belonging to one of these four climatic regions. We calculated I_{TAO} values separately for each species and thermal region and then performed a Spearman rank correlation test between thermal region pairs to assess how stable species' preferences are at country level.

Habitat changes and trends in butterfly assemblages

Vegetation encroachment. To assess vegetation changes at the monitored sites over time, we calculated the percentage of change occurring between the first and final botanical characterizations that were caused by vegetation encroachment. Depending on the duration of the sampling carried out at the site, changes in vegetation were assessed for periods spanning 6 years (two consecutive characterizations), 12 years (three characterizations), or 18 years (four characterizations).

For both the first and last characterisation, we calculated an average value of openness/closeness for the whole transect. This value was the sum of the product of the percentage of closed habitats in each section multiplied by −1, plus the product of the percentage of open habitats multiplied by +1. Thus, each section was assigned a value between −100 (totally closed) and 100 (totally open). A single value for each transect and characterisation was then obtained by averaging the values of each section corrected for their length. A simple difference in the overall value between the two characterizations indicated the degree of encroachment of plant communities along a particular transect.

TAO community index. To study changes in butterfly communities over time, we assessed butterfly counts from a total of 54 sites with records from 1997 to 2017 with 10 years or more of data (mean = 14 years, range: 10–21 years) (Fig. 1). Three of these sites are situated on the island of Menorca, five in Andorra and the remaining ones in Catalonia (NE Spain).

We followed the rationale of Julliard et al. (2006) and Devictor et al. (2012) to develop a community index (TAOc) for each butterfly assemblage and year. The contribution of each species to the community index was weighted by the square root of its annual abundance to avoid biases resulting from large differences in population densities between species. The TAOc was thus obtained for each year of sampling for each butterfly transect. The slopes of linear models with TAOc as the dependent variable and year as the independent variable showed the trends of each butterfly community toward openness/closeness over time. Positive slopes corresponded to communities that tended to become more dominated by open habitat species during the monitored period, while negative slopes tended to become more dominated by closed habitat species.

We used generalised linear models (GLM) to relate the slopes summarising site changes in the TAOc to the degree of vegetation encroachment and several other predictors (see below). We hypothesised that butterfly communities will have negative TAOc slopes (i.e., a trend of the community is to become dominated by species preferring closed habitats) whenever (i) the vegetation of the site showed a degree of encroachment during the study period. In addition to vegetation encroachment, we included the following predictors: (ii) the Shannon diversity index based on the percentage cover of the CORINE habitat types at every itinerary at the initial time of the series, as we predicted that there would be a greater buffer effect (i.e., a greater stability of the butterfly community against vegetation encroachment) at sites with a wider range of resources and habitats; (iii) the initial TAOc value, as we believe that the structure of the community at the start of the monitoring period could influence the regression slopes; (iv) the time spanned since the start of monitoring since longer monitoring periods could be associated with greater community changes; (v) the thermal region to which the site belongs (a categorical variable, with four classes), as different rates of plant growth between regions could result in different rates of encroachment. We also added (vi) the interaction between vegetation encroachment and the thermal region.

We used a dredge function for a model selection approach based on the akaike information criterion (AIC) to evaluate the strength of evidence for the relative influence of the predictors. The set of candidate models were derived from all combinations of predictors. Differences in AIC were used to rank the candidate models, using ΔAIC value <2 as a threshold for a model to be considered as receiving support. We then performed the five best models as individual GLMs. We also used a one way-ANOVA to test whether or not responses of the TAOc were similar for all four thermal regions considered and, as a comparison, we performed a similar analysis testing vegetation encroachment at each site. All the analyses were performed using Rstudio (R Core Team 2018) with the *MuMin* package (Bartón 2015) for the GLMs.

Species loss and population declines

To test whether or not vegetation encroachment could lead to population extinctions, we first identified all extinctions that had occurred in the 54 long-term monitored sites during the study period. We defined a local extinction as the absence of a species at the site during at least 4 years after a period with data of at least 4 years (see Pollard and Yates 1992); thus, an eight-year series at least was needed to detect an extinction event. If a species recolonized the site after becoming extinct but then became extinct again, we counted that as two extinction events. We then calculated two mean TAO index values for each of the 54 butterfly assemblages. The first was the average of the indices of all the species that suffered extinction events and no longer occured in the community, while the second was the average of the indices of those species not showing extinction events. Calculations were based on a total of 2515 butterfly populations at the 54 sites, considering only species with a minimum occurrence of half the total number of sampling years. We performed a paired *t*-test comparing the two mean TAO indices at each site, to test whether there were any differences between the species showing extinction events and those that do not. If vegetation encroachment was a primary driver of butterfly population dynamics, we would expect that species with a more positive TAO index would be more likely to experience local extinction events.

In addition, we modelled population trends at site level (calculated as the slope of butterfly counts against years) as a function of species' preferences for open or closed habitats, and the changes of plant communities at site level. A generalised linear mixed model (GLMM) was built, with trend slopes as the response variable (2484 butterfly populations with a calculated trend), the TAO index of each species, our measure of vegetation encroachment at the site where the species flies, and the interaction between the two variables as the three fixed factors, and 'itinerary' and 'species' as random factors.

Results

Species preferences for open/closed habitats

We obtained the I_{TAO} index for a total of 147 species of butterflies (Table A1). The average number of sites used for calculating this index was 50; the maximum was 121 sites for clouded yellow (*Colias crocea*), large white (*Pieris brassicae*) and small white (*Pieris rapae*). The mean value (±SD) of the index was 0.408 ± 0.566, with extreme values of −0.419 for speckled wood (*Pararge aegeria*), a species that prefers highly closed habitats (n° sites = 117), and 1 for olive skipper (*Pyrgus serratulae*), which was only recorded in open habitats (n° sites = 7). The mean value for I_{TAO} was highly positively skewed, indicating a strong association in most species with open habitats (Fig. 2). In total 91% of the species had positive values that according to our criteria correspond to open habitats.

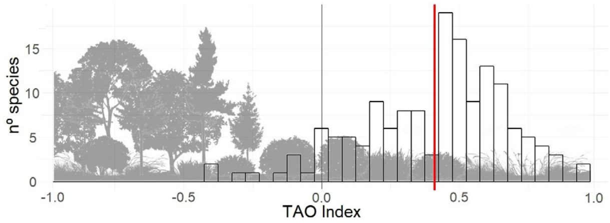

Fig. 2. Distribution of the I_{TAO} values for all 147 species along a (−1, 1) axis. In all, 91% of the species values show positive values, thereby indicating very strong preferences for open habitats. [Color figure can be viewed at wileyonlinelibrary.com]

Spearman correlations for the species indices between thermal regions were all positive and highly significant ($P < <0.01$ in nearly all pair-wise comparisons), the lowest ($P = 0.013$) correlation being between thermal region 1 (the coldest) and thermal region 4 (the warmest) (Fig. A1). Thus, species showed great consistency in their preferences for open or closed habitats regardless of the climatic conditions experienced by populations.

Habitat changes and trends in butterfly assemblages

Out of the 54 long-term monitored sites, in 41 (76%) there were changes toward greater vegetation encroachment. The overall increase in plant communities associated with closed habitats was in the range 0.1–31.7% between the first and final botanical characterizations. The 13 remaining sites changed in an opposite direction, moving toward a more open habitat (Fig. 3b). The TAOc values showed a similar pattern, with 39 butterfly communities (72%) becoming more dominated during the study period by species preferring closed habitats, and only 15 becoming more dominated by species preferring open habitats (Fig. 3a).

The five best models chosen with the AIC contain all the included variables except for the interaction between vegetation encroachment and thermal region (Table 1). Models 1 and 2 have delta<2 values and thus were selected as the best options out of all possible combinations. Vegetation encroachment had a significant relationship in all candidate models ($P < 0.05$), with greater encroachment (more negative values) being related to more negative TAOc slopes (Table 2). In the first two selected models, it had a very severe effect ($P < 0.01$). The Shannon index was also significant in all the models in which it was included, with a higher index being related to more positive TAOc slopes (i.e. a lesser response of the butterfly community to become dominated by species preferring closed habitats). Thermal region also had a significant response, with region 4 (the hottest) being associated with more negative trends. On the other hand, the initial TAOc number and the length of the

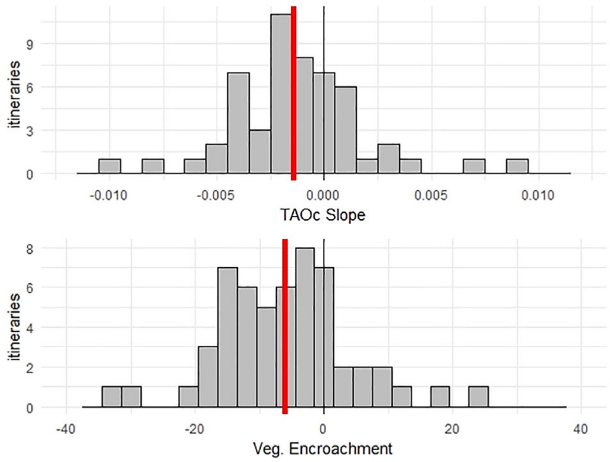

Fig. 3. Histograms showing TAOc slopes for all the 54 studied butterfly assemblages (a) and vegetation encroachment at the same 54 sites (b). The red bar situates the mean value of both data sets. In all, 72% of the itineraries show a negative TAOc slope indicating change toward butterflies that prefer closed sites, while 76% of the itineraries showed negative values for vegetation encroachment, indicating greater afforestation. [Color figure can be viewed at wileyonlinelibrary.com]

monitoring series were not significant in the models in which they appeared.

We observed significant differences between thermal regions (one-way ANOVA $P = 0.0219$) for TAOc slopes, with more negative slopes in warmer regions (Fig. 4a). Vegetation encroachment also showed significant differences between regions (one way ANOVA $P = 0.0309$). The pattern was similar to the TAOc, although the highest level of encroachment was not recorded in the warmest region but in thermal region 3 (Fig. 4b).

Species loss and population declines

A total of 126 extinction events occurred at 40 of the 54 studied sites; 15 sites had no recorded extinction events during the studied period. Extinction events were recorded in 5% of the populations that were monitored. Twelve extinction events were followed by colonisation and so in 114 cases a population of a species was never again recorded at the site in question (4.53% of the studied populations). The mean TAO index value for extinct populations was 0.393 ± 0.153, while the value for the remaining populations was 0.33 ± 0.050 (Fig. 5). A paired *t*-test showed significant differences ($t = 2.4857$, df = 39, $P = 0.017$) in the TAO index between species with extinction events and those with no extinction events, indicating that extinctions occurred more frequently in species preferring open habitats.

The GLMM performed for the butterfly trends at itinerary level showed no direct relationship with the values of the TAO index ($P = 0.964$) or vegetation encroachment ($P = 0.667$). Nevertheless, there was a highly significant relationship with the interaction of these variables (estimate = 1.37×10^{-3}, $df = 2390$, $t = 4.646$, $P = 3.57 \times 10^{-6}$). This indicates that species with higher TAOc indices had more negative trends when there was

Table 1. Model selection table of the best models according to the akaike information criterion. Models 1 and 2 are the best fitted models as delta<2.

	Main effects	Interaction	df	logLik	AICc	Delta	Weight
Model1	VegEnc + Shannon + ThReg	-	7	240.323	−464.21	0	0.283
Model2	VegEnc + Shannon + TAOinitial +ThReg	-	8	241.484	−463.76	0.442	0.226
Model3	VegEnc + ThReg	-	6	237.843	−461.89	2.313	0.089
Model4	VegEnc + Shannon + Timeseries + ThReg	-	8	240.37	−461.54	2.669	0.074
Model5	VegEnc + Shannon + TAOinitial + Timeseries + ThReg	-	9	241.536	−460.98	3.231	0.056

VegEnc, vegetation encroachment; Shannon, Shannon index of vegetation diversity; ThReg, thermal region; TAOinitial, initial TAOc value; Timeseries, series length.

Table 2. Results for the five best generalised linear models (GLMs) with their estimate values and *P*-values.

	MODEL 1		MODEL 2		MODEL 3		MODEL 4		MODEL 5	
	Estimate	Pr(>ltl)	Estimate	Pr(>ltl)	Estimate	Pr(>ltl)	Estimate	Pr(>ltl)	Estimate	Pr(>ltl)
(Intercept)	-5.18×10^{-3}	0.0276*	-9.28×10^{-3}	0.014*	-7.24×10^{-4}	0.4651	-5.75×10^{-3}	0.06306*	-9.85×10^{-3}	0.02185*
VegEnc	1.23×10^{-4}	0.0073**	1.58×10^{-4}	0.00266**	1.15×10^{-4}	0.0145*	1.25×10^{-4}	0.00775**	1.61×10^{-4}	0.00287**
Shannon	2.26×10^{-3}	0.0367*	2.72×10^{-3}	0.0161*			2.32×10^{-3}	0.03719*	2.78×10^{-3}	0.01668*
TAOinitial			9.61×10^{-3}	0.15729					9.61×10^{-3}	0.16127
Timeseries							3.37×10^{-5}	0.7738	3.40×10^{-5}	0.76929
Th Region2	7.70×10^{-4}	0.5295	1.18×10^{-3}	0.34545	9.94×10^{-4}	0.4321	7.13×10^{-4}	0.56892	1.12×10^{-3}	0.3796
Th Region3	1.69×10^{-4}	0.8924	6.60×10^{-4}	0.60748	3.61×10^{-4}	0.7802	1.30×10^{-4}	0.9187	6.20×10^{-4}	0.63445
Th Region4	-3.61×10^{-3}	0.0179*	-3.25×10^{-3}	0.03288*	-3.01×10^{-3}	0.0503	-3.63×10^{-3}	0.01862*	-3.27×10^{-3}	0.03385*

VegEnc, vegetation encroachment; shannon, shannon index of vegetation diversity; ThReg, thermal region; TAOinitial, initial TAOc value; timeseries, series length. Significant values with Pv<0.05 are marked with "*" and values with Pv<0.01 are marked with "**".

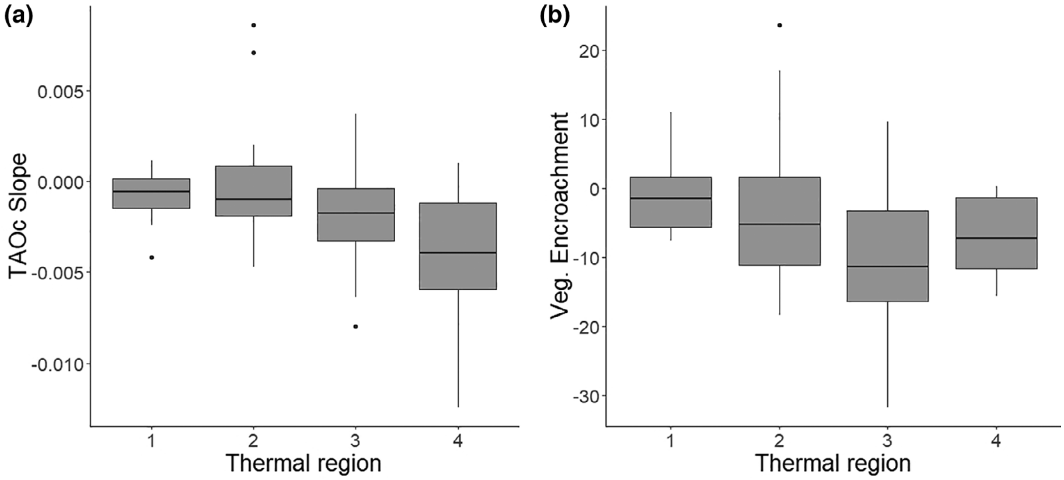

Fig. 4. Boxplots for TAOc slopes and vegetation encroachment by thermal region. Thermal regions numbering run from the coldest (1) to the warmest (4).

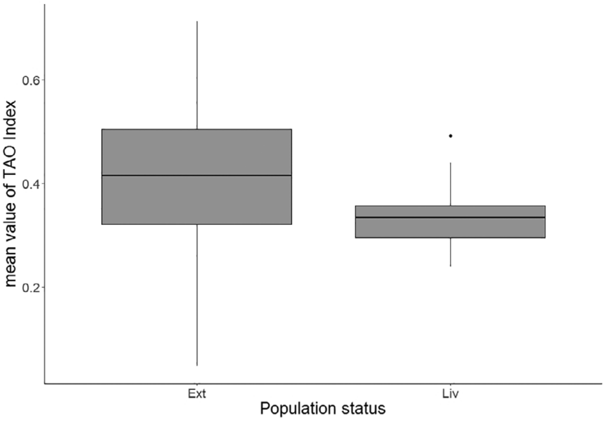

Fig. 5. Boxplot showing the mean value of the TAO index for all the extinct (Ext) and not extinct (Liv) species at each of the 54 studied sites.

vegetation encroachment, while species with a negative TAO index tended to exhibit the opposite trend (Fig. 6). This difference is exemplified by two species with very different preferences for open or closed habitats, speckled wood (*Pararge aegeria*, $I_{TAO} = -0.419$, slope = −72.74, $P = 0.198$) and mallow skipper (*Carcharodus alceae*, $I_{TAO} = 0.626$, slope = 114.12, $P = 0.009$) (Fig. 6).

Discussion

In this work, we used a large Mediterranean butterfly data set to derive an index of preference for open/closed habitats for 147 species. We adapted the index from the original formula developed by Suggitt et al. (2012) to evaluate butterfly responses to year-to-year microclimatic variation in relation to habitat use. Our results show the strong preference of Catalan butterfly species for open habitats, with only a few species exclusively associated with forest habitats. Although this preference is widely recognised in temperate Europe (e.g. van Swaay et al. 2006), to our knowledge this is the first time that a precise measure based on population densities across plant communities has been provided for what is one of the continent's richest butterfly fauna.

Interestingly, we found consistent preferences in butterfly species across thermal regions, which in our study area range widely from very hot Mediterranean conditions in lowland south-western sites to cold climates in the high Pyrenean mountains. Thus, although butterfly species may compensate for differences in environmental temperature by shifting to more open or closed habitats with, respectively, warmer or cooler microclimates, as noted by Suggitt et al. (2012), thermal habitat sensitivity is in fact small. This means that species preferences remain fairly stable and that our general index values are applicable under different environmental conditions. Likewise, although values will vary with additional population data, changes will be small as current values are based on 25 years of data from more than 150 monitoring sites, which make them sufficiently robust to be used to explore changes in butterfly communities without the need for regular updates.

The highly skewed preference of the butterfly fauna toward open habitats indicates that this group of insects will respond very strongly to vegetation encroachment. Here, by analysing long-term data on the structure of over 50 butterfly communities, we tested this possibility in the north-west Mediterranean basin, a region where the increase in forest cover is one of the major changes that has taken place in the landscape in recent decades (Debussche et al. 1999; Blondel et al. 2010; Feranec et al. 2010; Gerard et al. 2010; Marull et al. 2015).

More than 70% of our studied sites have experienced vegetation encroachment in the past two decades, which wholly confirms the importance of this phenomenon as part of landscape change in our region. Indeed, this was matched by a shift in

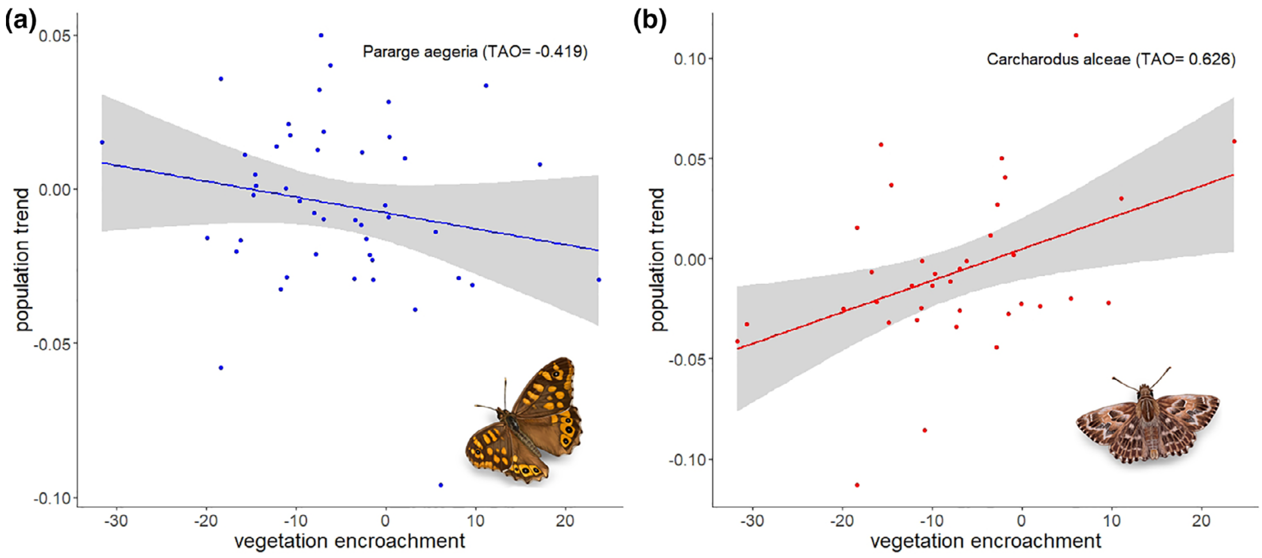

Fig. 6. Population trends according to vegetation encroachment at site level of two species with very different TAO index values. Populations of speckled wood (*Pararge aegeria*, TAO = −0.419) tended to decline wherever the habitat became open (n°. sites = 46, $R^2 = 0.03$, $P = 0.198$). Populations of mallow skipper (*Carcharodus alceae*, TAO = 0.626) declined strongly when there was habitat encroachment (n°. sites = 36, $R^2 = 17.97$, $P = 0.009$). [Color figure can be viewed at wileyonlinelibrary.com]

76% of the analysed butterfly communities toward domination over time by species preferring more closed habitats, as revealed by the community index (TAOc). Furthermore, the GLM models confirm that vegetation encroachment acted as the major factor in changes in the structure of butterfly communities.

It may be argued that the changes we recorded are not representative of major changes occurring at landscape level, as we only measured plant and butterfly communities along the transect routes (e.g., in a five-metre-wide band). However, in the last two decades, an increase in forest cover of 4% has also been recorded in buffer areas of 1 km surrounding a large number of our monitoring sites (Herrando et al. 2015), indicating that this phenomenon is very widespread and may be a primary driver of changes in biodiversity in our region. Our results thus complement those of Herrando et al. (2015), who found that an increase in forest cover was having an impact on both butterfly and bird populations, as revealed by a multi-species indicator based on monitoring data.

Changes in communities being dominated by closed-habitat-loving species were more marked in sites with less vegetation diversity (according to the Shannon diversity index). This may be because heterogeneous landscapes promote population stability offering greater ranges of resources and microclimates (Oliver et al. 2010). To a lesser extent, changes in the composition of butterfly communities were also affected by the thermal region, with the strongest changes occurring in the hottest regions (Fig. 4). This probably reflects the more severe encroachment processes occurring in Mediterranean habitats, which are linked, above all, to socioeconomic factors affecting agricultural abandonment that modify natural and cultural landscapes (Vidal-Macua et al. 2018). However, butterfly responses were qualitatively similar between regions, as shown by the nonsignificant interaction between thermal region and vegetation encroachment.

Contrary to our expectations, we found no relationship between the length of the time-series at each monitored site and the degree of butterfly community change. This result indicates that the response to encroachment is not time dependent, probably because change in the community structure is very rapid once vegetation encroachment has begun (see also Stefanescu et al. 2009). Similarly, dung beetles have been shown to respond more quickly than vegetation to pastoral practices (Tocco et al. 2013). This important finding indicates that the main reason for such rapid responses are insects' short generation time coupled with their precise habitat requirements, which accords them great value as indicators of environmental change (e.g. Thomas et al. 2004; Krauss et al. 2010). We also found no relationship between the slope and the initial TAOc value, which highlights the role of vegetation encroachment as one of the ecological drivers that affects butterfly populations regardless of the initial composition of the community.

A remarkable but worrying result was revealed by the analysis of extinction events. The finding that 4.53% of our monitored butterfly populations are already extinct is highly alarming. Extinct populations belonged to species with higher TAO values, which shows the threat that vegetation encroachment represents for open habitat species. Habitat loss is the major cause of species extinctions (Tilman et al. 1994) and it has been shown that the extinction risk in Mediterranean butterflies strongly decreases with suitable habitat availability (Fernández-Chacón et al. 2014). To date, butterfly population declines have been assessed using climatic and ecological factors; however, more work is needed to understand the mechanisms whereby declines are leading to extinction events at local and regional scales. In our region, lowland populations of some species have been shown to be more vulnerable toward extreme climatic events (i.e. summer drought) (Carnicer et al. 2019). We also found that vegetation encroachment was more important in warmer areas and so affects butterfly assemblages in typical Mediterranean habitats more severely. Therefore both climatic and landscape changes interact to ensure that butterfly species from Mediterranean habitats exhibit more negative trends (Herrando et al. 2019). All in all, our results indicate that most species in our region cannot cope with global change, which leads to mismatches affecting the overall butterfly assemblage (e.g. Devictor et al. 2012).

We believe that the TAO index and our community approach provide a very useful tool for local managers aiming to promote biodiversity conservation, even more so considering the indicator role of butterflies in insect communities (Thomas et al. 2004). Insect conservation is known to be important for saving endangered species and guaranteeing ecosystem processes at different scales (Kim 1993), and the protection of open landscape diversity has often been described as an important aim (Lindborg et al. 2008). Reintroduction of traditional grazing and farming would help revert this problem (MacDonald et al. 2000; Verdú et al. 2000; WallisDeVries et al. 2007; Stefanescu et al. 2009, 2011; Tomaselli et al. 2013).

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Supporting information

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

Table A1 List of all the I_{TAO} for the 147 studied species, ordered from the lowest to the highest value. Nitins refers to the number of itineraries where a species occurred. I_{TAO} desvest is the standard deviation of the TAO index.

Figure A1. Correlation heatmap for the TAO Index calculated for different thermal regions. Values indicate Spearman's Rank correlation. All relations resulted in a positive significant relationship (reg1~reg2: p = 6.1e-09; reg1~reg3: p = 2.2e-16; reg1~reg4: p = 0.013; reg2~reg3: p < 2.2e-16; reg2~reg4: p = 4.9e-05; reg3~reg4: p = 3.36e-05).

Table A2. CORINE biotope codes and habitat description in with their binary value for open (+1) or closed (−1) habitats (OPCL). The number of square meters of each habitat type in the first and last botanical characterizations of the 54 long term monitored sites are given in the "First" and "Last" columns, respectively.

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Heterogeneidad en las respuestas demográficas asociadas al gradiente altitudinal: el caso de las mariposas en el noreste ibérico

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Heterogeneidad en las respuestas demográficas asociadas al gradiente altitudinal: el caso de las mariposas en el noreste ibérico

Resumen: Los impactos del cambio global sobre la biodiversidad muestran con frecuencia heterogeneidad de respuestas a nivel espacial. Los programas de ciencia ciudadana como el *Catalan Butterfly Monitoring Scheme* (CBMS) permiten estudiar el estado de las poblaciones de mariposas a largo plazo y en amplias escalas espaciales, y entender así los motores de cambio global que las afectan. En este trabajo se han calculado, utilizando una nueva metodología, las tendencias de un centenar de especies con los datos del CBMS para tres regiones climáticas: alpina, mediterránea húmeda y mediterránea árida. Se han comparado las tendencias de algunas especies comunes entre regiones, así como la relación de dichas tendencias con las características ecológicas de las especies. También se ha estudiado la evolución y cambios de índices ecológicos a nivel de comunidad a partir de transectos de la región alpina con series temporales largas. Los resultados muestran que en las tres regiones el porcentaje de especies en declive supera el de especies en incremento, aunque las comparaciones se han hecho mayormente con especies generalistas y probablemente subestiman el declive que pueden estar experimentando las especies raras. Para las especies comunes, las regresiones han sido más severas en la región mediterránea árida que en la región alpina. En esta última región no se ha encontrado una relación entre las tendencias poblacionales y los índices ecológicos de las especies, pero por el contrario sí se detectan cambios significativos de diferentes índices de la comunidad a nivel local, como resultado principalmente de procesos de abandono del pastoreo y el avance de especies termófilas hacia mayores altitudes.

Palabras clave: mariposas; cambio climático; cambios de hábitat; tendencias; indicadores; regiones climáticas

Heterogeneity in demographic responses associated with the altitudinal gradient: the case of butterflies in north-eastern Iberia

Abstract: The impact of global change on biodiversity often has heterogeneous responses at a spatial scale. Citizen science programs such as the Catalan Butterfly Monitoring Scheme make it possible to study butterfly responses in the long term and over wide spatial scales, which thus helps understand the drivers of global change that are affecting them. In this work a novel methodology and the CBMS data have been used to calculate trends for a hundred species from three climatic regions: Alpine, humid Mediterranean and arid Mediterranean. A comparison between regions of the trends of a number of common species was made, as well as the relationship between these trends and species' ecological characteristics. Changes in the communities at a number of long-term monitored sites were also studied in the Alpine region using several community indices. The results show that in the three regions the percentage of species in decline exceeds that of the species that are increasing. Nevertheless, these comparisons were made using a mainly generalist fraction of the fauna and probably underestimate the declines that certain rare species are suffering. In common species, declines were more severe in the arid Mediterranean region than in the Alpine region. In this latter region there was no relationship between population trends and the ecological indices of the species. Conversely, significant changes were detected in certain community indices at local level, mainly due to the abandonment of grazing and the movement of thermophilic species towards higher altitudes.

Keywords: butterflies; climate change; habitat change; trends; indicators; climatic regions

Introducción

Existen numerosas evidencias del impacto que el cambio global, con sus múltiples manifestaciones, está teniendo sobre la biodiversidad a escala global (p.e. Dirzo et al. 2014; Wagner 2020). No obstante, la magnitud de este impacto en las comunidades naturales varía considerablemente a nivel espacial. Por ejemplo, en el hemisferio norte, el calentamiento global, durante las últimas dos décadas ha sido comparativamente más intenso en las latitudes altas y ello ha conllevado avances fenológicos también más marcados en esas latitudes (Post et al. 2018). El cambio climático también puede influir de forma distinta en la dinámica de las especies según las poblaciones se encuentren en el centro o en los extremos del área de distribución. En general, las poblaciones situadas en los extremos son más sensibles a las variaciones climáticas (Mills et al. 2017) y, comparativamente, las tendencias suelen ser más positivas en las poblaciones que corresponden al extremo frío que las que corresponden al extremo cálido, tanto latitudinalmente como altitudinalmente (Hampe y Petit 2005; Wilson et al. 2005; Franco et al. 2006; Thomas 2010).

A escalas más finas, los cambios en los usos del suelo - el otro gran motor del cambio global- generalmente muestran heterogeneidad, y ello puede generar mosaicos en las respuestas de la biodiversidad. Por ejemplo, los problemas derivados de la destrucción y fragmentación de los hábitats pueden paliarse en parte de un territorio a partir de diseños adecuados de zonas protegidas. Así, recientemente se ha comprobado que cerca del 50% de las especies de aves, especialmente aquellas con preferencias por los ambientes forestales, muestran tendencias poblacionales más positivas en el interior y proximidad de la red europea Natura 2000 que en áreas colindantes, pero más alejadas y no protegidas (Pellissier et al. 2020). Ese mismo trabajo, sin embargo, ponía de manifiesto que los efectos pueden variar de forma acusada según el grupo taxonómico considerado: a diferencia de lo que ocurre con las aves, las especies de mariposas diurnas se veían muy poco afectadas, un resultado que alerta de las limitaciones del diseño actual de esta red de áreas protegidas para favorecer a este grupo de insectos.

La posibilidad de detectar estas respuestas heterogéneas al cambio global se ve frecuentemente limitada por la dificultad de disponer de datos de un número suficiente de especies a escalas espaciales y temporales adecuadas. No obstante, en las últimas décadas, este problema se ha visto crecientemente solventado gracias a la consolidación de programas de monitoreo de la biodiversidad basados en la ciencia ciudadana, capaces de recabar información sobre grupos bioindicadores en áreas extensas (Pocock et al. 2018). Afortunadamente, en el ámbito ibérico se dispone de programas de seguimiento de la biodiversidad bien consolidados, por ejemplo, en el caso de las aves (Martí y Del Moral 1997; Herrando et al. 2008) y de las mariposas (Munguira et al. 2014). Para este último grupo, en particular, el programa Catalan Butterfly Monitoring Scheme está documentando, desde mediados de la década de los 90, los cambios que experimentan las comunidades de mariposas en un gran número de localidades distribuidas por Cataluña, Andorra y las Islas Baleares. Estas localidades se distribuyen en ambientes muy diversos, sometidos a distintas presiones antrópicas y a climas dispares, una situación óptima para abordar la cuestión de la heterogeneidad de las respuestas de la biodiversidad al cambio global a unas escalas espacial y temporal adecuadas.

Recientemente, para facilitar la comparación de las tendencias de las mariposas a nivel europeo a partir de datos de monitoreo, se ha desarrollado una metodología que mejora ostensiblemente las estimas poblacionales (Schmucki et al. 2016). El método produce curvas fenológicas de las especies en regiones con un clima homogéneo, asumiendo que dentro de una región climática las poblaciones de una determinada especie muestran una fenología similar. La curva fenológica patrón permite interpolar con mucha mayor fiabilidad los datos no disponibles en localidades concretas y producir así índices de abundancia más fiables. En este trabajo hemos aplicado esta metodología para explorar el nivel de coincidencia en las tendencias poblacionales de mariposas diurnas comunes en el noreste peninsular en las 2-3 últimas décadas, distinguiendo tres regiones con climas bien diferenciados, el ambiente alpino, el ambiente mediterráneo húmedo y el ambiente mediterráneo árido. Partiendo de resultados recientes que sugieren que las especies de mariposas que han sufrido regresiones más fuertes en el noreste peninsular son las que prefieren los ambientes más áridos (Herrando et al. 2019), esperamos que, en conjunto, las tendencias poblaciones en la región de montaña serán más positivas que en las dos regiones mediterráneas.

En un segundo análisis hemos intentado relacionar las tendencias poblacionales con características ecológicas de las especies. Para ello, utilizamos cuatro medidas del nicho ecológico, dos de las cuales están relacionadas con las preferencias de hábitat de los adultos, y dos con el nicho climático de las especies. Ambos tipos de medidas han sido identificadas como predictores de las tendencias generales en estudios anteriores (Stefanescu et al. 2011b; Melero et al. 2016; Herrando et al. 2019; Ubach et al. 2020).

Además de las tendencias poblacionales, el monitoreo a largo plazo en localidades fijas proporciona la posibilidad de explorar los cambios que se producen a nivel de comunidad. Para ello se pueden calcular fácilmente varios índices de comunidad basados en las estimas de nicho de las especies, ponderadas según su abundancia, y estudiar qué aspectos ecológicos son más relevantes en los cambios recientemente observados (Devictor et al. 2012). En este contexto, en un tercer análisis nos hemos centrado en unas pocas comunidades de áreas de montaña, que han sido monitorizadas regularmente en períodos de al menos 14 años, para identificar las tendencias más importantes que han tenido lugar.

Material y métodos

Área de estudio y muestreo de mariposas

Para este trabajo se han utilizado los datos del programa de seguimiento Catalan Butterfly Monitoring Scheme (CBMS). En este programa de ciencia ciudadana se obtienen datos de la abundancia de las poblaciones de mariposas mediante conteos realizados en transectos fijos. La metodología de muestreo es común a la de otros programas similares en países europeos, y se basa en la desarrollada originalmente en el Reino Unido (Pollard y Yates 1993). Los conteos de mariposas adultas se llevan a cabo a lo largo de itinerarios, generalmente de 1.5-2 km de longitud, considerando únicamente una franja de 5 x 5 m (2.5 m a ambos lados y 5 m enfrente del investigador) mientras se progresa a un ritmo constante. El itinerario está dividido en un número variable de secciones, que se corresponden con distintos tipos de hábitats. Idealmente, los censos se repiten un total de 30 semanas, desde la primera de marzo hasta la última de setiembre, siempre y cuando las condiciones meteorológicas sean adecuadas y permitan la actividad normal de las mariposas.

El CBMS se inició en 1994, y hasta 2020 se han obtenido datos de 188 especies de mariposas, en 185 itinerarios o estaciones de muestreo distribuidas por el conjunto de Cataluña, Andorra e Islas Baleares (**Fig. 1**). Las series temporales varían según la localidad, con un 40% de las estaciones con datos de 10 o más años. Para más información sobre el CBMS, se puede consultar http://www.catalanbms.org.

Análisis de datos

Cálculo de tendencias poblacionales

Los niveles poblacionales anuales de las especies se han estimado mediante índices de abundancia calculados a partir de la suma de los conteos en cada itinerario. Para la estimación de los conteos de semanas no muestreadas se ha ajustado una curva de vuelo a partir de los conteos de diferentes itinerarios de una región climática determinada mediante un GAM regional (Schmucki et al. 2016). Esto consiste en ajustar un modelo general aditivo a los conteos de una especie en función de su fenología en los distintos itinerarios dentro de una región climática. La curva fenológica resultante, adaptada según la abundancia de la especie en cada localidad, permite entonces estimar los índices de abundancia a nivel local. En una segunda fase, se utiliza un GLM para generar un índice anual regional colapsando los índices locales de las localidades donde hay poblaciones viables de la especie en un solo valor por año. El modelo corrige el sesgo de que algunos itinerarios dispongan de más datos que otros repartiendo el peso de los datos locales según el porcentaje de curva fenológica muestreada en cada localidad. También estima indirectamente el valor de años que no tienen suficientes datos para cumplir el umbral establecido. Posteriormente, se ajusta un modelo lineal para calcular la tendencia temporal de este índice anual, añadiendo unos intervalos de confianza del 95% a partir de un método *bootstrap*, que repite hasta 500 veces los cálculos con submuestras aleatorias de los datos. El paquete estadístico en R para realizar estos cálculos se puede descargar en Schmucki et al. (2021).

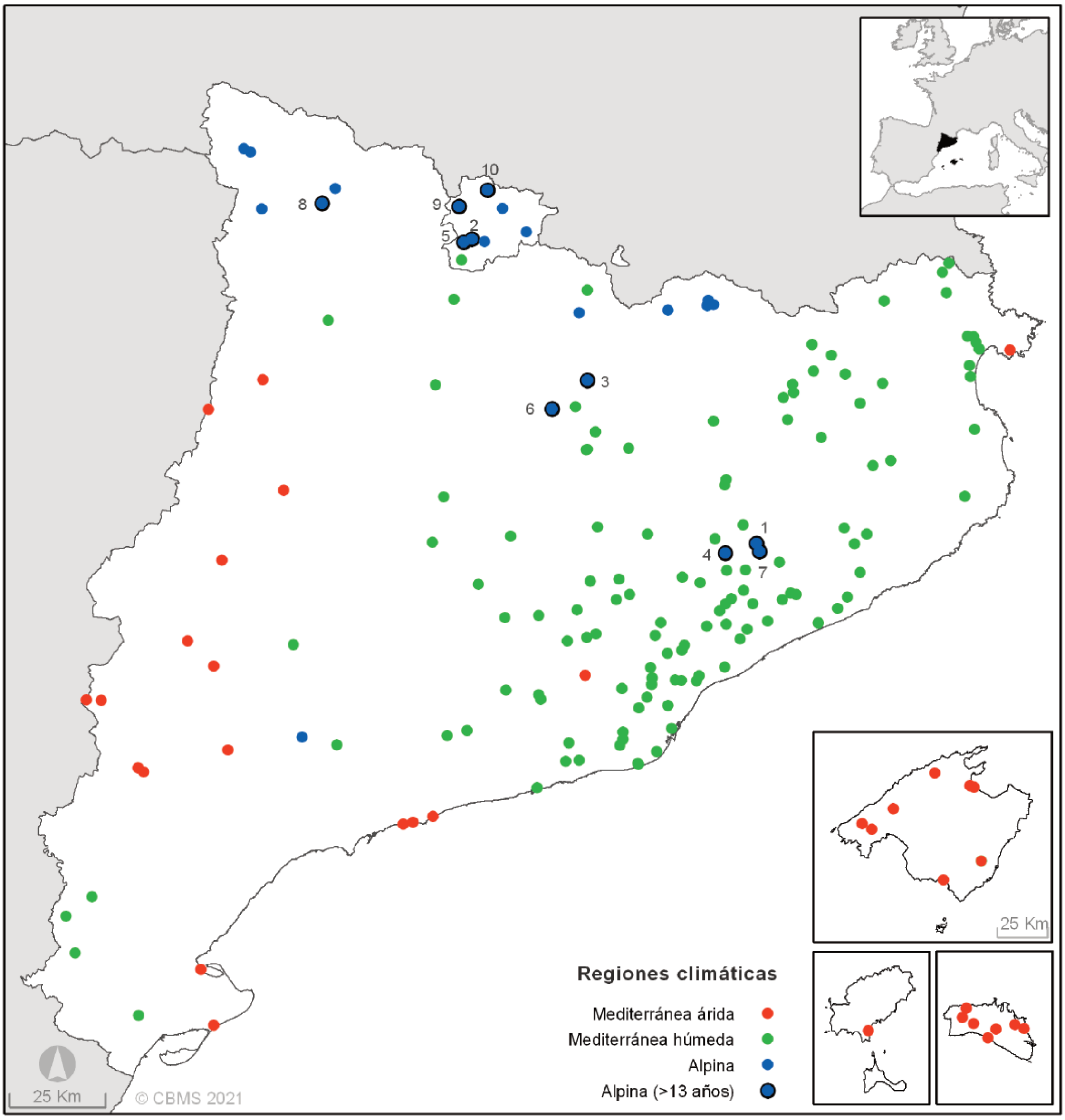

Figura 1. *Mapa de la región estudiada con los itinerarios presentes en la red CBMS desde el inicio del proyecto. El color es indicativo de la pertenencia de un itinerario a una de las tres regiones climáticas estudiadas (azul: alpina, verde: mediterránea húmeda, rojo: mediterránea árida). Los 10 itinerarios de la región alpina con más de 13 años de datos se encuentran numerados.*

Figure 1. *Map of the study region with all the itineraries in the CBMS network since the beginning of the project. The colour indicates the climatic region of each itinerary (blue: alpine, green: Mediterranean – humid, red: Mediterranean – arid). The 10 itineraries from the alpine region with >13 years of data are numbered.*

En el presente trabajo se han diferenciado tres regiones climáticas en las cuales se ha aplicado la técnica del GAM regional. Estas regiones se han establecido utilizando un umbral de 21DDG (número de horas por año en que se supera una temperatura de 21ºC; datos proporcionados por el Servei Meteorològic de Catalunya) y corresponden mayoritariamente con las clasificadas por Metzger et al. (2013) como: (1) región alpina (≤ 0-150 DDG), (2) región mediterránea húmeda (entre 150-400 DDG), (3) región mediterránea árida (≥ 400 DDG). El número de estaciones del CBMS disponibles para cada una de las regiones es, respectivamente, 24, 123 y 33 (**Fig. 1**).

Se han establecido unos criterios mínimos para estimar la tendencia de una especie en una región. El índice anual de abundancia solo se ha calculado cuando para la especie se tienen datos para un mínimo de cinco poblaciones con dos o más conteos positivos, es decir, la especie ha aparecido al menos dos semanas esa temporada. Además, la tendencia temporal solo se ha calculado en especies con series de cuatro o más índices anuales. De acuerdo con estos criterios, se han podido calcular las tendencias de 58 especies en la región alpina, 89 en la región mediterránea húmeda y 21 en la región mediterránea árida (**Tabla A1**).

Comparación de tendencias entre regiones climáticas

Se han utilizado modelos lineales mixtos (LMM) para comprobar si existen diferencias en los valores de las tendencias poblacionales entre regiones. En estos modelos la variable dependiente es la magnitud de la tendencia poblacional de una especie, es decir, la pendiente de la tendencia obtenida con el modelo lineal (ver apartado anterior), la región es un factor fijo, y la especie es un factor aleatorio. En este análisis se han seleccionado aquellas especies con series temporales de un mínimo de 10 años. Este criterio es mucho más conservador que el de los cuatro años utilizados en el cálculo de tendencias poblacionales (ver apartado anterior) y, por tanto, reduce el número de especies que pueden compararse entre regiones. De este modo, las tendencias corresponden a segmentos temporales suficientemente amplios y representativos de la situación en las dos últimas décadas. Las comparaciones se han hecho por pares de regiones (tres modelos en total). Para los modelos LMM se ha utilizado el paquete *lme4* en RStudio versión 1.3.1.

Tendencias poblacionales y características ecológicas de las especies

Para relacionar las tendencias regionales con las características ecológicas de las especies, se han utilizado cuatro indicadores del nicho ecológico, dos relacionados con el clima (STI y SPI), y dos con el hábitat (SSI y TAO).

El STI (*Species Temperature Index*) corresponde al promedio de la temperatura media anual que experimenta la especie en el conjunto de su distribución ibérica (según datos actualizados de García-Barros et al. 2004). El SPI (*Species Precipitation Index*) es un índice equivalente para la precipitación anual acumulada. Para más detalles sobre el cálculo de estos índices, véase Herrando et al. 2019.

El índice TAO sitúa la preferencia de una especie a lo largo de un gradiente que va desde ambientes cerrados (forestales) a ambientes abiertos (prados). El índice se calcula a partir de datos de la densidad de las especies en las secciones de los itinerarios del CBMS, previamente clasificadas como “abiertas” o “cerradas” en función de las comunidades vegetales dominantes. La metodología de cálculo de este índice, que queda acotado entre -1 (para una especie totalmente forestal) y +1 (para una especie totalmente ligada a ambientes abiertos) se describe en Ubach et al. 2020.

El SSI (*Species Specialization Index*) estima el grado de especialización de una especie respecto al uso de los diferentes tipos de hábitat. Se calcula a partir de la distribución de la densidad de los adultos en las secciones de los itinerarios del CBMS, previamente asignadas a 19 categorías de hábitat según la adaptación del código Corine a las comunidades vegetales de Cataluña (Carreras et al. 2015). El cálculo del índice sigue la fórmula descrita por Julliard et al. (2006), estando los valores situados entre 0 (para una especie totalmente generalista, sin ningún tipo de preferencia) hasta valores positivos no acotados (aunque con los datos del CBMS, los máximos especialistas no superan nunca un valor de 4).

Para relacionar las tendencias poblacionales con estos indicadores se han construido modelos lineales en cada región, siendo la variable dependiente la tendencia de la especie en esa región, y los predictores los cuatro índices de nicho. En los modelos también se han incluido las interacciones bivariantes entre las variables climáticas y las de hábitat. Sin embargo, debido a la alta colinealidad entre el SPI y STI (-0.81 en la región alpina, -0.68 en la región mediterránea húmeda, -0.47 en la región mediterránea árida, mediante la correlación de Pearson), se ha optado por realizar modelos utilizando las dos variables de hábitat solo con el STI o con el SPI. Previamente a la modelización, las variables se han escalado debido a su diferente magnitud de valores utilizando la función “scale” de R.

Indicadores de comunidad

Se han seleccionado 10 itinerarios de la región alpina con 14 o más años de seguimiento como muestra de las tendencias ecológicas que han mostrado las comunidades de montaña en las dos últimas décadas. Se han utilizado los mismos cuatro indicadores específicos del nicho ecológico (SSI, TAO, STI, SPI) para derivar los correspondientes indicadores de comunidad. El índice de comunidad de un año y lugar concreto se resume como la suma de los índices específicos multiplicados por el índice de abundancia relativa de la especie (calculado con el GAM regional), dividida por la suma de todas las abundancias. De acuerdo con los criterios mínimos establecidos, para un determinado año las especies que han aparecido en un solo conteo se han excluido de la comunidad al ser consideradas como ocasionales. En estos cálculos, las abundancias relativas se han transformado con una raíz cuadrada para minimizar las diferencias de densidad que existen entre las distintas especies. Los análisis sin esta transformación proporcionan, sin embargo, resultados cualitativamente similares. Posteriormente, se ha contrastado con un modelo lineal si existen cambios significativos en la evolución de los índices de comunidad, que representan entonces los factores principales de cambio a nivel local. Este método ha sido ampliamente utilizado en trabajos previos, por ejemplo, para poner de manifiesto cómo las comunidades europeas de mariposas y aves han pasado a estar progresivamente dominadas por especies más termófilas (Devictor et al. 2012) o por especies más generalistas (Le Viol et al. 2012) a causa del cambio global.

Resultados

Se ha calculado la tendencia (series temporales de cuatro o más años) para un total de 105 especies de mariposas, aunque el número varía fuertemente según la región (**Tabla 1**). En la región mediterránea húmeda, con más itinerarios (**Fig. 1**), se han estimado tendencias para 89 especies y a partir de series temporales generalmente de más de dos décadas. Debido a la alta diversidad lepidopterológica, en la región de montaña se han estimado más del doble de tendencias (58) que en la región mediterránea árida (21), si bien las series anuales son similares en ambas regiones (aproximadamente unos 15 años de media).

Independientemente de la región, las especies con regresiones poblacionales (tendencias negativas significativas) son mucho más frecuentes que las especies con aumentos (tendencias positivas significativas). Las tendencias estables ocupan una posición intermedia. Alrededor de un tercio de las tendencias son inciertas en las dos regiones mediterráneas, siendo este número notablemente más elevado en la región alpina (59%). Esta proporción tan alta se debe a un número todavía bajo de itinerarios combinado con series anuales relativamente cortas en esta región (**Tabla A1**).

La comparación de las tendencias entre regiones se ha limitado a las especies con series anuales de por lo menos 10 años. De éstas, las que más han aumentado son *Pararge aegeria* y *Lysandra bellargus* en la región alpina, *Gonepteryx cleopatra* y *Brintesia circe* en la región mediterránea húmeda, y *Celastrina argiolus* en la re-

Tabla 1. *Resultado general de las tendencias calculadas para las tres regiones climáticas, con los porcentajes de cada una de las categorías proporcionadas por el software rBMS.*

Table 1. *General results of population trends for the three climatic regions, with the percentages of trend categories given by the rBMS software.*

Región climática	Alpina	Mediterránea húmeda	Mediterránea árida
Nº Especies	58	89	21
Nº Años serie	13.88±5.54	22.84±5.41	16.71±5.54
% especies regresión	22.41	31.46	28.57
% especies incremento	3.45	2.24	14.29
% especies estable	15.51	30.33	23.81
% especies incierta	58.63	35.95	33.33

gión mediterránea árida. Entre las que han disminuido más fuertemente se encuentran *Satyrus actaea* en la región alpina, *Aporia crategi*, *Euphydryas aurinia*, *Glaucopsyche melanops*, *Melanargia occitanica* y *Erynnis tages* en la región mediterránea húmeda, y *Pontia daplidice*, *Callophrys rubi* y *Aricia cramera* en la región mediterránea árida. En la **Tabla A1** se encuentran las tendencias de todas las especies calculadas por cada región con el valor multiplicativo de la tasa de cambio anual.

La magnitud de las tendencias poblacionales no difiere significativamente entre las regiones alpina y mediterránea húmeda para las 35 especies comparadas (P=0.66), ni tampoco entre las regiones mediterráneas húmeda y árida para las 17 especies comparadas (P=0.429). Por el contrario, las tendencias sí son significativamente más negativas en la región mediterránea árida respecto a la región alpina (P=0.002), si bien la comparación se basa solamente en 10 especies.

Los modelos estadísticos a partir de los indicadores específicos se realizaron por separado con el STI y el SPI debido a la alta colinealidad entre ambos (**Tabla 2**). En la región alpina, ninguno de los índices de nicho, ni sus interacciones, tienen poder predictivo sobre la magnitud de la tendencia poblacional. En cambio, sí se observan relaciones significativas en las regiones mediterráneas. En la región húmeda el índice TAO es altamente significativo en el modelo que incluye el SPI, indicando que las especies con mayor preferencia por ambientes abiertos son las que tienen una tendencia más negativa. En este modelo, la interacción entre TAO y SPI indica, además, que las tendencias más positivas se observan para la combinación de especies que prefieren ambientes cerrados y relativamente secos. Tanto en el modelo que utiliza el STI como el que utiliza el SPI, aparecen efectos significativos de la interacción entre el TAO y el índice de especialización de hábitat (SSI), que se interpreta como una tendencia más fuertemente negativa en las especies que prefieren los ambientes abiertos y además son marcadamente especialistas.

A pesar del bajo número de especies, en los modelos de la región mediterránea árida aparecen muchos factores significativos. Las especies especialistas (altos valores de SSI) son las que muestran tendencias poblacionales más negativas, tanto con el STI como con el SPI. Además, el SSI interacciona con ambos factores climáticos en sus respectivos modelos, indicando que las especies generalistas asociadas con un índice pluviométrico bajo o un índice térmico alto tienen un mayor declive poblacional. Aun así, para comprender esta aparente contradicción hay que notar que para esta región no disponemos de datos de tendencias de auténticos especialistas, siendo el valor máximo de SSI de solo 1.20 (para *Leptotes pirithous*), lo cual limita la interpretación de estos resultados. El modelo con STI apunta a otras relaciones significativas con los indicadores de hábitat y climáticos. Las especies con preferencia por ambientes abiertos y las más termófilas muestran tendencias más negativas. Además, se observa una interacción significativa entre los índices TAO y STI que indica declives poblacionales más fuertes en especies asociadas a espacios abiertos y con menor índice térmico.

Los índices de comunidad en los 10 itinerarios monitorizados entre 14-27 años en la zona de montaña muestran numerosas tendencias significativas (**Tabla 3**). Las dos relaciones más extendidas son la disminución del índice TAOc y el aumento del índice térmico (CTI), ambas observadas en el 60% de los itinerarios (**Fig. 2**). En el primer caso, la tendencia negativa refleja un dominio progresivo de las especies que prefieren los ambientes forestales en detrimento de las especies propias de ambientes abiertos (**Fig. 2a**), mientras que en el segundo caso se observa una tendencia a un mayor predominio de las especies más termófilas (**Fig. 2b**). Además, en el 40% de los itinerarios también se observa un cambio significativo en el nivel de especialización de hábitat, siempre hacia un aumento relativo de las especies más generalistas (tendencia negativa del CSI). El índice CPI muestra solo tres relaciones significativas, y además con signos opuestos según los itinerarios.

Tabla 2. *Resultado de los modelos lineales generalizados para explicar qué indicadores específicos predicen la magnitud de las tendencias poblacionales en cada una de las tres regiones bioclimáticas. SSI: índice específico de especialización de hábitat, TAO: índice específico de preferencia por ambientes cerrados-abiertos, STI: índice específico de preferencia térmica, SPI: índice específico de preferencia pluviométrica. Se realizaron dos análisis por separado con STI y SPI debido a la alta colinealidad entre estas dos variables.*

Table 2. *Results of the generalized linear models examining species indicators that predict the magnitude of population trends in all three climatic regions. SSI: species specialization index. TAO: species index for open-closed habitat preference, STI: species temperature index, SPI: species precipitation index. Two models were made separately with STI and SPI given the high collinearity between both variables.*

	Alpina(58 spp.)		**M. húmeda (89 spp.)**		**M. árida (21 spp.)**	
	Coeficiente	p-valor	Coeficiente	p-valor	Coeficiente	p-valor
Modelos con SPI						
SSI	0.334	0.169	-2.46e-1	0.38	-12.04	0.04**
TAO	-0.747	0.325	-9.68e-1	6.09e-5***	2.871	0.208
SPI	0.001	0.170	-3.39e-4	0.406	-0.009	0.077
SSI:TAO	0.107	0.351	3.36e-1	0.016*	2.39	0.012*
SSI:SPI	-0.001	0.064	7.66e-5	0.827	0.017	0.005**
TAO:SPI	0.001	0.362	9.14e-4	0.003**	-0.006	0.057
Modelos con STI						
SSI	0.089	0.713	-0.309	0.229	-39.16	0.001**
TAO	0.685	0.345	0.208	0.630	-13.95	0.001**
STI	0.021	0.531	0.006	0.802	-3.12	0.001***
SSI:TAO	0.059	0.619	0.356	0.007**	0.20	0.832
SSI:STI	-0.016	0.434	0.008	0.699	3.04	0.001**
TAO:STI	-0.057	0.298	-0.044	0.164	1.06	0.005**

***Tabla 3**. Direcciones de cambio en 10 comunidades de mariposas de montaña monitorizadas entre 14-27 años. Se han aplicado modelos lineales entre los distintos índices de comunidad (calculados a partir de los correspondientes índices específicos) y los años de monitoreo para el índice de especialización (CSI), abierto-cerrado (TAOC), térmico (CTI) y pluviométrico (CPI). El sentido de la flecha indica la dirección de cambio y el número de flechas indica el nivel de significación (↑: $P < 0.05$, ↑↑: $P < 0.01$, ↑↑↑: $P < 0.001$).*

***Table 3**. Changes of 10 mountain butterfly communities monitored between 14-27 years. Linear models were applied to different community indices (calculated from the corresponding species indices) and monitoring years for the specialization index (CSI), open-closed index (TAOC), temperature index (CTI) and precipitation index (CPI). Arrow directions indicate the direction of the change, while the number of arrows corresponds to the significance level (↑: $P < 0.05$, ↑↑: $P < 0.01$, ↑↑↑: $P < 0.001$).*

Itinerario	Mapa	Altitud	Años	CSI	TAOC	CTI	CPI
El Puig	1	1030	27	↓↓	↓↓↓	↑	
Rec del Solà	2	1103	14		↓↓	↑	
Nou de Berguedà	3	1124	18	↓↓	↓↓↓		↑↑
Pla de la Calma	4	1193	24	↓		↑↑	↓↓
Enclar	5	1208	15		↓		
Campllong	6	1288	18		↓↓↓	↑	
Turó de l'Home	7	1656	14			↑	
Sant Maurici	8	1702	17	↓	↓↓	↑	↓
Comapedrosa	9	1782	15				
Sorteny	10	1946	15				

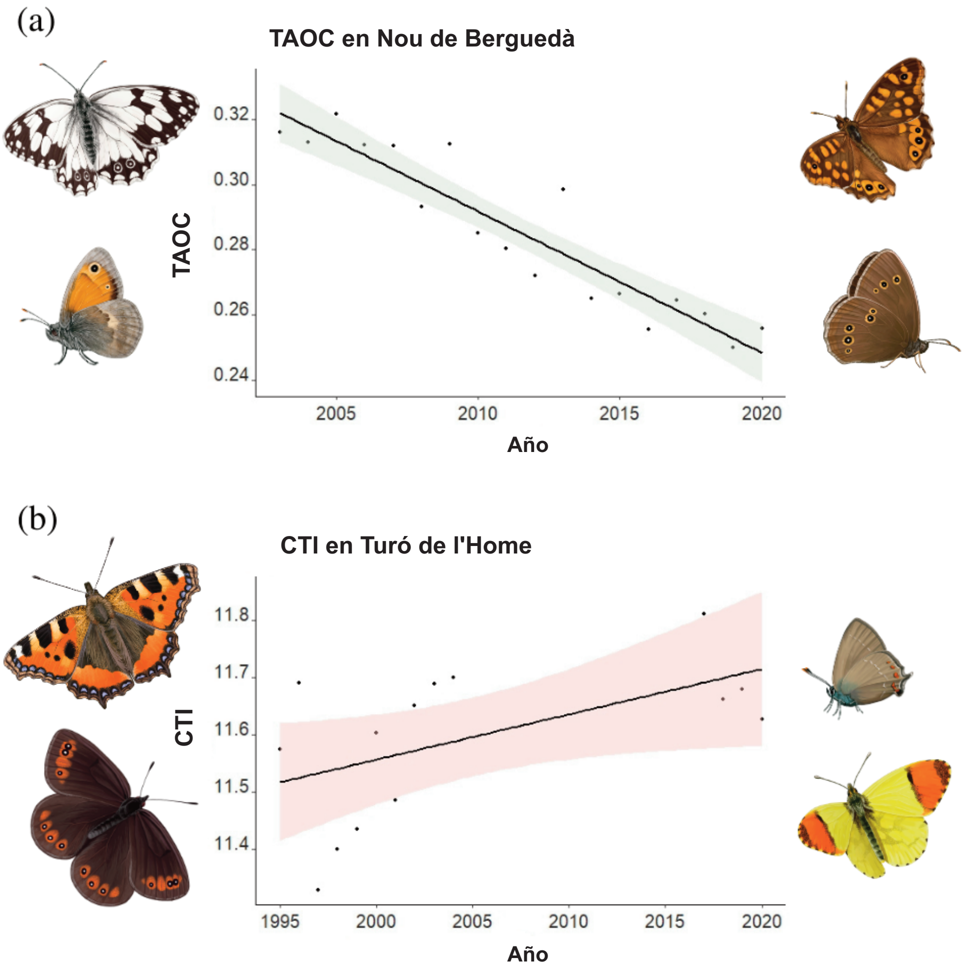

Figura 2. *Evolución de los índices de comunidad en las últimas dos décadas, ilustrativos de los diferentes motores de cambio. (a) En La Nou de Berguedà (1124 m), en el Prepirineo, se observa una disminución significativa del índice abierto-cerrado (TAOC), y una progresiva sustitución de especies de ambientes abiertos (Melanargia lachesis (TAO=0,458), Coenonympha pamphilus (TAO=0,657)) por otras de ambientes cerrados (Aphantopus hyperanthus (TAO=0,219), Pararge aegeria, (TAO=-0,416)). (b) En el Turó de l'Home (1656 m), en la cima del Montseny, se observa una tendencia regresiva de especies montanas (Aglais urticae (STI=10,51), Erebia meolans (STI=8,73)) y un aumento en las poblaciones de especies termófilas (Satyrium esculi (STI=12,94), Anthocharis euphenoides (STI=11,88)).*

Figure 2. *Community index trends in the two recent decades illustrating different drivers of global change. (a) Nou de Bergueda (1124 m), Prepyrenees: A significant TAOC decline and a progressive substitution of open space species (Iberian marbled white, Melanargia lachesis (TAO=0.458), small heath, Coenonympha pamphilus (TAO=0.657) by more forest-preferring species (ringlet, Aphantopus hyperanthus (TAO=0,219), speckled wood Pararge aegeria, (TAO=-0.416)). (b) Turó de l'Home (1656 m), Montseny summit: an observed regression of montane species (small tortoiseshell, Aglais urticae (STI=10.51), piedmont ringlet, Erebia meolans (STI=8.73)) and an increase on thermophilic species (false ilex hairstreak, Satyrium esculi (STI=12.94), Provence orange tip, Anthocharis euphenoides (STI=11.88))*.

Discusión

En este trabajo hemos utilizado datos del programa de seguimiento CBMS para comprobar si existen diferencias en las tendencias poblacionales recientes de las mariposas diurnas en tres regiones climáticas del noreste peninsular. A partir de la herramienta analítica que propone el GAM regional y su implementación en un paquete estadístico de libre acceso (Schmucki et al. 2016; 2019), hemos podido mejorar las estimas de las abundancias anuales en las localidades de muestreo y, posteriormente, calcular tendencias poblacionales ajustadas a regiones que presentan condiciones climáticas homogéneas. Este aspecto supone una mejora importante respecto a cálculos anteriores en los que las tendencias se estimaban para todo el conjunto del noreste peninsular, sin valorar la posibilidad de que las tendencias específicas varíen en ambientes tan distintos como la alta montaña o los ecosistemas mediterráneos áridos. Como contrapartida, esta división implica reducir la muestra disponible en cada región y, en último término, reducir el número de tendencias que pueden calcularse.

Los resultados coinciden con las estimas previas generales al mostrar un porcentaje mucho mayor de especies en regresión que de especies en aumento (Stefanescu et al. 2011b; Melero et al. 2016). Este predominio en las tendencias negativas es una constante en estudios que evalúan la situación reciente de los insectos, y de las mariposas en particular (Thomas 2016; Sánchez-Bayo y Wickhuys 2019; Wagner 2020; Seibold et al. 2020), y es una muestra clara del impacto mayoritariamente negativo que supone el cambio global sobre este grupo. No obstante, en nuestros análisis, la relación entre especies en regresión y en aumento, varía acusadamente según la región climática. Así, en la región mediterránea árida se detectan el doble de especies en regresión que especies en aumento, pero esta proporción aumenta hasta 6 y 14 veces más en la región alpina y mediterránea húmeda respectivamente. Con toda probabilidad, la disparidad de valores es, en buena parte, un artefacto relacionado con las limitaciones del muestreo. La región mediterránea húmeda, la más extensa y habitada, tiene una mayor concentración de itinerarios del CBMS. Gracias a ello, se pueden calcular tendencias poblacionales para muchas más especies que en las otras dos regiones, incluyendo las de mariposas más raras y de carácter más especialista que son, justamente, las que acusan más rápidamente los efectos negativos del cambio global y muestran tendencias regresivas más evidentes (p.e. Warren et al. 2001; Ekroos et al. 2010; Eskildsen et al. 2015; Habel et al. 2019). En las otras dos regiones, el número más limitado de itinerarios significa que las tendencias solo se pueden calcular para las especies más generalistas, ampliamente distribuidas. Este es un aspecto importante a tener en cuenta cuando se evalúan los resultados que proporcionan programas de monitoreo, sobre todo cuando éstos se basan en pocos puntos de muestreo; en estos casos, es muy posible que tiendan a subestimar la pérdida de biodiversidad por el sesgo hacia el componente más generalista del grupo estudiado.

A pesar de estas limitaciones, cuando la comparación de las tendencias poblacionales se restringe a especies compartidas entre regiones climáticas y, además, con series anuales largas, se obtienen resultados interesantes que parcialmente confirman nuestras predicciones. Concretamente, se observa una diferencia significativa en las tendencias entre las dos regiones más extremas, siendo las de la región mediterránea árida más negativas que las de la región alpina. En un trabajo reciente con datos del CBMS, Herrando et al. (2019) encontraron un patrón general según el cual las especies con preferencia por ambientes más áridos han sufrido declives más fuertes que las de ambientes húmedos en las dos últimas décadas. Los autores especulaban que la razón más probable de ello es el impacto negativo del cambio climático (especialmente la creciente frecuencia de los episodios de sequía) sobre la supervivencia de los estadios inmaduros de los lepidópteros que habitan las zonas más cálidas y secas. En el presente análisis, este patrón interespecífico se refuerza a nivel intraespecífico, de manera que dentro de una especie las poblaciones que ocupan los ambientes más áridos son también las que han experimentado una regresión más acusada. Esta situación, de hecho, ya se había puesto de manifiesto en el caso de *Pieris napi* (Carnicer et al. 2019), si bien esta especie no aparece entre las incluidas en la comparación entre la región alpina y la mediterránea árida por su rareza en esta última. Nuestra comparación se basa en tan solo 10 especies, todas ellas muy comunes (**Tabla A1**) pero, aun así, la diferencia es muy apreciable. El conjunto de las poblaciones de la zona árida tiene una tasa multiplicativa de cambio anual inferior a 1 (media±SD: 0.973±0.025), que denota un declive, y que contrasta con la tendencia a un ligero aumento en la zona alpina (1.004±0.0232). Estos resultados están en la línea del trabajo de Stefanescu et al. (2011a), que ya apuntaban a una regresión de las especies generalistas en los ambientes más áridos del noreste peninsular a causa del calentamiento global combinado con la intensificación agrícola.

El intento de identificar características del nicho ecológico de las especies que explique la magnitud de las tendencias ha tenido un éxito variable según la región climática. Los índices utilizados no tienen poder predictivo en la región alpina, pero sí en cambio en las regiones mediterráneas. En éstas, se pone de manifiesto que las especies asociadas a los ambientes más abiertos, especialmente las más especialistas, sufren declives más acusados. Tal como hemos apuntado en ocasiones anteriores, el abandono del pastoreo en extensas áreas de nuestra geografía está afectando muy marcadamente a los especialistas de prados (Herrando et al. 2016), un proceso que también se observa en otras regiones de la Europa meridional (Slancarova et al. 2016) y que en último término comporta extinciones locales (Ubach et al. 2020). Los modelos indican, además, que los cambios relacionados con los usos del suelo interaccionan con el cambio climático y aceleran el declive en las poblaciones que ocupan los ecosistemas mediterráneos (véase Stefanescu et al. 2011a; Herrando et al. 2019). La ausencia de relaciones significativas en la región alpina sugiere, nuevamente, que la afectación negativa de este conjunto de factores sobre la fauna de mariposas es menor. No obstante, ello no significa que esos mismos factores no estén actuando también en las zonas de montaña. Precisamente, el análisis de los cambios a nivel de comunidad en 10 localidades de montaña monitorizadas por períodos de 1-2 décadas muestra inequívocamente como la composición está variando en relación con los procesos del cambio global.

Al trabajar con toda la comunidad es posible utilizar información de todas las especies, incluidas las que no son suficientemente comunes para estimar tendencias poblacionales. En este sentido, los cálculos a nivel de comunidad permiten detectar patrones en la zona alpina que no quedaban reflejados en el análisis anterior, como por ejemplo las consecuencias del abandono del pastoreo y el avance de especies termófilas hacia mayores altitudes. Por ejemplo, la tendencia del índice TAO hacia valores más negativos en más de la mitad de los casos estudiados muestra el aumento relativo de las especies asociadas al bosque y matorral en detrimento de las típicas de prados. Esta tendencia es muy general en el noreste peninsular y, como ya hemos comentado, es consecuencia del abandono del pastoreo extensivo y un aumento progresivo de las masas forestales, bien documentado por Cervera et al. (2019). Estos autores identifican, además, la altitud como un factor que favorece la velocidad de este proceso, puesto que es en las zonas de montaña donde el éxodo rural ha sido más intenso y rápido. Los itinerarios de Campllong y la Nou de Berguedà, situados en el Prepirineo, representan ejemplos excelentes de esta problemática (**Fig. 2a**). En estos ambientes, encontramos numerosas especies propias de ecosistemas abiertos en declive local, como *Melanargia lachesis*, *Coenonympha glycerion, Coenonympha pamphilus* o *Plebejus argus*. Las especies en incremento son típicamente forestales, como *Pararge aegeria*, *Limenitis camilla*, *Polygonia c-album* o *Aphantopus hyperantus*.

El calentamiento global también actúa como un motor de cambio en las comunidades de mariposas de las montañas, tal como ha sido demostrado en varios estudios y se deriva de nuestros datos. A nivel ibérico, el desplazamiento de especies más termófilas hacia mayores altitudes ha sido bien estudiado y documentado en la Sierra de Guadarrama para un período de más de cuatro décadas, con métodos diversos incluido el cálculo del CTI (Wilson et al. 2005, 2007; Nieto-Sánchez et al. 2015). En el Mediterráneo oriental, Zografou et al. (2014) también han constatado aumentos del CTI en comunidades de mariposas para un período más corto de 15 años, en un área montañosa de Grecia de altitud moderada (un máximo de 650 m).

En el presente trabajo, 6 de las 10 comunidades seleccionadas han experimentado aumentos del CTI en los últimos 14-27 años, que se asocian con el éxito creciente de las especies termófilas en zonas de montaña. Un ejemplo evidente lo proporciona el macizo del Montseny, que con sus 1712 m destaca como el punto más alto del prelitoral catalán, y donde diversas especies de ambientes mediterráneos están colonizando las partes altas del macizo en detrimento de aquéllas con preferencia por ambientes más fríos (véase también Peñuelas et al. 2007). Los datos del CBMS muestran como mariposas como *Argynnis aglaja*, *Lycaena alciphron* o *Cyaniris semiargus* -especies típicas de montaña-, se encuentran en declive en El Puig (a 1030 m), mientras que *Erebia meolans* o *Aglais urticae*, que mantienen pequeñas poblaciones en las zonas culminares, han disminuido significativamente en el itinerario del Turó de l'Home (1656 m). En este punto culminante, se han registrado hasta tres nuevas especies en los tres últimos años, todas ellas provenientes de zonas bajas de la montaña (*Brintesia circe*, *Limenitis reducta*, y *Pyronia bathseba*). Además, especies mediterráneas como *Anthocharis euphenoides* o *Satyrium esculi* se encuentran estables o en incremento en estas localidades. Nuestros resultados contrastan con los de Devictor et al. (2012), que no detectaron un descenso global del CTI en los datos del CBMS. Sin embargo, en ese trabajo se descartaron los itinerarios situados por encima de 1000 m, un factor que podría haber contribuido a ese resultado. Además, los casi diez años transcurridos desde entonces pueden perfectamente haber supuesto cambios adicionales del CTI.

En definitiva, en este estudio aportamos evidencias de que los cambios negativos que experimentan las mariposas en las montañas del noreste peninsular en relación con el cambio global por ahora están siendo menos severos que los que se registran en los ambientes mediterráneos áridos. Sin embargo, las comparaciones entre regiones climáticas se basan mayoritariamente en la fracción más generalista de la fauna, y ello muy posiblemente subestima las regresiones que podrían estar experimentando muchas especies raras. De hecho, los efectos previsibles del cambio climático y del paisaje se detectan muy claramente en las comunidades de mariposas de montaña cuando se analizan las tendencias en varios índices de la comunidad durante las últimas dos décadas.

Contribución de los autores

Andreu Ubach: Conceptualización, Análisis de datos, Redacción. Ferrán Páramo: SIG, Gestión de la Base de Datos. Constantí Stefanescu: Conceptualización, Redacción, Supervisión.

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Apéndice

Tabla A1. *Tendencias de las especies calculadas en cada región climática. Se indica para cada especie cuál es la serie temporal disponible y cuál es la tasa multiplicativa de cambio anual. Se indican varias categorías en la tendencia poblacional, según la clasificación que proporciona el software rBMS.*

Table A1. *Species trends calculated in each climatic region. It is indicated for each species the available time series and the multiplicative rate of annual change. Several categories are indicated in the population trend, according to the classification provided by the rBMS software.*

	Región alpina			**Región mediterránea húmeda**			**Región mediterránea árida**		
Especie	**Años**	**% cambio**	**Tendencia**	**Años**	**% cambio**	**Tendencia**	**Años**	**% cambio**	**Tendencia**
Aglais io	15	1.009	Incierta	26	1.003	Estable			
Aglais urticae	18	0.971	Incierta						
Anthocharis cardamines	15	0.994	Estable	27	1.002	Estable			
Anthocharis euphenoides				24	0.969	Regresión moderada			
Apatura ilia				15	0.954	Incierta			
Aphantopus hyperanthus	5	0.835	Regresión fuerte						
Aporia crataegi	22	0.960	Regresión moderada	21	0.897	Regresión fuerte			
Araschnia levana				7	0.532	Regresión fuerte			
Argynnis adippe	15	0.965	Incierta						
Argynnis aglaja	18	0.973	Incierta						
Argynnis paphia	18	0.945	Incierta	27	1.007	Estable			
Aricia agestis	17	0.960	Incierta	21	0.963	Regresión moderada			
Aricia cramera				24	0.982	Estable	18	0.931	Regresión moderada
Boloria dia	18	0.971	Incierta	26	1.025	Incierta			
Boloria euphrosyne	15	0.972	Incierta						
Brenthis daphne				11	0.835	Regresión fuerte			
Brintesia circe	17	1.000	Incierta	27	1.016	Incremento moderado			
Cacyreus marshalli				24	0.942	Regresión moderada			
Callophrys rubi	15	1.039	Incierta	27	0.952	Regresión moderada	19	0.947	Regresión moderada
Carcharodus alceae				27	0.999	Estable			
Celastrina argiolus	4	0.696	Regresión fuerte	27	0.990	Estable	15	1.136	Incremento moderado
Charaxes jasius				27	0.992	Estable			
Coenonympha arcania	17	1.002	Estable	27	0.956	Incierta			
Coenonympha dorus				21	0.964	Regresión moderada			
Coenonympha pamphilus	18	0.942	Regresión moderada	27	0.966	Regresión moderada	5	1.233	Incremento fuerte
Colias alfacariensis	6	1.070	Incierta	21	0.954	Incierta			
Colias croceus	22	0.992	Estable	27	1.005	Estable	20	0.964	Incierta
Cupido argiades				13	0.981	Regresión moderada			
Cupido minimus	7	0.908	Regresión moderada	10	0.829	Regresión fuerte			
Cupido osiris				11	0.912	Regresión fuerte			
Cyaniris semiargus	7	0.908	Incierta						
Erebia meolans	15	0.974	Incierta						
Erebia neoridas	14	0.972	Incierta						
Erynnis tages				21	0.901	Regresión fuerte			
Euchloe crameri				27	1.023	Incierta			
Euphydryas aurinia				27	0.906	Regresión fuerte			
Glaucopsyche alexis				21	0.931	Incierta			
Glaucopsyche melanops				24	0.879	Regresión fuerte			
Gonepteryx cleopatra	4	0.694	Regresión fuerte	27	1.047	Incremento moderado	20	0.978	Incierta
Gonepteryx rhamni	22	0.990	Estable	27	1.016	Estable			
Hipparchia fagi				20	1.016	Incierta			
Hipparchia fidia				24	0.964	Regresión moderada	4	0.802	Incierta
Hipparchia hermione	5	0.875	Regresión fuerte						
Hipparchia semele				20	1.023	Incierta			
Hipparchia statilinus				26	0.953	Incierta			
Iphiclides feisthamelii	17	0.990	Estable	27	0.982	Regresión moderada			
Issoria lathonia	22	1.000	Estable	27	1.010	Estable			
Lampides boeticus	6	0.942	Incierta	27	0.979	Estable			
Lasiommata maera	5	0.875	Regresión fuerte						

Continuación Tabla A1.
Table 1 continuation.

	Región alpina			**Región mediterránea húmeda**			**Región mediterránea árida**		
Especie	**Años**	**% cambio**	**Tendencia**	**Años**	**% cambio**	**Tendencia**	**Años**	**% cambio**	**Tendencia**
Lasiommata megera	22	0.989	Incierta	27	1.002	Estable	20	0.953	Regresión moderada
Leptidea sinapis	17	0.980	Regresión moderada	27	0.963	Regresión moderada			
Leptotes pirithous				27	1.008	Estable	6	1.973	Incremento fuerte
Libythea celtis				21	1.042	Incierta			
Limenitis camilla				15	0.975	Incierta			
Limenitis reducta				27	0.978	Regresión moderada			
Lycaena phlaeas	9	0.985	Incierta	27	0.983	Estable	17	0.923	Incierta
Lycaena tityrus	7	0.848	Regresión moderada						
Lycaena virgaureae	8	1.026	Incierta						
Lysandra bellargus	15	1.074	Incremento moderado	24	1.027	Incierta			
Lysandra coridon	15	0.974	Incierta	13	0.964	Incierta			
Maniola jurtina	17	1.019	Incierta	27	1.008	Estable	18	0.984	Incierta
Melanargia lachesis	22	1.003	Incierta	27	0.948	Regresión moderada			
Melanargia occitanica				21	0.877	Regresión fuerte			
Melitaea cinxia	14	0.986	Incierta	20	0.950	Incierta			
Melitaea deione				25	0.984	Incierta			
Melitaea didyma	12	0.938	Regresión moderada	26	1.013	Estable			
Melitaea parthenoides	4	0.868	Incierta						
Melitaea phoebe	15	0.897	Incierta	24	0.968	Incierta			
Melitaea trivia				11	1.103	Incierta			
Neozephyrus quercus				25	1.048	Incierta			
Nymphalis antiopa				20	0.930	Regresión moderada			
Nymphalis polychloros				19	0.944	Incierta			
Ochlodes sylvanus	11	0.981	Incierta	27	0.969	Incierta			
Papilio machaon	5	0.992	Incierta	27	0.977	Regresión moderada	20	1.012	Estable
Pararge aegeria	18	1.031	Incremento moderado	27	0.993	Estable	20	1.009	Estable
Pieris napi	15	1.056	Incierta	27	0.984	Estable			
Pieris rapae	17	0.993	Estable	27	1.013	Estable	20	0.990	Estable
Piers brassicae	22	1.017	Incierta	27	0.989	Estable	20	1.006	Estable
Plebejus argus				21	1.093	Incierta			
Polyogonia c-album	15	1.002	Incierta	27	1.000	Estable			
Polyommatus celina							9	1.100	Incierta
Polyommatus escheri				21	0.941	Regresión moderada			
Polyommatus hispana				24	0.984	Estable			
Polyommatus icarus	17	0.992	Estable	27	0.987	Estable	20	0.956	Regresión moderada
Polyommatus thersites				20	0.945	Regresión moderada			
Pontia daplidice				27	0.983	Estable	20	0.973	Regresión moderada
Pseudophilotes panoptes				24	0.964	Incierta			
Pyrgus armoricanus				11	1.098	Incierta			
Pyrgus malvoides				26	1.005	Incierta			
Pyronia bathseba				27	0.985	Estable			
Pyronia cecilia				27	0.934	Regresión moderada	20	0.958	Incierta
Pyronia tithonus	15	0.973	Incierta	27	0.948	Regresión moderada			
Satyrium acaciae	7	0.908	Incierta	12	0.972	Incierta			
Satyrium esculi	14	0.944	Incierta	27	1.022	Incierta			
Satyrium ilicis				10	1.032	Incierta			
Satyrium spini				15	0.977	Incierta			
Satyrus actaea	15	0.898	Regresión fuerte						
Spialia sertorius				20	0.992	Incierta			
Thymelicus acteon	7	0.936	Regresión moderada	27	0.990	Estable			
Thymelicus lineola	15	0.976	Incierta						
Thymelicus sylvestris				19	0.965	Incierta			
Tomares ballus				15	0.973	Incierta			
Vanessa atalanta	15	1.005	Estable	27	0.990	Estable	20	0.985	Estable
Vanessa cardui	21	0.961	Incierta	27	0.974	Regresión moderada	20	0.936	Regresión moderada
Zerynthia rumina				20	0.976	Incierta			