

SPECIAL ISSUE ARTICLE

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 CO₂ 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; Wallis-DeVries 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.

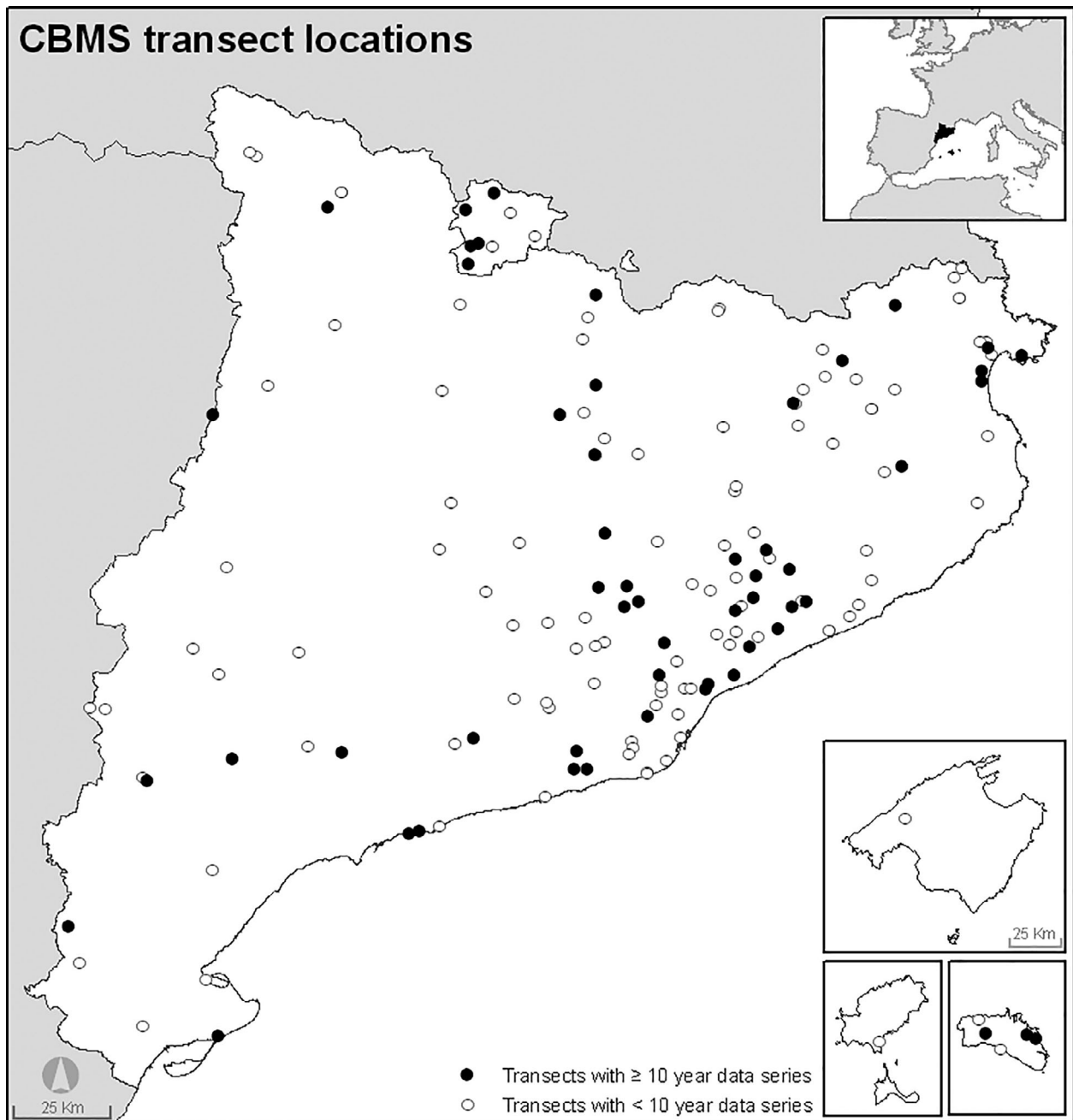


Fig. 1. Map of the study region. The locations of the 54 long-monitored transects (≥ 10 years) in the CBMS network used for this study are represented by black dots. White dots represent the remaining 106 CBMS transects that existed up to 2017 and were used for calculating an index of preference along 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 10.11 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:

$$I_{TAOi} = \frac{2 \times D_{\text{open}}}{D_{\text{open}} + D_{\text{closed}}} - 1$$

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 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 occurred 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 (\pm 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*

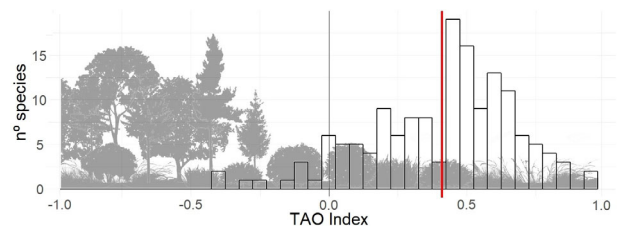


Fig. 2. Distribution of the I_{TAO} values for all 147 species along a $(-1, 1)$ axis. In all, 91% of the species values show positive values, thereby indicating very strong preferences for open habitats. [Color figure can be viewed at wileyonlinelibrary.com]

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.

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 $\Delta AIC < 2$ 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

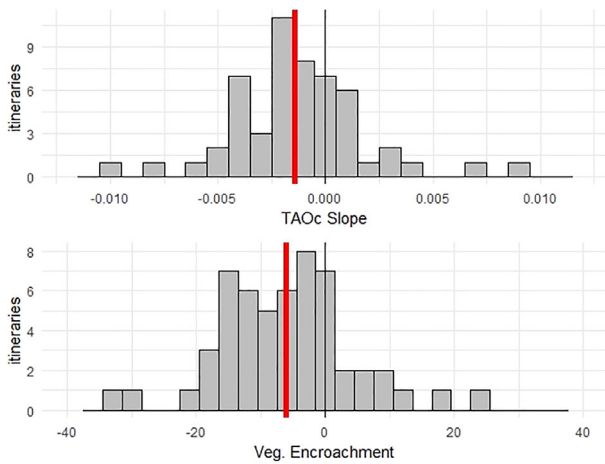


Fig. 3. Histograms showing TAOc slopes for all the 54 studied butterfly assemblages (a) and vegetation encroachment at the same 54 sites (b). The red bar situates the mean value of both data sets. In all, 72% of the itineraries show a negative TAOc slope indicating change toward butterflies that prefer 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(> t)	Estimate	Pr(> t)	Estimate	Pr(> t)	Estimate	Pr(> t)	Estimate	Pr(> t)
(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 $P < 0.05$ are marked with "*" and values with $P < 0.01$ are marked with "**".

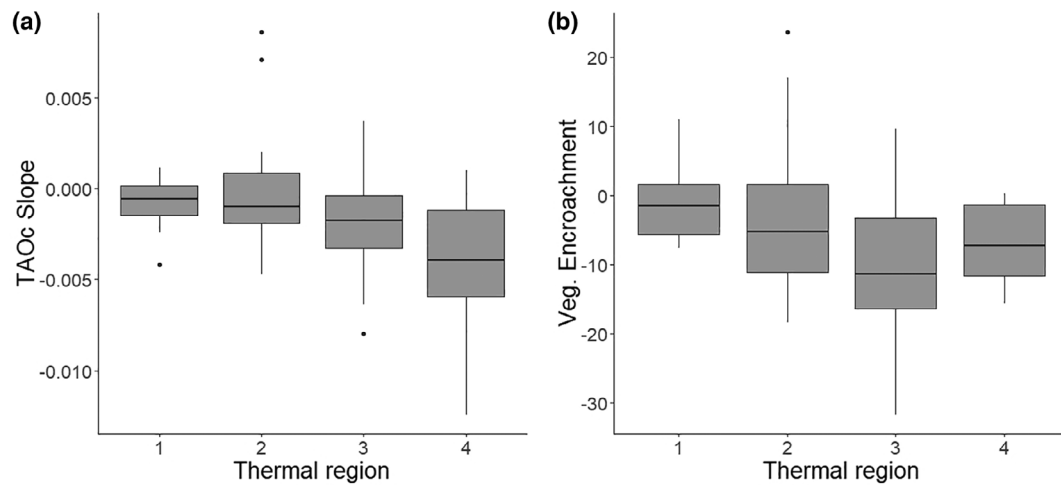


Fig. 4. Boxplots for TAOc slopes and vegetation encroachment by thermal region. Thermal regions numbering run from the coldest (1) to the warmest (4).

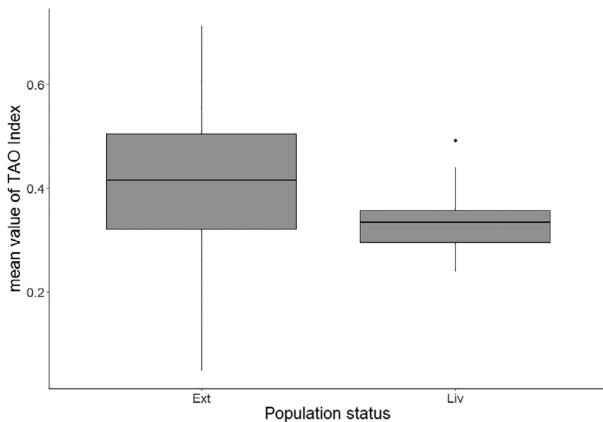


Fig. 5. Boxplot showing the mean value of the TAO index for all the extinct (Ext) and not extinct (Liv) species at each of the 54 studied sites.

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 southwestern 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

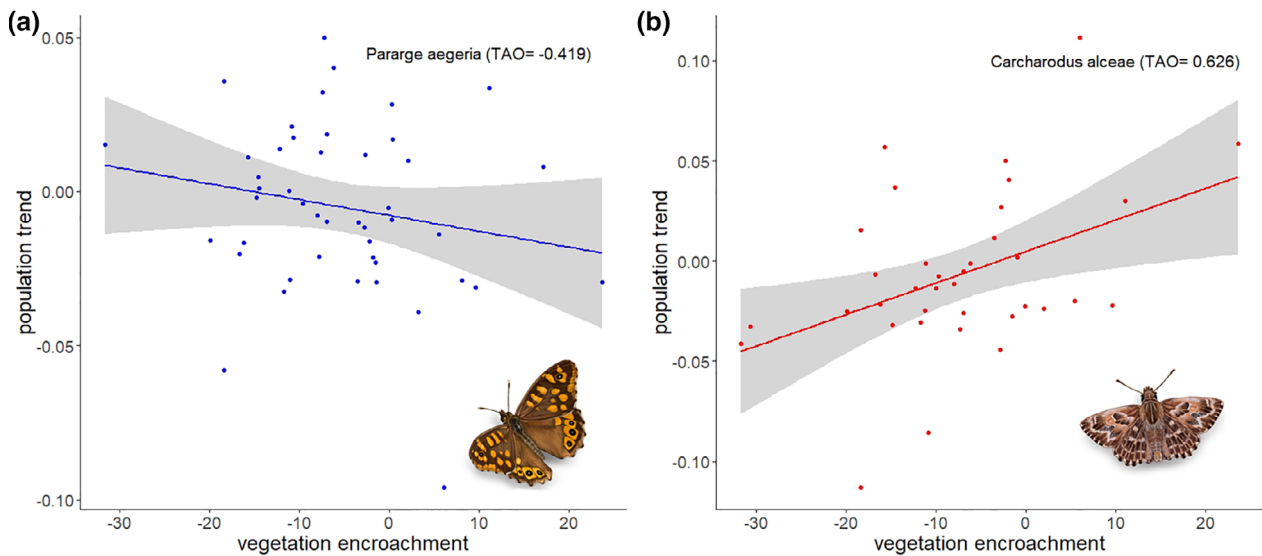


Fig. 6. Population trends according to vegetation encroachment at site level of two species with very different TAO index values. Populations of speckled wood (*Pararge aegeria*, TAO = -0.419) tended to decline wherever the habitat became open (n° sites = 46, $R^2 = 0.03$, $P = 0.198$). Populations of 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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