

Butterflies highlight the conservation value of hay meadows highly threatened by land-use changes in a protected Mediterranean area

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Abstract

Butterfly assemblages were used to characterize and evaluate the conservation value of the main habitat types in the Aiguamolls de l'Empordà Natural Park (north-eastern Spain), an important protected wetland area on the Mediterranean coast. Butterfly data were obtained from a number of transects walked as part of the Catalan Butterfly Monitoring Scheme, which uses a standardized methodology for monitoring butterflies. A Mantel test indicated a strong association between habitat types and the composition of butterfly assemblages and a principal component analysis ordinated individual butterfly species along a gradient from woodland to open areas, thereby indicating various degrees of shade tolerance. In addition, cluster analysis distinguished two main groups of habitats based on the similarities of their butterfly fauna: woodland and bramble clumps and a group of three different kinds of grasslands (traditionally hay meadows, pastures, and alfalfa fields). Hay meadows flooded in winter (the so-called *closes*) appeared always as the highest ranked habitat in terms of conservation evaluation: they have more butterflies and a slight tendency to harbor more and generally rarer species. This conclusion coincides with that of previous investigations that have indicated that the most diverse and rare plant communities in the whole Natural Park are present in the *closes*, and highlights the importance of traditionally managed hay meadows for wildlife. However, these hay meadows – one of the rarest habitats in the Mediterranean region – are in alarming decline and have become the most threatened habitat in this protected area: no longer profitable, we believe that the future of the *closes* will depend ultimately on the existence of agri-environmental schemes.

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1. Introduction

Situated on the shores of the Bahía de Roses, close to the eastern tip of the Pyrenees, the Aiguamolls de l'Empordà constitute one of the most important areas for wildlife on the Mediterranean coastline of the Iberian Peninsula. Traditionally, highly appreciated for its ornithological value (Sargatal and del Hoyo, 1989), this protected area (4784 ha) was declared a Natural Park in

1983 and has subsequently been included in the Ramsar list of Wetlands of International Importance. As well, it also harbors populations of several rare invertebrate taxa, especially those associated with wetland habitats (e.g., Pérez De-Gregorio, 1990).

The vegetation of the Aiguamolls de l'Empordà Natural Park (hereafter AENP) has also been studied in detail and analyses of the plant diversity occurring in the area as a whole (Farràs and Velasco, 1994; Watt and Vilar, 1997; Gesti and Vilar, 1999) and the impact of management policies on plant communities (Gesti, 2000) have been carried out. These studies have revealed the

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exceptional value of the so-called *closes*, one of the most limited and threatened habitats in the Natural Park. *Closes* are meadows enclosed by drainage canals lined by riverine forest that flood in winter and, depending on their production, are mowed for hay once or twice a year. A recent analysis by Gesti et al. (2003) has shown that the most typical plant community of the *closes* (*Arrhenatheretum elatioris* Br.-Bl., 1915) has the highest species richness and diversity of all plant communities present in the area, and is also home to the region's rarest taxa (i.e., those with the most restricted distributions in Catalonia, northeast Spain). Moreover, these authors warn that this habitat is disappearing rapidly. In 1956, 136.04 ha of *closes* were present in the area, but by 2002 this figure had dropped to just 26.75 ha as a result of agricultural improvement (e.g., conversion to the production of maize, sunflower, and rice) and the gradual change from hay to fodder as the main food source for cattle. The problem still exists, despite the declaration of the whole area as a Natural Park.

Unfortunately, evidence of the importance of the *closes* for other taxa is at present somewhat lacking. Stefanescu and Miralles (1994) studied moth assemblages in three sites located at different distances from the coastline corresponding to three well-defined and characteristic habitats of the AENP: a typical saltmarsh, an extensive reed bed and a traditional *closo*. Their analysis, based on data obtained by light trapping in two consecutive years, revealed important differences in the moth fauna of the three sites and showed that the *closo* site harbored the most diverse and species-rich moth assemblage. The bird communities of several *closes* have also been monitored in recent years (Montràs, 2004), mainly as a tool for understanding the phenological pattern of habitat use by different species. However, this study does not compare the bird communities of the *closes* with those present in other habitats within the Natural Park.

The lack of comprehensive studies of any taxonomic group other than higher plants undoubtedly represents an obstacle when trying to protect the remaining *closes* in the AENP. In fact, an increasing number of studies have shown a lack of agreement in cross-taxonomic patterns of species richness and endemism at scales of several orders of magnitude, including at the fine-scale patterns considered here (e.g., Prendergast et al., 1993; Oliver et al., 1998; Vanjaarsveld et al., 1998; Kremen et al., 2004). Obviously, this is good reason to avoid the former common practice of assessing the conservation value of wildlife areas using data from a single taxonomic group.

Apart from birds, butterflies stand out as the most intensively studied wildlife group in the AENP. Since 1988 several monitoring transects have been operated in different parts of the Natural Park as part of the Catalan Butterfly Monitoring Scheme or CBMS (Stefanescu,

2000), a monitoring program based on the standard methodology of the British Butterfly Monitoring Scheme (Pollard and Yates, 1993). The wealth of information accumulated throughout these years now enables us to assess the conservation value of various habitats in the AENP by using butterflies as a bioindicator group. This is important in the context outlined above, as it allows us to rank the *closes* by means of an independent data set provided by a well-studied and highly valuable indicator taxa. Moreover, this additional information seems especially pertinent in this case given that several works have shown a lack of correlation between butterfly and plant diversity (e.g., Stefanescu et al., 2004, using data from the CBMS) and butterfly and moth diversity (Ricketts et al., 2002) at the local scales considered in our study (0.1–10 km²). These potential disagreements could lead to serious conflicts in the designation of the areas or habitats most worthy of the greatest conservation efforts.

In this paper, we use data from the butterfly monitoring transects in the AENP to address several questions of obvious conservation interest in a protected area. First, we ask if butterfly assemblages are distributed homogeneously or heterogeneously across the different habitat types of the Natural Park. In the latter case, it may be possible to define regular associations of groups of species in particular habitats and select subsets of species that may be used as bioindicators of some particular environmental conditions. Secondly, once this question has been answered, we assess the conservation value of each habitat type on the basis of its butterfly fauna. Our results are compared with those from earlier botanical studies that have highlighted the ecological importance of the *closes*. Underlying this comparison is the fact that a coincidence in the results of both studies would provide stronger arguments for an effective protection of this threatened habitat. Finally, we also seek out correlations between habitat type and the different life history attributes of the butterfly species present, which, as recently shown, may have important implications for conservation (Dennis et al., 2004).

2. Material and methods

2.1. Transects and butterfly data

Butterfly data were obtained from six CBMS monitoring transects (Stefanescu, 2000), all of which were located within the AENP (Fig. 1). The transects were situated at various distances from the sea and provide a representative sample of the main biotopes found in the Natural Park: a mosaic of grasslands (hay meadows, pastures and alfalfa fields), rides delimited by woodland (mainly riverine forest), bramble and helophytic vegetation, and arable fields.

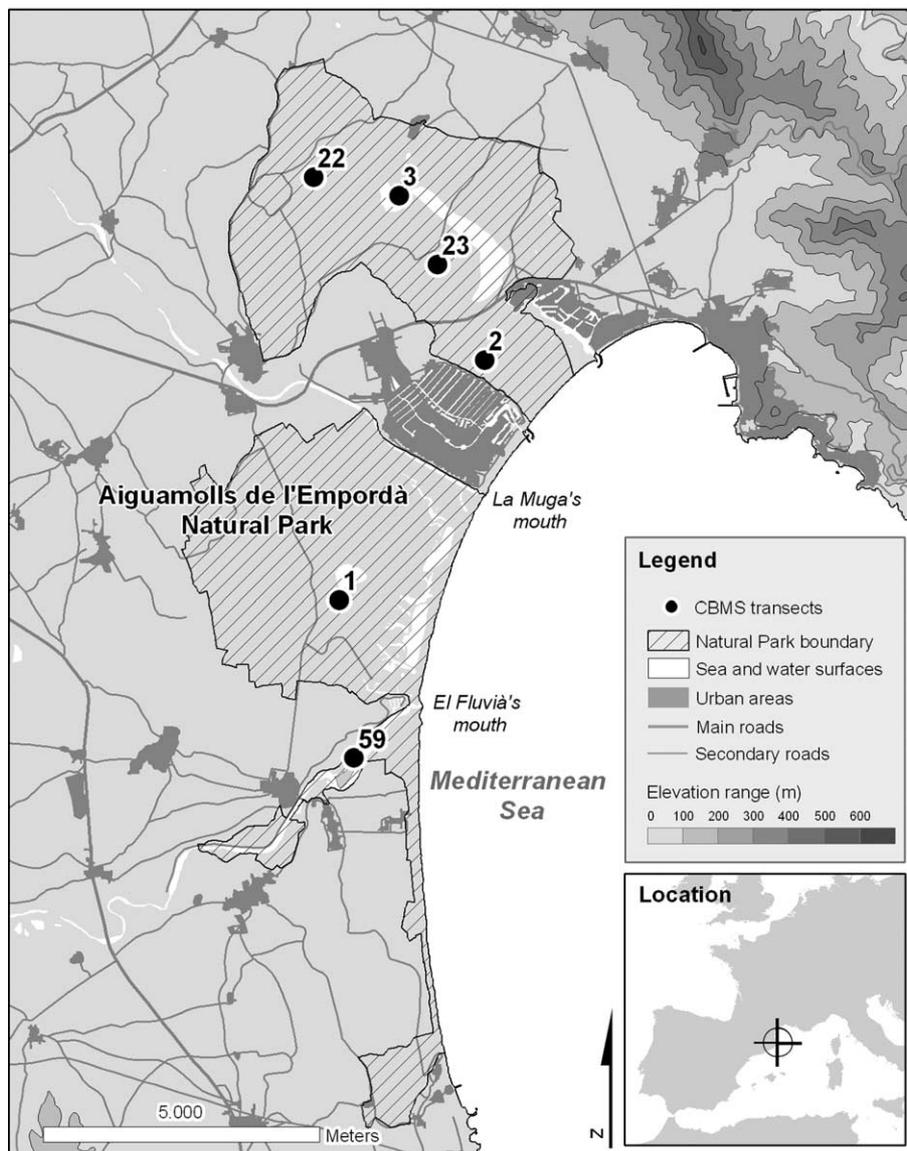


Fig. 1. Map of the Aiguamolls de l'Empordà Natural Park, showing the location of the six CBMS transects that provided the butterfly data. Numbers refer to the original codes of the transects in the CBMS: 1 – El Cortalet; 2 – La Rubina; 3 – Vilaüt; 22 – Closes de l'Ullal; 23 – Closes del Tec; 59: Mig de Dos Rius.

As per the standard methodology of the BMS (see Pollard and Yates, 1993, for details), recorders walked fixed routes and counted butterflies detected within 2.5 m on either side of the route and up to 5 m ahead. Counts were made on a weekly basis starting on March 1 and ending on September 26, a period of 30 recording weeks per year. Transects were divided into discrete sections, which coincided with obvious changes in vegetation type, and separate counts were made in each section. Five categorical variables were used to characterize the 46 sections included in this study: (i) relative cover of grasslands (0: <30% of the recording route; 1: >30%); (ii) absence (0) or presence (1) of cattle grazing in grasslands; (iii) relative cover of woodland (0: absence; 1: 10–30%; 2: >30%); (iv) relative cover of bramble hedges or

clumps (0: absence; 1: 10–30%; 2: >30%); (v) absence (0) or presence (1) of arable fields at the sides of the recording route. Data on the relative cover of vegetation types was extracted from the CBMS data base, which includes information on the percentage occupied by plant communities within the 2.5 m-belt on each side of the progression line of the transect routes, as characterized by a botanist in accordance with the CORINE Biotopes Manual (Moss et al., 1990). Plant communities were characterized in the first or second year of the monitoring of a transect; however, in El Cortalet, which has been recorded for the whole period 1988–2004, vegetation was characterized for a second time in 2000. A brief definition of the 46 sections, together with the values of each categorical variable, is given in Appendix A.

Because three of the six transects were only monitored for one year (La Rubina, 1988; Vilaüt, 1989; Closes de l'Ullal, 1996), in the other three transects we also only used data from one recording season to assess butterfly species abundance in each section. Data from Closes del Tec correspond to the first year of monitoring (1997), when they were actively managed as hay meadows or pastures. For El Cortalet and Mig de Dos Rius, we selected the year in which the plant communities were characterized (2000 and 2002, respectively). Moreover, we also included data from 1988 for six sections in El Cortalet that, at that time, sampled habitats that are no longer present in the transect (e.g., dry pastures and arable field margins). For each section, butterfly data were standardized as the individuals recorded in 100 m of transect throughout the season.

2.2. Correlation between butterfly assemblages and habitat types

The existence of a correlation between habitat types and the composition of butterfly assemblages was investigated using a Mantel test, which compares two similarity matrices computed for the same objects and obtained independently of each other (Legendre and Legendre, 1998). In our case, matrix Y contains similarities between the sites (i.e., the 46 studied sections) in terms of butterfly species composition, while matrix X contains similarities in environmental characteristics for the same sites (i.e., the scores of each of the five categorical variables used to characterize each section) listed in the same order. Calculations were made with the program Mantel (250 permutations) from the "R" package of multivariate analysis v. 3.0 (Alain Vauder, University of Montreal, Quebec, Canada). A one-tailed test was used to test for a positive correlation between the two matrices.

2.3. Indicator species

Species matrices were analyzed by ordination using principal component analysis (PCA) to identify sets of species characterizing the main habitat types in a reduced dimensional space. As input, data for both butterfly presence-absence and abundance adjusted for transect length, together with the habitat type variables, were used. Both analyses were performed on the complete data set (all 47 species observed) and for a reduced data set comprising only 27 of the "commonest species" (arbitrarily defined as those appearing with an abundance of at least one individual/100 m of transect in at least three sections). Although similar results were produced for both cases, we present here only the results obtained with the quantitatively reduced data set (abundance data for the 27 "commonest" species). This and all subsequent

analyses were performed using the STATISTICA package v. 5.0 for Windows (Statsoft, Inc., Tulsa, OK, USA).

2.4. Habitat types for butterflies: conservation value and ecological characterization

In order to detect the main habitat types that can be characterized by consistent butterfly assemblages, a cluster analysis was applied to the species abundance matrix. We used the reduced data set given the limited ability of the rarest species to reveal clear patterns. Thus, the final input matrix consisted of 46 columns (sections) and 27 rows (butterfly species). Linkage distance was chosen as the similarity coefficient and UPGMA as the clustering algorithm (e.g., Sneath and Sokal, 1973).

Each of the habitat types identified by the cluster analysis was characterized by several ecological parameters; differences between groups were analyzed using one-way ANOVA and LSD *post hoc* tests. Data were log transformed (or arc-sine transformed in the case of proportions) whenever assumptions of normality and homoscedasticity were not met. For this ecological characterization, we used the complete data set (i.e., comprising all 47 butterfly species appearing in the samples).

A first set of parameters, selected because of their frequent use as criteria for conservation evaluation, were chosen (e.g., Usher, 1986): (i) species richness, (ii) abundance, and (iii) rarity. Two measures of species richness were used: (a) all species recorded and (b) only those species that were recorded with an abundance of >1 individual/100 m of transect (i.e., excluding occasional or vagrant species). Abundance was defined as the number of butterflies recorded in 100 m of transect for all species combined. Rarity was measured at two different spatial scales: (a) within the Natural Park (i.e., local scale) as $1/n_i$, where n_i is the number of sections (out of a total of 46) where species i was recorded, and (b) within the CBMS (i.e., regional scale), again as $1/n_i$, where n_i is the number of CBMS transects in Mediterranean habitats (out of a total of 54) where species i was recorded. Thus, in the first case values ranged from 0.022 to 1, and in the second case from 0.019 to 1. Higher values corresponded to rarer species.

We also selected a second set of parameters that are widely used in studies aiming to relate insect life-cycle strategies to habitat characteristics (i.e., habitat permanence, habitat complexity, and resource diversity and availability; Brown, 1985; Steffan-Dewenter and Tscharntke, 1997; Dennis et al., 2004): (i) body size, (ii) overwintering stage, (iii) generations per year or voltinism, (iv) host-plant specialization, and (v) dispersal ability. Body size was estimated as the mean forewing length of males (data from Higgins and Riley, 1984). We calculated for each habitat type the relative contribution

(i.e., the proportion) of (a) species overwintering as egg, larva, pupa, adult, or unable to overwinter (i.e., migrant species), (b) species having one (univoltine), two (bivoltine), or three or more (multivoltine) generations per year, and (c) species feeding as larvae on a single host-plant genus (monophagous), on several genera within a single plant family (oligophagous), or on several genera belonging to a number of plant families (polyphagous). Biological data were obtained from Tolman and Lewington (1997) and from personal observations from within the study area. Finally, an overall index of dispersal ability was calculated after classifying each species into one of the following five categories: 0 – forming closed populations with very little dispersal; 1 – closed populations with more frequent dispersal; 2 – closed populations with common dispersal; 3 – open populations with non-directional dispersal; 4 – open populations with directional migration. Data on dispersal ability and population structure were obtained from various sources (e.g., Pollard and Eversham, 1995; Dennis and Shreeve, 1996; personal observations). The ecological attributes for the 47 butterfly species detected in our samples are summarized in Appendix B.

3. Results

3.1. Butterflies as indicators of habitat types

The Mantel test ($r=0.61$, $p=0.003$) indicated that the similarity matrices of butterfly composition and habitat types are strongly correlated. Therefore, a certain combination of vegetation units in our transect sections (i.e., the relative cover of grassland, bramble hedges or woodland along the transects) translates into a highly characteristic butterfly assemblage.

The nature of this close association was further studied by means of a PCA applied to the original matrices of butterfly abundance and habitat types. A 35.2% of variation in the data was accounted for by the first two axes in the new reduced multidimensional space (Fig. 2). The first axis (19.3% of variation) had a clear biological meaning and could be interpreted as a gradient between sections dominated by woodland and bramble (negative values) and sections mainly consisting of grasslands (both hay meadows and pastures; positive values). The position of arable fields near woodland and bramble clumps is explained by the coincidence of these three kinds of habitats wherever intensive farmland was sampled; for practical reasons the transect routes ran along the edges of arable fields, which mainly consisted of riverine forest or bramble patches.

The 27 commonest butterfly species were also ordinated along the first axis, showing their relative pref-

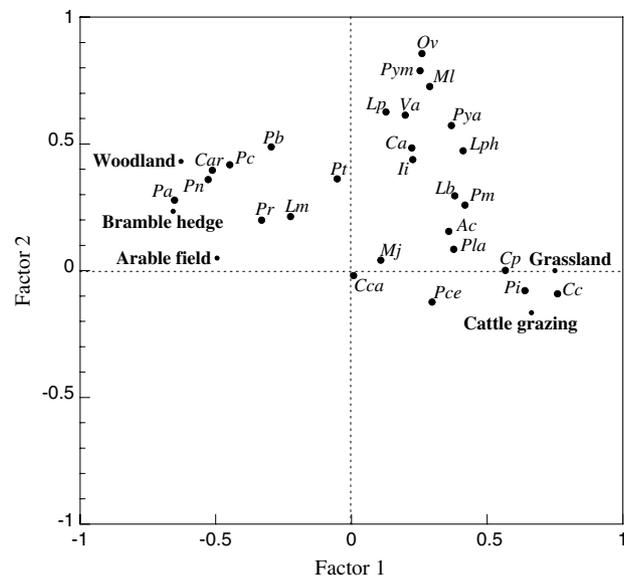


Fig. 2. Butterfly species and habitat variable distribution as a function of the two first principal axes in the PCA analysis conducted on the matrix of correlations between the depicted variables. Abbreviations for species: *Ac*, *Aricia cramera*; *Ca*, *Carcharodus alceae*; *Car*, *Celastrina argiolus*; *Cp*, *Coenonympha pamphilus*; *Cc*, *Colias crocea*; *Cca*, *Cynthia cardui*; *Ii*, *Inachis io*; *Lb*, *Lampides boeticus*; *Lm*, *Lasiommata megera*; *Lp*, *Leptotes pirithous*; *Lph*, *Lycaena phlaeas*; *Mj*, *Maniola jurtina*; *Ml*, *Melanargia lachesis*; *Ov*, *Ochlodes venata*; *Pm*, *Papilio machaon*; *Pa*, *Pararge aegeria*; *Pla*, *Plebejus argus*; *Pb*, *Pieris brassicae*; *Pn*, *Pieris napi*; *Pr*, *Pieris rapae*; *Pc*, *Polygonia c-album*; *Pi*, *Polyommatus icarus*; *Pya*, *Pyrgus armoricanus*; *Pym*, *Pyrgus malvoides*; *Pce*, *Pyronia cecilia*; *Pt*, *Pyronia tithonus*; and *Va*, *Vanessa atalanta*.

erence towards each habitat type. *Pararge aegeria*, *Pieris napi*, *Celastrina argiolus* and *Polygonia c-album* were the most characteristic species of woodland and bramble hedges and represent the most shade-tolerant butterflies in our study. At the opposite end of the axis, *Colias crocea*, *Polyommatus icarus* and *Coenonympha pamphilus* appeared strongly associated with grasslands; that is, they are typically found in the most open conditions. The PCA did not show a clear differentiation within each of the two extreme situations, i.e., no butterfly species appeared to prefer woodland to bramble hedges or hay meadows over pastures.

This ordination also suggested that several species with relatively low positive values (e.g., *Maniola jurtina*, *Pyrgus malvoides*, *Ochlodes venata*, *Melanargia lachesis*, and *Pyronia cecilia*) or relatively low negative values (e.g., *Pyronia tithonus* and *Lasiommata megera*) prefer habitats with intermediate characteristics of grasslands and woodland.

3.2. Major butterfly habitats

The cluster analysis allowed us to distinguish two main groups of habitats based on the similarities

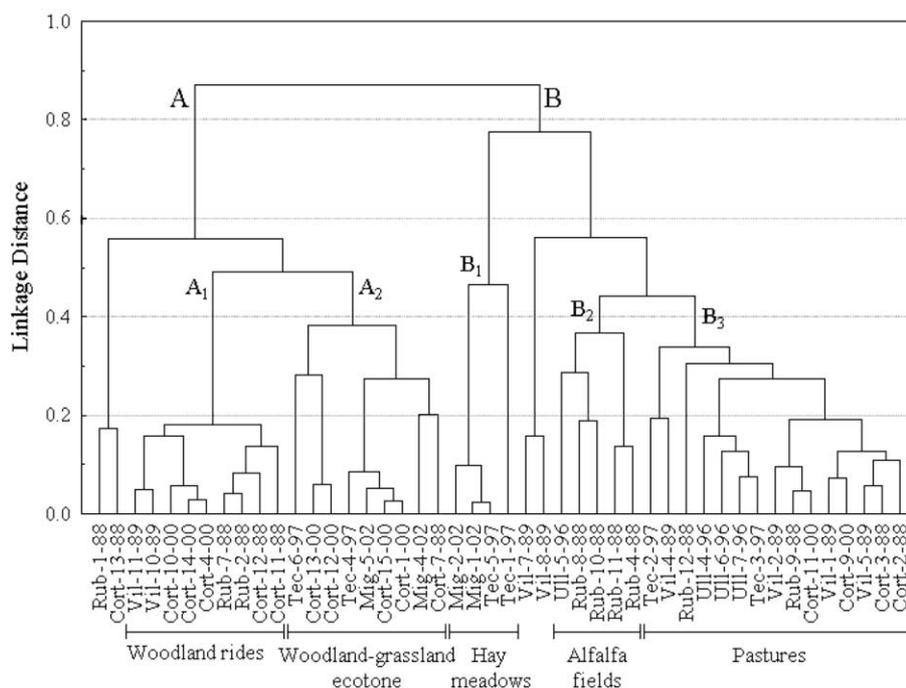


Fig. 3. Dendrogram based on the cluster analysis of 46 transect sections and 27 butterfly species. The between-samples measurement of similarity was 'Linkage distance', and the clustering algorithm was UPGMA. Main groupings of sections: A, woodland habitats; B, grassland habitats. The correspondences of further subdivisions of the two main groups to particular habitats (A1, A2, B1, B2, B3) are given below each cluster.

within the butterfly assemblages that live there (Fig. 3). In accordance with the PCA results, the first group (A) consisted of those sections dominated by woodland, by bramble clumps replacing former woodland, or both. The second group (B) corresponded to those sections that sampled a diversity of grasslands. However, further subgroups were evident within each main class, indicating a finer association between butterfly assemblages and the habitats occurring along the transects. In particular, we considered the five following major butterfly habitats (as defined from the cluster analysis when the linkage distance is set at around 0.5, Fig. 3), which represent useful ecological units:

- Subgroup A1: rides and arable field edges delimited by woodland, mainly elms (*Ulmus minor*), ashes (*Fraxinus oxycarpa*), and oaks (*Quercus humilis*), or bramble (*Rubus umilifolius* and *R. caesius*).
- Subgroup A2: open woodland interspersed with small grassy patches, and woodland-grassland ecotone.
- Subgroup B1: traditional hay meadows.
- Subgroup B2: alfalfa fields, harvested 2–3 times a year.
- Subgroup B3: pastures or hay meadows also used for grazing.

These units, which correspond to truly discernible broad habitat types, are characterized by means of their butterfly fauna below.

3.3. Comparison of butterfly habitats

The mean values (\pm SE) of the selected ecological parameters in the different groups are shown in Figs. 4 and 5.

3.3.1. Criteria for conservation evaluation

Of those criteria most often employed for conservation evaluation, we only found significant differences in butterfly abundances (log individuals/100 m of transect: $F=4.08$, $p<0.01$). Butterflies were more abundant in traditional hay meadows than in any other of the habitat types; few differences were detected within these other habitat types (Fig. 4(a)).

Hay meadows also ranked first for species richness, independently of which of the two sets of species was used, while woodland was determined as the most species poor habitat (Fig. 4(b)), although overall no significant differences were found between habitats.

Marginal significant differences between groups were also found for one of the two criteria of rarity used in this study (rarity at the regional scale: $F=2.21$; $p<0.1$; Fig. 4(c)). Hay meadows were again ranked as the most valued habitat (e.g., the one having the rarest species), with almost the same value as pastures. Significant differences were only found between pastures and woodland, which harbored the commonest butterfly species. Similar results were obtained when rarity was defined on a local scale. Both measures of rarity were highly correlated ($r=0.55$, $p<0.001$, $n=42$).

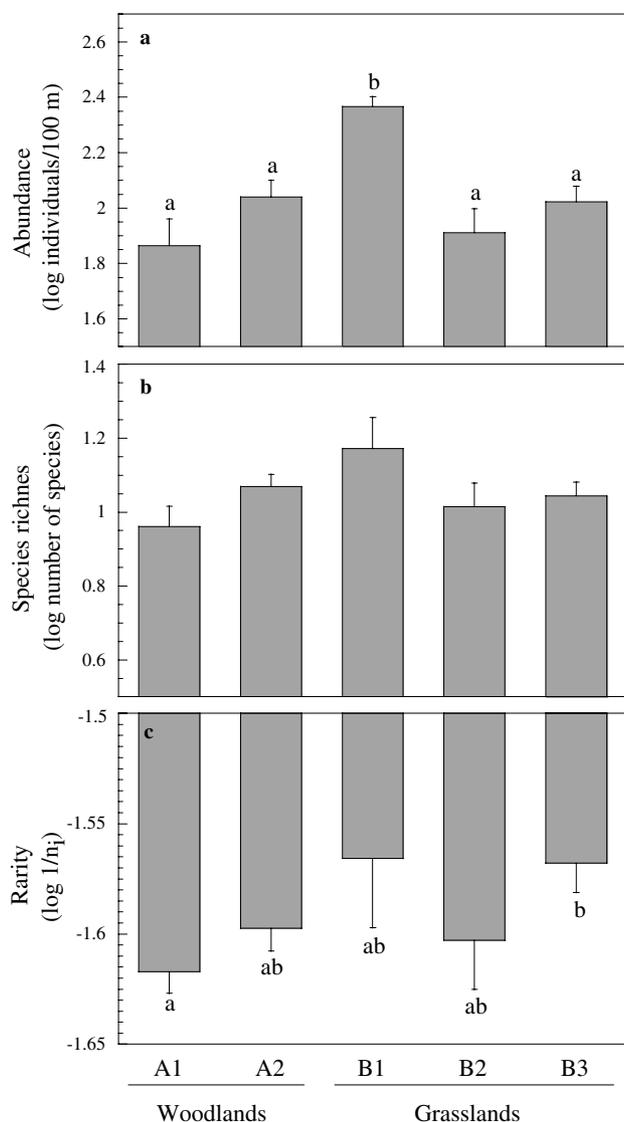


Fig. 4. Mean values (\pm SE) of three conservation evaluation criteria for different habitats according to their butterfly fauna. (a) Abundance of butterflies, (b) species richness (occasional species excluded), and (c) rarity (at the regional scale: $1/n_i$, where n_i is the number of CBMS transects from a total of 54 where species i was recorded). See Fig. 3 for the definition of habitat types. Different letters refer to significant differences ($p < 0.05$, LSD post hoc tests) among groups.

3.3.2. Life-history attributes

Changes in the composition of butterfly assemblages resulted in notable differences in some basic life-history attributes of the species (Fig. 5). Butterfly species tended to be smaller in hay meadows and pastures than in woodland (wing length: $F = 2.69$; $p = 0.046$; Fig. 5(a)). In addition, overwintering strategies clearly differed between woodlands and grasslands. Relatively more species overwintered as larvae in open habitats than in forested habitats ($F = 6.17$; $p < 0.001$), and the opposite was true for species overwintering as pupae ($F = 5.47$; $p < 0.01$) and, almost significantly, for adults ($F = 2.36$;

$p = 0.07$; Fig. 5(b)–(d)). Finally, dispersal ability was higher in alfalfa fields and woodland than in pastures ($F = 3.95$; $p = 0.009$; Fig. 5(f)). On the other hand, differences in host-plant specialization and voltinism were almost non-existent (with the exception of a likely higher proportion of bivoltine species in hay meadows and pastures: $F = 2.48$; $p = 0.06$; Fig. 5(e)).

4. Discussion

Butterflies have traditionally been viewed as an excellent group of bioindicators, mainly due to the complexity of ecological management required by many species (Thomas, 1991; New et al., 1995) and, more recently, to their great ability to act as indicators of climate change (Parmesan, 2003). Accordingly, several monitoring methods have been developed to provide detailed data on butterfly numbers and phenology.

One methodology that has proved particularly useful for monitoring butterflies in temperate countries is the so-called Butterfly Monitoring Scheme or BMS (Pollard and Yates, 1993). Reliable data on butterfly abundance and local distribution, as well as the effects of managing practices on butterfly populations, can be easily obtained by means of repeated visual censuses along a transect route. One advantage of the BMS is the fact that the transect route is divided into a different number of sections, coinciding with obvious changes in the vegetation, and thus provides finer scale data that can be used to assess biotope affiliations for butterfly species (e.g., Oostermeijer and van Swaay, 1998). Indeed, as shown by Shreeve et al. (2001), not only the requirements for precise larval host plants but also for other resources such as the hibernation site, adult feeding nectar sources, mate-locating locations, and basking sites have led, in many cases, to close associations of different groups of species or assemblages with particular habitats or biotopes. This makes it possible to assess the conservation value of different habitat types on the basis of their characteristic butterfly fauna.

In this study, data from the CBMS from six transects located in a Mediterranean Natural Park were used for this purpose. Data on butterfly abundance and vegetation characteristics from a total of 46 transect sections clearly indicated the existence of a strong association between butterfly assemblages and habitat type. This relationship was further examined by PCA and cluster analysis to reveal preferences of individual species and characteristic butterfly assemblages.

Individual species were ordinated along an axis representing a gradient from woodland (riverine forest and dense bramble clumps) to open areas (grasslands). Most of the species occupied intermediate positions along the positive side of this axis, suggesting a preference for

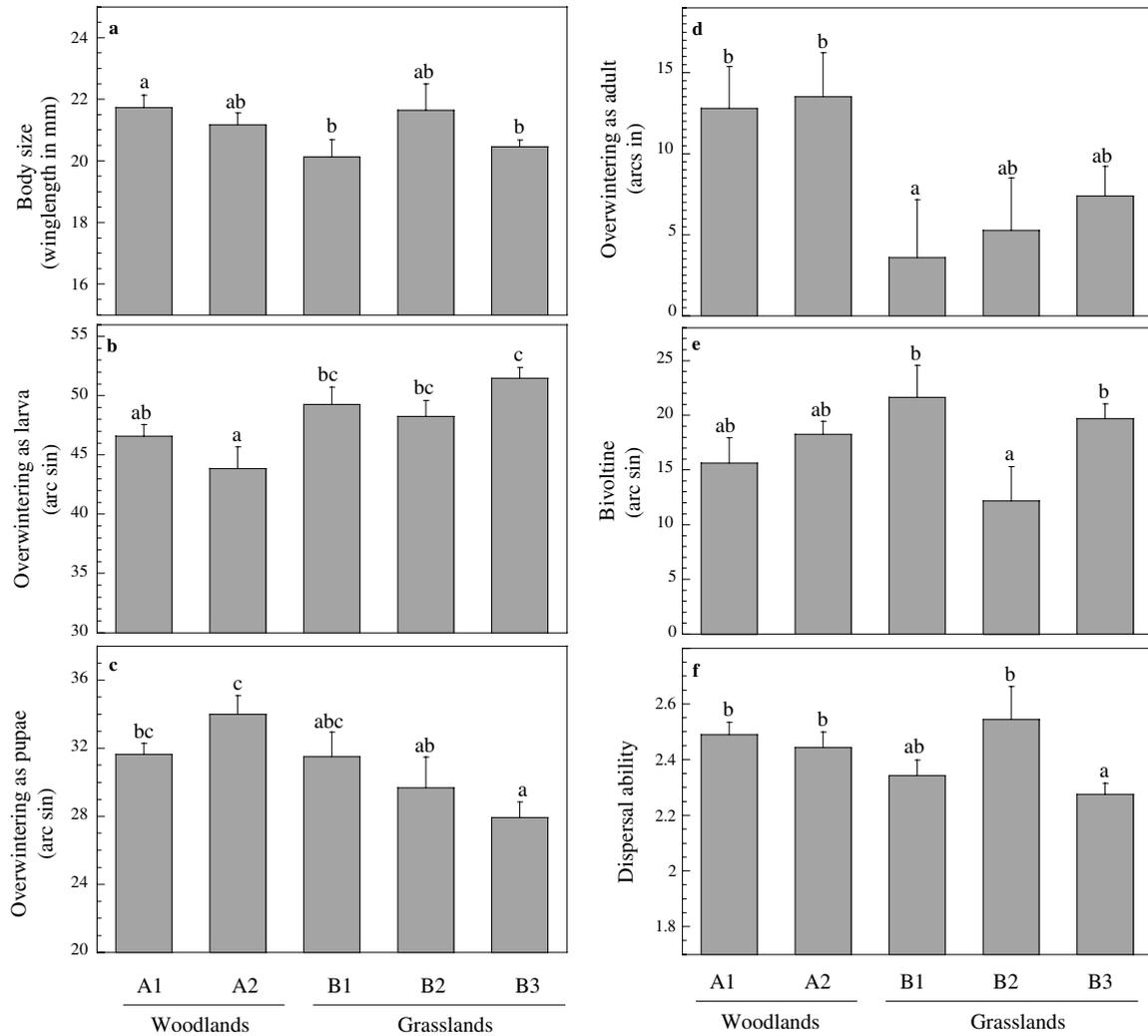


Fig. 5. Mean values (\pm SE) of six life-history attributes of butterfly species in five different habitats. (a) Body size, (b) proportion of species overwintering as larvae, (c) proportion of species overwintering as pupae, (d) proportion of species overwintering as adults; (e) proportion of bivoltine species, and (f) dispersal ability. Different letters refer to significant differences ($p < 0.05$, LSD post hoc tests) among groups. See the text for more details and Fig. 3 for the definition of habitat types.

open habitats with some presence of patches of woodland or shrubs. The most likely explanation for this finding is the need butterflies have for elements providing shelter and certain other resources (e.g., sites for perching males or protected egg-laying sites; see Dover et al., 1997; Quin and Burel, 2002), as well as their general preference for open areas. Moreover, a predictable decrease in many butterfly populations and, eventually, a loss of diversity occurs whenever these elements increasing landscape complexity are removed, as is currently occurring in farmland (van Swaay and Warren, 1999).

Our results also bear some resemblance to those of Warren (1985) and Greatorex-Davies et al. (1993), who defined a gradient of shade tolerance for butterflies occurring in English woodlands. For instance, *C. pamphilus* and *P. icarus* appeared at the extreme end of shade intolerance in the studies of Warren (1985) and Greatorex-Davies et al. (1993), and also as the most

characteristic grassland species in our data. At the other extreme, *P. aegeria* and *P. napi* appeared as the most typical examples of woodland butterflies in our study and as the most shade-tolerant species in English woodlands. An important issue to investigate further is how habitat preference of individual species varies across large geographical areas; that is, how their bioindicator properties change or remain constant under different environmental conditions (e.g., Thomas, 1993; Thomas et al., 1998). In this respect, the availability of BMS data from several European countries is essential and may help to predict trends in species that can be linked to widespread land-use changes in each country.

From the perspective of butterfly assemblages, cluster analysis clearly distinguished between two broad habitat types, i.e., those sections corresponding to basically open areas and those sections dominated by woodland. These categories could be further divided into several butterfly

habitats (Fig. 3), depending on more subtle characteristics related to vegetation and management practices (e.g., traditional hay meadows, pastures, and alfalfa fields were separated as distinct grassland habitats). A key aspect of the present study was the assessment of the conservation value of these habitats and, more particularly, of hay meadows for butterflies. Interestingly, although significant differences were only found for one (on a significance level of $p < 0.05$) or two (on a significance level of $p < 0.1$) of the three selected criteria (abundance, species richness, and rarity), traditional hay meadows *always* appeared as the highest valued habitat: they contain more butterflies and, as well, show a slight tendency to harbor more and generally rarer species. At the other extreme, woodland was generally ranked as the least valuable habitat.

Our conclusion broadly coincides with that of Gesti et al. (2003), who based their assessment of the conservation value of hay meadows on higher plants. It has to be said, however, whereas these authors found a notably greater species richness amongst higher plants in hay meadows than in other habitats, in our study this trend could only be suggested. In any case, this discordance is not surprising considering the lack of a general correlated pattern between butterfly and plant species richness (e.g., Kremen, 1992; Hawkins and Porter, 2003; Stefanescu et al., 2004). Most probably, the high abundance of butterflies in these hay meadows can be explained in terms of the high nectar supply (C. Stefanescu, unpublished data) and the abundance of key larval host plants (e.g., various Leguminosae used by Lycaenids) in comparison to woodland habitats and, to a lesser extent, grazed meadows.

Apart from differences in the conservation value of habitats, our study also revealed striking differences in some basic life-history attributes in the butterfly assemblages. For instance, it was clear that the butterflies of hay meadows and pastures tended to be smaller and have a poorer dispersal ability than those of woodland and alfalfa fields. In addition, relatively more butterflies overwintered as larvae in all types of grasslands, while there was a tendency for species to overwinter as pupae or adults in woodland. These differences can be accounted for, albeit only partially, by some basic features of the habitats, as suggested in the seminal works by Southwood (1962, 1977). Thus, the greater dispersal ability of butterflies in alfalfa fields as opposed to that of the other two grassland habitats can be explained in terms of their lower habitat permanence (these fields are harvested three or even more times per season). On the other hand, the greater dispersal ability of butterflies in woodland, which corresponds to a late successional and more stable and competitive habitat, contradicts the above argument. Instead, this and other traits are better explained by host-plant strategies, as recently suggested by Dennis et al. (2004). These authors linked the three-strategy system developed by Grime (1974) to explain plant strategies

(competitive, stress-tolerant, and ruderal) to butterfly biology, and found significant correlations between some butterfly biological traits and host-plant strategies. For example, they predicted an increase in wing surface-area, mobility, and adult overwintering in butterflies associated with woodlands, and the opposite in butterflies living in meadows, as indeed occurred in our study. They also predicted an increase in larval overwintering and conservation status in butterflies associated with meadows, again just as we found in our study. On the other hand, some other predictions failed, especially those relating host-plant specialization and voltinism to host-plant strategies. Although with our limited data it is not possible to fully evaluate the applicability of Dennis et al.'s predictions, we believe that the coincidences are encouraging and deserve further investigation with broader data sets.

5. Conclusion

The so-called *closes*, one of the most characteristic habitats in this Spanish Natural Park (AENP), were ranked first in the conservation evaluation of several habitat types using butterflies as a bioindicator taxon: the same result was obtained when higher plants were employed as the selected bioindicator taxon. Thus, these two findings highlight the importance for wildlife of these traditionally managed hay meadows. This fact, together with the alarming decrease in extension of the *closes* in the AENP and the rarity of this kind of habitat in the Mediterranean region, lead us to consider them as the most threatened and one of the most valued habitats in this protected area.

Paradoxically, the declaration of the area as a Natural Park has not prevented the loss of the *closes* and has even accelerated the process. Thus, it has been estimated that 80% of the *closes* have been lost over the last 50 years, and that at least 60% have disappeared since the area became legally protected in 1983 (Gesti et al., 2003). There are two main reasons to explain this apparent anomaly. Firstly, most of the protected land is in private hands (a common situation in many Spanish Natural Parks), which hinders proper management based on the application of wildlife conservation criteria. Secondly, the traditional management of grasslands (e.g., as hay meadows or pastures) is no longer profitable, which eventually leads to the abandoning of these practices in the absence of any effective financial support.

We believe that the future of this and other grassland habitats in the Mediterranean will ultimately depend on the existence of agri-environmental schemes such as those already operating in countries in northern Europe (e.g., Ovenden et al., 1998). If this does not occur, then these man-managed habitats together with their exceptionally rich wildlife will soon disappear as just another example of a general trend affecting the whole Mediterranean region (Bacaria et al., 1999; Blondel and Aronson, 1999).

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Appendix A

Description of the 46 transect sections together with the values for each vegetation category variable

Section label	Habitat description	Categorical habitat variables				
		Grassland cover	Cattle grazing	Woodland cover	Bramble cover	Arable field
Cort-1-00	Open woodland ride	0	0	1	1	0
Cort-2-88	Dry pasture	1	1	0	0	0
Cort-3-88	Dry pasture	1	1	0	0	0
Cort-4-00	Woodland ride	0	0	2	1	0
Cort-7-88	Track delimited by rice fields and riverine forest	0	0	1	1	1
Cort-9-00	Hay meadow also used for grazing	1	1	0	0	0
Cort-10-00	Woodland ride	1	0	1	1	0
Cort-11-00	Hay meadow also used for grazing	1	1	0	1	0
Cort-11-88	Maize field edge	0	0	1	1	1
Cort-12-00	Woodland-hay meadow ecotone	1	0	1	1	0
Cort-12-88	Maize field edge	0	0	1	1	1
Cort-13-00	Woodland-hay meadow ecotone	1	0	1	1	0
Cort-13-88	Maize field edge	0	0	1	1	1
Cort-14-00	Woodland ride	0	0	1	1	0
Cort-15-00	Sun-flower field edge	0	0	0	1	1
Mig-1-02	Hay meadow	1	0	0	0	0
Mig-2-02	Hay meadow	1	0	0	0	0
Mig-4-02	Woodland-hay meadow ecotone	1	0	2	1	0
Mig-5-02	Open woodland ride	1	0	2	1	0
Rub-1-88	Track delimited by helophytic vegetation	0	0	0	1	0
Rub-2-88	Track delimited by helophytic vegetation	0	0	0	1	0
Rub-4-88	Alfalfa field	1	0	0	1	0
Rub-7-88	Track delimited by helophytic vegetation	0	0	0	1	0
Rub-8-88	Alfalfa field	1	0	0	1	0
Rub-9-88	Hay meadow	1	0	0	1	0
Rub-10-88	Alfalfa field	1	0	0	1	0
Rub-11-88	Alfalfa field	1	0	0	1	0
Rub-12-88	Alfalfa field also used for grazing	1	1	0	1	0
Tec-1-97	Hay meadow	1	0	1	1	0
Tec-2-97	Hay meadow also used for grazing	1	0	0	1	0
Tec-3-97	Hay meadow also used for grazing	1	1	0	0	0
Tec-4-97	Woodland-pasture ecotone	1	0	1	0	0
Tec-5-97	Hay meadow	1	0	0	0	0
Tec-6-97	Woodland-pasture ecotone	1	1	1	0	0
Ull-4-96	Hay meadow also used for grazing	1	1	0	0	0
Ull-5-96	Hay meadow also used for grazing	1	1	1	1	0
Ull-6-96	Hay meadow also used for grazing	1	1	0	0	0
Ull-7-96	Hay meadow also used for grazing	1	1	0	0	0

(continued on next page)

Appendix A (continued)

Section label	Habitat description	Categorical habitat variables				
		Grassland cover	Cattle grazing	Woodland cover	Bramble cover	Arable field
Vil-1-89	Dry pasture	1	1	0	0	0
Vil-2-89	Hay meadow also used for grazing	1	1	0	0	0
Vil-4-89	Hay meadow also used for grazing	1	1	0	0	0
Vil-5-89	Hay meadow also used for grazing	1	1	0	0	0
Vil-7-89	Dry pasture	1	0	0	1	0
Vil-8-89	Hay meadow	1	0	0	0	0
Vil-10-89	Woodland ride	0	0	2	1	0
Vil-11-89	Woodland ride	0	0	2	1	0

Relative grassland cover (0: <30%; 1: >30%); cattle grazing (0: absence; 1: presence); relative woodland cover (0: absence; 1: 10–30%; 2: >30%); relative bramble cover (0: absence; 1: 10–30%; 2: >30%); arable fields at the sides of the recording route (0: absence; 1: presence).

Appendix B

Summary of the life-history attributes for the 47 butterfly species considered in this study

	Body size (wing length in mm)	Overwintering stage	Voltinism	Host-plant specialization	Dispersal ability	Rarity1 (regional scale)	Rarity2 (local scale)
<i>Carcharodus alceae</i>	14.5	2	3	2	2	0.02	0.04
<i>Carcharodus boeticus</i>	13.5	2	3	2	0	0.11	1.00
<i>Ochlodes venata</i>	15.5	2	2	2	1	0.03	0.02
<i>Pyrgus armoricanus</i>	13	2	2	1	1	0.05	0.11
<i>Pyrgus malvoides</i>	12	3	2	2	1	0.03	0.08
<i>Spialia sertorius</i>	12	2	2	1	0	0.03	0.33
<i>Thymelicus acteon</i>	12	2	1	2	1	0.02	0.08
<i>Aricia cramera</i>	12	2	3	2	1	0.02	0.06
<i>Cupido alcetas</i>	14.5	2	3	1	2	0.10	1.00
<i>Celastrina argiolus</i>	15	3	3	3	3	0.02	0.05
<i>Cacyreus marshalli</i>	11.5	5	3	2	2	0.05	1.00
<i>Cupido argiades</i>	12.5	2	3	2	2	0.11	0.25
<i>Lampides boeticus</i>	16.5	5	3	3	4	0.02	0.06
<i>Lycaena phlaeas</i>	13.5	2	3	2	2	0.02	0.04
<i>Leptotes pirithous</i>	12.5	5	3	3	4	0.02	0.04
<i>Plebejus argus</i>	13.5	2	3	3	0	0.07	0.05
<i>Polyommatus icarus</i>	16	2	3	2	2	0.02	0.02
<i>Satyrium w-album</i>	15.5	1	1	1	0	0.25	1.00
<i>Cynthia cardui</i>	28	5	3	3	4	0.02	0.03
<i>Inachis io</i>	28	4	3	1	3	0.05	0.08
<i>Issoria lathonia</i>	21		3	2	3	0.05	1.00
<i>Melitaea cinxia</i>	18	2	2	1	1	0.07	1.00
<i>Melitaea didyma</i>	21	2	2	2	2	0.04	0.14
<i>Melitaea phoebe</i>	22	2	2	2	2	0.03	0.50
<i>Polygonia c-album</i>	23	4	3	3	3	0.04	0.06
<i>Vanessa atalanta</i>	29.5	2	3	3	4	0.02	0.05
<i>Papilio machaon</i>	35	3	3	3	4	0.02	0.05
<i>Anthocharis cardamines</i>	21.5	3	1	2	2	0.04	1.00
<i>Colias crocea</i>	25	2	3	2	4	0.02	0.02
<i>Euchloe crameri</i>	22	3	2	2	1	0.02	0.08
<i>Gonepteryx cleopatra</i>	27.5	4	2	1	3	0.02	0.20

Appendix B (continued)

	Body size (wing length in mm)	Overwintering stage	Voltinism	Host-plant specialization	Dispersal ability	Rarity 1 (regional scale)	Rarity 2 (local scale)
<i>Gonepteryx rhamni</i>	28	4	1	1	3	0.03	0.25
<i>Leptidea sinapis</i>	21.5	3	3	2	1	0.02	0.17
<i>Pieris brassicae</i>	30.5	3	3	2	4	0.02	0.02
<i>Pontia daplidice</i>	22.5	3	3	3	4	0.02	0.17
<i>Pieris mannii</i>	21.5	3	3	2	1	0.07	0.50
<i>Pieris napi</i>	25	3	3	2	3	0.03	0.02
<i>Pieris rapae</i>	25	3	3	2	4	0.02	0.02
<i>Brintesia circe</i>	34.5	2	1	2	1	0.03	0.17
<i>Coenonympha pamphilus</i>	15	2	3	2	1	0.04	0.03
<i>Lasiommata megera</i>	22	2	3	2	2	0.02	0.03
<i>Maniola jurtina</i>	25.5	2	1	2	2	0.02	0.04
<i>Melanargia lachesis</i>	26.5	2	1	2	1	0.03	0.03
<i>Melanargia occitanica</i>	26.5	2	1	1	0	0.06	0.50
<i>Pararge aegeria</i>	20.5	2.5	3	2	2	0.02	0.02
<i>Pyronia cecilia</i>	15.5	2	1	1	1	0.02	0.07
<i>Pyronia tithonus</i>	18	2	1	2	1	0.04	0.04

Overwintering stage: 1 – egg, 2 – larva; 3 – pupa; 4 – adult; 5 – no overwintering and/or migratory species (no category was assigned to *Issoria lathonia*, which overwinters as larva, pupa or adult; *Pararge aegeria* overwinters as larva or pupa). Voltinism: 1 – univoltine, 2 – bivoltine; 3 – multivoltine. Host-plant specialization: 1 – monophagous, 2 – oligophagous; 3 – polyphagous. Dispersal ability: 0 – forming closed populations, very little dispersal; 1 – closed populations, more frequent dispersal, 2 – closed populations, common dispersal, 3 – open populations, non-directional dispersal, 4 – open populations, directional migration. Rarity at regional scale is defined as the inverse of the number of CBMS sites in which a species occurred (from a total of 54). Rarity at the local scale is defined as the inverse of the number of sections in the AENP in which a species occurred (from a total of 46). Data from Higgins and Riley (1984), Pollard and Eversham (1995), Dennis and Shreeve (1996), Tolman and Lewington (1997) and personal observations.

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