Ecological trends in endemic Mediterranean butterflies

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Abstract

In our knowledge of Palaearctic insects there is a research gap concerning ecological and/or evolutionary features associated with Mediterranean conditions in general and with Mediterranean endemicity in particular. This subject is here addressed from the case study of one of the better known insect groups: butterflies (Lepidoptera Rhopalocera). Life-history traits of 23 Mediterranean endemic butterfly species (excluding mountain and island endemics), each one belonging to a different genus, are here compared with those of non-endemic species of the same genera with a widespread distribution outside as well as inside the Mediterranean Region. Endemic butterflies tend to have relatively fewer generations per year, earlier adult emergence, shorter flying period and a more restricted reported diet as caterpillars, with less diversity of host plant genera and a larger use of exclusive genera. No differences in wintering stage were found. The shorter flying period may be an effect of the higher altitude of the habitat of some endemics compared with that of their widespread counterparts. Evidence is presented supporting the hypothesis that the earlier start of the flying period is due to adaptive evolution in univoltine-bivoltine Mediterranean endemics in order to avoid the deleterious effects of summer drought in caterpillars. The origin of all these differences is discussed from the scope of metapopulation genetics.

Key words: Rhopalocera, phenology, voltinism, adaptation, summer drought.

Introduction

The Mediterranean Region stands out as one of the world's 25 biodiversity hotspots, which is mainly due to the abundance of endemics in many organism groups (Myers *et al*., 2000). This characteristic of the basin is in a great part the outcome of the geological and climatic history of the Mediterranean during the Cenozoic and especially the Pliocene and Pleistocene, when these territories became a crossroad of taxa from different continents as well as an important focus of speciation (Blondel and Aronson, 1999; Thompson, 2005; Hewitt, 2000). The characteristic ecology of Mediterranean plant endemics has recently been examined by Lavergne *et al*. (2004) in a work that has revealed that endemics are a coherent group unified by common ecological features (see also Thompson, 2005 and references therein). There are many other organism groups whose Mediterranean endemics remain to be examined from such a perspective; for example, insects. This is the case in spite of the extraordinary species richness of the Mediterranean entomofauna, which is estimated to represent approximately 75% of total European insect biodiversity and probably contains 150,000 species - may be 30% of them still neither described nor named (Baletto and Casale, 1991). Many of the Mediterranean insect species are endemics, especially in mountain ranges, where endemics could account for even 15-20% of total species richness (Blondel and Aronson, 1999).

The aim of the present work is to improve our understanding of the ecology and evolutionary history of Mediterranean endemic insects by making a case study of one prominent group: butterflies (Lepidoptera Rhopalocera). Butterflies are adequate subjects since they are very probably the best known insects of the Mediterranean Region: centuries of attention from entomologists and naturalists in general have provided a huge amount of biological, ecological and distributional data which

has no counterpart with any other group of Palaearctic insects (Tolman and Lewington, 2002).

European butterflies, Mediterranean endemics included, have clear Palaearctic (boreal) affinities, with very few Palaeotropical elements (Casevitz-Weulersse, 1992). In Southern Europe, the onset of Mediterranean climate, about 3.2 million years ago, brought a biologically hostile summer drought for the first time in the Cenozoic (see Thompson, 2005 and also Blondel and Aronson, 1999 for review), which probably affected the evolution of most organisms as it is well known in plants (Thompson, 2005). Later, the evolutionary history of butterflies and many other organisms in the Mediterranean Region was drastically influenced by geographic isolation due to Pleistocene climate changes (see Blondel and Aronson, 1999; Hewitt, 2000). This is suggested in butterflies by biogeographical patterns of biodiversity, with peaks around the Alps and most endemics located south of the mountain axis extending from the Cantabric Range to the Carpaths (Dennis, 1993). These Northern ranges of the Mediterranean basin probably contained many faunistic refuges for boreal butterflies during interglacial periods, and the relatively warm lands of Southern Europe could have contributed to maintain butterfly diversity in the basin as refuges during glacial epochs (Dennis *et al*., 1991). In this scheme, geographic isolation by mountain barriers appears as a driving force of butterfly diversity in the Mediterranean, as exemplified by the abundant mountain endemics of *Erebia* and *Agrodiaetus* and by the distribution of major taxa, which roughly coincides with natural geographical divisions (Dennis *et al*., 1995).

In spite of the biological relevance of the summer drought that delimits the Mediterranean Region (Emberger, 1930; Quézel, 1985), there are very few works that deal directly with the evolutionary consequences of Mediterranean climate in insects (for example, Lumaret, 1995) and no one is aimed towards the search of general

patterns in Mediterranean endemics. Tolman and Lewington (2002) wrote that Southern European species tend to start flying later in the year, but he does not cite any reference. The same idea is supported by the conclusions of García-Barros (1989): in a comparative study on the biology of two Satyrine butterflies in the Iberian Peninsula, the typically Mediterranean species *Neohipparchia (Hipparchia) statilinus* (Hufnagel) seems to start its flying period later than the more widely distributed and more boreal *Hipparchia semele* (L.). In this last species, García-Barros (1988) discovered a possible adaptation to summer drought, namely a delayed ovarian maturation in Spain. This could probably result in a reduced voltinism, in accordance with the general trend observed in butterflies as climate seasonality increases (Dennis, 1993). Unfortunately, there is insufficient information for a deeper evaluation of the possible ecological patterns that could be hypothesized for Mediterranean endemic butterflies.

Methods

In the search of differences between Mediterranean endemic butterflies and their close non-endemic relatives, the kind of characteristics available to analyze is limited by our knowledge of European butterflies. In spite of being relatively well known insects, there are still not many data about uncommon species such as a number of Mediterranean endemics. With this limitation on mind, in the present work the following variables are taken into account: (1) voltinism (preferably referred to the Mediterranean Region in non-endemic species, and excluding data from mountain habitats), (2) earliest reported month of flying adults, (3) latest reported month of flying adults, (4) the difference of both (flying period duration), (5) wintering stage (egg-caterpillar-pupa-adult), and (6) number of reported genera of host plants. The search of differences between endemic *vs.* non-endemic butterflies was carried on by OLS linear regression: data points with coordinates x = non-endemic species, y = endemic species of the same genera were plotted for each variable and the slope tested for significant differences with unity. This approach was adopted by Lavergne *et al*. (2004) in the same manner to study Mediterranean endemic plants, and it is considered by Felsenstein (1985) as an elegantly simple method to correct possible phylogenetic inertia in a data set; furthermore it is usually employed in plant studies (Thompson, 2005).

   Mountain and island endemics were not included due to their unrepresentative evolutionary ecology, since the latter are usually subjected to strong ecological drift that could easily mask evolutionary pressures in common with continental endemics, and the former live in an environment where the basic characteristics of the Mediterranean climate are diminished (lower mean temperature and mild to absent summer drought, see Thompson, 2005). In fact altitude is so important in butterfly biology that it was homogenised in the species selection by taking only those species with a reported minimum altitude below 700 m a.s.l., that is, below the Supramediter-

ranean bioclimatic level in most of the region, according to Quézel and Médail (2003). Anyway, reported minimum and maximum altitude were analyzed to search for any possible bias in the data set.

   The following criteria, ordered by importance, guided the process of species selection: (1) the genus contains a Mediterranean endemic taxon which is neither mountain nor insular, and also a widely distributed species; (2) the non-endemic species occupies the widest possible area inside as well as outside the Mediterranean Region; (3) the widely distributed species is the most similar to its corresponding endemic species in altitudinal range and both have been cited below 700 m a.s.l.. The aim of these criteria is to homogenise potentially confounding ecological factors that could lead to detect unrealistic evolutionary trends, *i.e.* not really caused by the only fact of being an endemic butterfly species in the Mediterranean Region. Species selection and data compilation was done using Tolman and Lewington (2002), which unifies data from more than a hundred original works and reviews on butterflies of Europe, North Africa and the Near East. Data about each non-endemic species were taken, when possible, from a clearly Mediterranean subspecies, or from the Mediterranean range of the species, or for Southern Europe, or for the Mediterranean North of Africa, in order to increase ecological homogenization with Mediterranean endemics. The methodological outcome is that Mediterranean endemics will be compared with close relatives that are non-endemics but as Mediterranean as possible, thus isolating Mediterranean endemicity as the main factor to explain any observed difference. Details about the selection process appear in table 1.

   The statistical distribution of each variable was examined for each species group (endemics *vs.* non-endemics), and significant differences between endemics and non-endemics were searched as previously described using Prism 5 for Windows. For each variable, significant differences were considered only when the diagonal line $x = y$ was not contained in the confidence band of the regression line. As this band was set at a confidence threshold of 99%, the significance level of the positive results is 0.01. This high α is preferred since the number of selected genera is relatively small and data error is unknown, with the result that the data set is potentially subjected to random noise. Finally, possible correlations between detected patterns were searched.

Results

Selection of species

   A sample of 23 species pairs were selected among all the butterflies of the Mediterranean Region (table 1). In this selection there is one genus of Papilionidae, 3 genera of Pieridae, 9 of Lycaenidae, 7 of Nymphalidae (4 of Satyrines among them) and 3 of Hesperiidae, which seems a reasonably equilibrate sample of butterfly biodiversity in the basin. It is noteworthy the boreal character of this selection, with the exceptions of the genera *Zerynthia* and *Muschampia*, whose species distribution is mainly South of the basin.

Table 1. Data set and comments on species selection. For each genus, the first species in the table is the non-endemic one, and the second is the Mediterranean endemic. A voltinism of 1.5, for example, means that the taxon has been cited as univoltine and bivoltine in the area here considered. HP = host plant, P = pupa, L = larva, E = egg.

Species	Voltinism	Earliest flying month	Latest flying month	Flying period (months)	Wintering stage	N° of HP genera	N° of HP genera in common	Minimum altitude (m a.s.l.)	Maximum altitude (m a.s.l.)	Notes
PAPILIONIDAE										
Zerynthia polyxena (Denis et Schiffermuller)	1	3	7	4	P	1		0	1700	Extended East of the Mediterranean Region
Zerynthia rumina (L.)	1.5	3	10	7	P	1	1	0	1500	*Zerynthia cerisy* ruled out since it only reach 1100 m in Europe
PIERIDAE										
Artogeia napi (L.)	3.5	3	10	7	P	10		300	1200	Voltinism and phenology for Southern Europe; altitude for the typically Mediterranean balcanic subspecies (it is better with the aim of comparing with *A. balcana*)
Artogeia balcana Lorkovic	2.5	4	10	6	P	?	?	300	900	The only posible endemic species of this genus in spite of the lack of data of HP
Euchloe ausonia (Hubner)	2	3	7	4	P	7		0	1600	Extended towards the Tibet
Euchloe tagis (Hubner)	1	2	5	3	P	1	1	300	2400	Data for North Africa and Europe
Anthocharis cardamines (L.)	1	3	6	3	P	6		0	2100	Clearly the most extended in the genus
Anthocharis belia euphenoides Staudinger	1	3	6	3	P	1	1	0	1800	An Iberian subspecies; the North African subspecies is ruled out since it enters the Sahara desert, outside the Mediterranean Region
LYCAENIDAE										
Satyrium w-album (Knock)	1	6	7	1	E	1		100	1300	The most widespread and also the most similar in minimum altitude to *S. esculi*, which is the only possible Mediterranean endemism in this genus
Satyrium esculi (Hubner)	1	5	8	3	?	1	0	500	2400	The only endemic Mediterranean species in this genus
Callophrys rubi (L.)	1	3	7	4	P	15		0	2300	Clearly the only one
Callophrys avis Chapman	1	3	6	3	P	4	1	100	1700	The only possible endemism
Lycaena phlaeas (L.)	3	2	10	8	L	1		0	2400	Voltinism and months for Southern Europe and North Africa
Lycaena ottomanus (Lefebvre)	2	4	8	4	?	1	1	50	1500	*Lycaena candens* (endemism of the Eastern Mediterranean) is ruled out since its altitudinal range is quite different: 900 to 2000 m a.s.l.
Cupido minimus (Fuessly)	1.5	4	9	5	L	1		50	2800	-
Cupido lorquinii (Herrich-Schaffer)	1	4	6	2	P	1	0	100	2700	*Cupido carswelli,* from the Sierra de Cazorla (Spain), is ruled out due to considerable differences in minimum altitude (850 m a.s.l.)
Glaucopsyche alexis (Poda)	1	4	7	3	P	15		25	1500	Clearly the best non-endemic Mediterranean species
Glaucopsyche melanops (Boisduval)	1	2	6	4	?	3	1	100	1100	Months and altitude for the Mediterranean subspecies *melanops* and *algirica*
Pseudophilotes vicrama (Moore)	2	4	8	4	P	2		0	1900	Clearly the most widespread North of the Mediterranean Region
Pseudophilotes panoptes (Hubner)	2	3	8	5	?	2	2	600	1900	The only possible species. *P. abencerragus* is also in Arabia, outside the Mediterranean Region
Plebejus argus hypochionus (Rambur)	1	6	7	1	?	2		600	2400	The best subspecies, from Andalousia; *P. idas* is worse
Plebejus allardi (Oberthur)	1	4	5	1	?	1	0	10	1500	Exclusively North African, generally cited above 480 m a.s.l.
Agrodiaetus amanda amanda Schneider	1	5	7	2	L	1		100	2000	The most widespread species of Europe in the genus. The North African subspecies *abdelaziz* is ruled out since its mountain afficinies (approx. 1500 m a.s.l.)
Agrodiaetus admetus (Esper)	1	6	7	1	L	1	0	50	1500	The only non-mountain endemism
Lysandra bellargus (Rottemburg)	2	5	9	4	L	2		100	2000	More Mediterranean than *L. coridon*. Possibly univoltine in Greece (not confirmed)
Lysandra hispana (Herrich-Schaffer)	2	4	10	6	?	2	1	400	1000	The closest match in terms of minimum altitude (*L. philippi* 600 m a.s.l., *L. albicans* 500 m a.s.l.)
NYMPHALIDAE										
Melitaea phoebe (Denis et Schiffermuller)	2	4	9	5	L	1		0	1900	More Mediterranean area than *M. cinxia*
Melitaea aetherie (Hubner)	1.5	4	9	5	L	2	1	25	1800	The only possible endemism.
Mellicta athalia celadussa (Fruhstorfer)	2	5	8	3	L	5		0	2600	Iberian subspecies. Univoltine above the subalpine level, which is here not considered
Mellicta deione (Geyer)	2	4	9	5	L	5	2	100	1800	Data for all subspecies since all are Mediterranean. More adequate than *M.parthenoides* in terms of minimum altitude (400 m a.s.l.). Univoltinism in Argelia is doubtful and therefore not included
Euphydryas aurinia beckeri (Herrich-Schaffer)	1	4	6	2	L	3		10	1800	The most Mediterranean among non-mountain subspecies
Euphydryas desfontainii (Godart)	1	4	6	2	L	5	2	50	2800	Subspecies *desfontainii* and *baetica* (N. Africa - Iberian Peninsula)

(Continued)

(Table 1 Continued)

Species	Voltinism	Earliest flying month	Latest flying month	Flying period (months)	Wintering stage	Nº of HP genera	Nº of HP genera in common	Minimum altitude (m a.s.l.)	Maximum altitude (m a.s.l.)	Notes
Melanargia galathea (L.)	1	5	7	2	L	10		0	2600	Clearly the most adequate. Subspecies *galathea* and *lucasi* (N. Africa) are included, since they are Mediterranean *pro parte* September has not been recorded as the latest month since it has been observed only in high altitudes in *lucasi*
Melanargia lachesis (Hubner)	1	6	8	2	L	6	5	0	1600	*M. arge* presents higher minimum altitude (350 m as.s.l.). *M. ines* has more African affinities (Libia). *M. occitanica* could be a good alternative to this species
Hipparchia semele semele (L.)	1	6	9	3	?	16		0	2000	The most Mediterranean among widespread species in the genus. Insular subspecies *leighebi* not included
Hipparchia aristaeus (Bonelli)	1	5	8	3	?	1	0	50	1800	Data for all subspecies excluding insular ones from the Aegean. Insular subspecies *blachieri* (Sicilia) and *maderensis* also ruled out for the same reason. The N. African subspecies *algirica* has not been included in voltinism data since this is uncertain. *H. mersina* is ruled out due to the lack of HP data
Pyronia tithonus (L.)	1	7	9	2	L	9		0	1700	Clearly the most widespread among Mediterranean species
Pyronia bathseba (F.)	1	4	7	3	L	2	1	300	1700	*P. janiroides* and *P. cecilia* don't show a distribution as widely Mediterranean as this species
Coenonympha pamphilus (L.)	4	2	11	9	L	6		0	2700	The most Mediterranean among widespread boreal species
Coenonympha dorus dorus (Esper)	1	6	8	2	?	5	1	100	1700	A subspecies from the Iberian Peninsula and Southern France. N. African subspecies are ruled out due to excessively high minimum altitude (*fettigii* 800 m a.s.l., *austati* 600 m a.s.l.). There aren't data of HP for *C. arcanioides* (N. Africa)
HESPERIIDAE										
Pyrgus malvae (L.)	1.5	4	8	4	P	4		0	1900	-
Pyrgus onopordi (Rambur)	2.5	4	10	6	?	1	0	0	2800	-
Muschampia tessellum (Hubner)	1	5	8	3	L	1		0	1100	The most widespread, it extends towards the Middle East
Muschampia proto (Ochsenheimer)	1	4	10	6	L	1	1	0	1700	*M. leuzeae* and *M. mohammed* are mountain endemics
Carcharodus alceae (Esper)	4	4	10	6	L	2		0	2000	-
Carcharodus boeticus (Rambur)	3	5	9	4	L	2	0	500	1600	Voltinism from Southern Spain

Voltinism

There is a clear trend towards having fewer generations per year in endemics, but obviously only if the corresponding non-endemic species is at least bivoltine (figure 1A). This includes the genera *Artogeia* and *Euchloe* (Pieridae), *Lycaena* (Lycaneidae), *Melitaea* and *Coenonympha* (Nymphalidae, the last a Satyrine) and *Carcharodus* (Hesperiidae); all of them fall below the $x = y$ line right of its cut with the confidence band thus contributing to create this general pattern.

Phenology and wintering stage

In figure 1B it is observed a difference in the earliest reported emergence month, since the line $x = y$ is above the confidence band right of approximately May. However, the border of the band is close to the line, so, from this basis, it can only be suggested that endemics tend to start its flying period earlier than their non-endemic relatives when these begin to fly from May onwards. This is the case of the genera *Lysandra, Plebejus* and *Satyrium* (Lycaenidae), *Mellicta, Pyronia* and *Hipparchia* (Nymphalidae, the last two being Satyrines), and *Muschampia* (Hesperiidae). As will be shown later in this work, there is important additional evidence that supports this difference is real and plenty of biological meaning.

No significant differences were observed in the plot of later reported flying month (figure 1C), but in figure 1D there is a pattern: endemics tend to have a shorter flying period provided that it lasts more than 6 months in their non-endemic relatives. The genera involved in this case are *Artoegia* (Pieridae), *Lycaena* (Lycaneidae), *Coenonympha* (Nymphalidae, Satirinae) and *Carcharodus* (Hesperiidae). No differences in wintering stage were detected: as shown in table 1, there is not a single species pair with internal differences in this variable.

Diversity of host plants

The clearest trend appears in this variable (figure 1E). Endemics are associated with fewer genera of food plants provided that their non-endemic relatives use at least 3 genera. This pattern is also the most extended: it is observed in the pairs *Anthocharis, Artogeia* and *Euchloe* (Pieridae), *Callophrys* and *Glaucopsyche* (Lycaenidae), *Mellicta, Coenonympha, Hipparchia, Melanargia* and *Pyronia* (all of them Satyrine Nymphalidae except the first one). However, since these have been obtained only from reported and confirmed host plants, some caution is recommended because perhaps there are additional host plant genera that have not been notified, especially in endemics. In spite of this, a further proof of real dietary change in endemics appears in figure 1F, which shows a significant trend towards the use of distinct genera of host plants in endemics (*i.e.* genera not reported for the corresponding non-endemic species). The slope of the regression line is 0.52 ± 0.10,
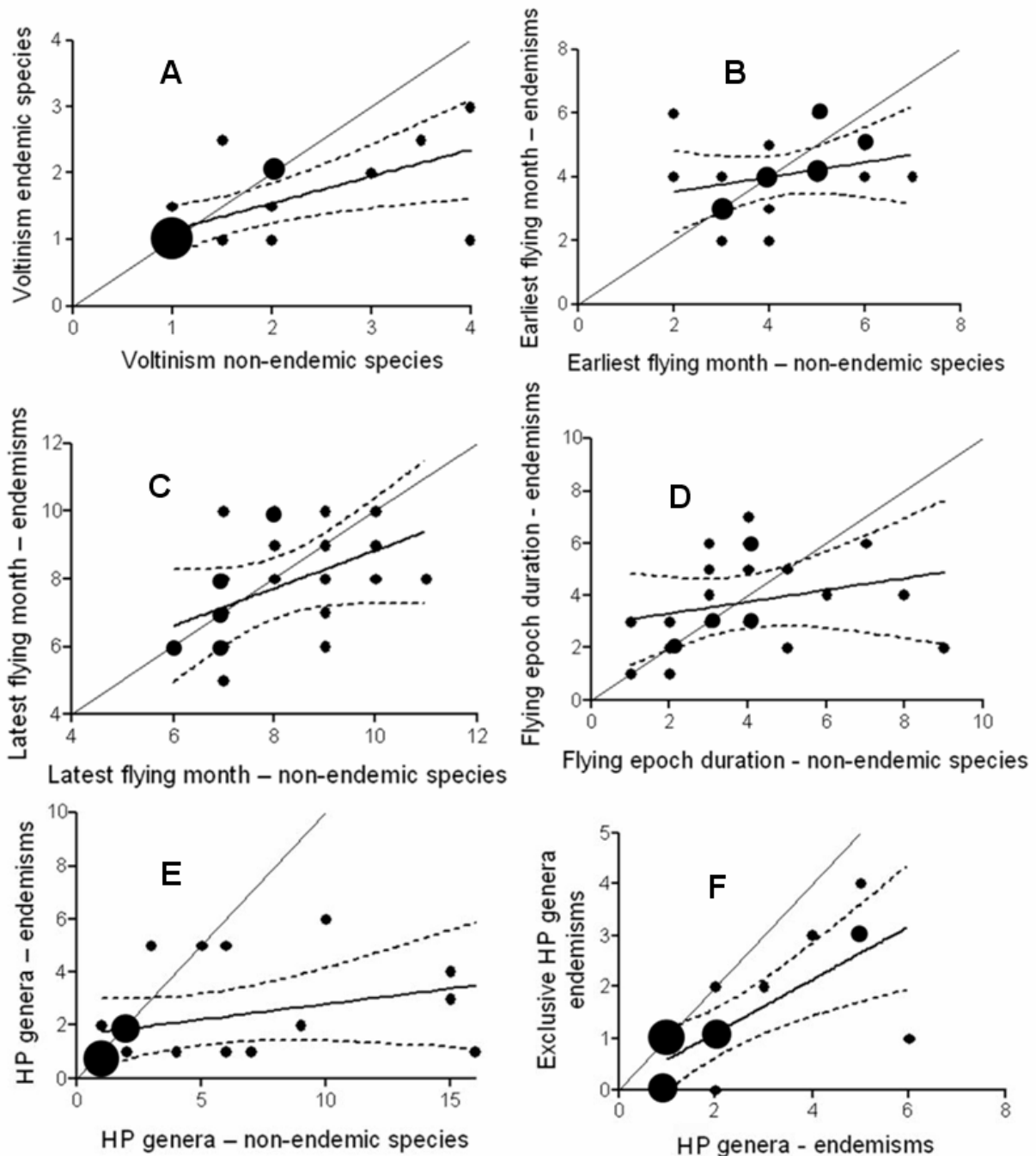
164

Figure 1. Plots of the variables under scrutiny: each point represents one genus, with the *x* coordinate being the value of the non-endemic species and the *y* coordinate being that of the endemic one. Dotted lines are 99% confidence bands of the OLS regression. The line $x=y$ is shown as a reference. HP = host plant.

so approximately half of the food plant genera reported for endemics have not been reported in their non-endemics counterparts. The only exception occurs when the non-endemic species only feeds on one genus: then the endemic species tends to use the same one. Leaving this exception apart, in figure 1F the pattern is quite linear, that is, the more plant genera eats the endemic species, the more distinct genera it uses compared to its close relative. Such a pattern suggests that exclusive host plant genera in endemics are a sub-sample of their total amount of food plant genera. All these results

probably indicate that, compared to non-endemic close relatives, Mediterranean endemic butterflies have a more restricted diet and feed on a substantially different amount of plant genera.

Possible altitudinal bias

There are no significant differences in minimum cited altitude (figure 2A), which indicates this factor has been adequately homogenised. However, the maximum altitude cited seems to be higher for endemic species when that of their non-endemic relative is below 1,600 m a.s.l.,
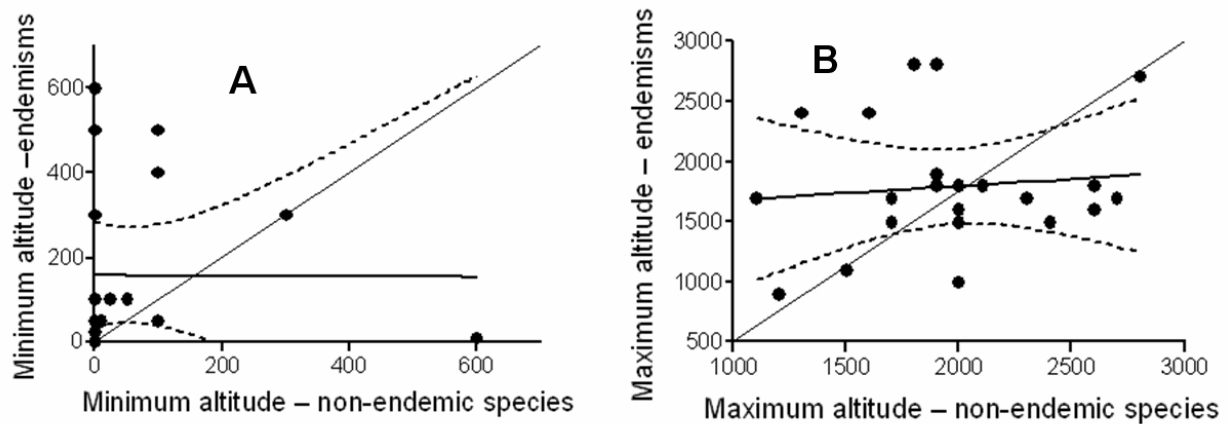
165

Figure 2. Plots of altitude of non-endemic species (*x* axis) *vs.* endemic species (*y* axis). Dotted lines are 99% confidence bands of the OLS regression. The line *x=y* is shown as a reference.

and lower when it is above 2,500 m (figure 2B). It is a curious pattern that could simply result from two geographical facts: (1) that the Mediterranean Region is plenty of medium-sized mountains, and (2) that its mountain ranges are relatively small compared with some mountains outside the limits of the basin, such as the Alps. However, even if there is a biological basis in this difference, it does not affect the conclusions of this work since mountain endemics, mountain subspecies and even data from mountains have been excluded (see table 1).

Correlations of results

A summary of the clearest trends detected appear in table 2. A total of 17 among the 23 genera show at least one trend. The six genera without any trend are *Zerynthia* (Papilionidae), *Agrodiaetus*, *Cupido*, *Pseudophilotes* (Lycaenidae), *Euphydryas* (Nymphalidae) and *Pyrgus* (Hesperiidae).

The most common pattern is the restricted diet, which does not have a significant correlation with any other

one (see table 3). Earlier emergence and shorter flying period show a significant correlation with one of the strongest trends, the reduced voltinism (p-value < 0.01 and < 0.001 respectively). This strongly suggests these three patterns are linked by some kind of biological mechanism. In this sense it is striking that not a single endemic species with earlier emergence has reduced voltinism (see table 1).

On the light of these results, two groups of endemic butterflies can be defined within those that display some trend: a) genera with reduced voltinism, and b) genera with earlier emergence. In the first group, voltinism in both endemic and non-endemic species tends to be higher than in the second group (mean voltinism: 2.46 ± 1.05 *vs.* 1.29 ± 0.47). In addition, when the monthly distribution of species richness (adults) is analyzed, in the first group there is a lack of endemics in early spring and early autumn (figure 3A), which helps to explain the correlation of reduced voltinism with shorter flying period. In the second group the pattern is the opposite,

Table 2. Summary of trends detected in endemic *vs.* non-endemic butterflies of the Mediterranean Region.

Ecological trends in endemic Mediterranean butterflies *vs.* non-endemic relatives (NER)		
Variable	Difference in endemics	Comments
Voltinism	Lower	
Earliest reported emergence month	Earlier	If that of NER > May
Duration of the flying period	Decreased	If that of NER > 6 months
Nº of genera of host plants	Restricted	
Nº of exclusive genera of host plants	About one half of total genera	

Table 3. Coefficients of correlation of the main trends detected in endemic butterflies. Numbers in brackets are non-directional p-values in the t-test of correlation significance. "Voltinism" refers to the trend towards a reduced number of broods, "Emergence" means earlier emergence month, "Flight period" refers to the shorter flying period and "Diet breadth" indicates a more restricted diet in plant genera.

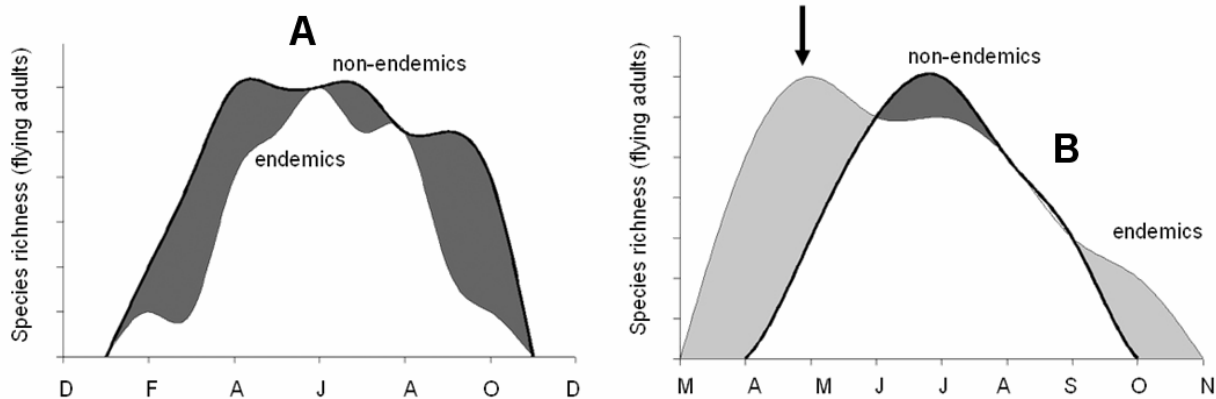|	Emergence	Flying period	Diet breadth
Voltinism	−0.62 (0.008)	0.75 (0.0005)	−0.13 (0.62)
Emergence		−0.46 (0.06)	−0.27 (0.29)
Flying period			−0.10 (0.70)

Figure 3. Species diversity of flying adults reported along the year in the group of genera whose endemics are characterized by reduced voltinism (A) and that whose endemic species show an forwarded emergence month (B). In this last plot it is remarkable the deviation of endemics towards spring months (arrow).

with more endemics in these epochs but less on July and a clear peak in spring, whereas non-endemic species reach their maximum in summer (figure 3B). These observations immediately suggest a negative influence of summer drought in this second group.

If we compare the flying period of each endemic with that of its non-endemic counterpart and we count the months where the non-endemic species flies but adults of the corresponding endemic taxon have not been observed, five cases will be registered in the second group and they appear only in summer months, from June to September. On June, *Plebejus argus hypochionus* (Rambur) flies but there are no citations of the endemic *Plebejus allardi* (Oberthur); on July the case is the same in this genera; on August this occurs in *Pyronia* and on September in *Pyronia* and *Hipparchia*. The same procedure reveals the pattern previously described for the first group: on February only the non-endemic species of *Coenonympha* and *Lycaena* have been cited as adults; on March the same is true in both genera and *Artogeia*, on April in *Coenonympha* and *Carcharodus*, on May only in *Coenonympha*, on July in *Lycaena* and *Coenonympha*, on October in both genera and *Carcharodus*, and on November in *Coenonympha* again. The scarcity of cases in summer months is remarkable in this group, which does not suggest any effect of summer drought, in contrast with the second group.
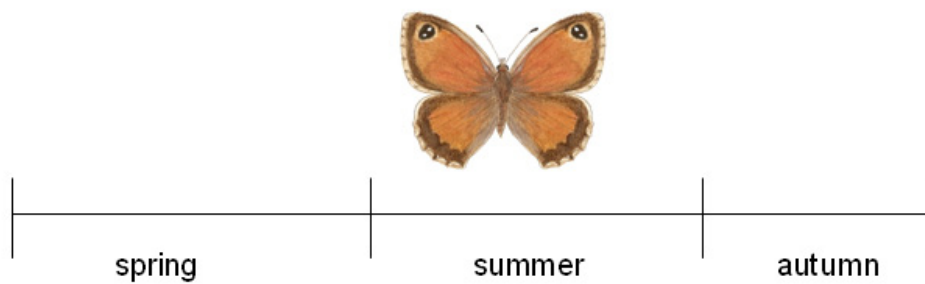
All these observations, as long as these data goes, can be interpreted from the scope that evolution of phenology in endemic Mediterranean butterflies strongly depends on the characteristic voltinism of ancestors. Boreal lineages with low voltinism – only 1 or 2 reproductive rounds –, which usually fly during summer months in the Palaearctic, would have a tremendous disadvantage if they loose any reproductive round due to the deleterious effects of Mediterranean summer drought. The endemics they have originated in the region seem to avoid this problem by means of an earlier emergence that could save the caterpillar from damages at the beginning of the hostile summer (figure 4). As will be discussed, natural selection appears as the most obvious mechanism for this phenological change.

Discussion

The trend towards reduced voltinism is not surprising if we take into account that the Mediterranean climate has higher seasonality than Atlantic-Eurosiberian ones. Higher seasonality, mainly due to summer drought, has been recognized as a cause of reduced voltinism due to the lower quality of the host plant caused by water stress (Dennis, 1993). This is supported by a number of observations; for example, in the Lycaenid *Cupido minimus* (Fuessly) it has been noticed that water stress in the host plant could even impede the second generation, a phenomenon that is also probably occurring in the Iberian endemic *Cupido carswellii* Stempffer (see Tolman and Lewington, 2002). On the other hand, the relatively soft and permeable cuticle of caterpillars probably makes them vulnerable to dangerous water losses due to the high temperatures and drought of the Mediterranean summer.

The inverse association between reduced voltinism and earlier emergence month seems explainable from an adaptationist perspective: the loss of one reproductive round is a minor problem for multivoltine species compared to univoltine or bivoltine ones, where it could imply the practical disappearance of the species in a habitat. Natural selection would therefore be expected to operate strongly in this last group in order to avoid the deleterious effects of summer drought. Thus it is easy to understand that univoltine-bivoltine endemic butterflies show an earlier emergence which could improve the survival options of caterpillars. In fact an avoidance of dry months has been observed in at least another group of Mediterranean insects, namely "dweller" dung beetles, which concentrate their activity on the relatively cool and wet months of early spring and autumn, when dung remains moist and therefore adequate for their life cycle (Lumaret, 1995). The idea that univoltine-bivoltine butterflies are intrinsically more prone to develop adaptations against summer drought fits with the finding of García-Barros (1988) that the univoltine butterfly *H. semele* presents delayed maturation of ovaries in the Iberian Peninsula, which was interpreted as an

167

A Boreal-Mediterranean species

spring | summer | autumn

B Endemic Mediterranean species

earlier emergence
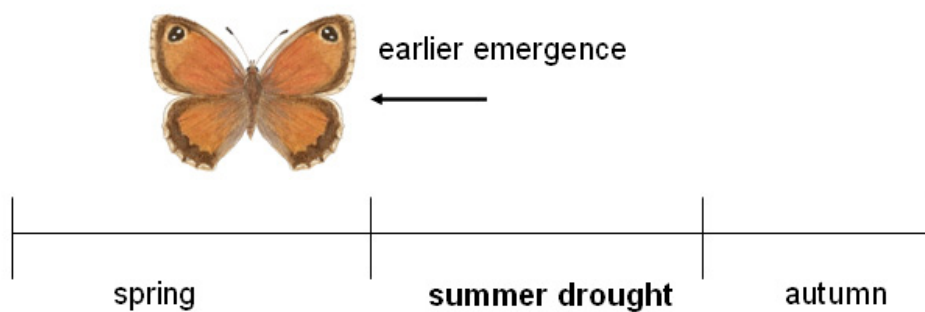
spring | **summer drought** | autumn

Figure 4. Diagram representing the trend towards an earlier emergence month in univoltine-bivoltine Mediterranean endemic butterflies, compared with their non-endemic counterparts of wide distribution of the same genera. This is probably to prevent the caterpillar from the deleterious effects of summer drought. A butterfly of the genus *Pyronia* is here shown (original drawing by the author).

adaptive feature in this sense. This last example suggests why endemics with earlier emergence also fly at the beginning of autumn: in this epoch, summer drought is over and caterpillars would be able to find adequate food during some still relatively warm months.

Against this view it can be argued that an earlier emergence is not the proof that the caterpillar is not exposed to summer drought. However, this criticism does not reveal serious problems: non-endemic species in this group emerge on May (3 species), June (3 species) and July (1 species), whereas their corresponding endemics emerge on April (5 species) and May (2 species). If we consider that the duration of the pupal phase is usually between 10 days and one month (García-Barros, personal communication), and that summer drought could start as early as on mid May in some years, then it is difficult to deny that caterpillars of these endemics are exactly avoiding the hostile summer season. In spite of this, it is true that all these results do not proof directly that the earlier emergence month is an adaptation to summer drought in these butterflies, since a direct link between fitness and emergence month has not been reported here. However, the most parsimonious and unifying explanation of all these facts is natural selection exerted by the Mediterranean climate on the caterpillar stage.

Interestingly, the forwarded emergence month suggests a possible way of speciation in Mediterranean butterflies. Early emerged adults would have a higher probability of copulate among them, thus possibly reinforcing any genetic basis of the forwarded emergence and thus likely initiating with this process an event of sympatric isolation. This idea adds another plausible possibility to the mainstream scheme of speciation by allopatric isolation by Pleistocene events in Mediterranean insects (see Blondel and Aronson, 1999).

The deleterious effect of winter appears as a first explanation for the relative lack of endemic butterflies with reduced voltinism in early spring and late autumn. But, being Mediterranean winters in general not as cold as those of boreal regions, the issue remains rather obscure. It can be hypothesized that the abundance of hills and small mountain ranges in the Mediterranean makes winter harder than one must expect on the basis of latitude in the habitat of many endemic butterflies. That is, an altitude difference rather than a biological one could be the answer. Mean minimum altitude is 212 ± 185 for these endemics and 50 ± 122 for their widespread counterparts, which indirectly supports this idea. Further research would be required to clarify this issue.

One might argue that the dietary specialization noticed in endemics could be the consequence of their restricted distribution compared to non-endemics. However, I considered only plant genera, and genera are inherently much more constant than plant species between areas of despair size. Even a few km² of Mediterranean vegetation usually have some hundredths of genera (*e.g.* more

than 100 genera in a patch of only 0.25 km^2, personal observation), and a larger patch would usually have many more species but not so more distinct genera since they are very redundant. For example, typical host genera such as legumes, *Centaurea*, *Sinapis*, etc., are almost always present in any area of biogeographically significant size for butterflies; this is obvious when we compare the geographical range described for butterfly species in Tolman and Lewington (2002) with those of plants species in Flora Europaea, or any regional flora, for the Mediterranean Region.

Dietary shifts seem to be more closely associated with endemics as a whole than earlier emergence. In this sense, the classical hypothesis of Ehrlich and Raven (1965) is here supported to the extent that new butterfly lineages (endemic species) are linked with new food plants. The capacity of eating a new genus of host plant that may be the only food available in a certain landscape could determine the survivorship of the butterfly in the zone. If this hypothetical site is separated from other populations of the butterfly, then genetically based diet differences could develop and finally originate an allopatric speciation event, possibly through isolation by phenological differentiation due to the life-cycle timing of the new plant genus.

If some of the patterns found here can be explained as adaptations to the Mediterranean climate, why, then, do not Mediterranean non-endemics display any of them? The answer is probably that they are not genetically isolated in the Mediterranean Region. Basic population genetics would demonstrate that even relatively small levels of immigration between boreal and Mediterranean populations could be enough to erase in practice the genetic basis of regional adaptations to Mediterranean climate. On the contrary, endemics are completely isolated in Mediterranean conditions and therefore are really able to develop adaptations without the "noisy" genetic influence of boreal immigrants with their own set of boreal-adapted alleles. That is, fine adaptation to Mediterranean conditions would be relatively impeded in non-endemic Mediterranean butterflies due to spatial effects of metapopulation genetics. Some lines of evidence fit with this idea by demonstrating a significant gene flow in butterflies at the scale of metapopulations (Nave *et al.*, 1996). This is an exciting hypothesis that would be very interesting for future research. From this scope, the possibility exists that the patterns here reported could also be found at the subspecies level - *i.e.* in Mediterranean subspecies within European butterfly species - , but gene flow between subspecies may erase any adaptive trend, thus making subspecies an inadequate unit to focus this kind of questions.

In conclusion, endemic Mediterranean butterflies (excluding mountain or insular species) tend to present reduced voltinism compared to their congeneric counterparts, which is probably the consequence of the high seasonality of Mediterranean climate. Univoltine or bivoltine endemics, the most sensitive to reductions of reproductive rounds, usually have earlier emergence that seems to prevent their caterpillars from suffering deleterious effects derived from Mediterranean summer drought. There is a strong trend towards a more re-stricted diet in genera of host plants in endemics – usually about half of the genera are exclusive of an endemic compared to a non-endemic species of the same genus. It is not clear to what extent these trends can be extended to other typically Mediterranean insects, but the present work at least offers a case study that could be useful in future research on this fascinating field of the evolutionary ecology of insects in the Mediterranean Region.

Acknowledgements

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