THE ORIGIN AND HISTORY OF THE BUTTERFLY FAUNA OF THE NORTH ATLANTIC ISLANDS

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ABSTRACT. The butterfly fauna of Macaronesia comprises only 31 species, of which 27 inhabit the Canary Islands, 15 the Madeiras and 7 the Azores. In contrast, the islands support rich floras and mollusc faunas. The butterfly fauna, while much more impoverished than expected from its latitude, has generated more than 300 publications over the last 150 years. However, errors abound in the literature and many, which we now correct, have become established.

The number of species and the number of endemic forms on each island are positively correlated with vegetation diversity and negatively correlated with distance from the nearest continent. There has been considerable inter-island differentiation in some genera, especially in *Hipparchia*, *Pararge*, *Gonepteryx* and *Pieris* and a classical double invasion of Madeira by *Pararge* from Europe.

The fauna consists of four elements: endemic taxa related to existing ones on the neighbouring continents; relict endemic descendants of an extinct Saharan fauna; recent (mostly post-fourteenth century) immigrants from Europe and Africa; cosmopolitan migrants. At least four species are known to have arrived in the last 150 years. Butterflies from four zoogeographical regions, Palaearctic, Nearctic, Afrotropical and Oriental, are represented. An unknown but substantial number of species, mainly from laurel forest, has probably become extinct since the islands were colonized by Europeans in the fourteenth century. Extinctions continue and several species or races on particular islands are under threat.

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INTRODUCTION

The North Atlantic Islands, collectively known as Macaronesia, comprise three main groups, the Azores, the Madeiras and the Canaries. All the islands are probably of independent volcanic origin though their positions and configurations are known to have changed considerably as a result of sea-floor spreading from the mid-Atlantic ridge. In general the older islands are those furthest from the ridge though there are exceptions. Many islands have changed in shape and size as a result of changing sea levels and continuing volcanic activity: for example, Porto Santo was many times its present area, and larger than Madeira, during the Pleistocene when sea levels were at times up to 200m lower than today. The relative position of the island groups is shown in Figure 1.
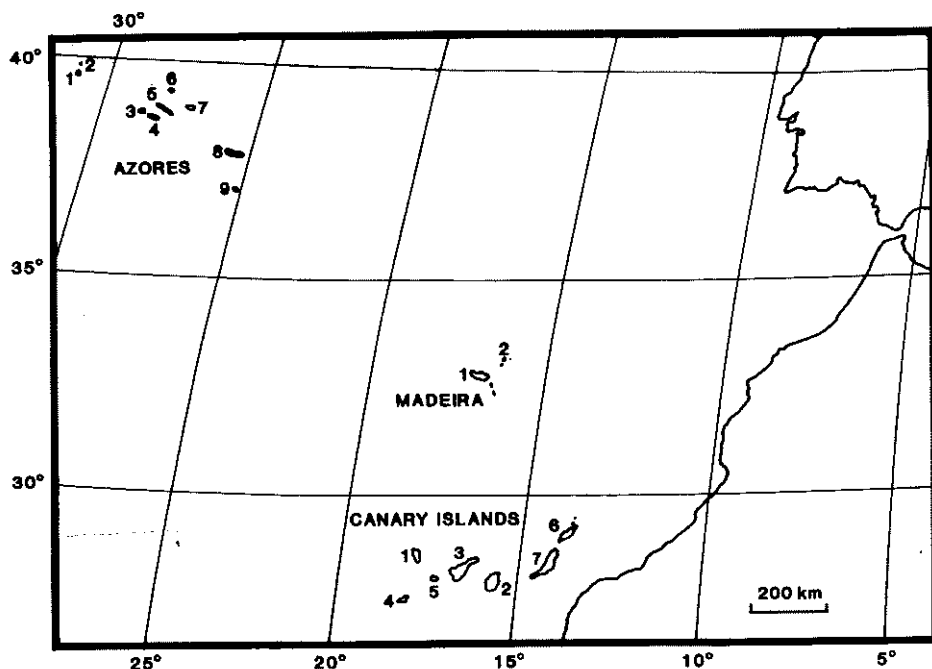

Figure 1. Positions of the North Atlantic Islands (Macaronesia). Azores: 1 = Flores, 2 = Corvo, 3 = Faial, 4 = Pico, 5 = Sâo Jorge, 6 = Graciosa, 7 = Terceira, 8 = Sâo Miguel, 9 = Santa Maria. Madeira: 1 = Madeira, 2 = Porto Santo. Canary Islands: 1 = La Palma, 2 = Gran Canaria, 3 = Tenerife, 4 = El Hierro, 5 = La Gomera, 6 = Lanzarote, 7 = Fuerteventura.

All the islands have a large array of endemic plants, some of which have evolved in isolation, others being relicts from a vegetation type that during the Tertiary extended over much of the Mediterranean region (Bramwell & Bramwell, 1974). They also have faunas rich in endemic molluscs (Wollaston, 1878), Coleoptera (Wollaston, 1854) and other animal groups.

The present butterfly fauna, in marked contrast, is much more impoverished than its southerly latitude would suggest: yet it comprises a curious mixture of species of Oriental, Afrotropical, Nearctic and (especially) Palaearctic affinity. In this paper we compare the butterfly faunas of the different islands and island groups and attempt to account for their origins. We suggest that the present assemblage of species has been primarily influenced by human alteration of the environment and recent invasions, which essentially began in the fourteenth century following European colonisation. A consequence of the human impact on the butterfly fauna is that a conventional biogeographical analysis of the relationship between species richness and island parameters such as vegetation diversity, area, altitude and distance from continental landmasses presents some unusual features as well as many familiar ones.

SOURCES

The butterfly fauna of Macaronesia is exceptionally well documented and we have been able to examine over 300 publications dating from the 1860s; only a selection is cited in this paper. Most publications are annotated lists of species found on the various islands or records of rare or unusual species. Many are reports of short visits by butterfly collectors, usually from Britain or Germany. There are also biogeographical reviews, evolutionary studies and, more recently, papers on population and community ecology. We have detected many inaccuracies, too numerous to document in detail, most of them errors in identification or recording, and it has even been difficult to establish which species occur on the various islands; indeed the wealth of published material has in some ways frustrated this task. One problem is that errors tend to be repeated in subsequent publications. So far as is possible we have corrected these errors.

Since 1984 we have visited all islands, except four of the Azores group, some of them repeatedly and at various seasons, in an attempt to gain a contemporary view of the habitats and status of all the species. With the exception of *Hypolimnus misippus* (which is rare and unpredictable) and *Cynthia virginiensis* (possibly now extinct or of erratic occurrence) we have seen all the 31 species listed in Table 1.

Table 1. List of butterfly species and subspecies recorded from Macaronesia with their status and probable biogeographical affinities.

Species & subspecies	M	S	T	C	G	P	H	F	L	A	Biogeographical affinity & status
PIERIDAE											
Pieris brassicae (L.)											Pa., res.
ssp. *cheiranthi* Hübner			x		(x)	x					end.
ssp. *wollastoni* Butler	x										end.
ssp. *azorensis* Rebel										x	end.
Artogeia rapae (L.)	x	x	x	x	x	x	x	x	o	o	Pa., mig.
Pontia daplidice (L.)			x	x	x	x	x	x	(x)		Pa., mig.
Euchloe belemia (Esper)											Pa., res.
ssp. *hesperidum* Rothschild			x	x			x				end.
Elphinstonia charlonia (Donzel)								x	x		Pa., res.
Catopsilia florella (Fab.)			x	x	x	x		x	x		Af., mig.
Colias crocea (Geoffroy)	x	x	x	x	x	x	x	x	x	x	Pa., mig.
Gonepteryx cleopatra (L.)											Pa., res.
ssp. *maderensis* Felder	x										end.
ssp. *cleobule* Hübner			x		x						end.
ssp. *palmae* Stamm						x					end.
LYCAENIDAE											
Lycaena phlaeas L.			x	x	x	x	(x)	x	x		Pa., res.
ssp. *phlaeoides* Staudinger	x	x									end.
Lampides boeticus (L.)	x	x	x	x	x	x	x	x	x	x	Co., mig.
Cyclyrius webbianus Brullé			x	x	x	x					Af., end.
Zizeeria knysna (Trimen)			x	x	x	x	x				Af., res.
Aricia agestis (D. & S.)											Pa., res.
ssp. *cramera* Eschscholz			x	x	x	x	x				Pa., res.
Polyommatus icarus (Rottemburg)								x	x		Pa., res.
NYMPHALIDAE											
Vanessa atalanta (L.)	x	x	x	x	x	x	x	x	x	x	Pa., mig.
V. indica (Herbst)											
ssp. *calliroe* Hübner	x	v	x	x	x	x	x	v			Or., end.
Cynthia cardui (L.)	x	x	x	x	x	x	x	x	x	x	Co., mig.
C. virginiensis (Drury)	(x)		x	(x)	x	(x)					Ne., mig.
Pandoriana pandora (D. & S.)			x		x	x	x				Pa., res.
Issoria lathonia (L.)	x	(x)			(x)	(x)					Pa., mig.
Hypolimnus misippus (L.)[1]	o		o	o	v	v			o		Co., mig.
SATYRIDAE											
Hipparchia azorina (Strecker)[2]										x	Pa., end.
H. algirica (Oberthür)[3]											Pa., res.
ssp. *maderensis* (Baker)	x										end.
H. wyssii (Christ)[4]											Af., end.
ssp. *wyssii* (Christ)			x	x							end.
ssp. *gomera* (Higgins)					x						end.
ssp. *tilosi* (Manil)						x					end.
ssp. *bacchus* (Higgins)							x				end.
Maniola jurtina (L.)											Pa., res.
ssp. *fortunata* Alpheraky			x	x	x	x	x				Pa., res.
Pararge aegeria (L.)	x										Pa., res.
P. xiphioides Staudinger			x	x	x	x					Pa., end.
P. xiphia (Fab.)	x										Pa., end.
DANAIDAE											
Danaus plexippus (L.)	x	x	x	x	x	x	x	x	x	x	Ne., mig.
D. chrysippus (L.)											Af./Or.
ssp. *kanariensis* Fruhstorfer[5]		(x)	o	x	x		x				end.
HESPERIIDAE											
Thymelicus acteon (Rottemburg)											Pa., res.
ssp. *christi* Rebel			x	x	x	x	x				end.
Total species (1960–90)	15	7	24	19	23	23	15	13	10	7	

Table 1 NOTES

x = recorded since 1960 as known or presumed breeding species; (x) = not reliably recorded since 1980 and possibly now extinct; o = old (pre-1960) or doubtful records which are unlikely to be confirmed; v = vagrant (occasional visitor not known to have bred). For further analysis in this paper, most (x) records are given the benefit of the doubt (see text) while all o records are excluded. v records are not included in the island totals.

Island abbreviations: M = Madeira, S = Porto Santo, T = Tenerife, C = Gran Canaria, G = La Gomera, P = La Palma, H = El Hierro, F = Fuerteventura, L = Lanzarote, A = Azores.

Biogeographical abbreviations: sp. = species, ssp. = subspecies, Pa. = Palaearctic, Ne. = Nearctic, Af. = Afrotropical (Ethiopian), Or. = Oriental, Co. = cosmopolitan, end. = endemic, mig. = migratory, res. = resident.

1 *Hypolimnus misippus* females have never been recorded in the islands and the species is accordingly considered a vagrant.

2 Oehmig (1983) split *Hipparchia azorina* Strecker into three species, *H. azorina* (with three subspecies, *azorina* (Pico), *ohshimai* (Faial) and *jorgense* (São Jorge)), *H. caldeirense* (Flores) and *H. miguelensis* (São Miguel). Following the discovery of two further populations on Terceira (1982) and Corvo (1984), Bivar de Sousa (1982, 1985), divided *H. azorina* into seven subspecies as follows: *H. a. azorina* Strecker (Faial), *H. a. miguelensis* Le Cerf (São Miguel), *H. a. picoensis* Le Cerf (Pico), *H. a. occidentalis* Bivar de Sousa (Flores), *H. a. jorgense* Oehmig (São Jorge), *H. a. barbara* Bivar de Sousa (Terceira) and *H. a. minima* Bivar de Sousa (Corvo). In our opinion Oehmig (1983) claims full speciation on insufficient evidence: though we prefer the classification of Bivar de Sousa, further work is clearly needed.

3 Erroneously figured (pl. 30, fig 2e) and assigned to *Hipparchia aristaeus maderensis* by Higgins & Riley (1970), the female specimen illustrated being *H. volgensis delattini* from Macedonia (Kudrna, 1977). Higgins & Riley (1980) failed to correct these errors and also state mistakenly that this species occurs in the Azores.

4 Incorrectly named *Pseudotergumia wyssii* by Higgins & Riley (1970, 1980) who raised the subgenus *Pseudotergumia* to generic status without comment or justification (Kudrna, 1977). The valid name is therefore *Hipparchia (Pseudotergumia) wyssii* (Christ). Two subspecies are recognized by Higgins & Riley (1980), three (*wyssii*, *gomera* and *bacchus*) by Kudrna (1977) while a fourth (*tilosi*) has recently been discovered on La Palma by Manil (1984).

5 This subspecies, which was not recognized by Talbot (1943) or Ackery & Vane-Wright (1984), also occurs on St. Helena (Fruhstorfer, 1899).

There is no previous account of the possible origin and history of the Macaronesian butterfly fauna. The most comprehensive attempt thus far is that of Leestmans (1975) who gives an exceptionally detailed review and an extensive bibliography of the Lepidoptera of the Canaries. This, together with Schmidt-Koehl (1971) and Rebel and Rogenhofer (1894), forms the basis for an understanding of the history of the Canary Island butterflies. Subsequent papers on the Canaries add little to the broad biogeographical picture. There are, however, accounts of the ecology and evolution of particular species, for example, *Cyclyrius webbianus* (Bacallado, 1976), *Pieris brassicae* (Schurian, 1975) and *Maniola jurtina* (Owen & Smith, 1990). There is also a small book on the butterflies of the Canaries (Fernández, 1978) which gives bionomic information on most (but not all) of the species, and an analysis of species diversity in relation to habitat on Tenerife (Aranguren & Báez, 1884).

During the second half of the nineteenth century, T. Vernon Wollaston, a cleric who for many years lived on Madeira and the Canary Islands, published detailed accounts of the beetles (Wollaston, 1854) and land snails (Wollaston, 1878). He made comparisons with other islands in the eastern Atlantic and became preoccupied with inter-island differences. Indeed he came within a whisker of appreciating the evolutionary significance of island biogeography (Wollaston, 1856) which so influenced Darwin and Wallace (1858) and Darwin (1859), following their studies in the Galapagos Islands and the Malay Archipelago, respectively. Wollaston also collected and observed butterflies and his records (Stainton, 1859; Baker, 1891) provide an earlier than usual overview of the fauna which, however, was not substantially different from what it is today. The butterflies of Madeira have been subsequently well studied, the more important recent publications being Oehmig (1977), Gardner and Classey (1960), Swash and Askew (1982) and Lace and Jones (1984).

The Azores are the least well documented. Some of the earlier publications are particularly unreliable and record species that in all probability never occurred there. The most reliable is Rebel (1940) who records all seven of the species now known to occur there and correctly questions the repeated records of *Artogeia rapae* which is absent (personal observation), except for perhaps the occasional imported stray. The list of species given by Carthy (1957) confirms Rebel's list, as indeed we were able to do in 1987.

TAXONOMIC DECISIONS

The taxonomic rank we have assigned to endemic subspecies and species listed in Table 1 is a compromise which, like most compromises, is provocative in the sense that there is ample room for disagreement. The literature on the butterflies of the North Atlantic Islands contains numerous decisions, revisions and opinions as to how many of the endemic subspecies and species should be named, but on balance we consider the arrangement offered in Table 1 the best approximation. The main modern sources of possible controversy are as follows:

On the basis of genitalia differences, *Pieris brassicae cheiranthi* (Figure 2) (Canary Islands) is designated a distinct species by Kudrna (1973) who, arguing from similarities in the structure of genitalia, retains *P. brassicae wollastoni* (Madeira) as a subspecies of *P. brassicae*. However, *P. brassicae brassicae* (from England) and *P. brassicae cheiranthi* freely interbreed in captivity, producing fully fertile F1 and F2 progeny in both sexes (A. G. Smith, Owen and D. A. S. Smith, unpublished): so, while acknowledging the genitalia differences, we consider all North Atlantic populations to be subspecies of *P. brassicae*.

The three island subspecies of *Gonepteryx cleopatra* have from time to time been regarded as distinct species and this view is upheld by Kudrna (1975), mainly on the basis of genitalia differences but also on differences of coloration. We treat them as subspecies. Conversely, genitalia similarities suggest that *Pararge xiphioides* (Canary Islands), to which we accord specific rank, could be considered a subspecies of the continental species *Pararge aegeria* (Swash and Askew, 1982). However, *Pararge xiphia* (Madeira) undoubtedly deserves specific rank as it apparently does not hybridise with sympatric *P. aegeria*, which colonised Madeira in the mid-1970s (Owen, Shreeve and Smith, 1986).

Vanessa indica calliroe and *Thymelicus acteon christi* have also been accorded specific rank (eg. Leestmans, 1975) and indeed it is possible to argue, though Kudrna (1977) disagrees, that some at least of the distinctive subspecies of *Hipparchia wyssii* merit specific recognition. However, for our purposes here the answer to the question whether or not island endemics, which have never been exposed to the breeding test, are designated subspecies or species is not crucial: what matters is that they are sufficiently distinct to indicate a relatively long period of isolation. On this criterion, the large whites (*P. brassicae*), cleopatras (*G. cleopatra*), speckled woods (*P. xiphia* and *P. xiphioides*), Indian

red admiral (*V. indica calliroe*) and the graylings (*H. wyssii*, *H. algirica maderensis* and *H. azorina*) are sufficiently distinct from their continental relatives to indicate an extended period of isolation. Other species with a claim to subspecific status on the islands are *Euchloe belemia*, *Aricia agestis*, *Lycaena phlaeas* and *Danaus chrysippus*. The timescales involved must vary widely and we cannot speculate on them. However, all these species, in addition to the endemic Canary blue (*Cyclyrius webbianus*), are probably relatively ancient inhabitants of the islands.
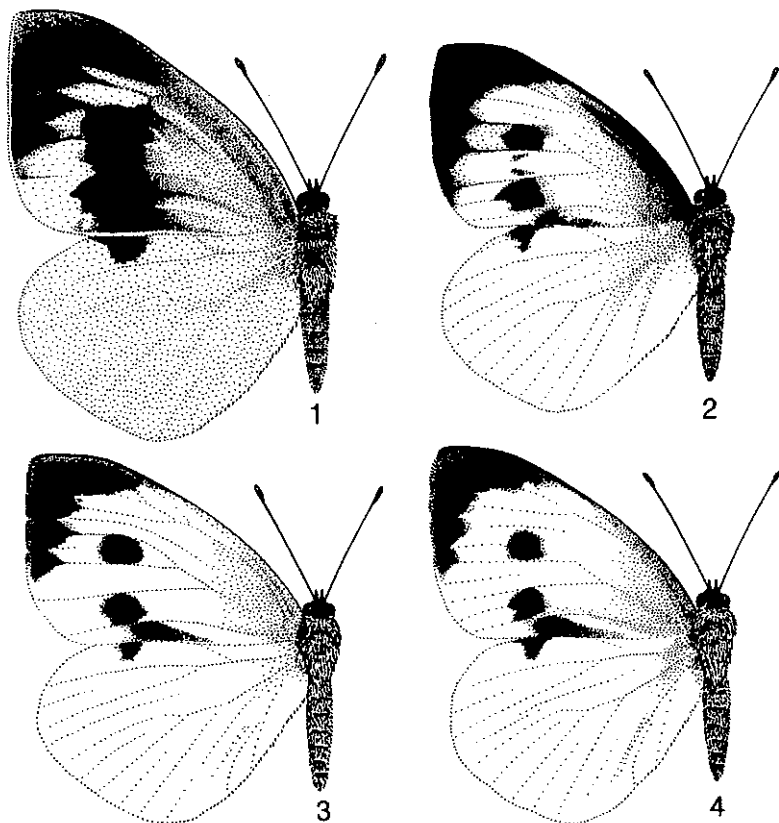

Figure 2. Geographical variation in female *Pieris brassicae* (L.). 1. *P. brassicae cheiranthi* (La Palma, Canary Islands); 2. *P. brassicae wollastoni* (Madeira); 3. *P. brassicae azorensis* (Pico, Azores); 4. *P. brassicae brassicae* (Oxford, England).

THE SPECIES LIST

All the 31 species and some of the subspecies listed in Table 1 are figured in colour by Higgins and Riley (1983). One error in Higgins and Riley (1983 and other editions) is noted in the footnote to Table 1.

The species list is provocative when, as in Table 1, it is necessary to decide the current status of each species on each island and when some of the modern literature persists in giving inaccurate information. For example, although *Cynthia virginiensis* is still claimed to be present we know of no positive records for any island since 1966 (Guichard, 1967). However, there are specimens collected in the 1970's on Tenerife and La Gomera in the Museo Ciencias Natureles de Tenerife. This is a migratory species, easily confused on the wing and at a distance with the abundant *Cynthia cardui*, and one that is likely to establish itself in an area and then disappear and perhaps reappear. *Hypolimnus misippus* has been sporadically recorded in the past on most islands and would have been omitted had it not been found recently (1970) on La Palma (Fernández, 1978) and on La Gomera in 1987 and 1988 (Feierabend, 1989). Likewise *Issoria lathonia* was obviously much more widespread in the past (Baker, 1891; Guichard, 1967; Leestmans, 1975) than it is now. The remarks about *C. virginiensis* apply equally to this species. We have failed repeatedly to find it in the Canaries though T. Shreeve and A.G. Smith (personal communication) have recently (1990) captured it in Madeira

Pieris brassicae wollastoni has not been reliably reported from Madeira for some years although recent "sightings" are claimed. However, on five separate visits to Madeira during the 1980s, neither the authors nor T. Shreeve and A.G. Smith (personal communication) have sighted or captured either adults or larvae. Since Swash and Askew (1982) collected it there are some reported local "sightings" (1987) but its present status is doubtful. Without question its range and abundance on Madeira have declined severely since Wollaston's day. Moreover, we have failed to find *P. brassicae cheiranthi* on four visits to La Gomera since 1984 and we fear *P. brassicae* may now be close to extinction on both islands.

Danaus chrysippus, which we have recorded on both La Gomera and La Palma, has apparently not been seen on Tenerife since 1970 and may now be extinct. Up to 1961, however, it was commonly reported from the Barranco Martiánez at Puerto de la Cruz, where one of its foodplants, *Asclepias curassavica*, was abundant (Gurney, 1928; Baynes, 1961; Goodall, 1961; de Worms, 1961). The Puerto de la Cruz site was extinguished by dumped rubble

when a new bridge was built over the Barranco Martiánez during construction of the autopista to Santa Cruz. The last recorded site for *D. chrysippus* on Tenerife is at Ten-Bel (Costa del Silencio) in the south of the island (Leestmans, 1975). We are reasonably convinced that *Elphinstonia charlonia* has never occurred on Tenerife and it is probable that the only traceable record (Holt White, 1894) is erroneous. Furthermore we agree with Leestmans (1975) that *Polyommatus icarus* has probably never occurred on the western Canaries and is confined to the eastern islands of Fuerteventura and Lanzarote where it flies mainly in winter (Owen, 1988). We can find no positive record for *Artogeia rapae* on the Azores, nor (perhaps more remarkably) from Lanzarote, despite repeated claims. Many species additional to those listed in Table 1 have been recorded on the islands. They are presumably vagrants, accidental or deliberate introductions, misidentifications, or just plain errors in the literature. One of the most remarkable is *Hipparchia statilinus* (Satyridae), a single specimen of which was collected by Wolff on Madeira in 1974 (Karsholt, 1988), undoubtedly a vagrant from the Iberian peninsula. Unfortunately, but nevertheless characteristically, this single occurrence has entered the literature in a way that suggests the species is established on Madeira (Higgins and Riley, 1983; Jones et al., 1987): "sightings" are again implicated. But the record is not without interest as it demonstrates that members of the genus *Hipparchia* are capable of long-distance dispersal. This is independently confirmed by the presence of endemic species and subspecies of *Hipparchia* on 13 of the 18 islands (*H. azorina* on seven of the Azores, *H. wyssii* on the five western Canary Islands and *H. algirica maderensis* on Madeira).

Most of the accidental introductions are probably from ships that call at the islands while travelling to and from Europe, South America and Africa. Leestmans (1975) lists many such species from the Canaries. Most are tropical South American or African and could easily have travelled on ships carrying fruit and vegetables. Cases of mistaken identity include the lycaenid *Callophrys rubi* (L.), still stated to occur on Tenerife (Higgins and Riley, 1983), presumably as a consequence of incorrect recording by Holt White (1894) who also noted other extremely unlikely species on the island. Hence our list for each island (Table 1) is the result of vigorous pruning and the omission of all doubtful records. How to treat doubtful cases has been largely decided by the results of our own field work. Nevertheless, we freely admit that deletions and additions are likely even before this paper is published.

BIOGEOGRAPHICAL ANALYSIS

Two of the biogeographical variables listed in Table 2 require explanation.

Vegetation diversity index (V)

This index should ideally be based on the number of plant species recorded for each island. However, this is an impossible task as the high and unknown numbers of introduced plants, many of which are used partially or exclusively by some butterflies as foodplants, must be included. Here we use an approximation based on the vegetation types, natural, semi-natural and man-made, recorded in our field notes. The 17 natural and semi-natural types are: Alpine, sub-alpine, montane scrub, montane grassland, *Pinus canariensis* forest, laurel forest (laurisilva), tree heath, juniper scrub, *Erica/Micromeria* heath, *Sphagnum* bog, marsh, xerophytic scrub, desert, dune, saltmarsh, lakes/reservoirs, streams/rivers. The 10 man-made habitats are: meadow, pasture, arable land, waste ground/road verges, coniferous plantations (eg *Pinus, Cupressus*), broad-leaved plantation (chestnut, oak, *Eucalyptus*, wattle etc.), vineyards, banana plantations, orchards, gardens (including botanic gardens). V is computed as the number of vegetation types recorded on the island divided by the total recorded (27) for all 18 islands.

Endemicity index (ê)

The measure of endemicity for each island is calculated as follows. Endemic species score 2 and subspecies 1 (as listed in Table 1). The island score for each species or subspecies is divided by the number of islands sharing the taxon. These scores are then summed for each island and divided by 2S (total species recorded x 2). The resulting index (ê) is a proportion ranging from zero (no endemicity) to unity (fauna consisting entirely of endemic species).

The other variables are explained in the footnote to Table 2.

Correlation analysis

The raw data for the 18 Macaronesian islands (Table 2) are analysed for number of species (S) and the explanatory variables V, A, C, H and I by simple and partial correlation (Table 3). S is positively correlated with V, A and H and negatively correlated with C. Partial coefficients remove the correlations with A and H (because V is itself correlated with H and H with A). S shows a positive

partial correlation only with V and a negative partial correlation with C. Thus we conclude that the important determinants of the number of species on each island are vegetation diversity (positive) and distance from the nearest continent (negative).

Table 2. Summary of the raw data for individual islands used for statistical analysis.

Islands	Explanatory variables					Dependent variables				
	A	H	V	I	C	S	E	ê	M	$\overline{M}$
Lanzarote	813	668	0.22	15	131	10	0	0.000	7	0.70
Fuerteventura	1725	807	0.30	15	94	13	1	0.022	7	0.54
Gran Canaria	1532	1950	0.54	56	188	19	8	0.074	10	0.53
Tenerife	2058	3718	0.67	35	263	24	11	0.079	10	0.40
La Gomera	378	1487	0.56	35	313	23	10	0.088	10	0.43
El Hierro	278	1501	0.59	69	344	15	5	0.066	7	0.47
La Palma	728	2423	0.56	49	375	23	10	0.099	9	0.39
Madeira	805	1862	0.63	50	640	15	7	0.190	8	0.53
Porto Santo	40	517	0.33	50	625	7	1	0.071	5	0.83
Santa Maria	97	590	0.33	81	1343	6	1	0.014	5	0.83
São Miguel	747	1105	0.44	81	1358	7	2	0.064	5	0.71
Terceira	400	1021	0.41	39	1552	7	2	0.064	5	0.71
São Jorge	246	1053	0.44	14	1614	7	2	0.064	5	0.71
Graciosa	62	400	0.41	37	1625	6	1	0.014	5	0.83
Faial	172	1043	0.52	8	1688	7	2	0.064	5	0.71
Pico	433	2351	0.56	8	1640	7	2	0.064	5	0.71
Flores	143	914	0.48	19	1898	7	2	0.064	5	0.71
Corvo	18	770	0.33	19	1890	7	2	0.064	5	0.71

A = area (km^2), H = maximum altitude (m), V = vegetation diversity (see text), I = distance from nearest island (km), C = distance from nearest continent (km), S = number of species (see text), E = number of endemic species & subspecies, ê = island endemicity index (see text), M = number of migratory species, $\overline{M}$ = proportion of species migratory.

Table 3. Values of r (point-biserial correlation coefficient) for the major variables listed in Table 2 (partial coefficients in italics).

	S	V	A	C	H
V	0.636**				
	0.555*	**V**			
A	0.600**	(0.258)			
	(0.107)	*-*	**A**		
C	-0.731***	(-0.103)	-0.661**		
	-0.821***	*-*	*-*	**C**	
H	0.705**	0.783***	0.585*	(-0.318)	
	(0.069)	*-*	*-*	*-*	**H**
I	*(0.177)*	*(0.131)*	*(0.392)*	*(-0.233)*	*(0.031)*

S = number of butterfly species, V = vegetation diversity index, A = area (km^2), C = distance from nearest continent (km), H = maximum altitude (m), I = distance from nearest island (km).

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; coefficients in parenthesis are not significant. The simple coefficients have $n = 18 - 2 = 16$ degrees of freedom (df); the partial coefficients have $n = 18 - 2 - 3 = 13$ df.

Our finding that the number of species inhabiting each island is negatively correlated with the distance of the island from the source of recruitment and positively correlated, albeit indirectly, with altitude and area, is a common and expected feature of oceanic island faunas (MacArthur & Wilson, 1967).

The endemicity index (ê) is correlated (positively) only with V ($P < 0.001$). In contrast, the proportion of migratory species (M) is correlated positively with C ($P < 0.001$) but negatively with V ($P < 0.001$). It is not of course surprising that the proportion of migratory species should be higher on the more remote islands.

Comparison of the Macaronesian archipelagos

The three archipelagos are compared in Table 4. Formal statistical analysis is not possible here as there are only three "cases". In general, the number of species per island, number and proportion of endemics and number and proportion of resident, non-endemic species (shared with the continent) all

decline with increasing distance from the continent. Vegetation diversity shows a trend similar to the variables based on butterflies. The proportion of migratory species, though not the raw number, shows the opposite trend as expected.

Table 4. Summary of variables examined in a comparison of the three Macaronesian archipelagos.

Factor	Canaries	Madeira	Azores
Number of species (1960-90)	27	15	7
Mean number of species per island	18.1	11	6.8
Number of species endemic at specific or subspecific level	10	6	2
Endemicity index for archipelago	0.37	0.40	0.29
Resident species*	6	1	0
Proportion resident species*	0.22	0.07	0.00
Number of migrant species	11	8	5
Proportion of species migratory	0.41	0.53	0.71
Total land area (km^2)	7512	845	2318
Mean area of islands (km^2)	1073	423	258
Maximum altitude (m)	3718	1862	2351
Vegetation diversity index	0.81	0.67	0.56
Distance from nearest continent (km)	94 (Africa)	597 (Africa)	1343 (Europe)

*Residents are species shared with a continent which breed on the islands but show neither endemicity nor migratory behaviour.

ORIGIN OF THE FAUNA

Twenty of the 31 species recorded since 1960, listed in Table 1 and analysed in Table 5, are Palaearctic or have Palaearctic affinities. They almost certainly colonised the islands from western Europe or North Africa. That this process continues is demonstrated by the arrival in the mid-1970s and subsequent explosive increase in numbers of *Pararge aegeria* on Madeira

(Owen, Shreeve and Smith, 1986). Thus Madeira is now the only place in the world with two sympatric species of *Pararge*. The resulting interspecific competition between the invader and the endemic *P. xiphia* has already resulted in a marked contraction of the range of the latter and the situation is under close scrutiny (Shreeve & Smith (1992) and Jones & Lace (1992). It is singularly fortunate to have the opportunity to study the ecological adjustment and evolutionary change following a double invasion similar to the one which is presumed to have occurred on Gran Canaria and Tenerife when the common chaffinch *Fringilla coelebs* arrived to compete with the endemic blue chaffinch *Fringilla teydea* (Lack & Southern, 1949).

Table 5. Biogeographical affinities of the Macaronesian butterfly fauna   (percentages in parenthesis).

Archipelago	S	P	A	N	O	C
Canaries (7 islands)	27	16 (59.3)	4-5 (16.7)	2 (7.4)	1-2 (5.6)	3 (11.1)
Madeira (2 islands)	15	10 (66.7)	0 (0.0)	2 (13.3)	1 (6.7)	2 (13.3)
Azores (9 islands)	7	4 (57.1)	0 (0.0)	1 (14.3)	0 (0.0)	2 (28.6)
Macaronesia (18 islands)	31	20 (64.5)	4-5 (14.5)	2 (6.5)	1-2 (4.8)	3 (9.7)

S = number of species, P = Palaearctic, A = Afrotropical, N = Nearctic, O = Oriental, C = cosmopolitan.

Artogeia rapae first appeared on Madeira in 1971 (Swash and Askew, 1982) and there was a mass invasion, presumed to be from Portugal, in 1974 (Wolff, 1975). In April 1985, the species was "widespread but by no means common" (Owen, Shreeve and Smith, 1986). However, in June 1987 it was abundant all over the island (DASS, unpublished). *A. rapae* is also one of the few abundant species on Porto Santo and it is not known when it first appeared there. As Porto Santo is closer than Madeira to Europe, *A. rapae* may have island-hopped from the former to the latter. It is possible that the recent decline in numbers and range contraction of *P. brassicae wollastoni* on Madeira may result from the recent establishment of *P. rapae* though it must be admitted that the two species coexist sympatrically on Tenerife and La Palma.

Two species are Nearctic and one of them, *Danaus plexippus*, has extended its range to many parts of the world in the last 150 years (Ackery and Vane-Wright, 1984), probably as a result of the cultivation and deliberate or accidental introduction of suitable larval food-plants (Owen & Smith, 1989), possibly abetted by genetic changes. The other Nearctic species, *Cynthia virginiensis*, is migratory and, although often collected on Madeira and the Canaries in the past, the last published sighting is by Ward and Guichard on Gran Canaria, Tenerife and La Gomera in 1966 (Guichard, 1967). Although neither Leestmans (1975) nor we and our colleagues (T. Shreeve and A.G. Smith, personal communication) have seen it, there are specimens collected in Tenerife and La Gomera in the 1970's in local museum collections.

The Afrotropical element, with only four or five species, depending on what is counted as truly Afrotropical, is poorly represented, despite the fact that the Canaries and Madeira are closer to Africa than to Europe. The closest relatives of two species (*Cyclyrius webbianus* and *Hipparchia wyssii*) are not found in tropical Africa proper and a third, *Danaus chrysippus*, extends far beyond Africa, which further weakens the Afrotropical element.

Danaus chrysippus is possibly the most abundant butterfly in sub-Saharan Africa. Although the small and precariously established populations in the Canaries may be derived from there, this is by no means certain. On Fuerteventura its main foodplant is *Caralluma burchardii* (Asclepiadaceae), a cactus-like endemic, but elsewhere it probably feeds on alien asclepiads, *Asclepias curassavica* and *Gomphocarpus fruticosus*; on the western Canaries it might be expected on various endemic species of *Ceropegia*, a genus recorded as a foodplant in Africa (Ackery & Vane-Wright, 1984). Although the species does not occur, at least on a permanent basis, in that part of Africa closest to the Canaries (Morocco and Rio de Oro) it may have done so in the recent past when the Sahara was less arid: moreover it is a notorious migrant. It also occurs, at least seasonally, in subtropical parts of the Palaearctic, throughout the Oriental and Australian regions and on most tropical and subtropical islands of the eastern Atlantic, Indian and western Pacific Oceans. There are signs that it may currently be extending its range in North Africa and southern Europe (Bretherton, 1984), perhaps for the same reasons that seem to account for the range expansion of *D. plexippus*.

However, we agree with Larsen (1990) that on morphological criteria the Canary Island populations appear more closely related to the Asian subspecies *chrysippus* rather than the various Afrotropical races. It is certainly not derived from West Africa where the species is monomorphic for the white hindwinged

form *alcippus*. Although *D. chrysippus* form *alcippus* has been recorded in the Canaries, only four of 54 specimens of *D. chrysippus* in the collections of the British Museum (Natural History) (24) and the Hope Department of Entomology, University of Oxford (30) are of this form, all collected in the nineteenth century. One of us (DFO) found two form *alcippus* in a sample of 33 collected on Fuerteventura in 1991, but in both specimens the white on the hindwing is less developed than in West African specimens. We believe that the Canary Island *D. chrysippus* are derived from the population which now inhabits Egypt (Larsen, 1990), the Middle East and mainland tropical Asia, rather than tropical west Africa. In the past subspecies *chrysippus* probably had a continuous distribution across Palaearctic North Africa and reached the Canaries from there. Whether the Canary race, shared with St. Helena, deserves subspecific status in its own right has been and remains debatable (Talbot, 1943; Ackery & Vane-Wright, 1984).

One genuine and abundant Afrotropical species, *Catopsilia florella*, first arrived in the Canaries in the mid-1960s and has subsequently spread to all islands where its larval food-plant, *Cassia didymobotrya*, has been introduced from Africa as an ornamental.

Much more remarkable is the lycaenid *Cyclyrius webbianus*, a distinctive and abundant endemic on all the western Canary Islands except El Hierro. All its many recorded larval food-plants are endemic species of Papilionaceae. The nearest relative of *C. webbianus* and its only congener is *Cyclyrius mandersi* (Druce), another endemic found only on the Indian Ocean island of Mauritius (technically within the Afrotropical region). *Cyclyrius* is absent from mainland tropical Africa and the present disjunct distribution of the genus appears enigmatic though it is paralleled by a number of plant genera (D. Bramwell, personal communication).

The case of *Hipparchia wyssii* (Figure 3), which occurs on all five of the western Canaries, presents some similar features. Assigned to the subgenus *Pseudotergumia* (see footnote to Table 1) by Kudrna (1977), he considers that the species most closely related to *H. wyssii* on genitalia characters is *Hipparchia (Pseudotergumia) tewfiki* (Wiltshire), a relict endemic confined to the south-west of the Arabian peninsular (Larsen, 1984), where it is the only intruder of this genus into the Afrotropical fauna. If Kudrna's taxonomic judgment is correct, then both *C. webbianus* and *H. wyssii*, as well as *D. chrysippus*, may be relicts descended from ancient (Pliocene or earlier) species or subspecies which once had continuous distributions across North Africa and beyond (Larsen, 1984). This interpretation is feasible given the palaeoclimatic evidence

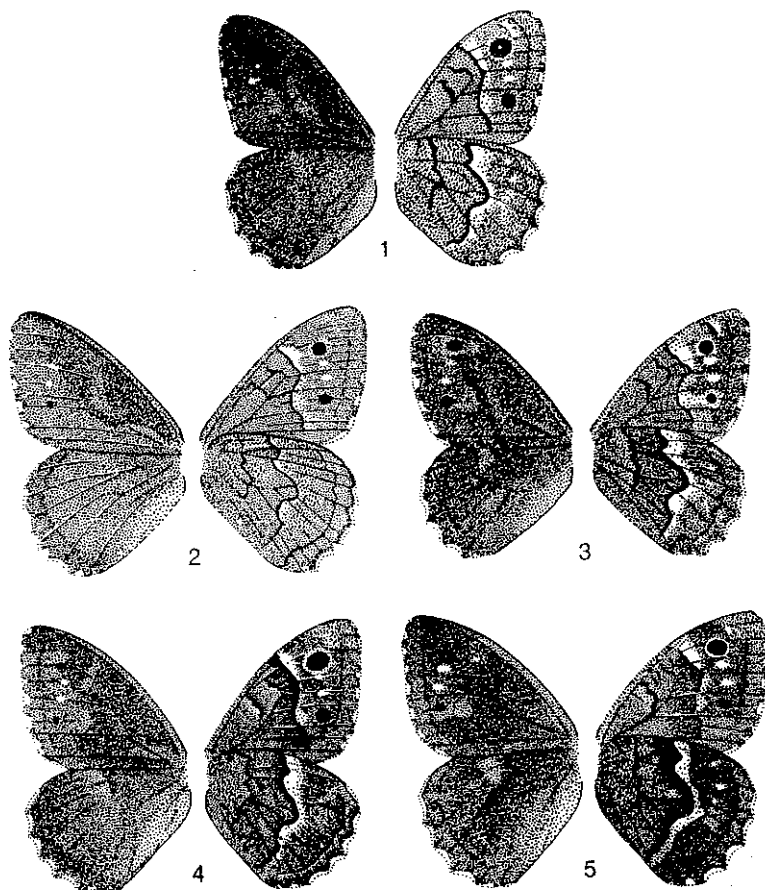and the biogeographical relationships with north-east Africa of some endemic Canary plant genera (eg. Aeonium).

Figure 3. Inter-island variation in male *Hipparchia (Pseudotergumia) wyssii* (Christ) in the Canary Islands. 1. Gran Canaria; 2. Tenerife; 3. La Palma; 4. La Gomera; 5. El Hierro. In each figure, the upperside is on the left and the underside on the right. Each island form is distinguishable by constant differences in pattern, mainly on the underside, which suggests visual selection for background matching as the butterflies normally rest with the wings closed.

H. wyssii shows island subspeciation within the Canaries and is thus a relatively ancient inhabitant: so far three subspecies are described from La Gomera, El Hierro and La Palma with Gran Canaria and Tenerife sharing a fourth subspecies *wyssii* (Table 1). However in the light of recent unpublished collections from Gran Canaria (DASS, 1990-91), we disagree with Kudrna (1977) and are now confident that Gran Canaria and Tenerife butterflies are subspecifically distinct for several constant morphological characters: we intend to describe a fifth subspecies from the former island. In contrast to *H. wyssii*, *C. webbianus* has not undergone visible island subspeciation. Its absence from El Hierro, where apparently suitable endemic foodplants occur, may be explained by the comparatively recent origin of this island.

Equally enigmatic is *Vanessa indica calliroe*, the only definite representative of the Oriental region. It is well established and common on Madeira and the five western Canaries. (It formerly occurred and still occurs as a vagrant on Fuerteventura and Porto Santo.) Wallace (1889), quoting Wollaston, remarked that *V. indica* "is permanently smaller in the small and bare island of Porto Santo than in the larger and more wooded adjacent island of Madeira". Wallace compared *V. indica* on Porto Santo with *Vanessa* (=*Aglais*) *urticae* on the Isle of Man "which is only about half the size of the same species in England and Ireland".) The Macaronesian populations are certainly at least subspecifically distinct from *V. indica* in India and south-east Asia (Bernardi, 1961; Leestmans, 1975), suggesting a considerable period of separation and ruling out accidental introduction by man. And yet there is general agreement that *V. indica* has not noticeably subspeciated further within the islands. It is possible that, during the Pliocene or earlier, *V. indica* or its ancestor occurred in the Mediterranean basin, south of the Tethys Sea or that *V. indica* itself survived the Pleistocene in the north of the Sahara region, which was generally much less arid than it is today (Moreau, 1966). In post-glacial times the Atlantic island populations would have been further isolated by mainland desertification, becoming remnants of a formerly wide geographical distribution, across North Africa and West Asia, when both climate and vegetation were more suitable. On all the islands where it occurs *V. indica* is much more common than *Vanessa atalanta*, a Holarctic species which is probably a recent arrival or frequent migrant from western Europe.

The three species listed in Table 1 as cosmopolitan are all widespread and abundant in many parts of the world; all three are regularly found on even quite small and remote islands (eg. St. Helena). Two, *Cynthia cardui* and *Lampides boeticus*, are migratory, while *Hypolimnus misippus*, also migratory, could additionally be described as irruptive as it typically has long periods of

scarcity followed by short bursts of superabundance. It is possible that *C. cardui* migrates every year to and from the eastern Canaries and western Europe (Owen, 1989). On the other hand, as neither females nor young stages of *H. misippus* have ever been recorded in the Macaronesian islands, in the absence of any evidence of breeding, we consider its status to be that of a rare vagrant.

INTER-ISLAND AND MACARONESIAN DIFFERENTIATION

Five species, *Pieris brassicae*, *Gonepteryx cleopatra*, *Hipparchia wyssii*, *Hipparchia azorina* and *Lycaena phlaeas*, show formally recognized inter-island differentiation and at least two others, *Pararge xiphioides* and *Aricia agestis*, also do so although subspecies have not yet been described or named. All of these subspecies are based on geographical differences in coloration, in some cases on differences in the structure of genitalia, and in size. The Madeiran subspecies of *L. phlaeas* is the least convincing but the remainder are good examples of inter-island differentiation. Our guess is that inter-island differentiation in *P. brassicae* (Fig. 2) is maintained by or associated with climatic (temperature) selection, while in *H. wyssii* (Fig. 3) selection for crypsis may also be involved. There is scope for investigation here and we also predict that isozyme electrophoresis would reveal further examples of differentiation, possibly including differentiation within islands.

There are seven endemic subspecies and species in which inter-island differentiation has not yet been recognised or described, but at least in some instances it probably exists at the biochemical if not at the morphological level. One endemic, *Pararge xiphia*, is confined to a single island (Madeira); the remainder are found on two or more islands. All the remaining species, which are either resident or migratory (Table 4) are considered at present to be identical to mainland forms although admittedly various authors have in the past tried to recognise Macaronesian subspecies.

HUMAN INFLUENCES

The Azores and the Madeiras were not, and had never been, populated until the Europeans arrived in the fourteenth century. The Canaries were inhabited by the Guanches, an isolated group possibly derived from the adjacent coast of North Africa. Although the Canaries were known to the Romans they were effectively "discovered" by Lanzarote Malocello in 1336. Thereafter successive waves of Europeans arrived and fought the Guanches who were exterminated, chiefly it seems, through the introduction of diseases (Crosby,

1986). The Guanches cultivated grains and husbanded some domestic stock but their population size was probably never more than a few hundred thousand and their impact on the environment was small compared to what the Europeans would achieve in the next five centuries.

Before the fourteenth century Madeira was completely forested and one of the first actions by the colonising Europeans was to destroy as many trees as possible. Although the timber was valuable on the European market, demand was not sufficient for the necessary rapid removal of trees and so the forest was burnt. Opinions differ but there are reports of a forest fire raging on Madeira for seven consecutive years (Crosby, 1986). The result must have been devastating for the native flora and fauna.

The first domestic grazing animals were introduced to the Azores in 1439. In addition rabbits were brought in to many islands and became abundant: Porto Santo is reported to have been over-run by them and there is little doubt that the present appearance of the island is largely the result of rabbit grazing.

The Macaronesian islands became the first Atlantic colonies outside Europe. Tropical crops could be grown and many species were tried, along with temperate species. However, sugar cane became dominant, especially on Madeira, but also on the Canaries. The European demand for cane sugar seemed insatiable. Terracing was necessary and water courses had to be constructed because, with extensive deforestation, water became scarcer. Much of the heavy work on Madeira was done by Guanches brought in as slaves from the Canaries. The results of exploitation were overgrazing and, its inevitable consequence, erosion, fewer native plants and more and more alien plants, including many familiar European weeds. Among them was bramble which has today infiltrated just about every remotely suitable habitat. Honeybees had been introduced by the mid-fifteenth century (Crosby, 1987) and there is every reason to suppose that a multitude of other insect species arrived, almost all of them from Europe.

The attraction of the islands to Europeans was the rich, volcanic soil and a climate where both tropical and temperate crops could be grown. Once the Guanches had been disposed of, the Canaries provided an ideal environment for European settlement along with a huge array of European biota. The Azores with their equable, warm and damp climate, provided the Portuguese, after clearance of the dense laurel forest, with valuable pasture, scarce in their homeland, for raising beef and dairy herds. Centuries later the same was to happen to other islands, notably New Zealand.

It is against this background of change that the present butterfly fauna of the islands must be interpreted. The endemic species and subspecies listed (Table 1) can be viewed as the survivors of European settlement. But what of the remainder? We know that *Pararge aegeria* is a recent and successful coloniser of Madeira and that *Catopsilia florella* has only recently established itself in the Canaries. There is considerable evidence that *Artogeia rapae* is in the same category. To these may be added *Danaus plexippus* which apparently arrived on the islands in the nineteenth century. All four of these species are extending their range and abundance in other parts of the world, all except *P. aegeria* in response to direct human influences. Human influence cannot be ruled out even for *P. aegeria* as it is a butterfly of woodland clearings and edges where there is plenty of grass. Furthermore, its chief foodplant on Madeira is *Brachypodium sylvaticum*, a grass introduced from Europe.

Maniola jurtina is typically a butterfly of open grassland and even if it is a pre-European resident, its distribution and abundance must have increased enormously with the felling of forests and the creation of meadow and pasture for domestic stock. The subspecies *fortunata*, shared between the Canaries and North Africa, is larger and brighter than Iberian butterflies. On the basis of a statistical analysis of the number and distribution of spots on the undersides of the wings we suggest that the island populations were derived from North Africa although inter-island heterogeneity also raises the possibility of more than one invasion (Owen & Smith, 1989).

Pontia daplidice, *Elphinstonia charlonia*, *Zizeeria knysna*, *Polyommatus icarus* and *Pandoriana pandora* could also be post-fourteenth arrivals: indeed, apart from the well-differentiated endemics, all species are candidates for this category.

There must also have been losses of both old and post-fourteenth century species but there is no way of knowing which butterflies occurred on the islands before the European invasion: no fossils like those left by molluscs (shells) or by birds (skeletons) have been found. But what is apparent is that the present butterfly fauna is impoverished and we consider it likely that an unspecified number of species, including endemics, were exterminated soon after the arrival of the Europeans. The discovery in Quaternary sands on Madeira of several species of flightless rail, a quail, a large species of *Turdus* and several fringillids, all now extinct, suggests a rich and varied endemic bird fauna (Pieper, 1985) and there is every reason to suppose that the same was true for butterflies.

This viewpoint is not new. Regarding the Lepidoptera of Madeira, Cockerell (1923) wrote, "Among the butterflies the skippers, *Papilio, Melitaea, Euchloe, Aglais, Limenitis* and many other familiar genera are wholly absent. The Lycaenidae are represented only by *Chrysophanus* (=*Lycaena*) *phloeas* and *Polyommatus* (=*Lampides*) *boeticus* .... The poverty of the Lepidopterous fauna, considering the climate and physical features generally, is extraordinary. Yet the Coleoptera are numerous, with many endemic species, and indeed a considerable number of endemic genera." He goes on, "I am convinced that a very large proportion of the present fauna of the Madeiras was introduced by man during the hundreds of years of occupation ...... I would earnestly beg lepidopterists to explore the Madeiras while there is still a chance to find peculiar species and races ...... The native flora is giving place to innumerable introduced species, and the native Lepidoptera must certainly tend to diminish or disappear." Since this was written one species, *Pieris brassicae*, has become local and rare if not extinct and two others, *Pieris rapae* and *Pararge aegeria*, have successfully colonised the island. There seems, however, no prospect of finding additional endemic species.

The superior survival of endemic land snails, beetles and angiosperms, compared to butterflies and birds, is not surprising. Populations of the former two groups are much better equipped to survive prolonged adverse conditions in extremely small pockets of habitat and they are, moreover, less dependent on the survival of individual species of plant or special types of plant community. The survival of a multitude of endemic angiosperm species can be explained by the long periods for which many seeds may remain dormant and viable.

THE PRESENT FAUNA

We do not know and presumably never will how many endemics disappeared followed the European colonisation of the islands. In particular there seem to be too few endemics and indeed too few butterfly species on Madeira compared to the western Canaries, which strongly implicates the effects of man and especially the destruction wrought by the great fire.

In our opinion the laurel forests on El Hierro, La Palma, La Gomera, Tenerife and the Azores ought to support more species of butterfly than they do, even though the forests are now much reduced in extent. The forest is particularly well conserved on La Gomera and La Palma, yet even on these islands there are few species especially associated with it. The most conspicuous are *Gonepteryx cleopatra* and, on La Palma, *Pieris brassicae cheiranthi* although some others, notably the two endemic species of Pararge,

Vanessa indica calliroe and *Pandoriana pandora* are more common in forest than in other habitats. *Artogeia rapae*, almost certainly a recent colonist in the islands, is strongly associated with forest on La Gomera, behaving like *Artogeia napi* (L.) which in many parts of Europe is found mainly in broad-leaved woodland, while *A. rapae* is generally found in open habitats. It is possible that *A. rapae* in the Canaries and Madeira has expanded its niche in the absence of its close relative *A. napi*.

Leaving aside the problematical status of *Danaus chrysippus*, only one endemic, *P. brassicae cheiranthi*, seems to be on the decline, at least on some islands. As already mentioned, it may be close to extinction on La Gomera and Madeira and is now local on Tenerife. However, on recent visits to La Palma (July 1990, August 1991), it was found to be abundant throughout the extensive swathe of laurel forest which clothes the eastern slopes of the Caldera de Taburiente at intermediate altitudes. Eggs and all larval instars were numerous on the endemic crucifer *Crambe strigosa*, many of which had been defoliated. In contrast, neither adults nor larvae were seen in the towns and villages, where the latter occurred on *Tropaeolum* (which was mainly desiccated in July), as they had been in the spring of 1986. The summer distribution and extraordinary abundance of *P. brassicae* on La Palma strongly supports the view, which is not new, that it is essentially a laurel forest species. Perhaps its predominantly urban distribution on Tenerife (around Puerto de la Cruz where its food-plant is *Tropaeolum*) results from scarcity of *C. strigosa* in the severely depleted laurel forest. If this interpretation is correct, the restricted range of *P. brassicae* on Tenerife and its rarity on La Gomera and Madeira, may result from deforestation. Interspecific competition with the recently arrived *Artogeia rapae* may also have contributed to its decline. *P. brassicae cheiranthi* may once have inhabited Gran Canaria where the laurel forest has been reduced to a vestige.

The relatively low number of species on the islands is in marked contrast to the abundance of some individual species. The endemic lycaenid, *Cyclyrius webbianus* occurs in enormous numbers: hundreds can be seen at once in June and July and neither of us can recall seeing other species of lycaenid in such abundance, especially when, as is often the case, no other lycaenid is in the vicinity. Similarly, we have never seen a species of *Gonepteryx* in such abundance as *G. cleopatra* in the laurel forests of La Gomera and Tenerife. The forests are often shrouded in mist but when the mist clears the butterflies appear everywhere and offer a remarkable spectacle. The various endemic *Hipparchia*, too, are locally common as are *Pararge*, especially on Madeira.

The distinctive and striking subspecies *cheiranthi* of *P. brassicae* on the Canaries (Fig. 2) is regarded as highly desirable by butterfly collectors and in our view there is some danger of over-collecting. The same might apply to the distinctive and attractive subspecies of *Gonepteryx cleopatra* which, despite their abundance, could be threatened by collectors who come from Europe to take a series from each of the islands where it occurs. *Vanessa indica* and the various species and subspecies of *Hipparchia* are other "desirable" butterflies which may not be immune from over-collecting.

From a biogeographical viewpoint islands are well known for the phenomenon of double or multiple invasions from the adjacent mainland and the subsequent establishment of two or more sympatric species. The Atlantic Island chaffinches are a famous and well-documented example (Lack and Southern, 1948; Grant, 1979). Chaffinches, *Fringilla coelebs*, the same species as in the western Palaearctic, occur on most islands and have undergone considerable inter-island subspeciation. They occur effectively in all wooded habitats (but are absent from very high elevations) except on Gran Canaria and Tenerife where they are absent from the *Pinus canariensis* forest. Here their place is taken by the blue chaffinch, *Fringilla teydea*, a distinct species presumed to have evolved from an earlier invasion by *F. coelebs* from the western Palaearctic. In the presence of *F. teydea*, the habitat and niche of *F. coelebs* is more restricted than on islands where the former is absent.

No exact parallel exists for butterflies although in view of the likelihood of man-induced extinctions, it may have done so in the past. However, the recent successful colonisation of Madeira by *Pararge aegeria* and its possible interactions with the endemic *Pararge xiphia* presents an opportunity for analysis of competitive exclusion and of habitat and niche differentiation (Shreeve & Smith, 1992; Jones & Lace, 1992). Both species are abundant and already there are indications that *P. aegeria* is establishing itself best in marginal and man-made habitats (eg. non-native forest). We therefore predict that the habitat of *P. xiphia* will become more restricted and that there is the possibility of rapid evolutionary change in the two species, especially as each has three or four breeding generations a year. In the 1980s we collected large samples of both species and these will be available for analysis if or when the two species "divide up" the available Madeiran habitat in a manner reminiscent of what is believed to have occurred in *Fringilla* on Gran Canaria and Tenerife. Hence although the Atlantic island butterfly fauna is believed to be impoverished as a result of human disturbance of the environment during the last five hundred years, there are opportunities for observing ecological and evolutionary adjustments as colonisation proceeds.

We end on a note of euphoria. It is possible to stand in the Botanic Garden at Puerto de la Cruz, Tenerife, and see at the same time butterflies representative of four of the six zoogeographical regions of the world: Palaearctic (*Vanessa atalanta*), Oriental (*Vanessa indica*), Afrotropical (*Catopsilia florella*) and Nearctic (*Danaus plexippus*). Where else in the world can this be done?

ACKNOWLEDGEMENTS

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