DIVERSIFICATION OF LEGUME-FEEDING PSYLLIDS (HEMIPTERA, PSYLLOIDEA) AND THEIR HOST PLANTS (LEGUMINOSAE, GENISTEAE)

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Declaration

I declare that the work recorded in this thesis is entirely my own, unless otherwise stated, and that it is my own composition. No part of it has been submitted for any other degree to any institution.

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Abstract

Psyllids ('jumping plant lice') are small phytophagous insects that are related to aphids, scales and whiteflies (Hemiptera, Sternorrhyncha). Psyllids are highly host specific, occurring on one or a few closely related hosts, and they predominantly feed on dicotyledonous angiosperms. In the subfamily Arytaininae (Psylloidea, Psyllinae) there are five psyllid genera that feed exclusively on shrubby legumes in the Genisteae (Leguminosae, Papilionoideae), and the species diversity for both plant and insect groups is highest in the Mediterranean. I made a detailed field survey of psyllids on Genisteae hosts in the western Mediterranean, including southern Iberia, NW Africa and two of the Macaronesian archipelagos (Canary Islands and Madeira). These collections (over 300) of both psyllids and legumes provided the basis for the taxonomic, phylogenetic and co-diversification analyses presented in this study.

I have reassessed the classification of the legume-feeding psyllids native to Macaronesia, and I have revised the taxonomy of one genus (*Arytainilla*). I present evidence that the largest Macaronesian group has a unique island origin distinct from the predominantly continental genera. This Macaronesian group, which also has three continental members, is described as a new genus in order to clarify the monophyly and placement of this group within the Arytaininae. Seventeen new psyllid species in four arytainine genera, discovered in continental and Macaronesian regions, are proposed.

I constructed phylogenies for both the arytainine psyllids and their legume host plants, in order to compare colonization, biogeographic patterns and island radiations. I present a phylogenetic study of the Palaearctic arytainine psyllids that incorporates both morphological data (adult and nymphal characters) and molecular data (mitochondrial genes: cytochrome oxidase I and II, including the intervening tRNA leucine; and the small ribosomal subunit rRNA). To investigate the evolution of the island legumes and to establish the relationships between continental and island host plants, a molecular

phylogeny of part of the Genisteae was generated from sequences of the nuclear region: ITS1-5.8S-ITS2. The legume phylogeny shows a Mediterranean origin for the Canarian Genisteae (*Adenocarpus*, *Genista* and *Teline*), and a diphyletic origin for *Teline* – with two distinct island groups nested within *Genista*. The psyllid phylogeny shows that the two largest genera are paraphyletic, but there is some evidence that the Genisteae-feeders, as a whole, are monophyletic. The phylogenetic analyses for both psyllids and legumes highlight the problems of establishing host-parasite interactions using traditional morphological classifications alone. Colonization and biogeographic patterns among the island psyllid species implies a close correlation between the radiation of psyllids and the diversity of their host plants.

Psyllid and legume phylogenies are compared in order to establish the extent of phylogenetic congruence between the insects and their host plants. To test assumptions of cospeciation, an absolute time scale is applied to both plant and insect phylogenies. A comparison of psyllid and legume phylogenies suggests that, whilst rare cospeciation events may play a significant role in promoting diversification, historical reconstructions of psyllid-legume interactions are complicated by systemic host switching. Psyllids appear to be opportunistic specialists with host switching occurring when the plant lineage fluctuates in geographical abundance, population structure or through dispersal. However, preadaptation is evident in many cases where selection of a new host may be constrained by plant chemistry and architecture. Successful establishment by a psyllid colonist is more likely when available hosts are phylogenetically and ecologically related to the original host. A history of parallel cladogenesis between psyllid and legume lineages is rejected in favour of a fluctuating lineage model of co-diversification which presents a more realistic interpretation of the present day pattern of host associations.

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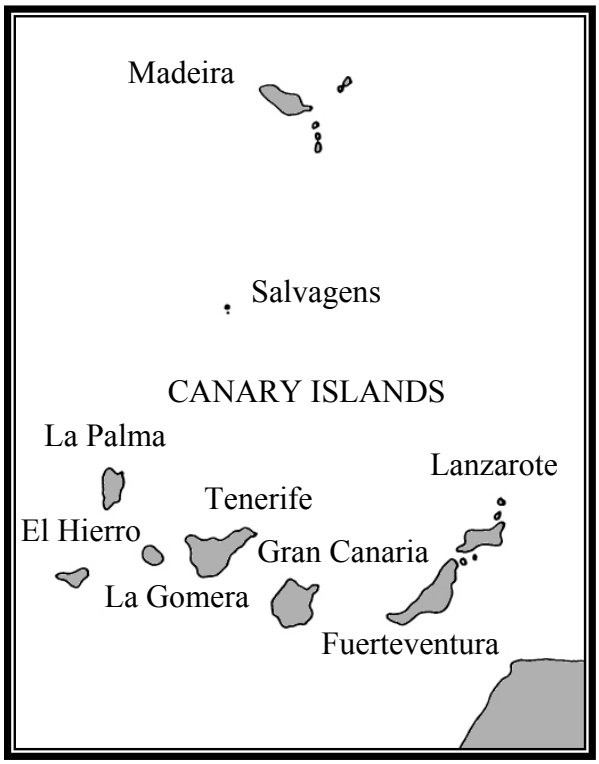
Above: The Macaronesian region showing the five archipelagos (north to south: Azores, Madeiras, Salvagens, Canaries, and Cape Verdes) which lie off the west coast of North Africa and southern Europe, between 15° and 40°N latitude. The geological ages of individual islands range from 1-30 Myr.

Right: The centrally positioned Canary Islands (27°-29°N) and Madeira (33°N) are the focus of this study. Only the five central and western Canary Islands (east to west: Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro) support the habitat type in which the insects and host plants in this study occur.



CHAPTER ONE
INTRODUCTION

1.1 Ocean island research

> 'By studying clusters of islands, biologists view a simpler microcosm of the seemingly infinite complexity of continental and oceanic biogeography ..... their very multiplicity, and variation in shape, size, degree of isolation, and ecology, provide the necessary replications in natural "experiments" by which evolutionary hypothesis can be tested.' (MacArthur & Wilson, 1967)

Island biogeography has influenced a broad range of biological investigation, including systematics, ecology and conservation (Grant, 1998). The science of island, or insular biogeography was made popular by MacArthur & Wilson (1967). It has since contributed significantly to the study of biotas on oceanic islands as well as those in habitat fragments on continents (Pickett & Thompson, 1978; Hanski & Gilpin, 1997). As MacArthur & Wilson (1967) pointed out, the inherent appeal of islands is the 'visibly discrete object that can be labelled with a name and its resident populations identified'.

Volcanic ocean archipelagos have presented biologists since Darwin and Wallace with natural laboratories in which to observe discreet and speciose systems. The most famous example is Darwin's Galapagos finches (Grant, 1986), but more recently the Hawaiian Drosophila with more than 1000 species (Kambysellis & Craddock, 1997) and island plant groups such as the woody composites of the Atlantic and Pacific archipelagos (Wagner & Funk, 1995; Givnish & Sytsma, 1997) have become model groups for the study of speciation processes. Understanding the mechanisms at work in ocean islands has been invaluable to a broader understanding of pattern and process in biogeography and evolution. Ideas that have germinated in the laboratories of ocean islands have proven applicable to continental land masses, where equivalent 'patchiness' in ecosystem patterns has resulted in equivalent 'island' dynamics or 'stepping stone' processes (e.g. the cichlid fish of Africa's Great Lakes, Rüber *et al*., 1998), but these are often more subtle and less easily studied than those found on real islands (Wu & Levin, 1997; Holt & Keitt, 2000).

1.2 Insect-plant interactions

1.2.1 *Introduction*

Insect-plant interactions have played an important role in defining models of interactive evolution such as coevolution and cospeciation (Futuyma & Slatkin, 1983). Although stricter terms of coevolution may be appropriate for some insect pollination and floral syndromes (Thompson, 1994), it is widely believed that herbivorous insect speciation is sequential in relation to the host plant (Jermy, 1976; Menken, 1996). Once insect host specificity is established, close tracking of ecological, phenotypic and chemical changes in closely related host plants may result in phylogenies similar to those arising from cospeciation or parallel cladogenesis. Determining the history of insect-plant associations is crucial to evaluating the cause and extent of associated evolution. Comparing host associations on the mainland with those found on islands provides an insight into preadaptation and the changes in host association that result from island colonization, radiation and ecological specialization.

1.2.2 *The role of insect and plant taxonomy*

Different approaches to the concept of species in the taxonomic treatment of plants and insects can present difficulties when comparing host and parasite phylogenies. Psyllids or 'jumping plant-lice' (Hemiptera, Psylloidea) are small, phytophagous, phloem feeding insects that are typically monophagous or oligophagous (i.e. specific to one or a few closely related hosts). They feed on a wide variety of dicotyledonous and a few monocotyledonous plants. Within the Psylloidea, six families are recognized (Burckhardt, 1987; White & Hodkinson, 1985) and within all families, a high degree of host specificity is typical. This study focuses on psyllids that feed on legumes in the tribe Genisteae (Leguminosae), a tribe which includes the common broom, gorse and related shrubs. The Genisteae has a complex taxonomic history that is littered with synonomy as a result of numerous taxonomic revisions. In contrast, the genistoid-feeding psyllids have been investigated by fewer workers and have been the subject of a limited number of taxonomic revisions. In addition, the legume host classification has numerous intraspecific taxa, while there is only one subspecific taxon among the entire 96 species of Palaearctic arytainine psyllids.

All of the 12 native Leguminosae genera represented in the Canarian archipelago are in the subfamily Papilionoideae, which is considered more evolutionarily advanced than the other two subfamilies, Mimosoideae and Caesalpinoideae (Käss & Wink, 1996).

Six of the Canarian legume genera (50%) are in the tribe Genisteae, which is one of four tribes retained by Bisby (1981) or six tribes delimited by Hutchinson (1964), after the subdivision of the Genisteae *sensu lato* of Bentham (1865).

The Canary Islands, with a history of discovery possibly stretching as far back as Phoenecian navigation of the African coast in 610 BC (Krüss, 1976), experienced a boom of scientific exploration in the late 18th and 19th centuries. Floristically, Macaronesia (with the exception of the Cape Verde Islands) is associated with a circum-mediterranean flora that would have been familiar to the creators of our present system of plant classification. Modern botany took shape in Europe (Walters, 1961) and is largely based on Eurocentric plant distributions. Approximately two thirds of all the genera in Linnaeus's 'Species Plantarum' (1753) are European. These beginnings, it has been proposed, are the root of the artifice constraining current plant taxonomy within a psychological and historical framework resulting in the psychohistorical process of 'chaining' (Cronk, 1989). 'Chaining' arises when taxonomic groups named by Linnaeus, or associated with pre-Linnaeun Medieval classifications have acted as 'nuclei' or 'sinks' for subsequently discovered taxa. This results in falsely 'skewed', large heterogeneous groups such as the genera *Rosa* (Rosaceae) and *Cassia* (Caesalpinioideae), and the subsequent splitting off of small anamolous taxa that can no longer be satisfactorily circumscribed within the larger group (e.g. the Canary Island genera *Dendrosonchus*, *Teline* and *Spartocytisus*). The result is a pattern of a few very large groups and many small groups.

Within the Leguminosae, the three subfamilies recognised today were known to Linnaeus but each was given a very different treatment according to the number and distribution of species familiar to Linnaeus. Hence *Mimosa* (mainly tropical) was established as a single genus to incorporate all of the then known species (39) of today's Mimosoideae (c. 2,820 species); the Caesalpinoideae was created for 19 genera, with the majority of species in the single genus *Cassia*; while the remaining majority of species (378) were placed in 45 genera under the Papilionoideae.

The historical legacy of this early bias is that the Leguminosae contains 18,000 species in 650 genera, and nearly a third of these taxa are in just six genera: *Astragalus, Crotalaria, Indigofera* (Papilionoideae), *Mimosa, Acacia* (Mimosoideae), and *Cassia sensu lato* (Caesalpinoideae).

However, taxonomic artifice alone is not the sole cause of this pattern, which though distorted in shape by human classification, is nevertheless reflective of biological trends within the Leguminosae. Namely, 1) the Caesalpinoideae is an ancient group, primarily of relict species which have undergone little recent speciation, 2) the

Mimosoideae are an ancient group which has undergone a massive bloom of recent speciation and 3) the Papilionoideae are a comparitively recently evolved group, resulting in large, poorly differentiated segregates with complex patterns of variation (Cronk, 1990).

The classification of the Canarian Leguminosae can be explained in the light of both taxonomic artifice and evolutionary trends in the Papilionoideae, with the additional component of adaptive radiation. Members of the Canarian Genisteae have all been incorporated in the large amorphous *Genista-Cytisus* generic group, probably due equally to the process of historical chaining, as to recent evolution in the Papilionoideae, resulting in poorly divisible genera. Both of these genera, *Genista* and *Cytisus* have acted as linked nuclei for a huge complex of species (c. 230 species). Amongst the Canary Island genera, two groups are an example of the budding off of morphologically anomalous taxa – *Teline* and *Spartocytisus* – which have been recognised by some but not all workers as distinct from the *Genista-Cytisus* group, but which molecular data have clearly shown, belong within one or other group (Käss & Wink, 1997; Chapter 4)

Compounding the problems of artifice in plant classification is the dilemma of regional research by many different workers (often lacking communication with one another), versus monographic work done by a few co-workers. This problem is evident in the tropics today and was faced by Linnaeus with access to only a part of the worlds floristic diversity. It is alluded to by Bentham (1875) in discussing Linnaeus's treatment of the Leguminosae 'a disproportionate treatment probably aggravated by the circumstances of the small number of botanists who have access to good working materials in *Cassia* and Mimoseae'. In assessing the amount of synonymy that accumulated during the 18th and 19th century exploration of Macaronesia, it is apparent that a certain degree of 'buccaneer' taxonomy by those working in isolation resulted in a somewhat lawless classification.

It is also possible to examine the reliability of the host plant taxonomy from the perspective of phytophagous insects. Incorporating phytophagous insect preferences into the systematic treatment of plants may prove to be useful, especially in the case of complex species groups. In the Canarian Genisteae, as might be expected, the phytophagous insect 'taxonomy' has tended to lump where human taxonomy has tended to split. The psyllid 'taxonomy' supports many of the species delimitations in the present classification but frequently does not recognise intraspecific taxa which are more likely to be a product of human artifice. The psyllid fauna supports the *Cytisus-Genista* split but suggests that *Adenocarpus* should be sister to the *Genista* group, which contradicts the placement of *Adenocarpus* as an outlier of a monophyletic *Cytisus-Genista* group. However, using molecular data (Käss & Wink, 1997) there is insufficient resolution at the base of the

Genisteae, to contradict or confirm either placement. In another example, psyllid preference appears to contradict all other data – according to the psyllid fauna, *Chamaecytisus* has an intermediate position between the *Cytisus* and *Genista* groups, but the morphological (Cristofolini, 1991) and molecular (Käss & Wink, 1997) data place this genus unequivocally in the *Cytisus* group. Characteristics determining host preference may not reflect phylogeny, i.e. convergences in chemistry and plant architecture, and the plasticity of such characters within the plant group is likely to determine the usefulness of phytophagous insects to plant taxonomy.

1.2.3 *Relative endemic diversity of native legume-feeding psyllids and their host plants*

Comparative numbers for endemic insect diversity in the Canary Islands indicate that psyllids (Psylloidea) have a relatively high endemic diversity when compared, either to the Homoptera as a whole (in which psyllids are included) or to other insect groups. Endemism is even higher (100%) for the native legume-feeding psyllids (Arytaininae) (Table 1). A similar comparison for the host plant group indicates that the genistoid legumes also have a high degree of endemism when compared to the angiosperms or dicotyledons as a whole (Table 2).

There is an association between the number of habitat zones per island and the diversity of native legume-feeding psyllids and genistoid legumes on each island (Tables 3, 4 & 5 and Table 1 Chapter 3). However, the number of endemic species is more closely associated with the proximity of the island to the African continent, although there is a need for caution in interpreting associations, given the small number of islands. The relative paucity of both legume-feeding psyllids and their hosts on Madeira is probably due to the more uniform habitat and climate on this island, and to the greater isolation of Madeira from large neighbouring islands or from a continental landmass (which could serve as sources of immigrants). The greater richness in psyllid fauna within the Canarian archipelago reflects the greater diversity of habitat, climate and variety of ecological niches, as well as greater diversity in host plant genera and species.

The isolation of Madeira increases the likelihood that species on this island will be endemic, and indeed endemism is 100% for the arytainine psyllids and their native hosts. Within the Canary Islands psyllid endemism is also 100% (all 21 species are endemic), but for each of the five islands endemism is consistently less than 50% (Gran Canaria 43%, Tenerife 36%, La Gomera 29%, La Palma 14%, and El Hierro 0%). This scale shows some

TABLE 1.

	no. endemic sp.	% endemic	
Orthoptera	31	37	
Dermaptera	16	66	
Homoptera	160	40	
Heteroptera	107	27	
Coleoptera	1160	59	
Diptera	331	31	
Lepidoptera	190	31	
Hymenoptera	194	23	
Psylloidea	**25**	**62.5**	– all psyllids
Arytaininae	**21**	**100**	– native legume-feeding psyllids

TABLE 2.

	no. endemic sp.	% endemic	
Angiospermae	519	27	
Dicotyledonae	497	31.4	
Genisteae	**17**	**94.1**	– genistoid legumes

Adapted in part from Báez *et al*. (2000) and Oromí & Báez (in press)

association with the distance of each island from the African continent, and its geological age. The highest level of endemism is found on Gran Canaria which is the oldest (14.5-16 Myr) and closest island to the African continent (245 km), while there are no endemic species on El Hierro which is the youngest (1.1 Myr) and furthest island from the continent (489 km) (Table 3).

In comparison, species richness – the total number of psyllid species present on each island – shows some association with island area: 11 species on the largest island of Tenerife (2058 km^2), seven species each on the islands of Gran Canaria (1534 km^2), La Palma (728 km^2) and La Gomera (378 km^2), and four species on the smallest island of El Hierro (277 km^2) (see Table 1 Chapter 3). However, a simple regression analysis using data from the five central and western Canary Islands (Table 1 Chapter 3) indicates that only two components are significantly correlated with species richness per island: altitude (which also dictates the variety of ecological niches, $r^2 = 78.6\%$, $P = 0.045$, d.f. = 4) and the number of potential host plants in the Genisteae ($r^2 = 79.6\%$, $P = 0.042$, d.f. = 4). Yet, the latter component is not a functional correlate, as up to one third (17–33%) of potential host plants (i.e. host congenerics) on an island may not be utilized as hosts. When species richness in the host plant group is assessed using the same predictors, there is a significant correlation with altitude only ($r^2 = 92.8\%$, $P = 0.008$, d.f. = 4), implying that habitat diversity may operate independently on host plant and psyllid groups to promote speciation.

Classification of habitat zones which are primarily determined by altitude and leeward (southern) or windward (northern) locations:

1 – xerophytic lowland, 0-600 m, typically a southern zone
2 – lowland scrub and sabinar (*Juniperus phoenicea*), 100-600 m, northern regions
3 – laurel forest, 600-1000 m, northern regions
4 – fayal-brezal (*Erica arborea* and *Myrica faya*), 800-1200 m, northern regions
5 – pine forest, 600-1900 m
6 – sub-alpine 1900-3700 m

Opposite page:

HABITATS

Top – high altitude subalpine zone on Tenerife, showing El Teide (3717m) in the background and the host plant *Spartocytisus supranubius* in the foreground.

Centre left – cloud sea on the northern slopes of Tenerife

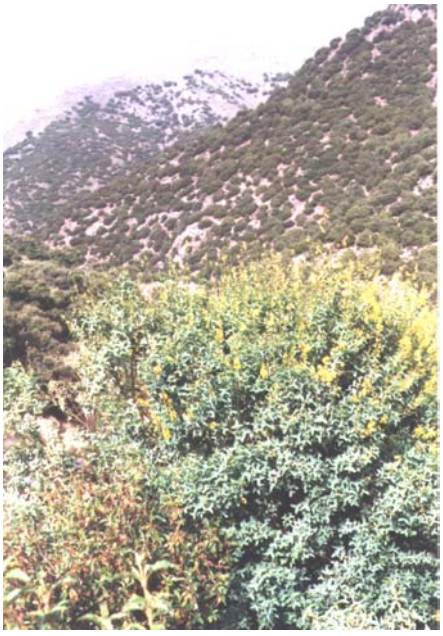
Centre right – pine forest on La Palma

Bottom left – mesic laurel forest on Madeira

Bottom right – lowland xeric scrub on Tenerife, with the host plant *Retama monosperma*.


HOST PLANTS: *Teline splendens* (La Palma) and *Teline stenopetala* (La Gomera)

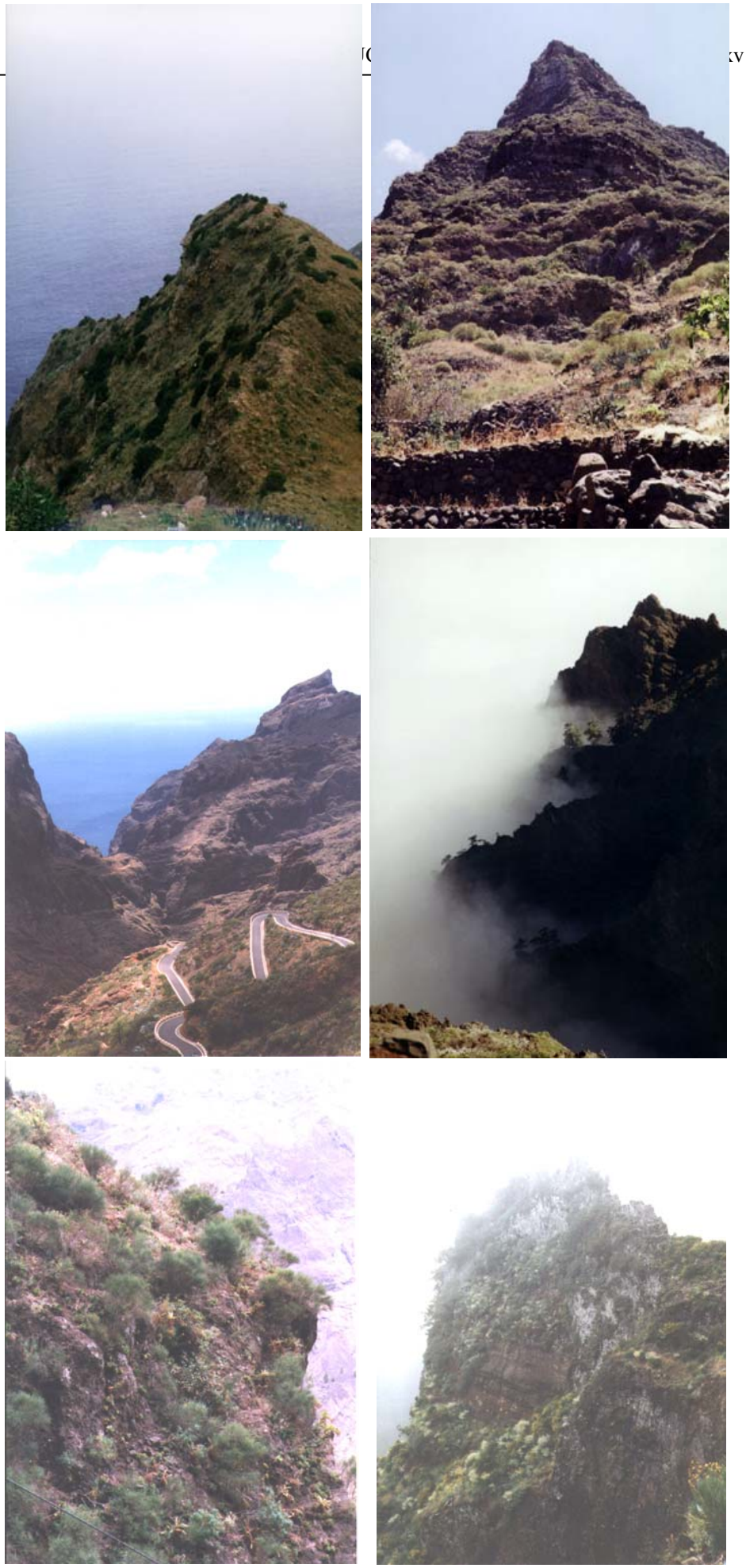

Chamaecytisus proliferus, flowers (Tenerife) and fruit (Gran Canaria)

Cytisus grandiflorus (Andalusía) and *Adenocarpus anagyrifolius* (Moroccan High Atlas)

PSYLLIDS: Adults are usually 2-4 mm in length, left, the largest Canary Island species, *Livilla monospermae* on the host plant *Retama monosperma*. Right, ovipositing female of *Arytinnis proboscidea* on the host *Adenocarpus viscosus*.

NYMPHAL FEEDING SITES: above left and below, eggs and nymphs are usually found on leaves and leaf buds of *Chamaecytisus proliferus*, but above right, nymphs of psyllid species feeding on *Teline* hosts are usually found on the flowers.



The terrain of volcanic islands is often steep and many of the places in which the host plants grow are difficult to access. *Top*: La Gomera. *Centre left*: Tenerife, *centre right*: La Palma. *Bottom left*: La Palma, *bottom right*: Madeira.

ANTHROPOGENIC EFFECTS: Cultivation of the native host plant *Chamaecytisus proliferus* increases host abundance (e.g. on El Hierro, top photo) and may promote psyllid abundance on cultivated and wild populations. Above, a large number of psyllids collected from a single wild individual.

Genista benehoavensis (top) and *Spartocytisus supranubius* (above) on La Palma where they are critically endangered from overgrazing by introduced rabbits and goats. In recent years, successful conservation programs have promoted the regeneration of these species in fenced off areas.

TABLE 3. Relative diversity of psyllids and legumes for each island:

island	no. of habitat zones	no. of Genisteae sp.	no. of psyllid sp.	no. of endemic Genisteae	no. of endemic psyllids
Gran Canaria	5	7	7	3 (43%)	3 (43%)
Tenerife	6	11	11	2 (18%)	4 (36%)
La Gomera	4	6	7	1 (17%)	2 (29%)
La Palma	6	9	7	2 (22%)	1 (14%)
El Hierro	5	5	4	1 (20%)	0

TABLE 4. Distribution of legume plant species (Genisteae) per island:

host plant genera	Gran Canaria	Tenerife	La Gomera	La Palma	El Hierro
Genista	0	0	0	1	0
Retama	1	1	1	1	1
Teline	4	5	2	2	1
Chamaecytisus	1	1	1	1	1
Spartocytisus	0	2	1	2	1
Adenocarpus	1	2	1	2	1

TABLE 5. Distribution of psyllid species (Arytaininae) per island:

psyllid genera	Gran Canaria	Tenerife	La Gomera	La Palma	El Hierro
Arytainilla	0	0	0	1	0
Livilla	0	1	1	1	1
Arytaina	1	2	2	2	1
Arytinnis gen. nov.	6	8	4	3	2

1.2.4 *Host plant specificity*

Strict cospeciation (matching phylogenies) would predict a single psyllid species to be present on each legume species, and in fact the total number of psyllid species in the Canary Islands (21) is only marginally greater than the total number of Genisteae (18) and remains comparable when each island is taken separately (Table 3). However, as mentioned earlier, the number of species in each group are subject to different species concepts and different approaches to taxonomic treatments. The situation is further complicated by the presence of many psyllid species on some legumes, while other legumes do not appear to have a psyllid fauna. In some cases, where a single plant species appears to host many psyllids, these may be associated with intraspecific host taxa.

A more flexible and ultimately more realistic approach to the interactive evolution of plants and insects was championed by J. N. Thompson (1994) in his book 'The Coevolutionary Process'. Thompson (1994) challenged the conventional cospeciation model, pointing out that interactions between plants and insects may not result in prolonged historical associations that can then be mapped onto a phylogenetic tree; but instead there may be a shifting geographic mosaic of transient associations, as a result of differences in the physical environment and the local genetic and demographic structure of populations.

"Differential speciation rates of interacting taxa, differential extinction rates, differences in geographic ranges among interacting species, novel mutations, and new ecological opportunities together prevent complete concordance in almost all comparisons. A run of parallel speciation is soon broken by a shift in one or more parasite populations onto a phylogenetically unrelated host. The larger the number of species in the group, the lower the chance of sustained phylogenetic tracking." (Thompson, 1994)

Thompson (1994) suggested that localized coevolution could take place within a shifting landscape, as part of the fluctuating nature of plant and insect metapopulations; and the history of these transient interactions would not be detected by a strict model of pairwise species for species coevolution.

Primitively, insects were probably saprophagous with a shift to the more complex lifestyle of herbivory, a secondary adaptation (Mitter, Farrell & Wiegmann, 1988). Psyllid fossils have been found from the early Permian before the angiosperms evolved. Thus, psyllids may have primitively fed on gymnosperms, or even lycopods (Hodkinson, 1980). The explosive radiation of the angiosperms in the Cretaceous was paralleled by a massive

radiation of associated insects, and many of the morphological and metabolic characters that the angiosperms exhibit may have evolved as defenses against herbivorous insects (Ehrlich & Raven, 1964; Jermy, 1984).

Allocation of resources in plants can vary seasonally, within an individual plant, between individuals, and from species to species. An example of this is evident in the phenological changes in chemical profile of flowers, leaves, stems, and fruit of the legume genus, *Adenocarpus* (Greinwald *et al*., 1992) – a genus that is host to several Canarian and continental psyllid species. The changing character of an individual plant is a complex and challenging landscape to herbivorous insects (Wink, 1992). An insect that attains an adaptive peak on one plant species is likely to be in an adaptive trough on another species (Janzen, 1979).

1.3 The Macaronesian region

1.3.1 *Introduction*

Macaronesia encompasses the five Atlantic Ocean archipelagos of the Azores, Madeiras, Salvage Islands, Canary Islands and Cape Verde Islands, comprising aproximately 14,400 km^2 lying between 15˚-40˚N latitude. Of all the archipelagos, the most easterly point of the Canary Islands approaches closest to a continental landmass (only 115 km), with successively greater distances to the Salvage Islands (360 km), Cape Verde Islands (500 km), Madeira (630 km), with the Azores the most isolated at 1600 km from a continental landmass. A broad range of geological ages, from 1-30 Myr has been established for these islands (Table 6).

On oceanic islands the combination of altitude and climatic conditions are particularly important in the development of island biodiversity. A comparison of species richness and endemism for the flora of Macaronesia reflects the diversity of habitats in each archipelago (Table 7).

1.3.2 *The Canary Islands*

The Canary Islands occupies a central position within the Macaronesian region, extending over more than 500 km between 27˚37' and 29˚23'N, and 13˚20' and 18˚16'W. The Canaries are 1400 km north of the Cape Verdes and 170 km south of the Salvagens. These islands are exceptional in several respects: the greatest diversity of island ages, altitudes, habitat zones and species richness within Macaronesia are all to be found in the Canary Islands.

The two large, eastern islands, together with the small archipelago of La Graciosa, combine the largest land area in Macaronesia with the lowest altitudes (Table 10). This highly eroded profile and the geological dating of these land masses indicate a far greater age for the eastern islands than that extrapolated for the western islands, which some have taken to imply a continental origin and a rift from the bulge of Africa during the Cretaceous (Schmincke, 1976).

TABLE 6. Characteristics of the five archipelagos:

archipelago	no. of islands	total km^2	highest altitude (m)	latitude N	distance to mainland	distance to closest archipelago	origin Myr BP
Azores	9	2235	2351	37˚	1600	900	4-8
Madeiras	3	796	1861	33˚	630	260	30
Salvagens	2	14	183	31˚	360	170	10
Canaries	7	7273	3718	28˚	115	170	1-21
Cape Verdes	10	4033	2829	16˚	500	1400	6-20 (45)

TABLE 7. Data for angiosperms:

archipelago	no. of endemic species	% endemic	no. of endemic genera
Azores	44	5	0
Madeiras	120	11	1
Salvagens	1	1	0
Canaries	520	27	17
Cape Verdes	92	14	0

Adapted from Humphries (1979), Press & Short (1994), Báez, Martín & Oromí (2000).

Geology

The geological origins of the Canaries are still unresolved with a number of contradictory hypothesis still under debate. Largely disputed now as a piece of 'parascience', which nevertheless was contested academically during the first half of the 20th century, is the 'Atlantis' or sunken continent theory. It was proposed that all five of the Macaronesian archipelagos were part of a single landmass – Plato's Atlantis – which, having sunk, left exposed only the tips of the mountain ranges as aerial islands. Remaining theories still contested seriously are discussed below, and due in part to the variety of questions and resolutions sought, none appear to convince all workers.

It was proposed by Raven & Axelrod (1974) that the break up of the Pangean landmass, approximately 180 Myr BP set in motion the tectonic forces that would eventually result in the formation of the Macaronesian islands. Within the framework of these macrogeological events, the real debate surrounds the source and temporal origin of the individual islands. It is now widely accepted that all the Atlantic islands, with the possible exception of the eastern Canary Islands, are oceanic in origin (Ancochea *et al*., 1990; Carracedo *et al*.,1998). However, there remain some mystifying factors that would be explained more easily if some islands were fragments of the Old World's continental edges, which became isolated with the disappearance of earlier land-bridges and subsequent continental movements. Geologically it appears that the majority of the Macaronesian islands were formed *de novo* during ocean crust volcanism. Although this allows for no direct contact with neighbouring continents, current island size may not be equivalent with historical size. Islands may have been larger or smaller, sediment accumulation and uplifting may have resulted in inter-island or even mainland connections in the case of the eastern Canary Islands (Schmincke, 1976).

Several biological and palaeontological factors are at odds with the geological probabilities. These include the presence of fossil ostrich eggs of Miocene age in Lanzarote and fossils of terrestrial turtles of Pliocene and Pleistocene age in Tenerife. Biologists have found it difficult to come up with dispersal methods for flighless birds and giant land turtles required to explain their presence on ocean islands with no historic link to the mainland. Nor are the striking floristic and faunistic links between Macaronesia, the Mediterranean, Africa, Arabia and America easily explained by the evocation of long distance dispersal alone (Bramwell, 1976; Sunding, 1979).

The proximity of the eastern Canary Islands to the African Continent (only 111 km) (Table 10) combined with the shallowness of the intervening ocean shelf 1000-1500 m, as opposed to 1500-4000 m around the western Canaries, has favoured the hypothesis that the

eastern islands of Fuerteventura and Lanzarote are continental in origin. This is supported by the phytogeographical evidence, with a major split in the floristic element between the eastern and western Canaries (Humphries, 1979). Seismic and gravimetric studies reveal the presence of oceanic crust in the west becoming transitional under Gran Canaria, and possibly continental farther east. It is extremely difficult to determine the origin of the basal crust and the accuracy of these results may be compromised by the accumulation of sediment, hence most studies have focused on the historical development and geodynamics of individual islands (Ancochea *et al*., 1990; Guillou, Carracedo & Day, 1998; Carracedo *et al*.,1999) (Table 8).

There have been three volcanic eruptions this century – on Tenerife (1909) and on La Palma (1949 and 1971) (Table 9). The Canaries are the second most volcanically active archipelago in Macaronesia, and in the Atlantic Ocean region only Iceland and the Azores are more active. Volcanic activity produces stochastic environmental changes that are likely to have a critical influence on the evolution of the flora and fauna, effecting both extinction and creating new environments for colonization (Brown & Pestano, 1998; Emerson, Oromí & Hewitt, 1999).

The ocean floor around the Canaries is estimated to be around 180 Myr old, while the islands are considered to be much younger structures (1-21 Myr) (Table 10). The oldest sedimentary rocks are Cretaceous, from Fuerteventura. While some believe volcanic activity may have begun in the Canaries as early as the late Cretaceous, others believe there is no evidence for volcanism before the Oligocene (Schmincke, 1976).

The ‘Atlas structural trend’ or ‘African trend’ is thought to be associated with the orogenesis of the Atlas mountains, running NE-SW, which is reflected in the alignment of Fuerteventura and Lanzarote and the alignment of Hierro-Gomera-Tenerife. What is termed the ‘Atlantis fracture zone system’ or ‘Atlantic trend’, from which the islands may have arisen, runs NW-SE, and is reflected in the alignment of Gran Canaria-Tenerife-Palma (Schmincke, 1976). However, Carracedo *et al*. (1998) have proposed a ‘hot spot model’ unrelated to the Atlas tectonism, whereby the Canaries originated by an asthenospheric plume.

TABLE 8.

Ages of the shield-building lavas:

island	date Myr BP
Fuerteventura	12-17(20)
Lanzarote	5-11(19)
Gran Canaria	10-16
La Gomera	8-12
Tenerife	4-8
La Palma	0-2
El Hierro	1

TABLE 9.

Dates of volcanic eruptions in the Canaries:

island	date
Fuerteventura	c. 3000 BP
Lanzarote	1730, 1824
Gran Canaria	c. 3075 BP
Tenerife	1704, 1705, 1706, 1798, 1909
La Palma	1585, 1646, 1677, 1712, 1949, 1971
El Hierro	c. 2900 BP

Adapted from: Schmincke (1976), Ancochea *et al*. (1990), Carracedo *et al*. (1998).

TABLE 10. Characteristics of the Canary Islands:

island	altitude m	area km^2	distance from mainland	distance to closest island	origin Myr BP
Tenerife	3717	2058	303 km	27 km – Gomera	7.5-11.5
La Palma	2426	728	489 km	54 km – Gomera	2
Gran Canaria	1950	1534	245 km	57 km – Tenerife	14.5-16
El Hierro	1501	277	489 km	61 km – Gomera	1-1.1
La Gomera	1487	378	417 km	27 km – Tenerife	10-12
Fuerteventura	807	1731	111 km	11 km – Lanzarote	16-20.6
Lanzarote	670	796	112 km	11 km – Fuerteventura	15.5-19

TABLE 11. Canary Island endemism

group	no. endemic sp.	% endemic
Plants	528	21.1
Invertebrates	> 3,054	51
Vertebrates	20	16.1

Adapted from Humphries (1979), Báez *et al*. (2000) and Oromí & Báez (in press)

History

There are several parallels between the anthropological history and the biogeographic history of other fauna and flora groups in the Canary Islands, such as repeated colonizations from the continent, patterns of inter-island colonization and genetically isolated island lineages. The arrival and settlement of humans on these islands is likely to have altered the ecology, with mostly negative effects on the biodiversity (especially the endemic element) evident today (Báez, 1988).

It is thought that the pre-hispanic, aboriginal Canary Island population stemmed from northwest Africa, but was early isolated through founder effect and genetic drift in small colonizing populations which then became distinct, both from the mainland and from populations on other islands. At least three waves of immigration have been proposed to account for the diversity of anthrolpological remains (Schwidetzky, 1976). The first wave of immigrants arrived around 2000 BC and the most recent in early Christian times, around the 1st century AD. Cultural differences between islands is explained by the failure of the most recent immigrants to reach all the islands. There is a distinct gradation from the oldest populations to the most recent, with La Gomera and Tenerife only inhabited by the oldest immigration group, the 'Guanches'. The patchy diaspora is established from skull characters with the extremes represented by the broad, prominent browed cromagnoid type found in La Gomera to the slim, gracile type found in the coastal regions of Gran Canaria. Prevailing winds and ocean currents from north to south combined with the levant winds from the Sahara would have made ocean travel from the continent to the islands far easier than the reverse journey from the islands back to the continent.

Scriptorially (the cave 'inscriptions' of El Hierro) and linguistically there are links to North Africa, with Berber, Egyptian and Libyc associations (Schwidetzky, 1976). Further cultural links are to be found in the ceramics, jewellery, leatherwork, obsidian knives and particularly the ancient Canarian custom of mummifying the dead. Despite associations with developing continental cultures, a lack of basic technological advancement has puzzled investigators. At the time of the Spanish Conquista in the 15th century, there was no use of metals. This led to the belief that the culture was neolithic and estimates of latest immigrations were much earlier than is believed today. Also puzzling is the lack of ship building in the archaeological record. This is strange in a people whose initial colonization must have been by boat, but contributes towards the explanation of the marked isolation of the different island populations.

A more tentative historical record can be found in ancient mythology. It has been suggested that several ancient names refer to the Canary Islands. The 'Elysian Fields' from

Homer (c. 800 BC), the 'three Gorgones' and the 'three hesperides' from Hesiod (c. 800 BC), and the 'Atlantides' from Plato (c. 400 BC). It is thought unlikely that any of these authors knew of the Canary Islands, but it is certain that they were known of by Ptolemy (200 BC) as he placed his '0' meridian through the islands, and until the discovery of the New World, the Canaries were considered the most westerly point on earth. In later mythology, the Canaries were widely alluded to as the 'Happy Islands' due to the absence of snakes and abundance of wild fruit, wine and honey (Virgil, Horace and Pliny 70 BC-70 AD). The Phoenicians knew of the island of Madeira but it is still doubtfull as to whether they visited the Canarian archipelago in their navigation of the African coast (c. 610 BC). It has been suggested that they were responsible for locating Homer's 'Islands of the Cyclops' with the associated idea of barbarism somewhere in the Atlantic, possibly in the Canary Islands. The first incidence of the current archipelago name is 'Canariae Insulae' from Anobius (330 AD) (Krüss, 1976).

Origin of the flora and fauna

The 'Macaronesian' concept was first introduced, not for a geographical or political region, but as a phytogeographical term by the botanist Philip Barker Webb in the 19th century. The diversity of habitats appears to be one of the main factors responsible for the rich Macaronesian flora, which includes c. 780 endemic species, while the diversity and endemism of the invertebrates is even more impressive (Table 11).

The Canary Island biota has the greatest affinity with the biotas of adjacent continental regions (Mediterranean and NW Africa) (Kunkel, 1976). However, there are several groups (both animal and plant) that show remarkable disjunctions, with the closest relatives of the island species found in Australasia, SE Asia, South Africa and South America (Bramwell, 1976; Báez, 1987). Fossil evidence indicates that the present day Macaronesian laurel forest was once the dominant element of a widespread subtropical Tertiary flora, remnants of which still survive around the Mediterranean as well as in southern Africa, Asia and the Americas (Bramwell, 1976; Sunding, 1979). The presence of species associated with the laurel forest ecology in Macaronesia suggests that these islands have acted as refugia, buffered by a relatively temperate oceanic climate, from the massive extinction and migration of plants and animals during periods of glaciation and desertification on the continent (Bramwell, 1976; Sunding, 1979). However, the relictual status of certain plant groups has been controversial. Bramwell (1976) argued that a number of woody island plant groups, based on cytological and morphological evidence, were relictual (e.g. *Bencomia*, *Echium*, and *Senecio*), but these have been shown by

molecular analyses to be recently derived from herbaceous, Mediterranean ancestors (Kim *et al*., 1996; Böhle, Hilger & Martin, 1996; Helfgot *et al*., 2000). These neoendemic groups are examples of spectacular and speciose adaptive radiations, and partly for this reason have been preferentially selected for molecular studies. However, genuine palaeoendemic elements in the Canary Islands may be less amenable to molecular studies because of a lack of suitable outgroups still living today.

The uniqueness of island biotas is partly attributed to adaptations (or loss of adaptations) to features that are peculiar to islands, such as the absence of predators, competitors or specialist pollinators. The diversity of these adaptations may be preserved by the insularity of each island and reinforced following an adaptive reduction in dispersal mechanisms (Carlquist, 1974). However, islands, which are therefore a 'nursery' for evolution and diversity, have proven to be drastically susceptible to aggressive competition and predation from introduced continental elements. This has led to a stability paradox on islands – there is long term stability protecting the diversification and the survival of palaeoendemics, but there is extreme instability when confronted with foreign invasions from recently introduced elements (Cronk, 1997). Thus, isolation may be the cause of a rich and unusual diversity, but also of great vulnerability. As islands are avenues for evolution they can also be cul-de-sacs of extinction.

Effects of seasonality and climate on the flora and fauna

Climate is one of the key features determining the floristic and faunistic character of the Canary Islands. As with other ocean archipelagos, the islands are subject to a relatively milder climate than the continental landmasses due to a temperate oceanic influence. However, the Canary Islands have a far from uniform climatic profile. There are certain prevailing conditions that result in a somewhat predictable pattern but the Canaries also come under the influence of more unpredictable weather systems.

The principle air masses blowing over the Canaries are associated with the Azores anticyclone over the North Atlantic region. Winds blowing outward and eastward from this region acquire a northeasterly direction as they turn towards the south under the influence of equatorial and continental low pressure zones. These winds from the north and northeast form the prevailing trade winds that blow throughout the year and are the most consistent influence of climatic factors in the Canaries (Fernandopullé, 1976).

The lower layer of the trades is thin, usually only 1000-1500 m, and humidity is acquired during traversion of the cool ocean waters resulting in a characteristic formation of extensive strato-cumulus clouds. These winds also attain the highest mean wind speeds,

27 km/hr (Lanzarote) to 14 km/hr (Tenerife) according to the shape and size of the geographic 'wind break' features.

Less prevalent winds blow from the NW, W and SW in association with winter depressions over the Atlantic. Anti-trade winds associated with hot, dry Saharan winds blow from the SE and sometimes E. The effect of the hot, dry anti-trades above the lower humidified trade layer results in a temperature inversion often forming at about 1000 m around the higher islands and resulting in the characteristic and dramatic cloud seas. The inversion layer shifts seasonally, being lower in summer and higher in winter. The winter cloud bank is therefore thicker but it is less persistent, while the summer cloud bank is permanent during the summer months of June and July.

Differences in climate between individual islands are determined primarily by the altitude of the island and by its proximity to the African continent. Mean monthly temperature varies with altitude from 27°C at sea level to 7.5°C above 3200 m. Local variation within islands becomes increasingly pronounced with altitude, and the higher islands rising above the inversion zone are subject to dramatic variation in temperature and precipitation between the northern (windward) slopes and the southern (leeward) slopes. Local land and sea breezes also effect the formation of the cloud banks. Clouds that are widespread over the sea, arrive on the windward side and pile up on the mountain slopes aided by sea breezes during the day, at night land breezes push the cloud bank offshore. In contrast, on the leeward slopes cloud banks may form 10-15 km offshore but do not form over land because of the heating effect produced by descent over the dry slopes (Fernandopullé, 1976).

Two forms of precipitation occur in the Canaries. Winter rains are the result of cyclonic depressions associated with North Atlantic air masses and northerly or north westerly polar maritimes. Occasional heavy precipitation results from humid tropical maritime air masses from the SW, and tropical cyclones originating over the African continent and arriving from the E. Sixty per cent of the yearly rainfall occurs between December-January, and in most cases the total annual precipitation occurs within 10-40 days of rainfall. The intensity of these rains is similar for northern and southern slopes but the number of rain days is higher in the north. Daily intensities vary with between 25-300 mm/24hr, indicating that 25-40% of the total yearly rainfall can occur in 24 hours. A second source of precipitation results from orographic uplift of the humid winds and horizontal precipitation from condensation by fog and mist associated with the cloud bank. Unlike the cyclonic winter rains, these forms of precipitation are exclusive to the northern slopes. Horizontal precipitation is believed by local people to be an important source of

water and there is a famous story of the ‘árbol de lluvia’ or ‘rain tree’ of El Hierro. The story relates how large cisterns (of which remnants survive today) were carved out of rocks beneath the tree, and collected sufficient water dripping from the foliage to meet the needs of the local people. On arrival of the Spanish Conquista this valuable resource was kept secret. However, a local girl who was enamoured of a Spanish soldier was persuaded by her lover to give the secret away, for which she was condemned to death by the islanders (Bramwell & Bramwell, 1990).

Orographic factors are the most important general distributors of rain in the islands, and as these factors are a result of altitudinal gradients, low islands such as Lanzarote and Fuerteventura lack the high relief barriers to catch the humid winds. Islands of medium height (El Hierro and La Gomera) are high enough to accumulate a large amount of cloud cover over the whole island, while the high islands (Gran Canaria, Tenerife and La Palma) rising above the cloud layer act as barriers which result in dramatically different climatic zones above and below the inversion zone. Thus low islands (Lanzarote and Fuerteventura) near the African coast have a semi-desert climate, while the central and western islands range from semi-arid southern areas to sub-tropical northern areas, and sub-alpine peaks with snow caps of 30-40 cm recorded for El Teide (Tenerife).

The summer is relatively quiescent compared to winter weather systems. The dry season lasts from May to August and in the height of the summer during July and August, heat waves from the Sahara influence weather conditions in the Canaries for up to 20-25% of the time. There is a clear pattern of increasing rainfall in a westerly direction away from continental Africa (Table 12).

TABLE 12. Mean rainfall for the period 1949-1967:

island	mean rainfall mm/yr
Lanzarote	135
Fuerteventura	147
Gran Canaria	325
Tenerife	420
La Gomera	410
El Hierro	426
La Palma	586

Adapted from Fernandopullé (1976).

1.4 Genesis and rationale for this study

The initial aim of this study was to select a plant-insect system that could be investigated against the backdrop of island biogeography. Preferably, a highly host specific insect group that was associated with one of the famously speciose plant groups, arisen from a dramatic adaptive radiation. The Macaronesian region, and in particular the Canary Islands, was selected primarily because these islands had been the focus of a number of exciting evolutionary studies in the last decade, but also important was the element of a logistically feasible field site (i.e. travel, expense, and facilities).

There had been several phylogenetic studies of independent plant and insect groups from Macaronesia, but there were no studies dealing specifically with interactions between native plants and insects. Selecting the plant and insect groups was the first step. I had narrowed the possibilities down to a hemipteran insect group, but I had little idea of which group would be suitable until the end of my first week collecting in the Canary Islands (1997). I noticed the legume-feeding psyllids quickly because I always found a member of this group on every legume I sampled, while there appeared to be less consistency (to my inexperienced eye at least) in the mixed assemblage of insects gathered from other target plant groups. However, it was not until sorting through these collections under a microscope at the University of La Laguna, that I began to realize that each psyllid from the different legumes sampled was a different species. In fact, this was the first major hurdle – learning how to identify psyllids, predominantly by characters of the genitalia. By the end of my first visit to the Canary Islands, I was convinced I had the right system and I had begun to sample systematically from every legume species/subspecies and population I could find, in the five central and western islands. The collecting I did in this first year produced five of the 10 new species discovered on the Canary Islands. A broader and more detailed survey in my second year included the Canary Islands, Madeira and continental regions – especially the Moroccan Atlas mountain ranges; and an additional twelve new species were discovered. This brought the number of new species I would need to name and describe to 17.

Although the focus throughout this study has been predominantly on the Canary Islands, the sampling in adjacent regions has provided a vital phylogenetic and biogeographic framework in which to view the evolution of the Canary Island psyllids. By far the most detailed sampling was undertaken in the Canary Islands, including repeated sampling of the same host populations at different times of the year and in different years, in order to monitor fluctuations in psyllid populations. A series of pilot host transplant

experiments in the field showed a high level of mortality among psyllids transplanted to foreign hosts, as well as an association in the rate and extent of mortality with the phylogenetic distance of the foreign host. Unfortunately, further research following up these preliminary hosts transplant experiments was beyond the scope of this PhD.

The taxonomy of the legume-feeding psyllids in this study was unsatisfactory when I started, and the need to describe and classify the new species I had collected led me undertake the revision of the genus *Arytainilla* presented in Chapter 2. As my work on the alpha taxonomy of the psyllid group progressed contemporaneously with the construction of the molecular phylogenies, I was able to cross reference between the two approaches, which I feel was advantageous to the interpretation and results of both. Molecular data provides an important contribution towards interpreting the monophyly or paraphyly of morphologically determined groups (particularly where there may be a high level of morphological homoplasy). Paraphyletic genera and taxonomic ambiguity in both insect and plant groups may reflect periods of rapid and, in some cases, recent diversification, resulting in poor differentiation of groups using either morphological or molecular data. In order to analyse the patterns of island and host plant colonization, I needed to resolve sister taxon relationships within groups. I determined that this would be best achieved by comparing and combining phylogenetic information from both morphological and molecular characters. In Chapter 3, I present the first phylogenetic analysis for the psyllid group. I compare and contrast molecular and morphological phylogenies, and I use both types of data to investigate the psyllid classification and evolutionary patterns in continental and island species.

An extremely confused taxonomy characterizes the legume classification (based on morphological data) and previous molecular phylogenies have inadequately sampled the major Canary Island host plant groups. Early on, it became apparent to me that accurate assessment of psyllid-legume interactions would be hindered without a detailed molecular phylogeny for the host plants. This led me to produce the molecular legume phylogeny, presented in Chapter 4, which has proved essential for interpreting the patterns of host preference and host switching in psyllids. For instance, the most polyphagous psyllid in the Canary Islands feeds on three legumes, but these three legume species have near identical sequences for the nuclear region sampled, suggesting that this psyllid, based on molecular evidence, is in fact monophagous. The construction of accurate phylogenies for both psyllids and legumes was the only way to address the question of cospeciation in Chapter 5, and to undertake the analyses required to test assumptions of parallel cladogenesis.

In many respects each aspect of this thesis, field surveys, taxonomy, morphological and molecular phylogenies as well as the combined synthesis, would all benefit from another three years study. However, in the past three years, I believe I have made some inroads into the complex and multilayered dimensions of insect-plant interactions. Perhaps my only regret is that I did not spend the entire three years of this study in the field, as there remains a great wealth of evidence to be gathered.

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