Chapter 13

Insect-plant interactions on islands: codiversification of legume-feeding psyllids (Psylloidea) and their Fabaceae hosts

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Introduction: species interactions on islands

The term codiversification can be used to describe variable degrees of interaction from strict pairwise cospeciation to more diffuse interactions between organisms that are implicated in some way in coevolutionary processes. To review and elucidate the origins and evolution of codiversification systems in an island context, I will reference empirical data from an endemic psyllid-legume (insect-plant) system in the Macaronesian islands. The colonization of islands, as well as the temporal patterns of establishment and diversification within these restrictive geographic areas, can greatly enhance our understanding of evolutionary processes in closely interactive systems.

Studying diversification in a lineage of organisms is challenging. An additional set of challenges, as well as opportunities, come into play when studying the interactions between two or more lineages (Silvieus *et al*., 2008). Added to the analysis of patterns and timing of speciation events in the individual lineages is the need to understand the history of the interactions between species through time. The question: “to what extent does one lineage influence the diversification of the other?” can only be understood fully within a historical framework, giving us some idea of how the interactions that we observe today originated.

Codiversification studies are, therefore, usually dependent on there being phylogenetic reconstructions for all lineages involved (Page, 2003). Furthermore, a means of calibrating the timing of speciation events implicit in the phylogenies is critical to our understanding of the evolutionary processes. Using island archipelagos that are oceanic in origin with established geological ages (e.g., the Macaronesian, Galápagos, and Hawaiian Islands) has provided us with some of the best known historical frameworks for studying speciation events (Craig *et al*., 2001; Emerson, 2008; Emerson & Gillespie, 2008).

Islands are famously known as natural laboratories because they provide natural geographic replicates of evolutionary processes, which, when compared between islands and archipelagos, provide clear and powerful evidence for the role of adaptation in species diversification (Grant, 1998). For instance, the development of inter-species interactions within an archipelago, such as those between a plant and an insect lineage, will shift and change between islands as the composition of species differs, providing natural comparisons of the different evolutionary outcomes. This, together with the often young age of oceanic islands compared to continents, so that much of the original speciation patterns remain observable due to low extinction rates, makes islands ideal places to study evolutionary processes such as complex, multi-lineage interactions that are an integral part of the diversification of island biotas.

Codiversification

The term codiversification may be taken to broadly encompass many different levels of interaction, including the more specialized terms cospeciation and coevolution. The terminology used usually implies different strengths of reciprocal selection. For example, gene-for-gene coevolution is sometimes used for pathogen-host interactions (Fenton *et al*., 2009); whereas cospeciation is frequently used to describe the endosymbiont-host relationship found in herbivorous insects (Clark *et al*., 2000; Gruwell *et al*., 2007). There are examples of genotypic variation in pea aphids feeding on alfalfa versus clover (Via & Hawthorne, 2005), and gene duplications are involved in the defence and counter-defense in plants and butterflies (Wheat *et al*., 2007). These studies indicate that even in relatively diffuse coevolutionary systems, such as plant-insect systems, reciprocal selection is likely, and selection may be acting on one or a few, to many, gene loci.

Broader analyses of codiversification patterns can be achieved with comparative phylogenetics that enable historical reconstruction for whole lineages of organisms (Becerra & Venable, 1999; Silvieus *et al*., 2008). Comparative phylogenetics approaches have been applied to the analysis of very different types of interaction from the assemblage of communities of species at the local level (Nyman *et al*., 2007), to the global spread of disease (Thompson, 2005; Leendertz *et al*., 2009).

A high level of parallel cladogenesis in a phylogenetic comparison of two or more lineages may be suggestive of cospeciation; but strict cospeciation requires both parallel cladogenesis and temporal synchronicity before the inference can be made that species divergence in both lineages occurred concurrently (Percy *et al*., 2004). If there is evidence for parallel cladogenesis but not temporal synchronicity, then the processes of speciation that we can infer differ from those under a strict cospeciation model (McKenna *et al*., 2009). For instance, if a parasite lineage did not speciate at the time the host speciated, but nevertheless, the speciation event in the host led, at some later date, to a speciation event in the parasite, then the process – in this case sequential speciation with host tracking – is different from synchronous cospeciation. Sequential host tracking was proposed as a common mode of host selection and diversification in phytophagous insects by Jermy (1976) and is similar in process to the "escape and radiate" coevolution proposed by Ehrlich and Raven (1964).

Increasing numbers of time calibrated molecular data sets are proving that asynchronous diversification, with the insects diversifying on already diversified plant lineages, is the norm for phytophagous insects (Winkler & Mitter, 2008). Other cases where there is evidence for near contemporaneous speciation events require further testing but could prove to warrant the term cospeciation (Farrell, 2001; Becerra, 2003).

The psyllid-legume system in Macaronesia

The psyllid (insect) -legume (plant) system in the central Macaronesian islands consists of species that belong to a broader diversification of both psyllid and legume lineages in continental Europe and Africa. Macaronesia is an assemblage of islands over a large geographic area between latitudes 15˚–40˚N, from the temperate northern Azores; through the central Madeira, Salvagens, and Canary Islands with Mediterranean and North African affinities; to the more tropical sub-Saharan Cape Verde Islands in the south. The psyllid-legume system described here is found on the central Macaronesian islands of Madeira and the Canary Islands (27˚–33˚N).

I first established the patterns of species diversity independently for the psyllids and legumes to address questions such as: "how many colonization events were responsible for the current diversity of psyllids and legumes?", "how many insular speciation events occurred within islands versus between islands, and allopatrically versus sympatrically?", and "how many plant species does each psyllid species feed on?". With these general patterns established, I could then address the question: "how did patterns of colonization and speciation in psyllids and legumes influence the interactions between the two lineages?".

Phylogenetic reconstruction and thorough taxon sampling are both important when testing for codiversification where the evolutionary branching pattern and sister taxon relationships are essential to the interpretation of cospeciation. Sampling is critical because unsampled taxa can influence the inference of species relationships. Using island systems is advantageous in this regard because smaller, discrete geographic units are easier to sample thoroughly.

The insects – psyllids

Psyllids are small (2-8 mm), plant sap-feeding insects in the Psylloidea (Hemiptera), commonly called "jumping plant lice". They are related to whiteflies (Aleyrodoidea), scales (Coccoidea) and aphids (Aphidoidea). Collectively, these four insect groups are known as the Sternorrhyncha and all are considered to be plant parasites. There is some anecdotal evidence to suggest that aphids and psyllids may competitively exclude one another (Fagundes *et al.*, 2005), and therefore the presence of one or the other may indirectly benefit the plant by limiting the diversity of parasitism that the host plant is subject to; and observers witnessing the congregation of adult psyllids on floral structures (e.g., *Salix* catkins) and the presence of pollen on these insects have considered whether they could effect pollination. A number of Macaronesian psyllids lay their eggs on or near floral structures, and nymphs are also found on these organs, but to date there is no evidence of any interaction other an insect parasite-plant host interaction in the psyllid-legume system in the Macaronesian islands (Percy, 2003a).

Using both molecular and morphological data, I established the taxonomic and phylogenetic relationships of the 23 native legume-feeding psyllids in the Canary Islands (21 species) and Madeira (two species), all of which are endemic (Percy, 2002, 2003a, 2003b). The phylogenetic analysis revealed that the native Macaronesian psyllid fauna of 23 species was derived from probably five, but possibly four, colonization events; but that only one of these resulted in a significant species radiation giving rise to the genus *Arytinnis*, with 18 endemic island species (16 species in the Canary Islands and two species in Madeira). Although not an endemic island genus, *Arytinnis* very likely originated in the Canary Islands where the centre of diversity lies (16 of the 21 species). The two Madeiran and three continental species are nested within the Canarian *Arytinnis*, and it is likely that both Madeira and the continent were colonized from the Canary Islands (Percy, 2003b).

The other island colonization events (all to the Canary Islands) resulted in either no species radiation (three colonization events giving rise to a single species in the genus *Livilla*, a single species in the genus *Arytainilla*, and a single species in the genus *Arytaina*), or a very modest species diversity of two species after a second colonization in the genus *Arytaina* (Percy, 2003b). This asymmetry in levels of diversification in these groups raised two questions:

"why did only one colonization event give rise to a significant radiation of species?", and "what are the constraints limiting radiation after colonization in the different psyllid genera?".

The legume host plant association for each psyllid species was established with field surveys of the placement of eggs, presence of non-winged immature stages, and the presence of adults on different host populations (Percy, 2003a). A simple numerical comparison of the number of psyllid species and genera with the number of legume species and genera, and the distribution of psyllids on legumes, suggested that the level of host plant diversity was the most likely factor promoting or constraining psyllid diversity (Figure 1). A majority of the 23 psyllid species in Macaronesia were found to be monophagous (20 species) – feeding on a single legume species – and only three species were found to feed on more than one legume species (Figure 2; Percy, 2003b).

I used sister species comparisons to assess the causes of speciation in this psyllid system and found that the majority of psyllid speciation events involved allopatry, either jointly with a host switch to a closely related host (six examples) or without a host switch, i.e., allopatrically on the same host (four examples). Only two sister species pairs, one continental and one in the Canary Islands, may have involved speciation sympatrically via colonization of unrelated legumes (Percy, 2003b). The colonization of distantly related plants together with subsequent formation of host races through strong diversifying selection and reproductive isolation may be necessary for sympatric speciation in psyllid-plant systems, as well other phytophagous insects (Nyman, 2009). Although the dominant pattern involved in the psyllid-legume system is psyllid speciation via shifts to closely related legumes, there were at least two host switches in the Canary Islands from the *Teline* host group to plants in unrelated legume genera (*Adenocarpus*, and *Chamaecytisus* in the *Cytisus* host group).

The host switch to *Adenocarpus* gave rise to two psyllid species, one on each of the two common *Adenocarpus* species; and host switches to *Chamaecytisus proliferus*, an endemic Canarian species, apparently occurred twice or even three times (Figures 3 & 4). All of these host switches occurred within the most diverse psyllid genus, *Arytinnis*. The other colonizations of the Canary Islands did not involve any wide host switching, only diversification on closely related legumes. For instance, the endemic legume genus, *Spartocytisus*, with two species, is host to two endemic psyllid species as a result of a colonization from the continent; two legume genera (*Chamaecytisus* and *Retama*) each represented by a single island species are host to psyllid species that independently colonized from the continent but did not, thereafter, undergo further species diversification.

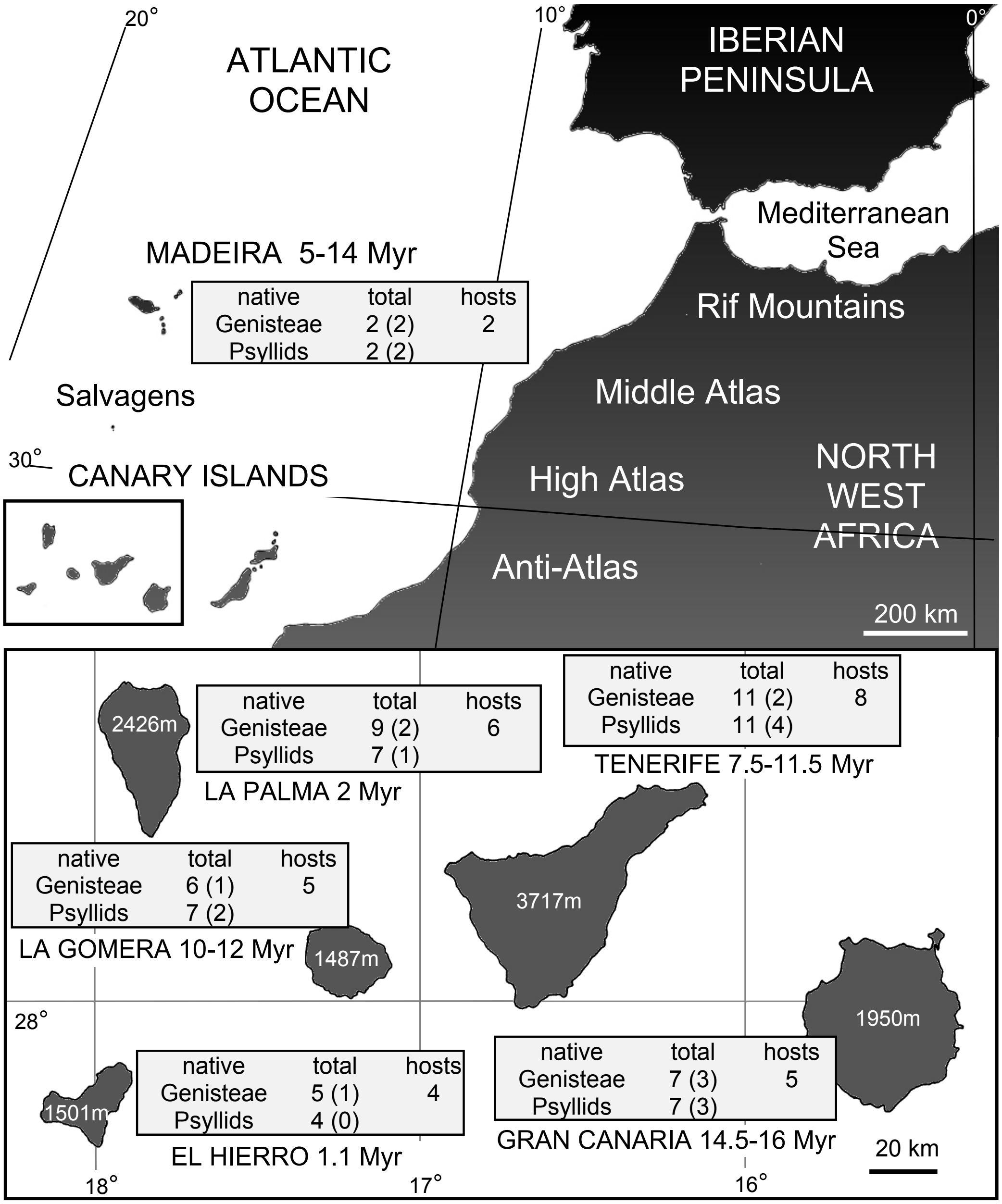

Figure 1. Map of the Macaronesian islands and adjacent continental areas surveyed for this study. Boxes give the number of native legume species (Genisteae) and psyllids (Arytaininae) on Madeira and each of the central and western Canary Islands (number of endemic species in parenthesis), and the number of Genisteae species on which psyllids are found (modified from Percy, 2003b).

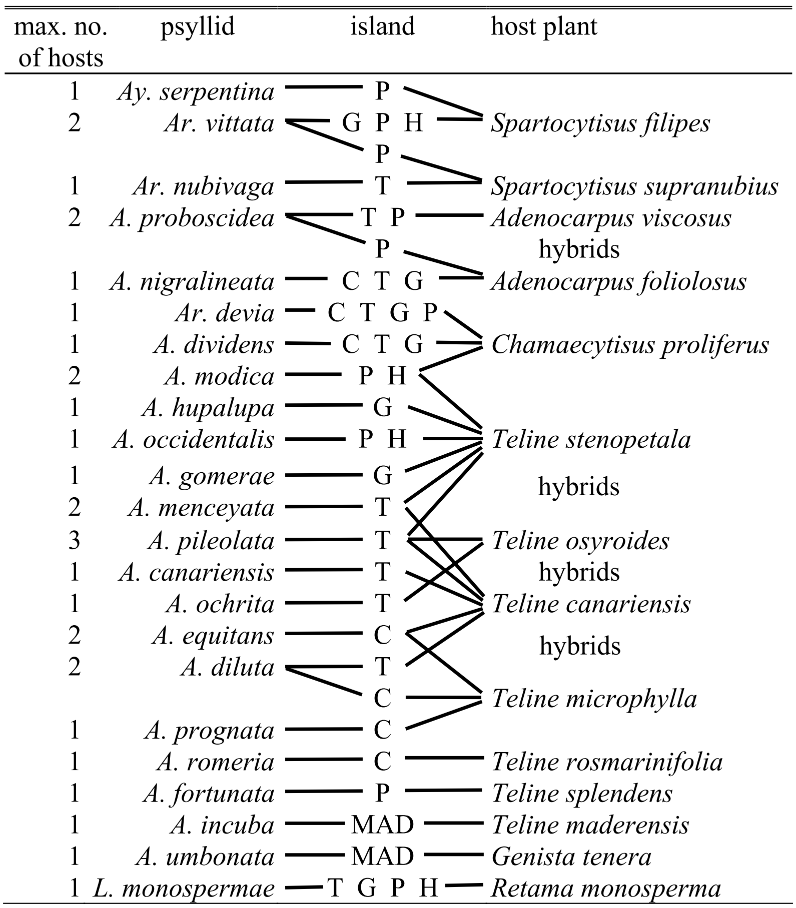

Figure 2. Summary of the distributions and host associations for the 23 Macaronesian island psyllid taxa (A. – *Arytinnis*, Ar. – *Arytaina*, Ay. – *Arytainilla*, L. - *Livilla*). Multiple psyllids on a single host often occur on different host subspecies (e.g., the five subspecies of *Teline stenopetala*) (Percy, 2003a). Hybrids between host plants are indicated where these have been recorded (Lems, 1958; Arco Aguilar, 1983; Suárez Rodgríguez, 1991) (modified from Percy, 2003b).

Another pattern found in the Canary Islands, as well as in other psyllid-plant systems, is for common and widespread host plants to accumulate multiple psyllid species. A number of legumes in the Canary Islands, particularly widespread ones occurring on multiple islands (e.g., *Chamaecytisus proliferus* and *Teline stenopetala*), are host to multiple psyllid species (Figure 2).

The legumes – brooms

The legumes in this study are members of the Genisteae commonly called “brooms”. The centre of diversity for this group is circum-Mediterranean. The phylogenetic analysis of the brooms revealed that, as for the psyllids, there were multiple colonizations of the Macaronesian islands, but only one genus, *Teline* (12 species), underwent a radiation; although, as it turned out, the molecular data revealed this to be two smaller radiations of five, and seven species, from two independent colonizations (Percy & Cronk, 2002). As well as being polyphyletic, *Teline* was also found to be nested within the larger broom genus, *Genista*. Interestingly, there is some evidence that, as with the psyllid genus *Arytinnis*, both continental and Madeiran *Teline* taxa may be derived from the Canary Islands, although low resolution at the base of this *Teline* clade prevented definitive conclusions about the directions of colonization (Percy & Cronk, 2002).

Each of the nine colonizations of Macaronesia by brooms resulted in different patterns of diversification within Macaronesia that appear to have strongly influenced psyllid diversification. For instance, the two *Teline* groups are characterized by single island endemics and within island diversification, whereas the two *Adenocarpus* species exhibit horizontal diversification whereby species are distributed over multiple islands according to altitudinal and ecological niches (Percy & Cronk, 2002). These patterns and extent of diversification, such as the partitioning of ecological and altitudinal niches, are often closely mirrored in the patterns of psyllid species diversity (Percy, 2003b).

Once we had established species diversity, geographic distributions, and host plant associations, for both legumes and psyllids, we proceeded to test whether congruence between the phylogenies, given the interaction between a psyllid and a legume species, indicated a likely cospeciation event (Percy *et al*., 2004).

Cospeciation analysis

A number of striking similarities were immediately apparent when comparing patterns revealed by the psyllid and legume phylogenies. Both the legumes and the psyllids have similar levels of species diversity in the Canary Islands and Madeira. For instance, there are six genera and 25 native species of genistoid legumes (Genisteae) and five genera and 23 species of genistoid legume-feeding psyllids (Arytaininae) (Percy & Cronk, 2002; Percy, 2003b; Percy *et al*., 2004).

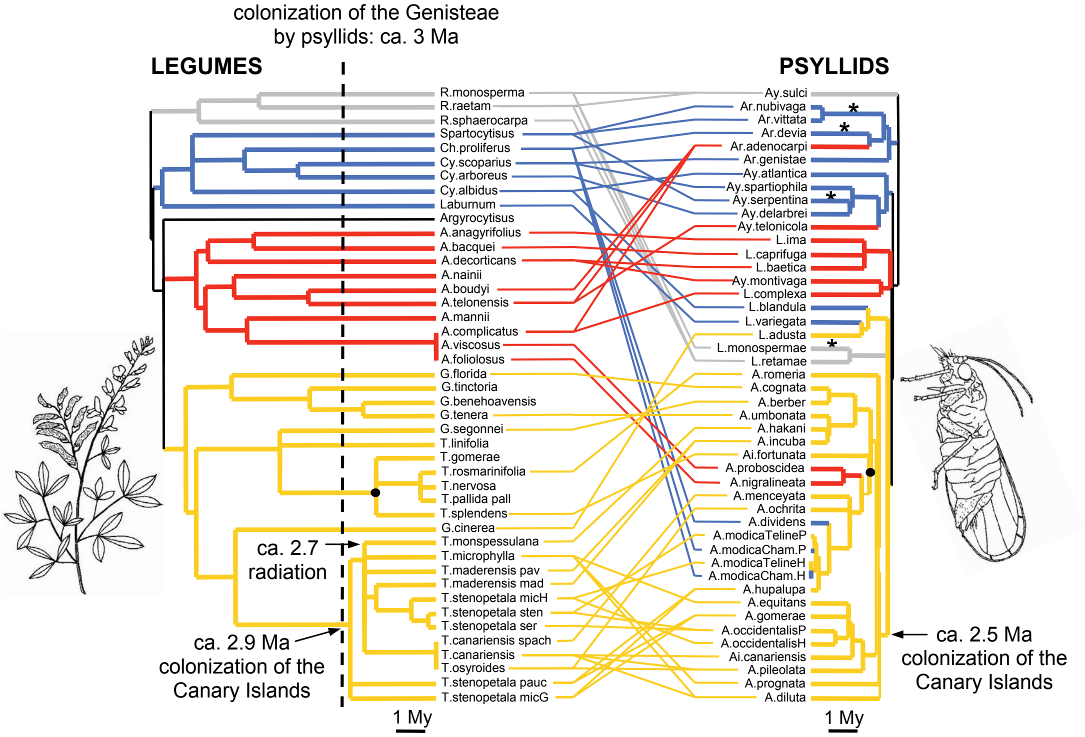

Figure 3. A ‘tanglegram’ from the program TreeMap (Page, 1994) of the insect-host plant associations for the legume-feeding psyllids (right) and their Genisteae (legume) hosts (left). Four main legume lineages are distinguished: *Retama* (grey), *Cytisus* (blue), *Adenocarpus* (red) and *Genista* (yellow). The psyllids specific to these legumes are indicated by the same coloured branches. In most cases, psyllid species within a group are associated with a single legume group, but some psyllid-legume associations have involved a wide host switch between legume groups. The dates on the psyllid tree are much younger than the dates on the legume tree, indicating a colonizing not a cospeciating psyllid lineage. Calibration points used to date the phylogenies are indicated by a black dot. Although there were several independent colonizations of the Canary Islands by legumes and psyllids, only one could have been contemporaneous (around 2.5 and 2.9 Ma), with a single potential cospeciation event during the radiation of legumes and psyllids in the Canary Islands. The evolution of other island psyllid lineages (indicated by asterisks) substantially postdate the evolution of their island legume hosts. Psyllid genera: *Arytaina* (Ar.), *Arytainilla* (Ay.), *Arytinnis* (A.), *Livilla* (L.); Legume genera: *Chamaecytisus* (Ch.), *Cytisus* (Cy.), *Genista* (G.), *Teline* (T.) (modified from Percy *et al*., 2004).

None of the psyllid genera and only one of the legume genera are endemic, but 24 of the 25 species of legumes and all of the 23 species of psyllids are endemic. In addition, the most diverse psyllid genus, *Arytinnis*, with 18 endemic species, includes 13 species which feed exclusively on *Teline*; and *Teline*, with 12 endemic species is the most diverse legume genus.

There are also biogeographic similarities. Both psyllid and legume groups in the Canary Islands and Madeira have their closest relatives in the Mediterranean/North African region, and there are several within archipelago and within island diversification patterns shared between legumes and psyllids, such as the predominantly single island endemism in the *Teline*-feeders and horizontal diversification in the *Adenocarpus*-feeders (Percy, 2003b).

These similar levels of diversity led to a hypothesize that cospeciation was an important process in this system. A cospeciation analysis using the program TreeMap (Page, 1994), which assesses the extent of parallel cladogenesis by mapping the psyllid and legume phylogenies onto each other, indicated that a significant number of speciation events could be correlated (i.e., there were a greater number of associated speciation events between the psyllids and the legumes than would be expected by chance alone) (Percy *et al*., 2004). In other words, a high degree of similarity in the phylogenetic branching patterns supported the hypothesis of relatively high levels of non-random cospeciation events.

However, as already mentioned, the inference of cospeciation requires evidence for the synchrony of the speciation events. In order to put dates on the cladogenic events in our phylogenies we used established geological ages for the younger island of La Palma to calibrate the psyllid and legume phylogenies independently (Percy *et al*., 2004). Comparing the two dated legume and psyllid phylogenies, we were able to rule out synchronous cospeciation for the majority of the associated speciation events (>98%). Instead, the dominant process that appeared to be driving speciation in the pyllids was diversification onto an already diversified legume lineage. Therefore, sequential host tracking, whereby psyllids preferentially switch to related or familiar plants was causing the partial similarity in phylogenetic branching patterns between psyllid and legume phylogenies. We estimated that >60% of the psyllid speciation resulted from host switching between related host plants, and <40% was due to wide switching to unrelated plants (Percy *et al*., 2004).

There is evidence in the psyllid phylogeny for two distinct periods of accelerated diversification, one when the psyllids first colonized the genistoid legumes, and secondly when the Canary Islands were colonized. Interestingly, the colonization of the Canary Islands by both psyllids and legumes occurred more or less contemporaneously, around 2.5-2.9 million years ago (Figure 3). One or more associated speciation events within these islands may therefore more closely fit the cospeciation model, and in our analysis one node was found to qualify as a cospeciation event during the early part of the psyllid-legume codiversification in the Canary Islands. However, speciation in both the legumes and the psyllids on colonization of these islands was rapid resulting in insufficient resolution to determine clearly the early sequence of speciation events immediately after colonization (Percy *et al*., 2004).

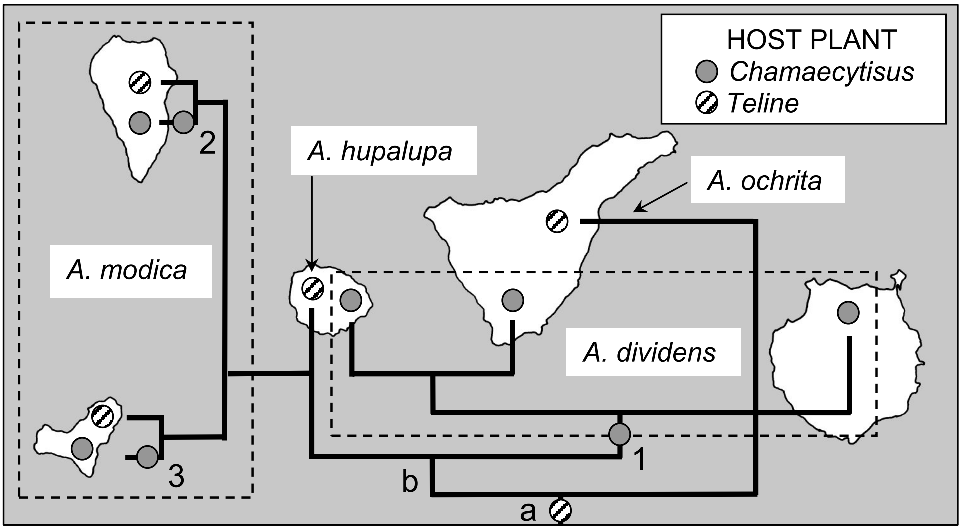

Figure 4. Distributions and mapped host plant associations in the *dividens*-*hupalupa*-*modica* subclade of *Arytinnis*. Three independent colonizations of *Chamaecytisus* from *Teline* are numbered. The nodes marked ‘a’ and ‘b’ denote where possible ancestral polyphagy at the base of the subclade could account for a propensity to switch between the same unrelated hosts with the re-emergence of polyphagy and putative host race formation on *Teline* and *Chamaecytisus* in *A. modica* on La Palma and El Hierro (modified from Percy, 2003b).

Interpreting temporal patterns

Mapping observed host associations onto a phylogenetic tree, together with an age calibrated framework for the phylogenies, can suggest historical temporal shifts that may have taken place. However, like all historical inferences, temporal shifts in dynamic host preferences are hard to reconstruct. For instance, although the majority of the legume nodes are considerably younger than the psyllid nodes, one of the legume nodes was markedly younger than the associated psyllid node. The two endemic Canarian *Adenocarpus* species, with no genetic variation either between them or with their continental sister taxon in our study (Percy & Cronk, 2002), are host to two endemic *Adenocarpus*-feeding psyllid species, which show reasonably high genetic divergence (Percy, 2003b; Percy *et al*., 2004). Explanatory scenarios for this outcome could include: hybridization and ongoing gene flow between *Adenocarpus* species, and/or evolution of the two *Adenocarpus*-feeding psyllids on different host plants before *Adenocarpus* colonized the Canary Islands followed by both psyllids subsequently switching to *Adenocarpus*. Further research to tease apart these historical scenarios will be challenging. In this case, it would require more extensive phylogeographic sampling, as well as a variety of molecular markers, to obtain greater resolution of the putative periods of island colonization.

Generalizations about insect-plant interactions from this study

When entering a new and unfamiliar environment such as colonizing an oceanic island, insects that are highly host specific and therefore possibly evolutionarily canalized in their adaptations to their environment may be faced with challenges not faced by habitat generalists: namely finding a specific environment required for survival. The degree to which an island's environment is "unfamiliar" to a newly arrived colonist will depend on a number of factors that are staples of classic biogeography (MacArthur & Wilson, 1967), including distance of an island from source biotas and the number of potential source biotas; island age and the age and proximity of any neighbouring islands; as well as island topography and geological history of the island. It will also depend on the ability of an insect to expand its host range. In the Macaronesian psyllid-legume system, it appears that psyllid diversity is strongly constrained by the presence and diversity of familiar plants. For this psyllid lineage, the presence of familiar plants in the central Macronesian islands is due to the relatively near-continent placement of these islands, increasing the likelihood that plants and animals will colonize from the same, or similar continental source areas.

However, what appears to be constraints in host preference may have different underlying causes. Host plant selection by a colonizing psyllid may be highly conserved by evolutionary canalization, in which case the psyllid will only survive if it finds the same, or a closely related host plant on entering a new environment. But there are also other factors to consider, such as opportunism (characterised as the opportunity to choose familiar versus unfamiliar plants) and competition (from other herbivorous insects). Competition may increase the likelihood that continental, or ancestral, host preferences are maintained on islands by the effect of competitive exclusion. Again, the proximity of an island to a continental source biota is likely to influence the strength of competition: less isolated islands are more likely to be colonized by multiple lineages that are closely related, and closely related herbivores with similar feeding habits that are already specialists are likely to exert competitive exclusion on each other, thus promoting the maintenance of host specificity. Conversely, a colonizing insect with no close relatives, for example, after colonizing a remote island, is expected to have more adaptive space available to it through less competition and predation; however, it is also likely to encounter fewer "familiar" plants; and these factors combined make it potentially more likely to expand its host range outside the norm (e.g., Hawaiian planthoppers and mirid bugs; Roderick & Percy, 2008; see also Nylin & Wahlberg, 2008); (Figure 5).

Differentiating the role of opportunism from host constraints is difficult (Janz & Nylin, 2008). We can ask: "in the absence of familiar plants would host selection have been wider, or, would the insect lineage have failed to establish?" To date, there are only preliminary and anecdotal data for the roles of opportunism and competition in the pattern of host constrained diversity in the Macaronesian islands. Preliminary host transplant experiments on the island of Tenerife found substantial mortality when psyllids were transplanted to legumes that were distantly related versus transplants to closely related legumes (Percy, 2001), implying that host selection is not simply opportunistic in the endemic legume-feeding psyllids. Only two speciation events involved wide host shifts to unrelated legumes in the legume-feeding psyllid lineage, and these appear to have occurred sympatrically. All other speciation events associated with colonizing a new geographic area/island involved no host shift, or a shift to a related legume, apparently confirming the role of preadaptation in constraining host selection (Percy, 2003b). The one or two cases of wide host plant shifts in the Canary Islands were within an island, and these shifts may occur via oviposition "mistakes" and sufficient contact time in sympatry for diversifying selection and adaptation to occur (Matsubayashi *et al*., 2010). Another factor that may promote wide host shifts is preadaptation to polyphagy through ancestral host preferences (Janz *et al*., 2001; Nylin & Wahlberg, 2008), discussed below. Although evidence that competition plays a role in maintaining host specificity in phytophagous, and other insect parasites, remains controversial (Kaplan & Denno, 2007; Johnson *et al*., 2009), there is at least one case in the Canary Islands that suggests a role for competition: the absence of one member of a psyllid species pair on the island of La Palma, versus the presence of both sister species on the island of Tenerife. On Tenerife host specificity is maintained, but on La Palma it is not. Host specificity on Tenerife may be maintained by competitive exclusion, possibly reinforced by adaptation to differing host plant phenologies (the host plants occur at either higher or lower altitudes, and the developing flowers on which the psyllids lay their eggs mature later or earlier respectively), but host specificity is not maintained on La Palma where only one of the sister species pair is present and feeds on both *Adencocarpus* host plants (Percy, 2003b).

Few studies have looked at the underlying causes of observed host specificity, and relatively little is understood about genetic constraints and the evolutionary canalization of host specificity. On the one hand, increasing host specialization in an insect lineage is thought to lead to a decrease in evolutionary flexibility in respect to host choice, resulting in the potential of an evolutionary "dead end" (Moran, 1988; Kelley & Farrell, 1998).

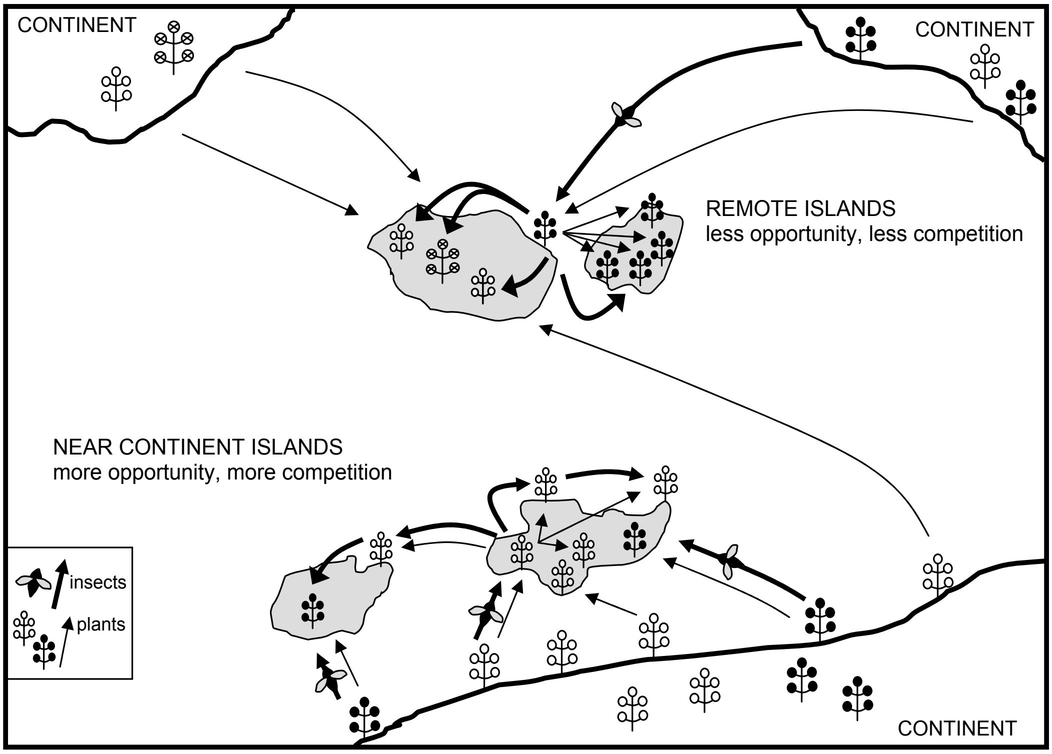

Figure 5. Illustration of the different levels of competition and opportunity expected on near continent islands and remote islands by colonizing specialist herbivores, with implications for the maintenance of host specificity discussed in the text. Opportunity is determined by the availability of "familiar" host plants; and competition is exerted by other specialist herbivores in the form of exclusion from particular host plants. In both near and remote islands, preadaptation to particular plants or plant lineages may act to filter colonizers. Opportunities to find familiar plants will be much greater on near continent islands because both plants and insects are more likely to come from the same source areas. Competition will also be greater on near continent islands because of the higher number of establishing insects that are specialists and that may also be closely related. Both more opportunity and more competition are expected to result in similar ranges of host specificity within an island insect lineage as those observed on the continent. In contrast, remote islands are more likely to have plants colonizing from many different source areas, reducing the likelihood that a colonizing insect will encounter familiar plants; post establishment insect diversification is therefore expected to involve relaxed specificity on remote islands due to less competition and fewer familiar plants. Finally, in both near and remote islands, an established insect lineage will have a greatly increased opportunity to diversify if an already colonized plant lineage undergoes an insular radiation; and host shifts between unrelated plants may be more likely within an island in sympatry. See text for discussion.

On a macroevolutionary scale, there appears to have been substantial extinction in insect lineages related to reduction in plant diversity (Wahlberg *et al*., 2009). From more microevolutionary scale studies, it now appears that generalist species may be as likely to evolve from within specialist lineages as from within generalist lineages (Nosil, 2002; Winkler & Mitter, 2008). It is a common pattern for plant-feeding insect lineages comprised predominantly of monophagous species to have at least some oligophagous or polyphagous members (Janz *et al*., 2001; Singer, 2008). A number of studies have provided evidence that specificity in plant-feeding insects may be more labile and evolutionarily flexible than patterns of observed host specificity would suggest (Janz & Nylin, 2008; Nylin & Wahlberg, 2008). Research, particularly work with Lepidoptera, has suggested that observed host specificity may mask adaptive variability in host choice, and cyclical developmental switches between generalist-specialist behaviours have been described as the oscillation hypothesis (Janz & Nylin, 2008).

Whether specialization in plant feeding insects is found to be evolutionarily canalized or evolutionarily plastic may be lineage specific. There is, nevertheless, evidence that a trend towards specialization is the norm in plant-feeding insects, with more than 80% classified as specialists (Winkler & Mitter, 2008). Even with the potential conflicts between adaptive fitness (specialists) and flexibility (generalists), it appears that specialization is strongly selected for in plant-feeding insects, and that shifts towards specialization, or even shifts from being a specialist on one plant to being a specialist on another plant, may happen quickly (Weingartner *et al*., 2006; Nylin & Wahlberg, 2008; Singer, 2008). What is less clear is how long lasting the specialist habit is within a lineage, what maintains it, and how often and under what conditions it breaks down (Janz & Nylin, 2008).

Are specialist insects poor island colonizers, especially of remote islands populated with unfamiliar plants? Studies of Hawaiian phytophagous insect groups suggest that constraints on host selection may also filter colonists to remote islands (Roderick & Percy, 2008). In Hawaiian delphacid planthoppers and mirid bugs, it is thought that the initial island host plants were those related to the putative ancestral continental host plants. This suggests that other potential herbivorous insect colonists may not have been able to establish if they were unable to locate familiar plants. However, there are notable differences in post-establishment diversification within the Hawaiian Islands versus the Macaronesian islands. In the remote Hawaiian Islands, there have been remarkable expansions onto unrelated host plants in a number of herbivorous insect radiations (Roderick & Percy, 2008). In contrast to these dramatic expansions in host range post colonization in the Hawaiian Islands, Canarian phytophagous groups (e.g., the legume-feeding psyllids and chrysomelid leaf beetles [Garin *et al*., 1999]) appear to have made far fewer wide host switches during diversification, supporting a role for the near-continent effect, with a greater range of familiar plants and more competitors, both acting to preserve ancestral host associations over time in Macaronesia (Figure 5). Wide host switches in both the Canarian psyllid and beetle groups have occurred but at a much lower frequency than switches to related hosts. There is evidence that specialist lineages of insects that include at least some oligophagous or polyphagous members are more likely to exhibit wide host switching (Weingartner *et al*., 2006; Winkler & Mitter, 2008). These findings emphasise the possible temporal nature of specialization and would be an interesting area of research in island insect-plant systems.

Interestingly, just as oscillations between specialist and generalist habits may be more common than previously thought, the distinctions between parasite and mutualist may also be less rigid and not easily classified as either purely parasitic or purely mutualistic (Thompson & Cunningham, 2002; Jones *et al*., 2009). An island-insect example is a lineage of moths (*Epicephala*) which lay their eggs in the developing ovaries of their host plant (*Glochidion*), but then as adult moths perform a highly specialized and efficient pollination service (Kawakita *et al*., 2004). The survival of this highly specialized insect-plant interaction, where the insect is both parasite and mutualist pollinator, may seem vulnerable to disturbance and local extirpation; yet these two moth and plant lineages have colonized many islands across the Pacific Ocean with the same close interaction apparently preserved as the lineages island hopped from one archipelago to another (D. Hembry, pers. comm.). This suggests an inherent robustness in systems that are sometimes characterized as evolutionary "dead ends" because of their high degree of relational specificity. In this moth-plant example, there may be conditions promoting synchronous dispersal and colonization of one archipelago after the other (e.g., prevailing weather systems or island stepping stones); but there may also be some underlying evolutionary flexibility allowing periods of mismatch in the association with re-association and re-establishment of the interaction opportunistically (Kawakita & Kato, 2006, 2009).

Much interesting work could be done on islands to tease apart these different evolutionary scenarios using comparative lineages of interacting insects and plants. Understanding the evolution of insect specialists and generalists, and the continuum in between, is key to understanding the processes of establishment and diversification of plant-feeding insects in novel environments. Islands offer an ideal framework for testing these hypotheses. The reconstruction of historical feeding habits can prove extremely challenging in such studies because adaptive shifts towards specialization may mask any periods of polyphagy during the establishment and evolution of an insect lineage. Tracing host preferences as a character on the insect phylogeny and comparing host preference in sister species and continental progenitors are some of the ways to infer historical host use, but comprehensive outgroup sampling would be key to these interpretations.

Conserving insect-plant interactions on islands

Island taxa are vulnerable to disturbance and invasive species, and the breakdown in interactions between native species are sometimes the first indicators of a critical level of disturbance. Some of the psyllid-legume interactions in the Canary Islands, as well as the species themselves may be threatened due to habitat disturbances that reduce host plant population sizes and increase isolation between plant populations. Using field data of psyllids on uncommon and rare legumes in the Canary Islands, I estimated a “critical host plant density”. A critical host plant density is the estimated minimum host plant population size required to sustain a host-specific psyllid fauna, and in the Canary Islands this appears to be > 2000 individual plants (Percy, 2001). If a plant species becomes rare, particularly if the remaining individuals are scattered in disjunct locations rather than forming a cohesive population, the likelihood of extinction in the associated insect fauna increases (Boggs & Ehrlich, 2008). I based my estimates of a critical host plant density on observations of psyllid presence/absence and abundance on rare legumes such as *Teline osyroides* and legumes with reduced, disjunct populations such as *Teline rosmarinifolia*.

Some rare legumes in the Canary Islands that do not host psyllids, may once have been more common and hosted psyllids in the past. A good example is *Genista benehoavensis*, this species is now threatened due to anthropogenic disturbance (only six individuals were known of in 1988), but it was once considered more common in the subalpine zone on La Palma (Palomares Martínez, 1997). The sister species on Madeira, *Genista tenera*, is common and is host to a psyllid species, but if there was a psyllid specific to *Genista benehoavensis* in the Canary Islands, it became extinct with the dramatic demise of the host plant. Conversely, the increasing rarity in La Palma’s subalpine zone of *G. benehoavensis*, and another legume, *Spartocytisus supranubius* (also here lacking a psyllid species that is present on *S. supranubius* on Tenerife, where both plant and psyllid are common), appears to have promoted the expansion and increased abundance in this zone of another native legume, *Adenocarpus viscosus*. Increased abundance of *A. viscosus* to dense, monotypic stands is accompanied by a parallel increase to unusually high densities of the *Adenocarpus*-feeding psyllid. Abnormally high densities of the native psyllid fauna on *Chamaecytisus* are also found where this legume is cultivated. Psyllid-legume interactions are, therefore, clearly impacted by anthropogenic changes to host plant distributions and abundance.

Future directions for research on insect-plant interactions in Macaronesia

There are several areas of future research that would be interesting to explore given the present knowledge we have of the central Macaronesian islands psyllid-legume system. In one respect, there needs to be an expansion outwards in focus to look at the comparative patterns found in other oceanic islands and archipelagos. Particularly useful would be a comparison between plant-insect interactions on remote versus near-continent islands. Such an approach could be used to address questions about plasticity in host choice during island colonization, as discussed above.

Another approach would be to focus in more closely at the suggestive patterns of host race formation, e.g., those found on El Hierro and La Palma in this study where the species, *Arytinnis modica*, found on two different legume genera, *Teline* and *Chamaecytisus*, may be in the process of undergoing host race formation (Figure 4). The two closest relatives of *A. modica* are found one on *Teline* and one on *Chamaecytisus*. I have hypothesized that this small clade of species may have had a polyphagous ancestor, or a historical period of polyphagy on *Teline* and *Chamaecytisus*, which gave rise to two specialized species (*A. dividens* and *A. hupalupa*), possibly via host race formation; and another reversion to polyphagy on colonization of La Palma and El Hierro is now being followed yet again by host race formation and specialization in *A. modica* (Percy, 2003b). The evocation of a polyphagous past in this clade of species despite observed host specificity in all the current species except *A. modica*, would fit with ideas discussed above of an underlying flexibility or plasticity in host choice that may be important during the colonization of novel environments, but temporal because of strong selection towards specialization (Janz *et al*., 2006). If host preferences are temporally dynamic and behavioural switches between specialist and generalist habits are not uncommon, then observed host race formation may in some cases be reflective of historical multi-host preferences, but these periods can rapidly become the “ghosts of polyphagy past” as adaptation shifts feeding behaviour back towards specialization.

The role of plant hybridization and psyllid species boundaries in plant hybrid zones is another area that needs further research. Hawaiian planthoppers have both increased and decreased diversity in different host plant hybrid zones (Drew & Roderick, 2005), and host plant hybrid genotypes have been shown to drive population divergence in a specialist mite herbivore (Evans *et al*., 2008). Several psyllid species (*Arytinnis diluta*, *A. equitans*, *A. pileolata*, *A. proboscidea*, and *A. menceyata*) are found on multiple hosts between which hybrids have been recorded (Figure 2). On Tenerife, hybrids between three legume species (*Teline canariensis*, *T. stenopetala*, and *T. osyroides*) are found around the Ladera de Güímar (Arco Aguilar, 1983; M. Arco Aguilar, pers. comm.), an area that was disturbed by early settlements of aboriginal Guanches. The most widespread psyllid on Tenerife (*A. pileolata*) is found on these three legumes. As hybrids are more likely to occur between closely related legumes, it is not clear whether the host range expansions occurred because the hybridizing legumes were related and therefore appeared familiar to the psyllid, or whether hybridization could have promoted host shifts via a “hybrid bridge” effect (Floate & Whitham, 1993). The *Adenocarpus*-feeding psyllids on Tenerife, where the host plants hybridize widely, maintain their host specificity, but both *Adenocarpus*-feeding psyllids are found in the plant hybrid zone. On La Palma, there is only one *Adenocarpus*-feeding psyllid and its host range has expanded to encompass both *Adenocarpus* host species as well as the hybrid zone. We do not know what role, if any, this and other plant hybrid zones play in the maintenance or breakdown of host specificity, or indeed if hybridization in host plants could promote hybridization in psyllids.

Lastly, an investigation of potentially cryptic speciation in taxa such as *Arytaina devia*, which has the largest intra-specific molecular diversity of any of the Canarian legume-feeding psyllids in this study (Percy, 2003b) may shed light on the role of drift in non-adaptive divergence, since *A. devia* is found on the same host plant throughout its geographic range across four islands.

Conclusions

Psyllid diversity in the Macaronesian islands is notably influenced by, and apparently constrained by, the presence and diversity of the host plants. When we compare continental and island host plant associations, preadaptation is evident in host selection in island psyllid lineages. 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 sequential host tracking model of codiversification. Further research is needed on the evolutionary determinants of preadaptation, host constrained diversification, the role of competition, and plasticity versus canalization of host preference in psyllid-plant systems; comparisons between Macaronesian and other oceanic island systems would provide fertile ground to tackle some of these questions.

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