

Herbivorous Insects and the Hawaiian Silversword Alliance: Coevolution or Cospeciation?¹

GEORGE K. RODERICK²

ABSTRACT: Numerous groups of herbivorous insects in the Hawaiian archipelago have undergone adaptive radiations. R. C. L. Perkins collected and documented species in nearly all of these groups. In this study I tested whether patterns of host plant use by herbivorous insects can be explained by host plant history. I examined a group of insects in the planthopper genus *Nesosydne* (Hemiptera: Delphacidae) that feed on plants in the Hawaiian silversword alliance, many of which are endangered or threatened. For these *Nesosydne* species feeding on the silversword alliance, mitochondrial DNA sequence data revealed a statistically significant pattern of cospeciation between these insects and their hosts. These planthoppers are highly host-specific, with each species feeding on only one, or a few closely related, plant species. Patterns of host plant use across the plant lineage, as well as within extensive hybrid zones between members of the silversword alliance, suggest that planthopper diversification parallels host plant diversification. Data collected thus far are consistent with, but do not directly demonstrate, reciprocal adaptation. For other herbivorous insects associated with members of the Hawaiian silversword alliance, patterns of host plant use and evolutionary history are not yet well understood. However, cospeciation appears not to be universal. For example, endemic flies in the family Tephritidae (Diptera) are less host-specific and demonstrate host-switching. Research is under way to reveal the mechanisms associated with cospeciation and host-switching for different insect groups associated with the Hawaiian silversword alliance.

INSECT LINEAGES at the generic and family levels appear to be largely conservative with respect to their host affiliations, and many species in such lineages are highly host-specific (Dethier 1954, Ehrlich and Raven 1964, Farrell and Mitter 1993, but see Dobler et al. 1996). Current patterns of host plant use by herbivorous insects can be explained by one of two hypotheses, both of which can lead to greater herbivore diversity: cospeciation with host plants and host-plant switching.

Cospeciation is the matching of speciation events in two lineages, such that the two phylogenies resemble one another (see Brooks 1979, 1988, Mitter and Brooks 1983, Hafner et al. 1994, Page 1995a). Cospeciation of plants and their herbivorous insects may increase herbivore diversity as insects track and diversify with their hosts. Coevolution can lead to cospeciation but is not required. For example, major vicariant events to which both lineages respond, followed by allopatric speciation, could also produce a pattern of cospeciation. Or one group may respond to vicariance, with the other lineage "following" again without the need for strict coevolution.

By contrast, host-plant switching is a change of hosts (see Futuyma 1983a,b, Thompson 1994) other than would be predicted by the host phylogeny, such that the two phylogenies are no longer congruent. Host-switching can result in greater herbivore diversity if, following a switch

¹ This research was supported by the University Research Council of the University of Hawai'i and the U.S. Fish and Wildlife Service. Additional support for our laboratory is provided by grants from NSF, USDA, California Department of Food and Agriculture, International Rice Research Institute, Rockefeller Foundation, and the Pacific Biomedical Research Center, University of Hawai'i. Manuscript accepted 3 February 1997.

² Center for Conservation Research and Training, 3050 Maile Way, Gilmore 409, University of Hawai'i at Mānoa, Honolulu, Hawai'i 96822.

to a new host, the herbivore becomes sufficiently isolated and divergent from the species on the original host. However, factors responsible for generating the diversity of herbivorous insects relative to their hosts are less clear. Compilations of research on herbivorous insects and their hosts indicate that although a few insect radiations do appear to be tightly correlated with radiations of their hosts, most insect radiations show evidence of host-switching (Mitter et al. 1988, 1991, Farrell and Mitter 1993, Funk et al. 1995).

Recently, it has been suggested that hybrids between host species may be associated with herbivorous insect diversity and, by extension, parasite diversity (Floate and Whitham 1993, Strauss 1994, Whitham et al. 1994, Christensen et al. 1995). Much ecological and genetic data have demonstrated that hybrid zones can represent very different environments for herbivorous insects (see Boecklen and Spellenberg 1990, Aguilar and Boecklen 1992, Floate et al. 1993, Floate and Whitham 1994, Fritz et al. 1994, Roderick and Metz 1997). Hybrid hosts not only create new adaptive zones, but also may allow specialized parasites an escape from the evolutionary dead end—hybrids may enable parasites to increase their host range, possibly leading to genetic diversification and speciation. This scenario has been termed the “hybrid bridge” hypothesis (Floate and Whitham 1993). Hybrid hosts thus can provide a means for host-switching.

Distinguishing between the relative importance of cospeciation and host-switching is difficult for several reasons. By necessity, much of our information concerning patterns of cospeciation or coevolution must come from inferring past events from current observations. Recent developments in both molecular biology and theory have made it possible to compare reconstructed phylogenies of pairs of interacting lineages and to test for significance of cospeciation (Mitter and Brooks 1983, Brooks 1988, Mitter et al. 1991, Maddison and Maddison 1992, Moran and Baumann 1994, Funk et al. 1995, Page 1995*a,b*). However, reconstructing past associations between species can be more problematic (Mitter et al. 1988, 1991, Wiegmann et al. 1993). For example, if cospeciation were to occur, it demands that both insect and plant (or parasite and host) have the potential to radiate

concurrently. However, for many insect/plant relationships studied, especially in North America, the radiations of plants and insects have not been coincident, usually with the plant group becoming established following retreat of the glaciers and the insects spreading northward at some later time (Farrell and Mitter 1993, Funk et al. 1995). For such interactions in mainland tropical regions, which are older than temperate ones, historical patterns of host association are likely also to be obscured by extinctions and incomplete knowledge (B. Farrell, pers. comm.). Such circumstances may bias evidence away from cospeciation, likely discounting its importance in the early stages of diversification of a plant lineage. To know about the relative ages of the cospeciation events requires some knowledge of the historical frameworks of both the insect and plant radiations.

Many radiations of herbivorous insects are endemic to Hawai'i (see Simon 1987, Howarth and Mull 1992, Nishida 1994, Asquith 1995, Eldredge and Miller 1995, Miller and Eldredge 1996, Roderick and Gillespie in press) and represent a unique opportunity to unravel the population genetic and phylogenetic processes that have led to current patterns of host plant affiliation and are responsible for the diversity of associated insects. The extreme isolation and historical framework provided by the Hawaiian archipelago makes possible the set of features necessary for the test of hypotheses to account for patterns of herbivore host affiliations and associated diversity. In particular, island and volcano age can be used to identify the age of particular insect/plant associations, independently from any information gained through molecular data. In this study, I examined the evidence for cospeciation and host-switching for species of planthoppers in the genus *Nesosydne* (Hemiptera: Delphacidae) that feed on the Hawaiian silversword alliance. Recently, Baldwin and Robichaux (1995) generated a phylogenetic hypothesis for the history of the species within the silversword alliance that makes this work possible.

The current threats to biological diversity have necessitated the understanding of the forces responsible for both its generation and demise (Wilson 1988, 1996). Nowhere on earth is the extinction crises more acute than in the Hawaiian

archipelago (Gillespie et al. 1997, Liebherr and Polhemus 1997, Gillespie 1997). As such, Hawai'i becomes a model system for the study of both the generation of biodiversity and its conservation.

MATERIALS AND METHODS

Study Organisms

SILVERSWORD ALLIANCE. The silversword alliance in Hawai'i comprises 28 species, presumably with one common ancestor (Baldwin et al. 1991, Baldwin and Robichaux 1995, Baldwin 1997). This radiation is among the most well studied of all plant lineages in Hawai'i (see Wagner and Funk 1995), with published works on ecology, physiology, systematics, conservation status, and hybridization (Carr 1987). Carr and colleagues (Carr 1985, 1990*a,b*) have investigated the extent of hybridization between members of the silversword alliance and have documented that many, if not most, members of the silversword alliance form natural hybrids in the field. Hybrid zones differ in (1) the plant species involved; (2) the relatedness of plant species that hybridize; (3) the range of ecological conditions occupied; and (4) the extent of overlap between the hybrids and one or both parental species. Hybrids and potential F₁s have been identified by leaf size and shape (Carr 1985), and recently by genetic data (Friar et al. 1996, V. Caraway and C. Morden, unpubl. data).

Recently, Baldwin and colleagues (Baldwin et al. 1991, Baldwin and Robichaux 1995, Baldwin 1997) used molecular genetic data to generate a hypothesis of evolutionary relationships among members of the alliance. The alliance appears to be monophyletic and to contain distinct clades within Hawai'i. Divergence among extant species is likely in the range of 4–6 myr, or no older than the age of Kaua'i (Baldwin and Robichaux 1995, Baldwin 1997). Conflicting evidence from nuclear, karyotype, and cytoplasmic DNA data suggests that some species may be of hybrid origin. The existence of a phylogenetic hypothesis for plant species in the silversword alliance is an essential element in the analysis presented here for several reasons: (1) it provides the basis for tests of cospeciation

of planthoppers and their host plants; (2) it gives insight into the degree of host specificity; and (3) it establishes the relatedness between parental plant species associated with each plant hybrid zone.

***Nesosydne* PLANTHOPPERS.** The genus *Nesosydne* in Hawai'i contains at least 80 species (Zimmerman 1948). In contrast to other delphacid planthoppers that are mainly grass feeders (Denno and Roderick 1990), species within *Nesosydne* in Hawai'i feed on plants in an astonishing 28 plant families (Figure 1) (Zimmerman 1948, Wilson et al. 1994). This diversity of host plants may be explained in part by the fact that *Nesosydne* is likely polyphyletic and may represent several independent colonizations of Hawai'i with subsequent radiations within the archipelago (Asche 1997). Despite this diversity of host plants, nearly all *Nesosydne* species are highly host-specific, with 88% of species using plants within a single family and 77% using a single plant species (Figure 2). At least 15

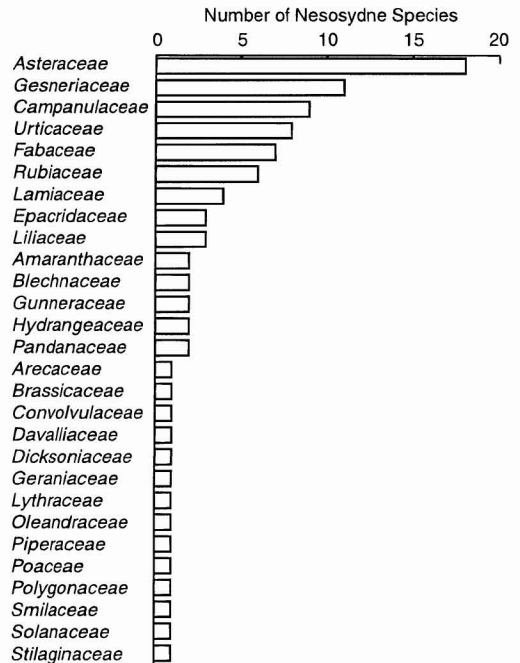


FIGURE 1. Number of Hawaiian *Nesosydne* species recorded on species in each plant family (compiled from Zimmerman 1948, Wilson et al. 1994). Number of species adds to more than total for Hawai'i because some planthoppers feed on plant species in more than one family.

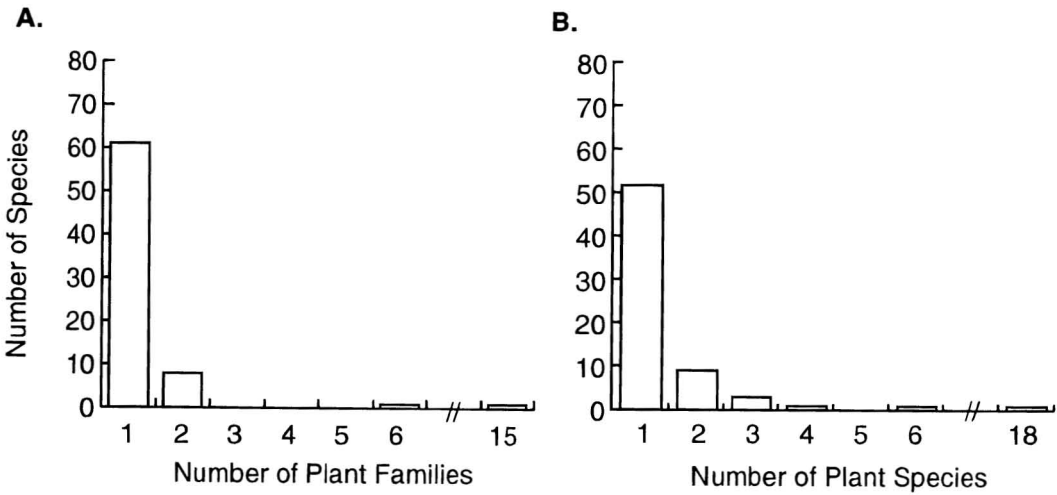


FIGURE 2. Host specificity of single *Nesosydne* species in Hawai'i. (A) Distribution of number of plant families on which single species have been recorded. Total plant families recorded in Hawai'i = 28. (B) Distribution of number of plant species on which single *Nesosydne* species have been recorded. *Nesosydne* species for which plant families (A) are recorded, $n = 71$; and for which plant species (B) are recorded, $n = 66$.

Nesosydne species are reported to be found only on plant species within the Hawaiian silversword alliance (Zimmerman 1948, Swezey 1954). Currently, it is not known whether these 15 species represent their own monophyletic clade.

Host Plant Associations

For the insects examined in this study, host plant associations for planthoppers on the silversword alliance were established by field collections of developing nymphs and the presence of male and female adults. Planthoppers were collected using an aspirator (puter) and sweeping. Insects were frozen at -80°C shortly after collection.

Planthopper History

A 441 base-pair region of mitochondrial cytochrome oxidase I DNA was amplified using primers C1-J-1751 'Ron' and C1-N-2191 'Nancy' (designed by R. Harrison laboratory [Simon et al. 1994]). Here, I present data from 20 individuals in six *Nesosydne* species. The frequency of transitions and transversions was determined for the group using several genetic distances: uncorrected pairwise percentage

divergence, Kimura (1980) 2-parameter, and Tamura-Nei (1993). A phylogeny was reconstructed using parsimony (PAUP [Swofford 1993]). Bootstrapping was used to provide a level of confidence associated with each node. Outgroups included another Hawaiian delphacid planthopper, *Nesosydne koae*, which feeds on *koa* (see O'Connell 1991), and a delphacid from the U.S. mainland, *Prokelisia marginata* (Roderick 1987, Denno et al. 1997).

Cospeciation between Planthoppers and Host Plants

A test of cospeciation was conducted using TreeMap (Page 1995b). This method and the corresponding computer program makes explicit the relationship between the host and "parasite" (here, insect herbivore) trees and allows a visually intuitive representation of that history (Page 1995a). In brief, reconstructions that maximize the number of cospeciation events are considered to have the greatest explanatory power and are preferred over reconstructions with fewer cospeciation events. In the method, host switches are also incorporated as an explanation of the observed pattern of host-"parasite" associations. The significance of the observed fit

between host and parasite trees can be evaluated by comparison with the distribution of the same measure of fit for random trees (Page 1995a). The program does place several constraints on the data. For example, each "parasite" may only be associated with one host, and the trees must be completely resolved.

The planthopper phylogeny was mapped on to Baldwin and Robichaux's (1995) phylogeny for the silversword alliance based on sequences of nuclear ribosomal DNA. A randomization test (by "randomizing" the planthopper tree using TreeMap [Page 1995b]) was used to test the significance of the observed level of cospeciation between planthoppers and their plant hosts.

RESULTS

Planthopper Host Plant Associations

Planthoppers have now been collected on 13 out of 28 members of the silversword alliance. Where a planthopper species has been recorded on more than one host species, the hosts were closely related and/or hybridize. These host records suggest that planthopper species feeding on the silversword alliance are highly host specific to either single plant species or closely related species.

Planthopper History

The 441 base-pair piece of cytochrome oxidase I amplified was one codon insertion longer than that of *Drosophila yakuba* (Clary and Wolstenholme 1985). Transitions were approximately double transversions for the range of genetic distances encompassing the *Nesosydne* planthoppers feeding on the silversword alliance, and both transitions and transversions increased linearly over this range of genetic distances. The linear increase indicates that cytochrome oxidase I is a good candidate for the evolutionary relationships investigated here and that both transitions and transversions contain useful information. If island age can be used as a rough time frame, these genetic distances correspond to approximately 2% base-pair divergence per million years. Although there may be other species not examined here that would fall within

those feeding on the silversword radiation, the group of species examined here was supported by multiple synapomorphies that distinguished it from *N. koae* (Figure 3). The time frame suggested here for the diversification of *Nesosydne* species that feed on the silversword alliance is consistent with a single origin of these insects in Hawai'i and corresponds to the age of the silversword alliance.

Cospeciation between Planthoppers and Host Plants

The comparison of planthopper and host plant phylogenies resulted in five cospeciation events (noted by letters in Figure 3). The randomization test shows that this number of cospeciation events is significant ($P < .01$). Note that the method identifies "cospeciation" events for the individual planthoppers collected on *Dubautia raillardoides* and *D. paleata*, and *D. ciliolata* and *D. scabra*, even though the planthoppers collected on each species pair are identified as the same species (see Figure 3). The comparison of phylogenies provides no evidence of recent host-switching. Whether the pattern of cospeciation will hold when all species of *Nesosydne* are included is one objective of current research.

Planthoppers were also collected from five extensive hybrid zones (Figure 4). Baldwin and Robichaux's (1995) data provide information on the relatedness of the plant species involved in each of these hybrid zones. In two hybrid zones between closely related plant species a single planthopper species spanned each entire hybrid zone: *D. paleata* and *D. raillardoides* (Kaua'i) and *D. ciliolata* and *D. scabra* (Hawai'i). In two other hybrid zones between close plant relatives, a single planthopper species was associated with only one parental plant species; in one of these, the planthopper also occurred on all identifiable hybrids, and in the other the planthopper's range was restricted to the parental species: *D. ciliolata* and *D. arborea* (Hawai'i) and *D. menziesii* and *D. platyphylla* (Maui). On intergeneric hybrids between *Argyroxiphium sandwicense* and *D. menziesii* (Maui) both parental plant species supported one planthopper species each and all apparent hybrids shared the species associated with *D. menziesii*.

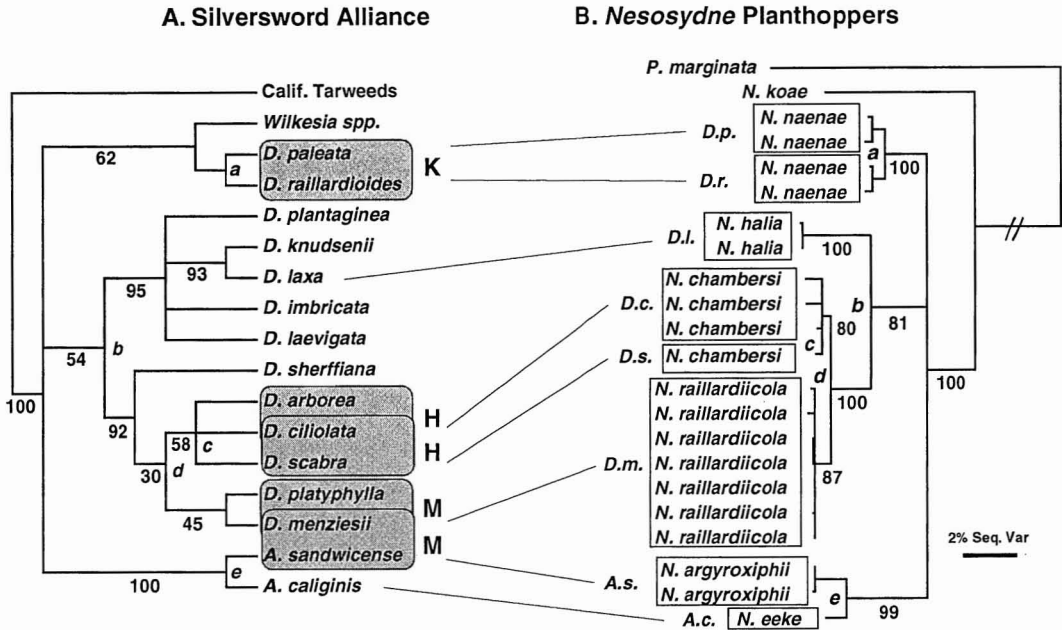


FIGURE 3. Comparison of phylogenies of (A) select species of the Hawaiian silversword alliance (data from Baldwin and Robichaux [1995]) with (B) associated *Nesosydne* planthoppers. Shaded ovoid areas in A represent plant species that hybridize. Boxes in B represent individuals of *Nesosydne* species collected on the same host plant noted. Letters a–e denote points of cospeciation as recovered by TreeMap (see text). Bootstrap percentages for each node are shown. The trifurcation near the base of both trees is left unresolved because of low bootstrap support. *Nesosydne koae* feeds on *koa* in Hawai‘i, and *Prokelisia marginata* is a salt marsh-inhabiting delphacid planthopper from the U.S. mainland (see text).

DISCUSSION

Though still in progress, work to date suggests that the *Nesosydne* planthoppers associated with the Hawaiian silversword alliance are highly host-specific, with each species feeding on one or a few closely related hosts. The significant pattern of cospeciation for the species examined to date suggests that species of planthoppers and members of the silversword alliance share parallel or cophylogenies and is consistent with reciprocal adaptation. Unfortunately, this result does not directly demonstrate reciprocal adaptation nor identify the processes that underlie the pattern of cophylogenies (Price 1996). For example, cophylogenies may arise through a number of processes that may include vicariance in one or both players, coevolution, or adaptation by only one player in response to the other. It is possible that major vicariance events, such as island and volcano formation, have shaped both planthopper and plant phylogenies concurrently, and that planthopper adaptation to hosts

may not be important in explaining significant cospeciation.

Some biological observations can shed light on this issue. Research on other delphacid planthoppers suggests that planthoppers can adapt to closely related novel hosts. For example, numerous studies have shown that the rice brown planthopper, *Nilaparvata lugens*, can overcome new “resistance genes” in rice in only a few generations, but that wider host-switching is limited (for a review see Roderick [1994]). Delphacid planthoppers contain yeastlike endosymbionts that may be involved in this adaptation, although their role has yet to be identified.

Investigation of hybrid zones presented here demonstrated that single planthopper species are not found on distantly related hosts, despite sympatry and the existence of intermediate hybrids. In two hybrid zones, planthoppers do not feed on one of the two parental species. These patterns of host association indicate that limits exist to host adaptation by planthoppers. Also, that single

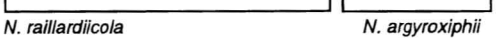
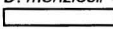


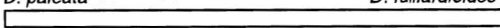
Locality of Host Hybrid Zone	Habitat	Relationship of 2 Host Parents	Host Parent... backcross ... F1 ... backcross ...Parent
A. Maui: Haleakala Crater	Hybrids and parents overlap on slopes and valley floor	distant (inter-generic)	<i>D. menziesii</i> ----- <i>A. sandwicense m.</i>  <i>N. raillardiicola</i> ----- <i>N. argyroxiphii</i>
B. Maui: Haleakala Outside slope	Hybrids and parents overlap in ravine	closest relatives	<i>D. menziesii</i> ----- <i>D. platyphylla</i>  <i>N. bridwelli</i>
C. Big Island: Mauna Kea	Hybrids and parents overlap on slopes and ravine	closest relatives	<i>D. ciliolata g.</i> ----- <i>D. arborea</i>  <i>N. chambersi</i>
D. Big Island: Saddle	Parents allopatric: <i>D.c.</i> on pahoehoe lava, <i>D.s.</i> and hybrid on aa lava	close relatives	<i>D. ciliolata g.</i> ----- <i>D. scabra</i>  <i>N. raillardiae</i>
E. Kauai: Alakai Swamp	Parents allopatric: <i>D.p.</i> on bogs, <i>D.r.</i> forest, hybrid on forest margins	closest relatives	<i>D. paleata</i> ----- <i>D. raillardioides</i>  <i>N. naenae</i>

FIGURE 4. Patterns of planthopper host plant use and characteristics of five hybrid zones between members of the Hawaiian silversword alliance (dashed lines). Range of hybrid use for each planthopper species is noted by rectangles. In two hybrid zones, parental plant species were found with no planthoppers.

species feed on some closely related hosts but not on others suggests that some closely related plant species have not diverged sufficiently to limit planthopper distribution. These observations are consistent with the hypothesis that diversity of *Nesosydne* planthoppers parallels and follows the diversity generated in the silversword alliance. Current work on this group includes reciprocal transplant studies to examine the role of plant hybridization in the diversification of *Nesosydne* planthoppers, population genetic assessments of planthoppers across plant hybrid zones, as well as a complete analysis of all Hawaiian *Nesosydne* planthoppers including species that feed on taxa other than the silversword alliance.

Preliminary observations of patterns of host use by other insect groups associated with the Hawaiian silversword alliance indicate that patterns of cospeciation are not universal. For example, endemic tephritid flies (Diptera: Tephritidae) associated with the Hawaiian silversword alliance are less host-specific, with many species feeding in flowers of more than one host. For example, only seven of 12 species have been reared from only one host species within the silversword alliance, whereas five

species have been reared from more than one species (Hardy and Delfinado 1980). Further, some of these species feed on distantly related taxa that are sympatric, indicating at least some degree of host-switching. Because some members of the silversword alliance can go for many years without flowering, using other hosts for flower feeding may be a necessity (although prolonged pupation as found in some North American tephritids may also occur [D. Papaj, pers. comm.]). Whether host-associated genotypes and/or sibling species exist (see Bush 1994), awaits further analysis. Other hypotheses to be tested with this group include whether the tephritids in Hawai'i stem from a single origin, whether gall forming is ancestral to flower feeding, and whether there has been a single host switch between another composite, *Bidens*, and the silversword alliance (Hardy and Delfinado 1980; Asquith, Seiler, Miramontes, and Messing, unpubl. data). Molecular work to address these hypotheses is under way.

The insects associated with the Hawaiian silversword alliance provide a unique opportunity to examine historical patterns of host plant use and, perhaps more important, the mechanisms that underlie those patterns. Whether patterns of

cospeciation are a consequence of coevolution has yet to be resolved and awaits further study.

ACKNOWLEDGMENTS

I thank U. Bergstrom, A. Isagawa, E. Metz, and B. Thorsby for technical help. For assistance in collecting, I am grateful to R. Gillespie, R. Bartlett (Maui Land and Pineapple), E. Metz, and R. Robichaux. B. Baldwin, R. Gillespie, E. Metz, S. Palumbi, R. Robichaux, and F. Villablanca provided helpful discussions and suggestions. Comments from R. DeSalle, B. Farrell, R. Gillespie, J. Liebherr, and D. Polhemus greatly improved the manuscript. Finally, I thank J. Liebherr and D. Polhemus for organizing the Perkins Symposium and the resulting publication.

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