BIODIVERSITY OF PLANTHOPPERS (HEMIPTERA: DELPHACIDAE) ON THE HAWAIIAN SILVERSWORD ALLIANCE: EFFECTS OF HOST PLANT PHYLOGENY AND HYBRIDISATION

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Abstract

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Many hypotheses have been advanced to account for the biodiversity of herbivorous insects. Here we test whether the diversity of a group of planthoppers, genus *Nesosydne* (Hemiptera: Delphacidae), can be explained by the history and patterns of hybridisation of their host plants in the Hawaiian silversword alliance, many of which are critically endangered or threatened. Molecular data (DNA sequences of mitochondrial cytochrome oxidase I) for planthoppers examined to date reveals significant co-speciation between these insects and their hosts. *Nesosydne* planthoppers are highly host specific with each species feeding on only one plant species or on closely related species that hybridise. There was no evidence to support the "hybrid-bridge" hypothesis as a mechanism by which herbivorous insects may switch hosts. Nor was there evidence that plant hybrid zones were centres of insect biodiversity. Rather, patterns of host plant use within plant hybrid zones suggests that planthopper diversification follows host plant diversification.

Introduction

The current threats to biological diversity have necessitated the understanding of the forces responsible for both its generation and demise (Wilson, 1988; 1996). Insects are among the most diverse organisms, with over 1 million described to date and perhaps another 10 to 30 million remaining to be discovered in tropical regions (Erwin, 1982; 1986). Herbivorous species form a major component of these insects (Strong et al., 1984) and most explanations for their diversity are linked to the diversity of plants on which they feed (Mitter et al., 1988; 1991; Farrell and Mitter, 1993; Thompson, 1994; Funk et al., 1995; Futuyma et al., 1995).

Much of the current insect biodiversity was present even before the radiation of the flowering plants (angiosperms) and appears to be coincident with the earlier diversification of seed plants (Labandeira and Sepkoski, 1993). Herbivorous insects may have further diversified with the radiation of angiosperms which required pollinators (Ehrlich and Raven, 1964); indeed, some radiations of insect species do appear to be correlated with those of flowering plants (Mitter et al., 1988; 1991). Insect lineages at the generic and family levels appear to be largely conservative with respect to their host affiliations and many species in these lineages are highly host specific (Dethier, 1954; Ehrlich and Raven, 1964; Farrell and Mitter, 1993). 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: co-speciation with host plants and host plant switching. Co-speciation is the matching of speciation events in two lineages, such that the two phylogenies resemble one another (see Brooks, 1979; Mitter and Brooks, 1983; Brooks, 1988; Hafner et al., 1994; Page, 1995a). Co-speciation may be a consequence of co-evolution, but may also arise through other mechanisms. By contrast, host-plant switching is a change of hosts (see Futuyma, 1983a; 1983b; Thompson, 1994) other than would be predicted by the host phylogeny, such that the two phylogenies are no longer congruent. Compilations of research on herbivorous insects and their hosts indicates that while 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 the frequent occurrence of hybrids between plant species may form centres of biodiversity or otherwise play a role in herbivore diversification (Floate and Whitham, 1993; Strauss, 1994; Whitham et al., 1994). Hybridisation between host species may also play a role in parasite diversification. Hybrid hosts not only create new niches, but may allow specialised parasites an escape from evolutionary dead ends (see Moran, 1988) — hybrids may provide a "bridge" to novel host species (Floate and Whitham, 1993). Whether "hybrid-bridges" are important in explaining the history and patterns of host plant use by herbivorous insects remains controversial (see Floate and Whitham, 1993).

The *Nesosydne* planthoppers (Homoptera: Delphacidae) in Hawaii are one of several insect radiations with members associated with the Hawaiian silversword alliance (Asteraceae) (see Roderick, in press). Here, we investigate factors underlying the biodiversity of these sap-feeding insects in light of the history and hybridisation of their plant hosts. We first test for the importance of "hybrid-bridges" by comparing phylogenetic histories of silversword plants and planthoppers. Secondly, we examine whether plant hybrid zones are centres for biodiversity, by examining planthopper species diversity across five hybrid zones.

Methods

Silversword Alliance.

The silversword alliance in Hawaii comprises 28 species, presumably with one common ancestor (Baldwin et al., 1991; Baldwin and Robichaux, 1995; Baldwin, in press). This radiation is among the most well-studied of all plant lineages in Hawaii (see Wagner and Funk, 1995) with published works on ecology, physiology, systematics, conservation status, and hybridisation (Carr, 1987). Carr (1985; 1990a; 1990b) has investigated the extent of hybridisation between members of the silversword alliance and has 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 hybridise,
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 F[1]s have been identified by leaf size

and shape (Carr, 1985), and recently by genetic data (RAPDs, V. Caraway and C. Morden, unpubl. data; Friar et al., 1996).

Recently, Baldwin and colleagues (Baldwin et al., 1991; Baldwin and Robichaux, 1995; Baldwin, in press) have used molecular genetic data to generate a hypothesis of evolutionary relationships among members of the alliance (fig. 1). The alliance appears to be monophyletic and to contain distinct clades within Hawaii. Divergence among extant species is likely in the range of 4–6 MY, or no older than the age of Kauai (Baldwin and Robichaux, 1995; Baldwin, in press). 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 co-speciation 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

Many radiations of insects, including delphacid planthoppers, are endemic to Hawaii (Simon, 1987; Howarth and Mull, 1992; Asquith, 1995; Eldredge and Miller, 1995; Miller and Eldredge, 1996). In contrast to other delphacid planthoppers which are mainly grass feeders (Denno and Roderick, 1990; Denno et al., 1991; Roderick, 1994), these planthoppers in Hawaii feed on a wide variety of plant families (Zimmerman, 1948; Swezey, 1954). The genus *Nesosydne* in Hawaii contains at least 80 species (Zimmerman, 1948). Systematic studies of the genus *Nesosydne* based on morphological characters are in progress (Asche, in press). *Nesosydne* is now thought to be polyphyletic and represent several independent colonisations of Hawaii with subsequent radiations within the archipelago (M. Asche, personal communication). At least 15 *Nesosydne* species are reported to be found only on plant species in the Hawaiian silversword alliance (Zimmerman, 1948; Swezey, 1954); whether these species form a monophyletic group within the *Nesosydne* has not been established based on morphological characters, although the molecular data presented here support monophyly. Presently, no other literature exists on abundance, life stages,

and seasonality of *Nesosydne* planthoppers on these different host plant species.

Host plants associations

Planthoppers were collected using an aspirator and sweeping on members of the silversword alliance including five extensive hybrid zones (see fig. 1). For these collections, R. Robichaux provided information on the likelihood that individual plants were hybrids, although in each hybrid zone there is a continuum of backcrosses between likely parental species. Insects were frozen at −80°C shortly after collection.

Planthopper history

A 441 base pair piece of cytochrome oxidase I was amplified using primers C1-J-1751 'Ron' and C1-N-2191 'Nancy' (designed by R. Harrison lab, Simon et al., 1994) To date, we have examined individuals in six *Nesosydne* species. The frequency of transitions and transversions was examined for *Nesosydne* species using several genetic distances: uncorrected pairwise percent divergence, Kimura (1980) 2-parameter, and Tamura-Nei (1993). A phylogeny was reconstructed using both parsimony (PAUP, Swofford, 1993) and neighbor-joining (Phylip, Felsenstein, 1993; MEGA, Kumar et

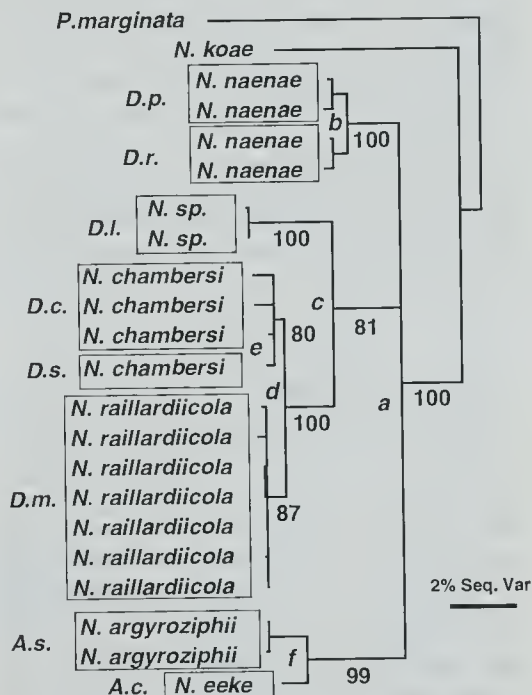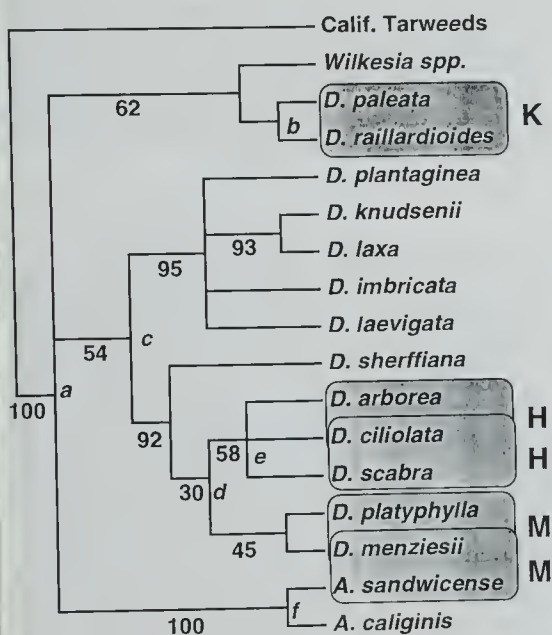## A. Silversword Alliance B. *Nesosydne* Planthoppers

Figure 1. A. Phylogenetic hypothesis of evolutionary relationships among selected plant species in the Hawaiian silversword alliance showing major clades (after Baldwin and Robichaux, 1995). The total number of species in the radiation is 28 (not all shown), which likely evolved from a single California tarweed species only in the past 4–6 million years (Baldwin, in press). Hybrid zones between pairs of taxa examined in the current study are shown by shaded boxes with islands noted to the right (K = Kauai, M = Maui, H = Hawaii). Bootstrap support (%) for particular clades are shown below branches. B. Phylogenetic reconstruction by parsimony of the history of *Nesosydne* species found on members of the Hawaiian silversword alliance using DNA sequence variation in mtDNA COI. Branch lengths are proportional to sequence variation. Numbers below branches denote bootstrap support (%) for nodes. Multiple individuals of the same species are shown with the same name. Boxes show host plant affiliations, with names to the left. On both reconstructions, points corresponding to co-speciation between planthoppers and their host plants are lettered a–f.

al., 1993). Bootstrapping (n=500) was used to provide a level of confidence associated with each branch. Outgroups included another Hawaiian *Nesosydne* planthopper, *N. koae*, which feeds on *Acacia koa* (see O'Connell, 1991) and *Prokelisia marginata*, a delphacid from the continental United States (see Roderick, 1987; Denno et al., in press).

Tests of hypotheses for herbivore diversity

The hybrid-bridge hypothesis predicts that host switching has occurred in the history of relationships between plants and their hosts. To test this hypothesis, the phylogeny of the planthoppers was compared to that of the silversword alliance. The planthopper phylogeny was mapped onto Baldwin and Robichaux's (1995) phylogeny for the silversword alliance based on sequences of nuclear ribosomal DNA. Events of hybrid switching and co-speciation, were reconstructed using TreeMap (Page, 1995b). A randomisation test (by "randomising" the planthopper tree using TreeMap, Page, 1995b) was used to test significance of the observed level of co-speciation between planthoppers and their plant hosts.

To test of whether plant hybrid zones are centres for insect diversity, the number of planthopper species was examined across five hybrid zones and compared to taxa and locations where hybridisation does not occur.

Results

Host plants associations

Nesosydne planthoppers have now been collected on 13 out of 28 members of the silversword alliance. Based on observations of both adults and developing nymphs, many earlier recorded associations are either spurious, site-specific, or no longer occur (Roderick, unpubl. data). On five plant species no planthoppers were found. On the other plant species, only one planthopper species occurred in sympatry on the same host plant species. Where a planthopper species occurred on more than one host species, the hosts were closely related and/or hybridise. These host records indicate that planthopper species in this group 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 *Drosophila yakuba* (Clary and Wolsten-

holme, 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 percent per million years (for island ages see Carson and Clague, 1995). Parsimony, neighbor-joining, and maximum likelihood gave identical trees with similar bootstrap values; only the parsimony tree is shown here (fig. 1B). While there may be other species not examined here that would fall within those feeding on the silversword radiation, this group was supported by multiple synapomorphies that distinguished it significantly from *N. koae*. 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 Hawaii and corresponds to the age of the silversword alliance.

Tests of hypotheses for herbivore diversity

The reconstruction of planthopper and host plant phylogenies resulted in 6 co-speciation events and no host-switching (fig. 1). It should be noted that the base of the tree for both host plants and planthoppers was unresolved. The randomisation test shows that this number of co-speciation events is significant (p < 0.01). Note that the method identifies a "co-speciation" events for the different planthopper haplotypes collected on *D. raillardioides* 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 fig. 1B). The reconstructed co-phylogenies provide no evidence of recent host-switching. Research is ongoing to determine whether this pattern of cospeciation is supported when all species of Hawaiian *Nesosydne* are included.

The reconstructed co-phylogenies provide no evidence to suggest that host-switching is important in the host associations documented here, as would be predicted by the "hybrid-bridge" hypothesis.

Planthoppers were collected over 5 extensive hybrid zones (fig. 2). Baldwin and Robichaux's
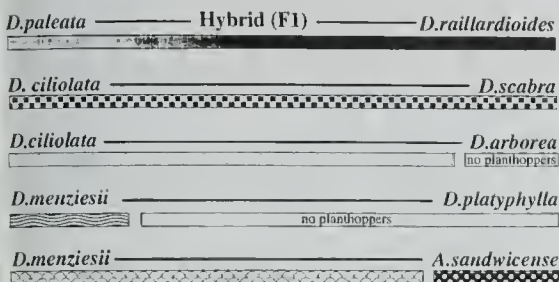
Planthopper Use of Hybrids: ▭

Figure 2. Patterns of planthopper host plant use and characteristics of five hybrid zones between members of the Hawaiian silversword alliance. Range of hybrid use for each planthopper species noted by shaded rectangles. In two hybrid zones, parental plant species were found with no planthoppers. See text for islands and degree of relatedness between plant taxa.

(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. raillardioides* (Kauai) and *D. ciliolata* and *D. scabra* (Hawaii). 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 while in the other, the planthopper's range was restricted to the parental species: *D. ciliolata* and *D. arborea* (Hawaii) and *D. menziesii* and *D. platyphylla* (Maui). On intergeneric hybrids between *A. 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*. No greater diversity of planthopper species was observed in these hybrid zones than on silversword taxa and locations where hybridisation does not occur: four of five hybrid zones supported only one planthopper species and one supported only two species. Thus, the evidence does not support the hypothesis that silversword hybrid zones are centres for planthopper biodiversity.

Discussion

The Hawaiian *Nesosydne* planthoppers are highly host specific, with each species feeding on one or a few closely related hosts. The significance of co-speciation demonstrates that species of planthoppers and members of the silversword alliance examined to date share parallel or co-phylogenies. Unfortunately, this result does not identify the processes that underlie the pattern (see Farrell and Mitter, 1993; Funk et al., 1995; Price, 1996). For example, co-phylogenies may arise though a number of processes that may include vicariance on one or both players, co-evolution, or adaptation by one player in response to the other. It is possible that major vicariant 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 co-speciation.

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 host-switching is limited (for review Roderick, 1994). Investigation of hybrid zones presented here demonstrate that the same planthopper species is not found on distantly related hosts, despite sympatry and the existence of intermediate hybrids. This pattern of host association indicates that limits exist to host adaptation by planthoppers. That single 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 likely follows the diversity generated in the silversword alliance.

Data presented here do not yet adequately address the role of hybridisation in the host species in causing differentiation of planthopper populations and species. For the taxa examined to date, hybrid bridges and host-switching do not explain current patterns of host use by planthoppers; patterns of host use can be predicted entirely on the basis of co-speciation of the planthoppers and hosts. Planthoppers are no more diverse in number of species than planthoppers; collected on non-hybrids. Whether genetic diversity within planthopper species is greater in hybrid zones remains to be tested. More rigorous tests for the role of plant hybridisation in the diversification of *Nesosydne* planthoppers are now underway and include reciprocal transplant studies, population genetic assessments of planthoppers across plant hybrid

zones, and a more complete molecular analysis of *Nesosydne* planthoppers on members of the silversword alliance and other host plants.

Acknowledgments

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