Speciation and phylogeography of Hawaiian terrestrial arthropods

G. K. RODERICK and R. G. GILLESPIE
Center for Conservation Research and Training, 3050 Maile Way, Gilmore 409, University of Hawai'i, Honolulu, Hawaii 96822, USA

Abstract

The Hawaiian archipelago is arguably the world's finest natural laboratory for the study of evolution and patterns of speciation. Arthropods comprise over 75% of the endemic biota of the Hawaiian Islands and a large proportion belongs to species radiations. We classify patterns of speciation within Hawaiian arthropod lineages into three categories: (i) single representatives of a lineage throughout the islands; (ii) species radiations with either (a) single endemic species on different volcanoes or islands, or (b) multiple species on each volcano or island; and (iii) single widespread species within a radiation of species that exhibits local endemism. A common pattern of phylogeography is that of repeated colonization of new island groups, such that lineages progress down the island chain, with the most ancestral groups (populations or species) on the oldest islands. While great dispersal ability and its subsequent loss are features of many of these taxa, there are a number of mechanisms that underlie diversification. These mechanisms may be genetic, including repeated founder events, hybridization, and sexual selection, or ecological, including shifts in habitat and/or host affiliation. The majority of studies reviewed suggest that natural selection is a primary force of change during the initial diversification of taxa.

*Keywords*: biodiversity, conservation, island biology

Introduction

Remarkable suites of endemic and often rare species are characteristic of isolated land masses. This is particularly true of the Hawaiian Islands, where the biota is well known for its extraordinarily high levels of endemism, with species frequently confined to minute distributional ranges. At the same time, anthropogenic disturbance, either direct or indirect, is causing rapid species decline. No other area in the USA has such a high proportion of endemic species nor suffers the impact from as many new species annually as the Hawaiian Islands (Dobson *et al*. 1997). As a consequence, the archipelago represents a microcosm for studies in evolution and conservation.

There are several geographical features that render the Hawaiian archipelago an unparalleled scientific laboratory for studying processes of evolution. First, the extreme isolation of the Hawaiian Islands has allowed repeated and explosive diversification of species from a single ancestor, often accompanied by radical shifts in

morphology, ecology and behaviour. These radiations are associated with high frequencies of endemism: greater than 81% in birds and an estimated 99% in terrestrial molluscs and arthropods (Eldredge & Miller 1995, 1997; Miller & Eldredge 1996). Second, the tremendous topographical range and consequent environmental diversity (wet and dry habitats; bogs, shrublands and forests; elevations from tropical coastlands to alpine deserts) provide a huge ecological spectrum for species differentiation. Third, the series of islands provides a replicated system for examining within- and between-island patterns of species formation across similar ranges of environmental extremes. Finally, because the high islands are arranged by age from Kaua'i (oldest) to Hawai'i (youngest), the archipelago allows examination of species formation within an identifiable chronological framework (Carson & Clague 1995) (Fig. 1). The initial stages of population subdivision can be found on the youngest island, with the dynamic volcanic state of the island providing shifting barriers to gene flow (Carson 1990a). Later stages in species formation can generally be found on the older islands. Upon this palette, the primary factors responsible for generating the high

Correspondence: R. G. Gillespie. Tel.: +01-(808)-956–8884; Fax: +01-(808)-956–9608; E-mail: gillespi@hawaii.edu
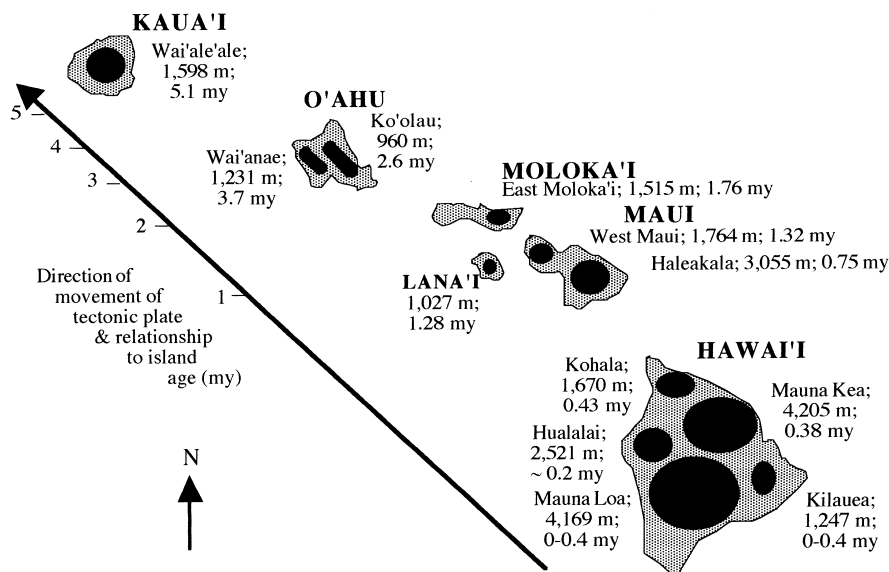
Fig. 1 Major land masses of the Hawaiian Islands. Dark circles mark the highest (> 900 m) volcanoes. Elevations and ages of the volcanoes are given (from Carson & Clague 1995).

diversity of endemic species of arthropods are genetic factors associated with small population sizes, and ecological factors arising from habitat and/or host shifts.

Here, we examine patterns of species formation and phylogeography within lineages of Hawaiian arthropods. Arthropods make up over 75% of the Hawaiian endemic biota (Eldredge & Miller 1997) and include some of the world's best-known species radiations. We first document phylogeographic patterns within lineages and then discuss mechanisms that have contributed to these patterns in different taxa. In this discussion we use currently recognized species designations and do not attempt to impose our own assessments of species boundaries. However, it should be noted that species designations are particularly problematic in Hawai'i, as hybridization may be a recurrent theme, and there is increasing evidence for the existence of a number of paraphyletic 'species' (see Discussion below). We consider phylogeography in its broadest context, 'the study of principles and processes governing the geographical distributions of genealogical lineages including those at the intraspecific level' (Avise 1994). While this definition may encompass a greater evolutionary spectrum than others in the volume, it is the relevant focus for many of the important patterns of evolution in Hawai'i.

Patterns

The phylogeographic pattern that predominates in most Hawaiian taxa, both species and populations, is a step-like progression down the island chain from the oldest to the youngest islands (see Funk & Wagner (1995) for a review of the progression rule as applied to Hawaiian

species radiations). This phenomenon was first described in the seminal papers of Carson (1970, 1974, 1987b) who used chromosomal sequences to infer phylogenetic patterns of the Hawaiian *Drosophila*. In addition, species (or populations) tend to have the narrowest ranges on the older islands (Gillespie *et al.* 1997). Species on the youngest island (Hawai'i) tend to be widely distributed over the island and in some groups these species are shared with Maui, the next-youngest island. A number of different within-island patterns may be superimposed on these general patterns. Here we discuss three categories of patterns found in the native Hawaiian taxa: (i) single representatives of a lineage throughout the islands; (ii) species radiations in which there are either (a) single endemic species on different volcanoes or islands, or (b) multiple species on each volcano or island; and (iii) single widespread species within a radiation of species that exhibits local endemism.

1. Single species in a lineage

A number of taxa in the Hawaiian Islands are represented by single species. Carson (1987a) has compiled genus:species ratios for selected Hawaiian taxa, and has suggested genetic mechanisms that could provide for the development of speciose vs. nonspeciose lineages. These single species are generally endemic to the archipelago, and are often morphologically unique. The fact that they have failed to proliferate has often been attributed to high dispersal abilities. For example, two species of dragonflies, *Anax strenuus* (Aeshnidae) and *Nesogonia blackburni* (Libellulidae), are both single representatives of Hawaiian lineages (Howarth & Mull

1992). The lack of diversification in these taxa is consistent with their tremendous dispersal abilities. In particular, the sister species of *A. strenuus* is *A. junius*, a species that is widespread throughout the Pacific. Among Lepidoptera, the two endemic Hawaiian butterflies, *Vanessa tameamea* (Nymphalidae) and *Udara blackburni* (Lycaenidae) are the sole representatives of their lineages in the Hawaiian Islands. Again, the nonspeciose nature of these taxa has been attributed to the fact that, at least for *Vanessa tameamea*, they belong to groups that are noted for migrations or strong flight (Howarth & Mull 1992). Among Hemiptera, the genus *Hyalopeplus* (Miridae) has not radiated ecologically or differentiated by island. The single endemic Hawaiian species, *H. pellucidus*, belongs to a genus that is widespread in the Pacific. This pattern contrasts to that of related mirids in endemic genera that have speciated extensively (Asquith 1997). Finally, the koa bug, *Coleotichus blackburniae*, is a lone representative of its lineage and is a strong flier (A. Taylor and P. Follett, personal communication).

Can dispersal abilities explain lack of differentiation?

The situations described above suggest that widespread, dispersive species have colonized the Hawaiian Islands, and have differentiated from mainland ancestors on the archipelago, yet have failed to undergo species proliferation because of their dispersal abilities. However, this argument begs the question of how proliferation has occurred in other taxa. The ancestors of many lineages that have undergone spectacular diversification in the Hawaiian archipelago are also highly dispersive. For example, the genus *Tetragnatha* has been found on every habitable land mass examined to date (Gillespie *et al.* 1994). Aerial sampling has shown the genus to comprise 96% of the aerial spider plankton collected offshore (400 km from land in the China Sea) (Okuma & Kisimoto 1981). Not surprisingly, *Tetragnatha* specimens have been found to be among the first and most persistent colonists on mangrove islands in the Florida Bay (Simberloff & Wilson 1968). However, in the Hawaiian Islands the genus has radiated into a tremendous diversity of ecologically specialized and narrowly endemic forms (Gillespie *et al.* 1997). Other radiations, including mirids (Asquith 1997) and delphacid planthoppers (Roderick 1997; Asche 1997) have arisen within groups that are known for their dispersal abilities. Given the dispersive nature of many of the colonists, under what conditions can proliferation occur? It may be that diversification is the general rule for colonizing taxa that are exposed to largely unexploited ecological space over a sufficient time period. Among species that have not diversified in the Hawaiian Islands, it may be

that colonization is relatively recent, or that possible habitats into which they could diversify have already been 'filled'.

Single representatives among relict taxa

An alternative explanation for the nonspeciose nature of certain taxa is that they may be relict lineages. Certain taxa are characterized by a suite of apomorphies which, in some cases, has even caused them to be placed in monotypic genera. For example, the spider *Doryonychus raptor* (Tetragnathidae) has abandoned the web-building behaviour characteristic of the family, and developed long claws at the ends of the tarsi of leg pairs I and II (Gillespie 1991b, 1992). The claws are employed in a unique behaviour whereby insects are impaled directly from the air. *D. raptor* has all the features characteristic of the genus *Tetragnatha*, but is phylogenetically basal when compared to *Tetragnatha* species worldwide (Gillespie *et al.* 1994). Such accumulation of autopomorphies among older clades appears to occur in a number of Hawaiian arthropod groups (Asquith 1995). The phylogenetic placement of *D. raptor*, coupled with its extraordinarily specialized foraging behaviour and confinement to very small pockets of forest on the oldest of the main Hawaiian Islands (Kaua'i) suggests that the species may be a relict of a previously diverse radiation of *Tetragnatha* (cf. Grimaldi 1988).

Possible effects of recent extinctions

It is possible that some lineages in the Hawaiian Islands appear to be nonspeciose as an artifact of extinction of a prominent component of the lineage. For example, in many species radiations the taxa within the radiation have very short branches, reflecting the rapid species formation that characterizes these groups. If all species except one were systematically removed from within one part of the radiation, the result would be a long branch to that part of the radiation. This long branch may then be 'attracted' to other long branches (Felsenstein 1978), such as those that characterize the outgroups, rather than to the short branches of the rest of the radiation. In the Hawaiian archipelago this situation may occur because of the extinction of much of the lowland entomofauna. For example, it is possible that the suggestion of multiple introductions of *Tetragnatha* spiders into the Hawaiian Islands (Gillespie *et al.* 1994) might be explained by this phenomenon: Based on 12S ribosomal DNA sequences, the few lowland representatives of this radiation (*T. hawaiensis* clade) were found to group outside the main radiation of Hawaiian *Tetragnatha*. As described above, this may be an artifact of possible extinction of lowland relatives of *T. hawaiensis*.

Table 1 Select Hawaiian terrestrial arthropods for which information exists concerning patterns of speciation and phylogeography. Species are categorized as described in the text: 1, single representatives of a lineage throughout the islands; 2, species radiations with (a) single endemic species on different volcanoes or islands or (b) multiple species on each volcano or island; and 3, single widespread species within a radiation of species exhibiting local endemism

Order: Family	Genus	No. of species	Reference
1. Single Species			
Araneae:Tetragnathidae	*Doryonychus raptor*	1	Gillespie (1991b, 1992)
Araneae:Tetragnathidae	*Tetragnatha hawaiensis*	1?	Gillespie *et al.* (1994)
Isopoda: Philosciidae	*Littorophiloscia hawaiiensis*	1	Taiti & Howarth (1997)
Odonata:Aeshnidae	*Anax strenuus*	1	Howarth & Mull (1992)
Odonata:Libellulidae	*Nesogonia blackburni*	1	Howarth & Mull (1992)
Lepidoptera:Lycaenidae	*Udara blackburni*	1	Howarth & Mull (1992)
Lepidoptera:Nymphalidae	*Vanessa tameamea*	1	Howarth & Mull (1992)
Hemiptera:Miridae	*Hyalopeplus pellucidus*	1	Asquith (1997)
Hemiptera:Scutelleridae	*Coleotichus blackburniae*	1	Howarth & Mull (1992)
(2a) Species radiations with single endemic species on different volcanoes or islands			
Araneae:Linyphiidae	*Labulla*	8	Hormiga (unpublished)
Isopoda:Philosciidae	*Hawaiioscia*	4	Taiti & Howarth (1997)
Orthoptera:Tettigoniidae	*Banza*	9	Strazanac (1996)
Orthoptera:Gryllidae	*Caconemobius*	9	Otte (1989); Shaw (1995)
Lepidoptera:Geometridae	*Eupethicea*	12	Montgomery (1983)
(2b) Species radiations with multiple species on each volcano or island			
Araneae:Tetragnathidae	*Tetragnatha*	≈ 60	Gillespie (1991a)
Psocoptera:Psocidae	*Ptycta*		Thornton (1984)
Odonata:Coenagrionidae	*Megalagrion*	22	Polhemus (1997)
Orthoptera:Gryllidae	*Laupala*	35	Otte (1989, 1994); Shaw (1995, 1996a,b)
Orthoptera:Gryllidae	*Prognathogryllus*	36	Shaw (1995)
Coleoptera:Carabidae	Platynini	128	Liebherr (1997)
Hemiptera:Delphacidae	*Nesosydne*	81	Asche (1997); Zimmerman (1948)
Diptera: Drosophilidae	*Drosophila*	500–1000	Kaneshiro & Boake (1987)
Diptera: Pibunculidae	*Cephalops*	36	DeMeyer (1996)
Diptera:Tephritidae	*Trupanea*	21	Hardy & Delfinado (1980)
(3) Widespread species within radiations of localized species			
Araneae:Tetragnathidae	*Tetragnatha quasimodo*		Gillespie (1991a); Gillespie *et al.* (1994)
Araneae:Theridiidae	*Theridion grallator*		Oxford & Gillespie (1996a,b,c); R. G. Gillespie & G. S. Oxford (unpublished)
Odonata: Coenagrionidae	*Megalagrion hawaiiense*		Polhemus & Asquith (1996); Polhemus (1997)
Diptera: Drosophilidae	*Drosophila grimshawi*		Piano *et al.* (1997)

2. Species radiations

(a) Isolation and single-island endemics

A number of lineages have progressed down the island chain, forming distinct species on each volcano or island on the way (Fig. 2a). For example, the spider genus *Labulla* (Linyphiidae) shows a pattern of single (occasionally two) species endemic to most volcanoes: two species on Kaua'i, one on the Wai'anae Mts. (O'ahu), two on the Ko'olau Mts. (O'ahu), one on Moloka'i, one on Maui, and one on Hawai'i (G. Hormiga and J. Coddington, unpublished). Preliminary work based on morphological and mtDNA sequences (cytochrome oxidase) indicates that

the radiation is monophyletic, and has formed new species in progression down the island chain. Similarly, the Hawaiian grasshopper genus *Banza* (Tettigoniidae) also has a single species on most volcanoes on Kaua'i, O'ahu, Moloka'i, and Maui, and one species on Hawai'i (Strazanac 1996). A phylogeny based on morphological characters indicates that the most ancestral species are on the oldest islands. Predatory caterpillars in the genus *Eupethicea* have also tended to form single species on different islands (Montgomery 1983). Based on cytochrome oxidase I mitochondrial DNA sequences (M. Heddle, G. K. Roderick, E. Metz, unpublished) the herbivorous species, *E. monticolens*, appears to be ancestral to the
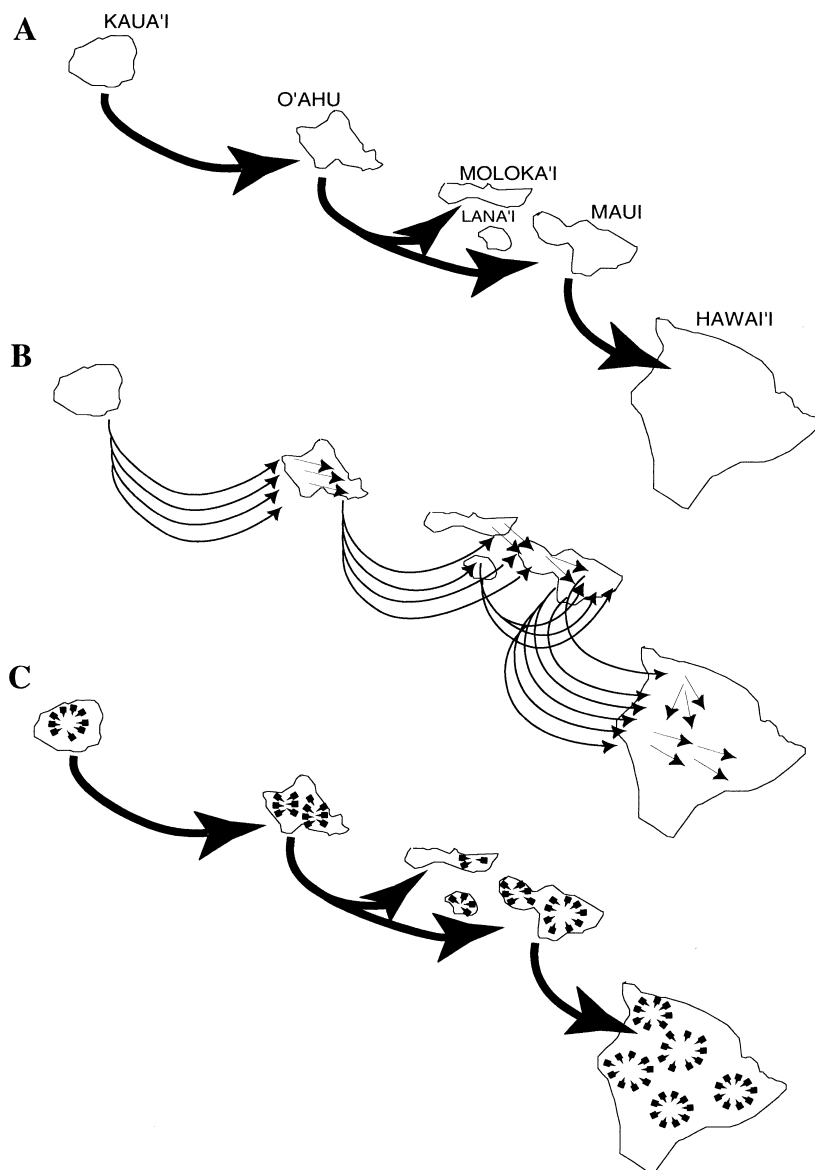
Fig. 2 A. Progression of lineages along the island chain, resulting in distinct species on each volcano or island. Arrows indicate direction of speciation events. B. Multiple speciation events between islands or volcanoes within islands, as a result of (for example) repeated founder events. Sexual selection has also been implicated in such founder events. C. Multiple speciation events within islands that may arise as a result of such effects as ecological shifts. Arrows are centred around the different volcanoes within which speciation occurs.

predatory species, with pollen feeding ancestral to predatory behaviour and a single shift to a predatory lifestyle.

In the genus *Hawaiioscia* (Isopoda: Philosciidae) (Taiti & Howarth 1997) there are four truly troglobitic species from caves on Kaua'i, O'ahu, Moloka'i, and Maui, respectively. These four taxa are morphologically very close, although they show some clear differences. All known populations of *Hawaiioscia* occur in lowland lava tubes near the coast. Mitochondrial (COI) evidence suggests that dispersal has permitted a stepwise progression down the island chain (M. A. Riverage, G. K. Roderick, unpublished). An alternative hypothesis to explain the phylogeography of the cave isopods is that they have colonized lava-tube caves independently

multiple times, perhaps from an as yet undiscovered widespread littoral species.

(b) Multiple species on each volcano or island

Factors implicated in the formation of multiple species on a single island may be divided into two broad categories: genetic and ecological. Genetic effects include founder events, hybridization, and sexual selection. Species that differentiate through these mechanisms will generally be expected to show a pattern in which sibling species are allopatric, usually on different (probably adjacent) volcanoes or islands (Fig. 2b). Species that differentiate as a result of ecological shifts (which may be associated with a habitat and/or a host) may be expected to show a pattern

whereby species proliferate within a given land mass (Fig. 2c). While we consider these mechanisms in turn, we do not imply that they are mutually exclusive. Several factors may be involved in any given radiation, and may operate together or in tandem.

A. Genetic effects

Genetic changes have frequently been implicated in species diversification of arthropods in the Hawaiian Islands. Particular factors that may be involved in such genetic changes include founder events, hybridization and sexual selection.

(i) Founder events and isolation

Colonization events involving small numbers of individuals may trigger rapid species formation (Carson & Templeton 1984; Coates 1992; Mayr 1954). Selective pressures are likely to be different and the environment of the small area occupied by these colonists is probably more homogeneous. More importantly, allele frequencies at some loci will differ from those of the parent population because of accidents of sampling (Templeton 1980). These conditions may provide key genetic variability for significant adaptive character change mediated by selection (Carson 1990b). In particular, traits controlled by few genes, with epistatic modifiers (type II, see Templeton 1981) are likely to be affected during founder events. As a result, the founder events that are generally considered to accompany colonization of new islands may lead to rapid differentiation (Fig. 2b). In addition, it has been suggested that the growing islands impose a shifting mosaic population structure, with populations continually undergoing recolonization and extinction as habitats are formed and destroyed by volcanic activity. Because volcanic activity has always been focused on the south-easternmost island of the archipelago, this growing 'front' may serve as an 'evolutionary crucible' (Carson 1990a). Accordingly, there appears to have been opportunity for founder events to have occurred between islands, between volcanoes within islands, and between sites as new volcanoes are formed. These multiple opportunities for isolation of small populations have been implicated in generating the tremendous diversity among the Hawaiian *Drosophila* (Kaneshiro & Boake 1987), and may also be responsible for rapid speciation in a number of other groups. For example, Thornton (1984) provided a phylogenetic estimation of the endemic *Ptycta* complex (Psocidae) based on morphological characters, and used it to propose that a combination of isolation of small populations and subsequent rapid divergence has been involved in species formation in this group. A similar analysis for the Hawaiian *Cephalops* (Pipunculidae) led to comparable conclusions (DeMeyer 1996).

Besides founder-induced isolation, there are several situations in which vicariant isolation may have allowed species differentiation. As mentioned above, taxa on the youngest island (Hawai'i) are frequently widespread over the entire island (comprising five volcanoes), although there are species that have already undergone differentiation between volcanoes here. The tendency for many species to be single-island (or volcano) endemics on the older islands may be due, in part, to vicariance within the island (or island complex). For example, the glacially mediated fluctuation in sea level alternatively flooded and exposed the land connecting islands of the Maui Nui complex (Moloka'i, Maui, Lana'i and Kaho'olawe). This may have allowed differentiation between the volcanoes, and the concomitant single-volcano endemism that is frequently observed. The highly dissected topography of the archipelago, particularly of the older islands, may also have contributed to isolation and species formation in many groups (Carlquist 1980). For example, isolation of this form may have played an important role in the diversification of Hawaiian crickets (Otte 1989). Among cave species, isolation among the different lava tubes on the same island may have allowed the formation of new species. For example, new species have formed among isolates of the cixiid planthopper *Oliarus polyphemus* that inhabit different lava tube systems on Hawai'i (Hoch & Howarth 1993).

(ii) Hybridization

Differential mixing of characters during segregation of populations and species may occur as a result of hybridization of newly divergent taxa (Endler 1989; Harrison 1993). Behavioural changes during founder events may facilitate hybridization, as it has been suggested that sexual interactions may lose specificity subsequent to a founder event (Kaneshiro 1989; see below). Closely related heterospecifics may therefore hybridize and/or introgress subsequent to colonizing a new land mass, but the extent of genetic exchange may differ between different regions of the genome (Desalle & Giddings 1986). Differences may be particularly pronounced between character sets involving nuclear and mitochondrial (mt)DNA. MtDNA differs from nuclear DNA because of: (i) its greater sensitivity to the effects of each founder event due to its smaller effective population size (25%) relative to nuclear DNA; (ii) its transmission through the female line only; and (iii) its existence as a single copy (Avise 1991; Roderick 1996). Analysis of mtDNA information will result in a gene genealogy, but will probably provide an incomplete history of the organisms if much hybridization has taken place. The occurrence of hybridization may explain differences that have been found between nuclear and mitochondrial phylogenies, in particular for the Hawaiian *Drosophila* (DeSalle *et al.*

1997). Indeed, natural hybridization with the formation of fertile hybrids has been documented between closely related species of *Drosophila* on the youngest island of Hawai'i (Carson 1989).

Among Hawaiian crickets, Shaw (1996a) comments on a discrepancy between phylogenies generated on the basis of song (Otte 1994) with that generated from mtDNA variation. Although the discrepancies could be explained by problems with current taxonomic boundaries, and problems with mtDNA lineage sorting, she argued that hybridization and introgression appear to be the most likely explanation.

While the number of species in which hybridization has been documented is presently small, it will probably grow as researchers accumulate phylogeographic knowledge about particular radiations.

(iii) Sexual selection

Sexual selection is frequently implicated in the acceleration of species formation. Based on the premise that founder events are the most important mechanism of speciation in the Hawaiian *Drosophila* (Fig. 2b), Kaneshiro (1976, 1983) has proposed models suggesting the importance of sexual selection in driving species proliferation in these insects. The basic tenets of these arguments are that, when a population becomes isolated and is released from interaction with related species, its sexual behaviour may become less constrained, resulting in simpler, more intraspecific variability (Kaneshiro 1983). Intrasexual selection may then operate to cause divergence of the sibling species during isolation because of a shift in the distribution of mating preferences during the founder/flush cycle (Carson 1986; Carson & Kaneshiro 1976). Some current research on the Hawaiian *Drosophila* is now focused on finding behaviour genes involved in this speciation process (Y. Nakano and K. Y. Kaneshiro, personal communication).

Sexual selection has also been implicated in the evolution of Hawaiian crickets in the genus *Laupala* (Otte 1989; Shaw 1996b). Phylogenetic analyses based on morphological (Otte 1994) and molecular (Shaw 1996a) characters indicate that extensive intra-island species formation has occurred in this group. Differentiation between closely related species is associated with changes in song, a character which is controlled by many genes of small effect (Shaw 1996b). These features of the *Laupala* system suggest that, unlike the Hawaiian *Drosophila*, founder events have not played a major role in the initial stages of species diversification (Otte 1989; Shaw 1996a, 1996b). Rather, differentiation appears to occur through the interaction of sexual selection on genetically well structured populations. More work is needed to understand the relative importance of these factors in the initial divergence of species in this group.

B. Ecological shifts

Diversification of ecological affinities is a common feature of taxa that have proliferated within islands (Fig. 2c). Species may shift habitat or host, or (in the case of cospeciation) shift habitat with their host.

(i) Habitat shifts

Howarth (1981, 1993) was the first to document the importance of adaptive shifts in species formation in the Hawaiian biota. He showed that many of the cave endemics in the different Hawaiian Islands had their closest relatives on the surface. Prior to this work, it had been thought that cave species evolved through a process of relict formation, with populations being isolated in caves subsequent to major climatic changes (Barr & Holsinger 1985). However, cave species on Hawai'i, the youngest island, cannot be more than a million years old and have never experienced conditions such as glaciation that might leave relicts. Accordingly, Howarth (1981) argued that these species must have evolved from the epigean fauna as a result of adaptive shifts. Likewise, adaptive shifts into caves may be responsible for species formation in the ground cricket genus *Caconemobius* (Otte 1989; Shaw 1995). In a similar manner, Liebherr (1997) has found that differentiation among marginal isolates may have played a role in species formation within the large radiation of Hawaiian carabid beetles: Using an assessment of phylogeny based on an extensive analysis of morphological characters, Liebherr found that on any one island higher-elevation species are generally more basal, a pattern consistent with speciation by peripheral isolation.

Among Hawaiian *Drosophila*, Kambysellis & Craddock (1997) have generated a phylogeny based on yolk protein DNA sequences, showing that clades are characterized according to whether they breed on fungi, leaves, fruit, or bark. Suites of reproductive characters (in particular, ovarian egg and ovipositor traits) appear to evolve together (Kambysellis 1993). Adaptive shifts to new breeding sites appear to have been important at least in the early diversification of the group, and in a few more-recent speciation events (Craddock & Kambysellis 1997; Kambysellis *et al.* 1995; Kambysellis & Craddock 1997) (Fig. 3).

Polhemus (1997) used morphological and ecological characters to generate a phylogeny which showed that the Hawaiian radiation of damselflies in the genus *Megalagrion* (22 species) cluster according to ecological affinity (gill shape and breeding ecology). Based on this analysis species initially differentiated on Kaua'i, or a preceding high island, and representatives of each of these clades then progressed independently down the island chain. This would suggest that diversification itself cannot be explained on the basis of ecological shifts in this group.
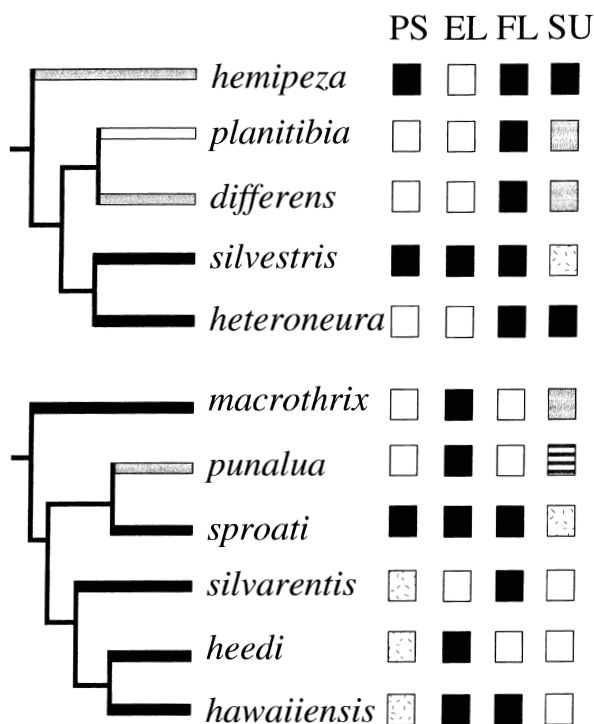
Fig. 3 Phylogeny of different clades of Hawaiian *Drosophila* showing ecological changes associated with speciation events. Bars on the cladogram indicate islands (grey, Oahu; stippled, Molokai; white, Maui; black, Hawaii). PS = predatory substrate (white, stems; black, bark; stippled, flux). EL = egg load (white, 1–100; black, > 100). FL = posterior filament length (white, moderate; black, long). SU = breeding substrate (white, flux; black, stems and bark; stippled, bark; horizontal bars, multi; gray, stems). Adaptive shifts or changes in morphology associated with the use of new breeding sites appear to have been important in both species groups shown here. (Adapted from Kambysellis & Craddock 1997).

Recently, Gillespie *et al.* (1997) have examined the role of adaptive shifts in the radiation of spiders in the genus *Tetragnatha* in order to determine the extent to which species splitting is associated with shifts in ecological affinity. A preliminary phylogenetic analysis based on morphological characters (Gillespie 1993) indicated that the 'spiny-leg' clade of Hawaiian *Tetragnatha* grouped according to ecological affinity, with species characterized as 'green leaf-dwelling', 'maroon', and 'gray/black bark-dwelling'. A phylogeny was then generated based on molecular data from ribosomal 12S and cytochrome oxidase I mitochondrial DNA, and allozymes; ecological associations were considered in the context of the phylogeny (Gillespie *et al.* 1997). The results of the molecular analysis indicated that species on any one island are generally most closely related to each other, and each of the different 'ecomorphs' appear to have evolved independently on the different Hawaiian islands (Fig. 4). This

study suggests the intriguing possibility that there has been a one-to-one convergence of the same set of 'ecomorph' types on each island in a manner similar to lizards of the Caribbean (Losos 1992; Losos *et al.* 1994).

(iii) Host switching

Host switching is a form of ecological shift which involves a change of hosts other than would be predicted by the host phylogeny, such that the two phylogenies are no longer congruent. Host switching can result in speciation if, following a switch to a new host, the specialized trophic level becomes sufficiently isolated and divergent from the species on the original host. Compilations of research on herbivorous insects and their hosts indicate 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 (Farrell & Mitter 1993; Mitter *et al.* 1991). Among Hawaiian insects, Asquith (1995; 1997) generated a phylogeny based on morphological characters for the genus *Sarona* (Miridae) and found that speciation within the genus appears to be largely host mediated. Species have differentiated extensively within islands as a result of host switching. Some clades have differentiated between closely related hosts, while others have differentiated between unrelated hosts. Similarly, in the Hawaiian cricket genus *Prognathogryllus*, Shaw (1995) used morphological characters from Otte (1994) to show that changes in host associations, coupled with geographical isolation, may underlie species formation.

(iii) Cospeciation

Another mechanism through which herbivorous arthropods can diversify and shift ecological affinity is by means of cospeciation and tracking the ecological shifts of the host. Cospeciation involves the matching of speciation events in two lineages such that the two phylogenies resemble one another (Brooks 1988; Mitter & Brooks 1983; Page 1995). Although still work in progress, Roderick (1997; Roderick & Metz 1997) has shown that *Nesosydne* planthoppers associated with plants in the Hawaiian silversword alliance (Asteraceae) are highly host specific, with each species feeding on one, or a few closely related, hosts (Fig. 5). The significant pattern of recent host tracking for the species examined to date suggests that planthoppers and their associated members of the silversword alliance share parallel phylogenies. Work is underway to include all *Nesosydne* species in this analysis. Unfortunately, the result of cospeciation does not directly demonstrate reciprocal adaptation or identify the processes that underlie the pattern of cophylogenies (Price 1996). For example, cophylogenies may arise through a
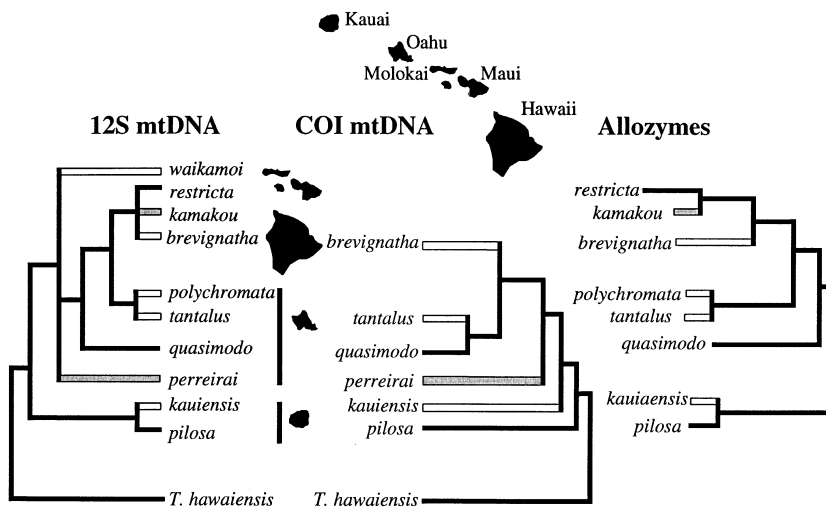
Fig. 4 Phylogeny of species in the spiny-leg clade of Hawaiian *Tetragnatha* (adapted from Gillespie *et al.* 1997). A. 12S mtDNA sequences; B. COI mtDNA sequences; C. allozymes. For the 12S tree, the strict consensus of 55 trees is shown. Bars on the cladogram indicate groups with which species are affiliated based on morphological characters (white, 'green leaf-dwelling' group; grey, 'maroon' group; black, 'grey/black bark-dwelling' group; see Gillespie (1993) for morphological characters that define groups).

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 speciation associated with colonization of an island or volcano has shaped both planthopper and plant phylogenies concurrently, and that planthopper adaptation to hosts (and/or vice versa) may not be important in explaining significant cospeciation.

Host hybrids as bridges for speciation. Recently, it has been suggested that hybrids between host species may be associated with herbivorous insect diversity (Strauss 1994; Whitham *et al.* 1994). Much ecological and genetic data have demonstrated that hybrid zones can represent very different environments for herbivorous insects and may allow genetic

diversification and speciation. This scenario has been termed the 'hybrid bridge' hypothesis (Floate & Whitham 1993). Hybrid hosts thus can provide a means for host switching. The Hawaiian archipelago again provides an ideal opportunity for examining the role of hybrid zones in species formation. In particular, the occurrence of natural hybrids between many members of the silversword alliance provides a unique opportunity to test the predictions of both host tracking and host switching among the planthoppers (*Nesosydne*) that feed on these plants. These hybrids also allow a phylogenetic assessment of the importance of plant hybridization in determining the diversity of associated insects, specifically the role of hybrid 'bridges' and hybrid zones as centres of diversity. Roderick & Metz (1997) have conducted preliminary investigations of silversword
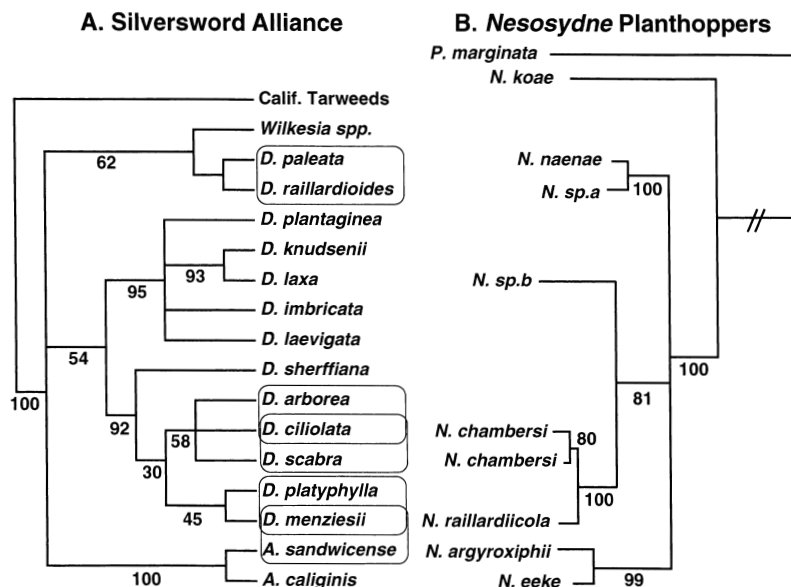
Fig. 5 Comparison of phylogenies of (A) select species of the Hawaiian silversword alliance (data from Baldwin & Robichaux 1995) with (B) associated *Nesosydne* planthoppers (after Roderick 1997). Ovoid areas in (A) represent plant species that hybridize. The trifurcation near the base of both trees is left unresolved because of low bootstrap support. *N. koae* feeds on koa in Hawaii and *Prokelisia marginata* is a salt marsh-inhabiting delphacid planthopper from the USA mainland.

hybrid zones and found that the existence of intermediate hybrids is insufficient to allow species of *Nesosydne* planthoppers to shift onto distantly related hosts. In two hybrid zones, for example, 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, the fact 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 follows the diversity generated in the silversword alliance: the hybrids are not used as 'bridges'.

3. Single widespread species within radiations

Most species that belong to large Hawaiian radiations occupy rather small ranges, with many species being endemic to single mountains. Nevertheless, many radiations also contain one or a few species that are widespread (a characteristic also of some continental radiations; D. A. Polhemus, personal communication). For example, in the Hawaiian *Drosophila*, *D. grimshawi* is widespread, with members distributed on all major islands. However, recent evidence (Piano *et al.* 1997) based on DNA sequences (yolk protein gene), chorion ultrastructure, and behaviour have suggested that the different populations do not undergo extensive gene flow. Instead, populations of this species are highly structured. In addition, *D. grimshawi* appears to be paraphyletic (O'ahu and Kaua'i populations *of D. grimshawi* are closer to *D. pullipes* than to other populations of *D. grimshawi*).

Among Hawaiian *Tetragnatha* spiders, *T. quasimodo* is widespread and found on all islands except Kaua'i, while the remaining species in this 'spiny-leg' clade are confined to much smaller areas (Gillespie 1991a). To examine this phenomenon, we have conducted a preliminary examination of population structure in *T. quasimodo* based on electrophoretic and mitochondrial and nuclear intron DNA sequence information of populations. Using populations from O'ahu, East Maui and Hawai'i (two populations) we estimated average heterozygosity based on allozyme frequencies (R. G. Gillespie & G. K. Roderick, unpublished). To measure genetic differentiation and gene flow among populations we used Wright (1951)'s F_{ST}, and hence $N_e m$, which showed a significant linear relationship with pairwise distances when plotted on a log scale (slope = 1.912, $P = 0.018$). For comparison, Nei's distance ranged from 0.05 (between adjacent populations on Hawai'i) to 0.59 (between the youngest population on Hawai'i and the oldest O'ahu population), and showed a significant linear relationship with geographical distance and volcano age. We also used an intron (see Palumbi 1996) within nuclear

DNA intron polypeptide chain elongation factor-1αF2 to examine population subdivision in this widespread species (G. K. Roderick & R. G. Gillespie, unpublished). The results all suggested sequential colonization of volcanoes from the oldest to the youngest, and also showed that populations were highly structured between islands, with little gene flow. Accordingly, as with the drosophilid *D. grimshawi*, it appears that extensive gene flow cannot explain the widespread nature of this species.

Another species of spider that is widespread throughout the islands, but appears to be part of a large radiation of taxa with smaller ranges, is the Hawaiian happy-face spider *Theridion grallator* (Gillespie & Tabashnik 1989). *T. grallator*, which is best known for its extraordinary colour polymorphism, is a small spider found on the undersides of leaves in mesic and wet forests in the Hawaiian Islands. Three characteristics of the *T. grallator* system suggest that colonizations of different islands have been rare events and have probably been associated with genetic bottlenecks: (i) island-wide genetic differences underlie the colour polymorphism in different populations (Oxford & Gillespie 1996a,b,c); (ii) pattern details of each morph differ between islands (R. G. Gillespie & G. S. Oxford, unpublished); and (iii) estimates of gene flow based on allozymes and fixed genetic differences between populations indicate that, as with *D. grimshawi* and *T. quasimodo*, populations of *T. grallator* are genetically isolated (R. G. Gillespie & G. S. Oxford, unpublished).

The damselfly *Megalagrion hawaiiense* occurs on all high volcanoes, but exhibits different colour morphs on different volcanoes (illustrations in Polhemus & Asquith 1996). This observation suggests that populations of the apparently widespread *M. hawaiiense*, as with *D. grimshawi*, *T. quasimodo*, and *T. grallator*, are much more differentiated than they appear based on gross morphology.

Thus, many of the apparently widespread 'species' within species radiations may in fact represent complexes of species. Why have these species maintained morphological similarity despite their genetic differences? As in each of these cases the habitats occupied on different islands is similar, it may be that morphological stasis is a result of similar selective pressures. However, it is not clear why these species should be different from others within their own radiation that have undergone morphological differentiation.

Conclusions

This review highlights the value of the Hawaiian archipelago in elucidating phylogeographic patterns. Because over 75% of the native Hawaiian terrestrial biota comprises arthropods, these groups offer great potential for allowing a general understanding of patterns and processes in species formation. A number of trends are

beginning to emerge. Many of the arthropods that have managed to colonize the Hawaiian Islands have descended from highly dispersive taxa. Yet, it remains unclear as to why certain groups have differentiated while others have not. Indeed, most groups that have colonized the Hawaiian Islands once appear to have done so repeatedly (e. g. *Tetragnatha* and *Argyrodes* spiders, mirid bugs, delphacid planthoppers). Subsequent radiation in the Hawaiian Islands is generally associated with loss of dispersal ability, although the interplay between these parameters and causal relationships are poorly understood. Lineages tend to progress down the island chain, with the most ancestral groups (populations or species) on the oldest islands. However, additional patterns may be superimposed on this general progression, the nature of which varies among taxa. Certain groups are represented by populations of a single species that may have failed to differentiate, or may be relicts of historical radiations. Other groups have species on different volcanoes. Among the major radiations, both genetic (founder events, hybridization, and sexual selection) and ecological (habitat shifts and host switches) factors have been implicated in the proliferation of different groups. No single mechanism can explain the diversification and speciation for all groups of Hawaiian arthropods.

This review does suggest that ecological parameters have played an important role in the diversification of Hawaiian terrestrial arthropods, and supports the view of naturalists in the earlier part of the century, that divergent natural selection is the ultimate cause of adaptive radiation (see Schluter 1996 for review). Mechanisms by which ecological shifts might occur among Hawaiian arthropods must still remain speculative. Other studies have suggested the importance of ecological character displacement and the evolution of reproductive isolation as a by-product of resource-based divergent natural selection (Schluter 1996). Because of the chronological arrangement of the Hawaiian archipelago, with a corresponding range in the development of species differentiation, it will be possible in the future to examine population phenomena associated with species proliferation. Preliminary evidence suggests that groups showing a tendency to proliferate within islands also tend to undergo expansion in ecological range among the representatives that have colonized the youngest island. One conjecture might be that local adaptation and specialization within different ecological environments may allow these populations to proliferate into an array of closely related species, as can be found on the next-older island. If substantiated, this scenario would implicate natural selection as the primary force of change during initial diversification, and would support the traditional view of the importance of divergent selection in adaptive radiation.

References

Asche M (1997) A review of the systematics of Hawaiian planthoppers (Hemiptera: Fulgoroidea). *Pacific Science*, **51**, 366–376.

Asquith A (1995) Evolution of *Sarona* (Heteroptera, Miridae). In: *Hawaiian Biogeography* (eds Wagner WL, Funk VA), pp. 90–120. Smithsonian Institution Press, Washington, DC.

Asquith A (1997) Hawaiian Miridae (Hemiptera: Heteroptera): the evolution of bugs and thought. *Pacific Science*, **51**, 356–365.

Avise JC (1991) Ten unorthodox perspectives on evolution prompted by comparative population genetic findings on mitochondrial DNA. *Annual Review of Genetics*, **25**, 45–69.

Avise JC (1994) *Molecular Markers, Natural History and Evolution.* Chapman and Hall, London.

Baldwin B, Robichaux R (1995) Historical biogeography and ecology of the Hawaiian silversword alliance (Compositae): new molecular phylogenetic perspectives. In: *Hawaiian Biogeography* (eds Wagner WL, Funk VA), pp. 259–287. Smithsonian Institution Press, Washington, DC.

Barr TC, Holsinger JR (1985) Speciation in cave faunas. *Annual Review of Ecology and Systematics*, **16**, 313–337.

Brooks DR (1988) Macroevolutionary comparisons of host and parasite phylogenies. *Annual Review of Ecology and Systematics*, **19**, 235–259.

Carlquist S (1980) *Hawaii: A Natural History.* Pacific Tropical Botanical Garden, SB Printers, Inc., Honolulu.

Carson HL (1970) Chromosome tracers of the origin of species. *Science*, **168**, 1414–1418.

Carson HL (1974) Patterns of speciation in Hawaiian *Drosophila* inferred from ancient chromosomal polymorphism. In: *Genetic Mechanisms of Speciation in Insects* (ed. White MJD), pp. 81–93. Australia and New Zealand Book Co., Sydney.

Carson HL (1986) Sexual selection and speciation. In: *Evolutionary Processes and Theory* (eds Karlin S, Nevo E), pp. 391–409. Academic Press, New York.

Carson HL (1987a) Colonization and speciation. In: *Colonization, Succession and Stability* (eds Gray AJ, Crawley MJ, Edwards PJ), pp. 187–206. Blackwell Scientific Publications, Oxford.

Carson HL (1987b) Tracing ancestry with chromosomal sequences. *Trends in Ecology and Evolution*, **2**, 203–207.

Carson HL (1989) Natural hybridization between the sympatric Hawaiian species *Drosophila silvestris* and *Drosophila heteroneura. Evolution*, **43**, 190–203.

Carson HL (1990a) Extinction and recolonization of local populations on a growing shield volcano. *Proceedings of the National Academy of Sciences USA*, **87**, 7055–7057.

Carson HL (1990b) Increased genetic variance after a population bottleneck. *Trends in Ecology and Evolution*, **5**, 228–230.

Carson HL, Clague DA (1995) Geology and biogeography of the Hawaiian Islands. In: *Hawaiian Biogeography Evolution on a Hot Spot Archipelago* (eds Wagner WL, Funk VA), pp. 14–29. Smithsonian Institution Press, Washington, DC.

Carson HL, Kaneshiro KY (1976) *Drosophila* of Hawaii: systematics and ecological genetics. *Annual Review of Ecology and Systematics*, **7**, 311–345.

Carson HL, Templeton AR (1984) Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annual Review of Ecology and Systematics*, **15**, 97–131.

Coates DJ (1992) Genetic consequences of a bottleneck and spatial genetic structure in the triggerplant *Stylidium coroniforme* (Stylidiaceae). *Heredity*, **69**, 512.

Craddock EM, Kambysellis MP (1997) Adaptive radiation in the Hawaiian *Drosophila*: ecological and reproductive character analyses. *Pacific Science*, **51**, 475–489.

DeMeyer M (1996) Cladistic and biogeographic analyses of Hawaiin Pipunculidae (Diptera) revisited. *Cladistics*, **12**, 291–303.

DeSalle R, Brower AVZ, Baker R, Remsen J (1997) A hierarchical view of the Hawaiian Drosophilidae. *Pacific Science*, **51**, 462–474.

DeSalle R, Giddings LV (1986) Discordance of nuclear and mitochondrial DNA phylogenies in Hawaiian *Drosophila*. *Proceedings of the National Academy of Sciences USA*, **83**, 6902–6906.

Dobson AP, Rodriguez JP, Roberts WM, Wilcove DS (1997) Geographic distribution of endangered species in the United States. *Science*, **275**, 550–553.

Eldredge LG, Miller SE (1995) How many species are there in Hawaii? *Bishop Museum Occasional Papers*, **41**, 3–18.

Eldredge LG, Miller SE (1997) Numbers of Hawaiian species: (Suppl. 2), Including a review of freshwater invertebrates. *Bishop Museum Occasional Papers*, **48**, 3–22.

Endler JA (1989) Conceptual and other problems in speciation. In: *Speciation and Its Consequences* (eds Otte D, Endler JA), pp. 625–648. Sinauer Association, Sunderland, MA.

Farrell BD, Mitter C (1993) Phylogenetic determinants of insect/plant community diversity. In: *Species Diversity in Ecological Communities* (eds Ricklefs RE, Schluter D). pp. 253–266. University of Chicago Press, Chicago.

Felsenstein J (1978) Cases in which parsimony and compatibility methods will be positively misleading. *Systematic Zoology*, **27**, 401–410.

Floate KD, Whitham TG (1993) The 'hybrid bridge' hypothesis: host shifting via plant hybrid swarms. *American Naturalist*, **141**, 651–662.

Funk VA, Wagner WL (1995) Biogeographic patterns in the Hawaiian Islands. In: *Hawaiian Biogeography Evolution on a Hot Spot Archipelago* (eds Wagner WL, Funk VA), pp. 379–419. Smithsonian Institution Press, Washington, DC.

Gillespie RG (1991a) Hawaiian spiders of the genus *Tetragnatha*. I. Spiny leg clade. *Journal of Arachnology*, **19**, 174–209.

Gillespie RG (1991b) Predation through impalement of prey: The foraging behavior of *Doryonychus raptor* (Araneae, Tetragnathidae). *Psyche*, **98**, 337–350.

Gillespie RG (1992) Impaled prey. *Nature*, **355**, 212–213.

Gillespie RG (1993) Biogeographic pattern of phylogeny among a clade of endemic Hawaiian spiders (Araneae, Tetragnathidae). *Memoirs Queensland Museum*, **33**, 519–526.

Gillespie RG, Croom HB, Hasty GL (1997) Phylogenetic relationships and adaptive shifts among major clades of *Tetragnatha* spiders in Hawaii. *Pacific Science*, **51**, 380–394.

Gillespie RG, Croom H, Palumbi SR (1994) Multiple origins of a spider radiation in Hawaii. *Proceedings of the National Academy of Sciences USA*, **91**, 2290–2294.

Gillespie RG, Tabashnik BE (1989) What makes a happy face? Determinants of colour pattern in the Hawaiian happy face spider *Theridion grallator*. *Heredity*, **62**, 355–363.

Grimaldi DA (1988) Relics in the Drosophilidae (Diptera). In: *Zoogeography of Caribbean Insects* (ed. Liebherr JK), pp. 183–312. Comstock Publishing Association, Cornell University Press, Ithaca, New York.

Hardy DE, Delfinado MD (1980) *Diptera: Cyclorrhapha III, Series Schizophora Section Acalypterae, exclusive of Family Drosophilidae*. Insects of Hawaii. University Press of Hawaii, Honolulu.

Harrison RG (1993) *Hybrid Zones and the Evolutionary Process*. Oxford University Press, Oxford.

Hoch H, Howarth FG (1993) Evolutionary dynamics of behavioral divergence among populations of the Hawaiian cave-dwelling planthopper *Oliarus polyphemus* (Homoptera: Fulgoroidea: Cixiidae). *Pacific Science*, **47**, 303–318.

Howarth FG (1981) Community structure and niche differentiation in Hawaiian lava tubes. In: *Island Ecosystems; Biological Organization in Selected Hawaiian Communities* (eds Mueller-Dombois D, Bridges KW, Carson HL), pp. 318–336. Academic Press, New York.

Howarth FG (1993) High stress subterranean habitats and evolutionary change in cave-inhabiting arthropods. *American Naturalist*, **142**, 565–577.

Howarth FG, Mull WP (1992) *Hawaiian Insects and Their Kin*. University of Hawaii Press, Honolulu.

Kambysellis MP (1993) Ultrastructural diversity in the egg chorion of Hawaiian *Drosophila* and *Scaptomyza*: Ecological and phylogenetic considerations. *International Journal of Insect Morphology and Embryology*, **22**, 417–446.

Kambysellis MP, Ho K-F, Craddock EM, Piano F, Parisi M, Cohen J (1995) Pattern of ecological shifts in the diversification of Hawaiian *Drosophila* inferred from a molecular phylogeny. *Current Biology*, **5**, 1129–1139.

Kambysellis M, Craddock EM (1997) Ecological and reproductive shifts in the diversification of the endemic Hawaiian *Drosophila*. In: *Molecular Evolution And Adaptive Radiation* (ed. Givnish TJ, Sytsma KJ), pp. 475–509. Cambridge University Press, New York.

Kaneshiro KY (1976) A revision of generic concepts in Hawaiian Drosophilidae. *Proceedings of the Hawaiian Entomological Society*, **23**, 255–278.

Kaneshiro KY (1983) Sexual selection and direction of evolution in the biosystematics of the Hawaiian Drosophilidae. *Annual Review of Entomology*, **28**, 161–178.

Kaneshiro KY (1989) The dynamics of sexual selection and founder effects in species formation. In: *Genetics, Speciation and the Founder Principle* (eds Giddings LV, Kaneshiro KY, Anderson WW), pp. 279–296. Oxford University Press, Oxford.

Kaneshiro KY, Boake CRB (1987) Sexual selection and speciation: issues raised by Hawaiian *Drosophila*. *Trends In Ecology And Evolution*, **2**, 207–212.

Liebherr J (1997) Dispersal and vicariance in Hawaiian platynine carabid beetles (Coleoptera). *Pacific Science*, **51**, 424–439.

Losos JB (1992) The evolution of convergent structure in Caribbean *Anolis* communities. *Systematic Biology*, **41**, 403–420.

Losos JB, Irscchick DJ, Schoener TW (1994) Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Evolution*, **48**, 1786–1797.

Mayr E (1954) Change in genetic environment and evolution. In: *Evolution as a Process* (eds Huxley JS, Hardy AC, Ford EB), pp. 156–180. Allen & Unwin, London.

Miller SE, Eldredge LG (1996) Numbers of Hawaiian species: (Suppl. 1). *Bishop Museum Occasional Papers*, **45**, 8–17.

Mitter C, Brooks DR (1983) Phylogenetic aspects of co-evolution (eds Futuyma DJ, Slatkin M), pp. 65–98. Sinauer, Sunderland, MA.

Mitter C, Farrell B, Futuyma DJ (1991) Phylogenetic studies of insect–plant interactions: insights into the genesis of diversity. *Trends in Ecology and Evolution*, **6**, 290–293.

Montgomery S (1983) Biogeography of the moth genus *Eupethicea* in Oceania and the evolution of ambush predation in Hawaiian caterpillars. *Entomology Gen*, **8**, 27–34.

Okuma C, Kisimoto R (1981) Airborne spiders collected over the East China Sea. *Japanese Journal of Applied Entomology and Zoology*, **25**, 296–298.

Otte D (1989) Speciation in Hawaiian crickets. In: *Speciation and its Consequences* (eds Otte D, Endler JA), pp. 482–526. Sinauer Associates, Sunderland, Mass.

Otte D (1994) *The Crickets of Hawaii: Origin, Systematics, and Evolution*. The Orthopterists' Society, Academy of Natural Sciences, Philadelphia, PA.

Oxford GS, Gillespie RG (1996a) Genetics of a colour polymorphism in the Hawaiian happy face spider, *Theridion grallator* (Araneae: Theridiidae) from Greater Maui. *Heredity*, **76**, 238–248.

Oxford GS, Gillespie RG (1996b) The effects of genetic background on the island-specific control of a colour polymorphism in the Hawaiian happy face spider, *Theridion grallator* (Araneae: Theridiidae). *Heredity*, **76**, 257–266.

Oxford GS, Gillespie RG (1996c) Quantum shifts in the genetic control of colour polymorphism in the Hawaiian happy face spider, *Theridion grallator* (Araneae: Theridiidae) from Greater Maui. *Heredity*, **76**, 249–256.

Page RDM (1995) Parallel phylogenies: reconstructing the history of host-parasite assmeblages. *Cladistics*, **10**, 155–173.

Palumbi SR (1996) Nucleic acids III: The polymerase chain reaction. In: *Molecular Systematics*, 2th edn (eds Hillis DM, Moritz C, Mable BK), pp. 205–247. Sinauer Association, Sunderland, MA.

Piano F, Craddock EM, Kambysellis MP (1997) Phylogeny of the island populations of the Hawaiian *Drosophila grimshawi* complex: evidence from combined data. *Molecular Phylogenetics and Evolution*, **7**, 173–184.

Polhemus D (1997) Phylogenetic analysis of the Hawaiian damselfly genus *Megalagrion* (Odonata: Coenagrionidae): implications for biogeography, ecology, and conservation biology. *Pacific Science*, **51**, 395–412.

Polhemus D, Asquith A (1996) *Hawaiian Damselflies*. Bishop Museum Press, Honolulu.

Price PW (1996) *Biological Evolution*. Saunders College Publishing, Fort Worth, TX.

Roderick GK (1996) Geographic structure of insect populations: gene flow, phylogeography and their uses. *Annual Review of Entomology*, **41**, 263–290.

Roderick GK (1997) Herbivorous insects and the Hawaiian silversword alliance: co-evolution or co-speciation? *Pacific Science*, **51**, 440–449.

Roderick GK, Metz EC (1997) Biodiversity of planthoppers (Hemiptera: Delphacidae) on the Hawaiian silversword alliance: effects of host plant history and hybridization. *Memoirs of the Museum of Victoria*, **56**, 393–399.

Schluter D (1996) Ecological causes of adaptive radiation. *American Naturalist*, **148**, S40–S64.

Shaw KL (1995) Biogeographic patterns of two independent Hawaiian cricket radiations (*Laupala* and *Prognathogryllus*). In: *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago* (eds Wagner WL, Funk VA), pp. 39–56. Smithsonian Institution Press, Washington.

Shaw KL (1996a) Sequential radiations and patterns of speciation in the Hawaiian cricket genus *Laupala* inferred from DNA sequences. *Evolution*, **50**, 237–255.

Shaw KL (1996b) Polygenic inheritance of a behavioral phenotype: Interspecific genetics of song in the Hawaiian cricket genus *Laupala*. *Evolution*, **50**, 256–266.

Simberloff DS, Wilson EO (1968) Experimental zoogeography of islands: The colonization of empty islands. *Ecology*, **50**, 278–296.

Strauss S (1994) Levels of herbivory and parasitism in host hybrid zones. *Trends in Ecology and Evolution*, **9**, 209–214.

Strazanac JS (1996) *Hawaii Endemic Copiphorini: Systematics and Acoustics (Orthoptera: Tettigoniidae: Conocephalinae)*. PhD dissertation, University of Hawaii, Honolulu.

Taiti S, Howarth FG (1997) Terrestrial isopods (Crustacea, Oniscidea) from Hawaiian caves). *Mémoires de Biospéologie.*

Templeton AR (1980) The theory of speciation via the founder principle. *Genetics*, **91**, 1011–1038.

Templeton AR (1981) Genetic architectures of speciation. In: *Mechanisms of Speciation* (ed. Barigozzi C), pp. 105–121. Alan R. Liss, New York.

Thornton IWB (1984) Psocoptera of the Hawaiian Islands Part III. The endemic *Ptycta* complex (Pscocidae): systematics, distribution and evolution. *International Journal of Entomology*, **26**, 1–128.

Whitham TG, Morrow PA, Potts BM (1994) Plant hybrid zones as centers of biodiversity: the herbivore community of two endemic Tasmanian eucalypts. *Oecologia*, **97**, 481–490.

Wright S (1951) The genetical structure of populations. *Annals of Eugenics*, **15**, 323–354.

Zimmerman EC (1948) *Insects of Hawaii, Vol 4. Homoptera: Auchenorhycha*. . University of Hawaii Press, Honolulu.