GEOGRAPHICAL CONTEXT OF SPECIATION IN A RADIATION OF HAWAIIAN *TETRAGNATHA* SPIDERS (ARANEAE, TETRAGNATHIDAE)

Rosemary G. Gillespie: Division of Insect Biology, University of California Berkeley, 137 Mulford Hall, Berkeley, California 94720-3114, U.S.A.

ABSTRACT. Adaptive radiation involves the diversification of species each adapted to exploit different ecological roles. I have studied a radiation of spiders in the genus *Tetragnatha* (Tetragnathidae) in the Hawaiian Islands to elucidate processes involved in such diversification. The temporal framework of the Hawaiian Islands allows examination of the changing pattern of adaptive radiation over time, as lineages have generally progressed down the island chain from older to younger islands. Species of *Tetragnatha* in the spiny-leg clade on any one island are typically most closely related to others on the same island, and the same set of ecological forms (ecomorphs) has evolved repeatedly on different islands. These results indicate that adaptive radiation frequently involves ecological divergence between sister taxa to allow multiple close relatives to co-occur in the same habitat. The current study examines the geographical context within which these species arose. I focus on a clade of 5 species that occur on the volcano of East Maui; at any given site 3 species can co-occur, one of each of 3 different ecomorphs. Mitochondrial DNA sequences from populations of these 5 species from throughout their distribution (Maui, Lanai and Molokai) were used to infer the geographic history of the species on East Maui and to determine whether diversification likely occurred in situ, or alternatively whether diversification occurred in allopatry on different volcanoes. Although ecological differentiation between taxa is evident, allopatry is clearly implicated in the initial divergence of taxa. Further study is required to understand the nature of the interplay between allopatry and ecological divergence in species formation.

Keywords: Adaptive radiation, biogeography, allopatry, parapatry, evolution

One of the most hotly debated aspects of the speciation process is its geographical context, and the nature and importance of isolation in the initial divergence of taxa (Coyne & Orr 2004). As a result of the influential work of Mayr (1963), ideas of speciation were dominated for many years by the importance of allopatry in initiating divergence (Coyne 1994; Howard & Berlocher 1998). However, theoretical studies have demonstrated that sympatric speciation can occur and can cause species to form much more rapidly than by allopatric speciation (Turelli et al. 2001; Gavrilets 2003). The importance of sympatric speciation in nature, however, remains questionable (Coyne & Orr 2004). Recent studies on species and speciation have started to recognize the validity of some of the predominant ideas of the earlier part of this century, including the role of both divergent natural selection (Schluter 2001) and hybridization (Seehausen 2004) in generating new species. In particular, ecological speciation, in which reproductive isolation evolves as a consequence of divergent natural selection on traits between contrasting environments, is now recognized as an important mechanism of speciation (Schluter 2001). However, the geographic context of speciation in situations of adaptive radiation, where multiple close relatives occur in sympathy, is still the subject of considerable debate (Glor et al. 2004).

The current study focuses on the Hawaiian Islands, the most isolated archipelago in the world and well known for some of the most extraordinary illustrations of adaptive radiation (Simon 1987; Wagner & Funk 1995). The Hawaiian island chain is a hotspot archipelago, arranged in chronological series, the youngest island being Hawaii, the oldest Kauai (Carson & Clague 1995; Price & Clague 2002). The biogeographic 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 (Wagner & Funk 1995), often with repeated bouts of diversification within islands (Roderick & Gillespie 1998).
Figure 1.—Map of the Hawaiian Islands. Names in bold type indicate islands that were the focus of the current study. Ages of the different volcanoes are given (myrs = million years).

Accordingly, the islands are considered a “natural laboratory” as they allow study of patterns of species formation on islands of different age (Gillespie 2004, 2005). Here, I focus on an adaptive radiation in the spider genus *Tetragnatha* (Tetragnathidae) in the Hawaiian Islands to examine the geographic context involved in the initial divergence of taxa.

The genus *Tetragnatha* is strikingly diverse in the Hawaiian Islands, with multiple species occurring in sympatry throughout the islands. Until 1991, only 8 species had been described from the islands. Over the last few years I have described an additional 29 species of Hawaiian *Tetragnatha* (Gillespie 1991, 1992a, 1994, 2002, 2003) and am currently describing approximately 15 more species. This species radiation encompasses forms representing a huge spectrum of colors, shapes, sizes, ecological affinities and behaviors. Many species are web builders, with their shapes modified to allow concealment within specific microhabitats (Blackledge & Gillespie 2004). Some species have modifications of the jaws, apparently to allow specialization on specific prey types (Gillespie 2005). However, several groups have abandoned the characteristic web-building behavior of the genus (Gillespie 1991, 1992b). For example, one entire clade, or lineage, of 16 species (the “spiny leg” clade), has “lost” web building behavior, with the concomitant development of long spines along the legs and adoption of a vagile, cursorial, predatory strategy.

Recent studies have shown that representatives of the spiny leg clade occur as four distinct ecomorphs associated with specific habitat types: “green spiny” on leaves; “maroon spiny” on moss, “large brown spiny” on tree bark, and “small brown spiny” on twigs (Gillespie et al. 1994; Gillespie et al. 1997). Similar sets of ecomorphs occur in most native habitats and phylogenetic analyses have shown that ecomorphs have arisen repeatedly and independently (Gillespie 2004). In particular, the most ubiquitous ecomorph, green spiny, has evolved (or been lost) at least once on each of the older islands, Kauai (*T. kauaiensis*), Oahu (*T. tantalus, T. polychromata*), and Maui Nui, the once connected volcanoes of Molokai, Lanai, and Maui (*T. brevignatha, T. macracantha, T. waikamoi*). Likewise, the maroon spiny has evolved independently on Oahu (*T. perreirai*) and Maui Nui (*T. kamakou*); both species are
closely related to species of the green spiny ecomorph. Also, one of the small brown spiny ecomorphs (T. restricta) has evolved independently on Maui. The island of Hawaii, presumably because it is still very young, contains mostly populations of the same species that occur on Maui (Gillespie 1991).

The distribution of ecomorphs across habitats is significantly different from random (Gillespie 2004): there is a remarkably similar representation of ecomorphs in different habitats. Not all habitats have all ecomorphs, but there is never more than one representative of a given ecomorph at a site. The finding that similar ecomorphs never co-occur is most striking on East Maui. Here, a representative of each ecomorph is found at almost every site on the volcano, yet the species composition of the array of four different ecomorphs changes quite markedly between different locations (Gillespie 2005). Different species of the same ecomorph have very clear cut parapatric distributions. Moreover, different ecomorphs that co-occur are frequently sister species, suggesting the possibility that ecological differences may have arisen in situ. However, populations of these species also occur on other volcanoes, suggesting a potential role for allopatry in the initial divergence of taxa.

Here, I focus on a group of sympatric species to determine how divergence may have occurred within the geographic context of the Maui Nui island complex. Specifically, I examined 5 species that are found on East Maui: T. kamakou (maroon spiny), T. restricta (small brown spiny), and T. waikamoi, T. macracantha, and T. brevignatha (green spiny). (The large brown ecomorph is represented at all sites by T. quasimodo, but this species falls outside the clade of 5 species which form the focus of the current study). Tetragnatha kamakou and T. restricta co-occur with each other and with one of the green spiny ecomorphs (T. waikamoi, T. macracantha, or T. brevignatha) at different locations on the volcano. The question addressed here is whether species in the Maui Nui clade formed through diversification within the single volcano of East Maui or alternatively whether divergence occurred in allopatry, prior to their current distribution.

METHODS

Study Sites and Organisms.—The study was focused on the more recent part of the Hawaiian archipelago, Maui Nui and Hawaii (Fig. 1). Maui Nui is a composite of 4 separate islands, Maui, Molokai, Lanai, and Kahoolawe. Until 300,000–400,000 years ago, these islands were all connected, much like the island of Hawaii is today (Carson & Clague 1995). Glacially mediated fluctuations in sea level have alternately flooded and exposed the land connecting islands of the complex of islands. Except for Kahoolawe, all islands of Maui Nui have been sufficiently high to maintain native forest. Each island has a single high volcano except for Maui itself, which has two. These volcanoes range in age from Molokai (1.8 MY), through Lanai and West Maui (1.3MY) to East Maui (0.8MY). The island of Hawaii is the largest in the archipelago and the youngest. It consists of 5 volcanoes, the oldest being Kohala (0.43MY), then Hualalai (0.40MY), Mauna Kea (0.38MY), Mauna Loa (0.20MY), and Kilauea (0.10MY).

The five focal species for the study were T. brevignatha, T. macracantha, T. kamakou, T. restricta, and T. waikamoi. Specimens collected from different sites are shown in Table 1.

As outgroups, I used two populations of T. quasimodo, East Maui, Waikamoi, Carruthers, 6100ft, 26 June 1994; and Hawaii, Puu Makaula, 11 July 1994.

Phylogenetic Hypotheses.—An approximately 730 base pair piece of Cytochrome oxidase subunit I (COI) was amplified using primers LCO-1628 (ATAATGTAATTGATCTGCTCATGC) and HCO-2396 (ATITGTAGCTGAGGTAAAATAAGCTCG) (Palumbi et al. 1996). Genbank accession numbers are given in Table 1. Historical hypotheses of phylogenetic relationships were reconstructed using three methods: (i) Maximum Parsimony as the optimality criterion in the program PAUP* version 4.0b10 (Swofford 2000). Heuristic searches were performed by step-wise addition of taxa, with TBR branch swapping and 1000 step-wise random taxon addition replicates. Characters were weighted (transversions: transitions) 2:1. Of the total characters: 543 characters were constant, 143 variable characters were parsimony-informative, and 44 characters were parsimony-uninformative. (ii) Maximum Likelihood as the optimality criterion. MODELTEST v. 3.04 (Posada and Crandall 1998), which makes use of log likelihood scores to establish the model of DNA evolution that best fits the data, was first
Figure 2.—Phylogenetic hypothesis based on DNA sequence of partial mitochondrial cytochrome oxidase I. Phylogeny reconstruction used Maximum Parsimony (tree length 523, Consistency index = 0.58, Retention index = 0.74), Maximum Likelihood (-Ln likelihood = 3376.47142), and Bayesian inference of likelihood, with each analyses producing a similar topology. Support for each node was assessed through bootstrap values ≥ 50% for Maximum Parsimony (below node) and for Maximum Likelihood (above each node, left), and Posterior Probabilities for the Bayesian analysis (above each node, right).
used to determine parameter values. The HKY85+G+I model was selected: negative log likelihood, 3381.6406, and Akaike Information Criterion (AIC), 6775.2812. This is a general time-reversible model of DNA substitution with a gamma distribution for the rate of substitution at a site and a shape parameter gamma distribution of 1.4870. The proportion of invariable sites (I) was estimated as 0.612. The base frequencies were estimated as: A, 0.2586; C, 0.1650; G, 0.2058; T, 0.3705 with a ti/tv ratio of 2.9285. (iii) Bayesian Inference of Likelihood with posterior probability of phylogenies approximated by sampling trees from the posterior probability distribution. The program MrBayes (Huelsenbeck 2000) uses Markov chain Monte Carlo (MCMC) to sample phylogenies according to their posterior probabilities, with the marginal probability of trees calculated from the trees visited during the course of the MCMC analysis. The proportion of the time any single tree is found in this sample is an approximation of the posterior probability of the tree. The estimates from MODELTEST were used as priors for the Bayesian inference of phylogeny using MrBayes 3.0. MacClade 4 (Maddison and Maddison 2000) was used to overlay ecomorph category on the molecular phylogeny and determine the most parsimonious scenario for ecomorph evolution. Both accelerated and delayed transformation optimization options were applied.

RESULTS

Phylogenetic estimation using Maximum Parsimony, Maximum Likelihood and Bayesian Inference gave a similar topology (Fig. 2). Support for nodes, which was provided by bootstrap support for Maximum Parsimony
and Maximum Likelihood and Posterior Probabilities for the Bayesian Inference of Likelihood, was generally high. Geographical locations were mapped against the tree topology to determine probable ancestral geographic affinities for each species/population. The results gave strong support for the following clades: “brevignatha Maui”; “brevignatha Hawaii”; “all macracantha Maui + Lanai”; “kamakou Maui”; “kamakou Molokai”; “all restricta Maui + Hawaii”; and “all waikamoi Maui”. There was also strong support for the clade “restricta + only kamakou Molokai”; this renders T. kamakou paraphyletic with respect to T. restricta. Most importantly, however, it suggests that, although T. restricta (Maui + Hawaii) co-occurs with T. kamakou on Maui, and T. kamakou is the sister species of T. restricta, the population of T. kamakou which is sister to T. restricta is not on Maui, but on Molokai, another volcano in the Maui Nui group of islands.

There was weak support for a clade of “brevignatha Maui” + “macracantha Maui + Lanai”, which, if upheld, would render T. brevignathha paraphyletic relative to T. macracantha.

The character reconstructions to examine the evolution of ecomorphs are shown in Fig. 3, using ACCTRAN, which minimizes parallel evolution. The topology indicates that a minimum of 3 character transformations are required, one with the divergence of T. kamakou from T. brevignatha + T. macracantha, the second with the divergence of T. restricta from T. kamakou Molokai. Also, based on the reconstruction, E. Maui appears to be the ancestral geographic locality, although this may be because E. Maui, with by far the largest land mass in the island complex, has the largest number of species and thus is the island most likely to have haplotypes represented across the tree.

DISCUSSION

Throughout the native forest on the volcano of Haleakala, East Maui, four species of spiny leg Tetragnatha can co-occur, and when they do, only one of each of the primary ecomorphs is found in any given location: green spiny (T. waikamoi, T. brevignatha, or T. macracantha), maroon spiny (T. kamakou), small brown spiny (T. restricta or T. kikokiko), and large brown spiny (T. quasimodo). In this paper I focused on five species of Hawaiian Tetragnatha that form a Maui Nui clade and are each others’ closest relatives (Gillespie 2004): T. waikamoi, T. brevignatha, T. macracantha, T. kamakou, and T. restricta. Tetragnatha kamakou, and T. restricta co-occur with T. waikamoi, T. brevignatha, or T. macracantha throughout their distribution. The predominant ecomorph and the ecomorph represented by the most number of species, is green spiny, with T. waikamoi being sister to the remaining species in the clade, and T. brevignatha and T. macracantha forming sister species.

Previous work has shown that different species of green spiny never co-occur (Gillespie 2004, 2005), suggesting that ecological divergence between taxa might involve some degree of isolation. The results presented here do not reject the hypothesis that isolation plays a role in the divergence of sister species of the same ecomorph. For example, the green spiny T. macracantha (from East Maui and Lanai) is monophyletic and sister to the East Maui population of green spiny T. brevignatha. However, because T. macracantha has a population on Lanai as well as East Maui, it is possible that divergence between these two taxa occurred in allopatry.

The most informative result comes from the clade including T. kamakou and T. restricta, which is sister to the clade comprising T. brevignatha and T. macracantha. In particular, the mitochondrial tree shows that East Maui populations of T. kamakou and T. restricta, which occur in sympathy throughout much of the volcano, are each more closely related to populations on other volcanoes: for example, T. restricta is most closely related to T. kamakou from Molokai and individuals of T. kamakou on East Maui are most closely related to individuals of T. kamakou on West Maui. One explanation for this pattern could be colonization of Hawaii by T. restricta, divergence in allopatry, and subsequent recolonization of Maui. However, given the tendency of taxa to colonize from older to younger islands, and not the reverse (Wagner & Funk 1995), this scenario would be unusual. A second scenario is suggested by the reconstruction of historical geographical areas (Fig. 3), which indicates that T. restricta diverged from T. kamakou on East Maui, with T. kamakou going on to colonize Molokai. However, it is difficult to suggest a process that might lead
Table 1.—Taxonomic and geographical information of the specimens included in the present study including GenBank accession numbers for COI sequences for each specimen. *, Genbank Accession Number. Collectors: MA, M. Arnedo; GB, Greta Binford; LB, Lindell Bromham; CE, Curtis Ewing; RG, Rosemary Gillespie; MH, Mandy Heddle; AM, A.C. Medeiros; GO, Geoff Oxford; DP, Dan Polhemus; MR, Malia Rivera; GR, George Roderick; KS, Kerry Shaw; AT, AnMing Tan.

| Species     | Volcano | Locality       | Elev. | Date         | Collector | Code | Genbank*  |
|-------------|---------|----------------|-------|--------------|-----------|------|-----------|
| *T. brevignatha* | E. Maui | Waikamoi, Fence | 4400ft | 21 October 1995 | RG,MH,MA,MR | J70  | DQ182752  |
|             | E. Maui | Waikamoi, Nr Flume | 4400ft | 9 November 1996 | RG         | GJ86 | DQ178958  |
|             | Mauna Loa | Kipuka at mile 18 | 5000ft | 9 March 1995 | RG         | D95  | DQ182753  |
|             |         | Kipukaas         | 5050ft | 13 June 2002  | RG,GR     | 14.1JG| DQ182754  |
|             | Kohala  | Kahua Ranch      | 3780ft | 11 June 2002  | RG,GR     | Tet2  | DQ182756  |
|             | Hualalai | Koloko Dr.       | 3200ft | 12 June 2002  | RG,GR     | Tet8  | DQ178961  |
|             | Mauna Loa | Kealakekua     | 3740ft | 9 March 1990  | RG         | Tet1  | DQ182759  |
|             | Kilauea | Puu Makaala      | 4300ft | 11 July 1994  | GB         | 11.2JG| DQ182755  |
| *T. macracantha* | E. Maui | Kipahulu         | 4000ft | 15 May 1990   | RG,AM     | J52   | DQ182765  |
|             |         | Puu Kukui        | 3000ft | 16 May 1990   | RG,AM     | J53   | DQ182766  |
|             |         | Kaumakani        | 3700ft | 7 June 1999   | CE, DP    | Tgs1  | DQ182767  |
|             | Lanai   | Munro Trail      | 3300ft | 20 June 1999  | MA        | Tgs2  | DQ182768  |
| *T. kamakou* | E. Maui  | Waikamoi, Carruthers | 6150ft | 17 November 1992 | RG | GJ81 | DQ182760  |
|             |         | Waikamoi, Nr Flume | 4400ft | 9 November 1996 | RG         | GJ72  | DQ178963  |
|             |         | Kaumakani        | 3700ft | 7 June 1999   | CE, DP    | TTk2  | DQ182761  |
|             | W. Maui | Puu Kukui        | 4550ft | 13-I-98       | RG, KS    | TTk1  | DQ182762  |
|             | Molokai | Puu Lua          | 3180ft | 15 June 1999  | MA        | Tgs3  | DQ182759  |
|             |         | Puu Lua          | 3180ft | 15 June 1999  | CE, DP    | 00006 | DQ178962  |
| *T. restricta* | E. Maui | Waikamoi, Fence | 4200ft | 3 July 1993   | RG        | GJ74  | DQ182763  |
|             | Mauna Kea | Hakalau, Maulua Tr. | 6000ft | 17 June 1999  | RG, GR, LB | 73    | DQ178964  |
|             | Mauna Kea | Hakalau, Maulua Tr. | 6150ft | 16 August 1997 | RG         | J35   | DQ182764  |
| *T. waikamoi* | E. Maui | Waikamoi, Nr Flume | 4200ft | 3 July 1993   | RG        | 00012 | DQ182771  |
|             | Hanawi  | 5000ft          | 6 May 1998 | 27 February 1993 | RG   | GJ28  | DQ182769  |
|             | Waikamoi Flume | 4300ft | 6 May 1998 | 27 February 1993 | RG   | GJ28  | DQ182769  |
|             | W. Maui | Puu Kukui       | 4550ft | 13 August 1994 | GS, AT    | J28   | DQ178965  |
|             | Puu Kukui | 4550ft | 13 January 1998 | RG, KS    | 00009 | DQ182772  |
| *T. quasimodo* | E. Maui | Waikamoi, Carruthers | 6100ft | 26 June 1994  | RG        | AY490287 |
|             | Kilauea | Puu Makaala      | 4300ft | 11 July 1994  | GB        | AY490308 |
to such an inferred sequence of events. Finally, a third scenario is that the divergence of T. restricta from T. kamakou was initiated by colonization from the older Molokai. For example, if East Maui were occupied by T. kamakou and the volcano was subsequently colonized a second time by T. kamakou from Molokai, disruptive selection could lead to the formation of a new, ecologically differentiated species. This final scenario of an older ancestor is also supported by the inferred time of divergence between T. restricta and T. kamakou: The maximal uncorrected pairwise genetic divergence between these species is 9.1%, an amount which, when scaled to a global arthropod rate of mitochondrial sequence divergence of 2.3% per million years (Brower 1994), minimally dates the ancestor to 1.98 MYA, the approximate age of Molokai. However, if T. restricta diverged from T. kamakou Molokai before E. Maui was formed 0.8MYA (Fig. 1) as the dating suggests, the geographical context of the divergence remains enigmatic as a result of unsorted ancestral variation (lineage sorting) or hybridization (Rokas et al. 2003). Among Hawaiian arthropods, studies of both flies (Drosophila) and crickets (Laupala) have shown marked differences between trees generated from nuclear DNA versus mitochondrial DNA. For example, interspecific hybridization has been a regular occurrence in the history of both Drosophila (DeSalle & Giddings 1986) and Laupala (Shaw 2002; Mendelson & Shaw 2005). However, for the Hawaiian Tetragnatha, there is no evidence that hybridization between species occurs regularly. Considerable work on the phylogenetic relationships among the species considered here based on nuclear loci (allozymes and minisatellites) (Pons & Gillespie 2003, 2004; Gillespie 2004) shows no evidence of unsorted historical variation or recent introgression between any of the species or populations within species. Thus, we can assume that the mitochondrial data do accurately represent the phylogenetic history of the species examined in the current study. That Tetragnatha do not hybridize, despite the young age of many species, is interesting in comparison with Drosophila and Laupala: In both the flies and crickets, sexual selection has been implicated as a major force in driving speciation (Kanehiro 1989; Shaw & Herlihy 2000). By contrast, sexual selection appears not to play such a key role in Hawaiian Tetragnatha (Roderick & Gillespie 1998); rather, ecological affinities appear to be of greater significance in the initial stages of differentiation. Although still largely conjecture at this point, ecological affinity may play a key role in reinforcing isolation of gene pools in Tetragnatha, a process that perhaps is not as important in Drosophila and Laupala.

Together with previous studies on the spiny leg clade (Blackledge & Gillespie 2004; Gillespie 2004), the results of the current study suggest that there is a strong ecological component to species diversification. These results corroborate similar findings that have appeared in the literature for other adaptive radiations. In particular, extensive within-habitat proliferation, and repeated evolution of similar ecomorphs in different habitats has been found in cichlid fish in the Great African Lakes (Ruber et al. 1999), sticklebacks in Canadian glacial lakes (Schluter & McPhail 1993; Schluter 1998; Schluter 2000), and Anolis lizards in the Caribbean (Losos et al. 1998). In most of these cases, species pairs
appear to have had an allopatric phase in their recent history (e.g., threespine sticklebacks and Darwin’s ground finches). The only exception in which no allopatric phase is indicated is that of the Rhagoletis flies (Feder et al. 1988; Filchak et al. 2000), although even here the possible role of allopatry cannot be ruled out (Coyne & Orr 2004). The radiation of Hawaiian Tetragnatha suggests, as do results from studies of other adaptive radiations, that allopatry, together with ecological differentiation, plays an important role in the formation of species. Future studies on the interplay between divergence in allopatry and ecological differentiation will be critical to understanding the mechanism of speciation within an adaptive radiation.

ACKNOWLEDGMENTS

The work reported here was supported by funds from the Schlinger Foundation, the National Science Foundation, the University of Hawaii Research Council, and UC Berkeley. Additional support was provided by the Bishop Museum, Haleakalā National Park, the Nature Conservancy of Hawaii, the State Department of Land and Natural Resources, and the Hawaii Natural Areas Reserve System. For help with collecting I owe particular thanks to M. Arnedo, G. Binford, L. Bromham, C. Ewing, M. Heddle, A.C. Medeiros, G.S. Oxford, D. Polhemus, M. Rivera, G. Roderick, K. Shaw, and A.M. Tan.

LITERATURE CITED

Blackledge, T.A. & R.G. Gillespie. 2004. Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. Proceedings of the National Academy of Sciences 101:16228–16233.

Brook, A.V.Z. 1994. Rapid morphological radiation and convergence among races of the butterfly Heliconius erato inferred from patterns of mitochondrial DNA evolution. Proceedings of the National Academy of Sciences 91:6491–6495.

Carson, H.L. & D.A. Clague. 1995. Geology and biogeography of the Hawaiian Islands. Pp. 14–29. In Hawaiian Biogeography Evolution on a Hot Spot Archipelago. (W.L. Wagner & V.A. Funk, eds.). Smithsonian Institution Press, Washington, D.C.

Coyne, J.A. 1999. Ernst Mayr and the origin of species. Evolution 48:19–30.

Coyne, J.A. & H.A. Orr. 2004. Speciation. Sinauer Associates, Sunderland, Massachusetts.

Desalle, R. & L.V. Giddings. 1986. Discordance of nuclear and mitochondrial DNA phylogenies in Hawaiian Drosophila. Proceedings of the National Academy of Sciences 83:6902–6906.

Feder, J.L., C.A. Chilcote & G.L. Bush. 1988. Genetic differentiation between sympatric host races of the apple maggot fly Rhagoletis pomonella. Nature (London) 336:61–64.

Filchak, K.E., J.B. Roethele & J.L. Feder. 2000. Natural selection and sympatric divergence in the apple maggot, Rhagoletis pomonella. Nature 407:739–742.

Funk, D.J. & K.E. Omland. 2003. Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology, Evolution and Systematics 34:397–423.

Gavrilets, S. 2003. Models of speciation: what have we learned in 40 years? Evolution 57:2197–2215.

Gillespie, R.G. 1991. Hawaiian spiders of the genus Tetragnatha: I. Spiny leg clade. Journal of Arachnology 19:174–209.

Gillespie, R.G. 1992a. Hawaiian spiders of the genus Tetragnatha II. Species from natural areas of windward East Maui. Journal of Arachnology 20:1–17.

Gillespie, R.G. 1992b. Impaled prey. Nature 355:212–213.

Gillespie, R.G. 1994. Hawaiian spiders of the genus Tetragnatha: III. Tetragnatha acuta clade. Journal of Arachnology 22:161–168.

Gillespie, R.G. 2002. Hawaiian spiders of the genus Tetragnatha: IV: New, small species in the spiny leg clade. Journal of Arachnology 30:159–172.

Gillespie, R.G. 2003. Hawaiian spiders of the genus Tetragnatha: V. Elongate web-builders from Oahu. Journal of Arachnology 31:8–19.

Gillespie, R.G. 2004. Community assembly through adaptive radiation in Hawaiian spiders. Science 303:356–359.

Gillespie, R.G. 2005. The ecology and evolution of Hawaiian spider communities. American Scientist 93:122–133.

Gillespie, R.G., H.B. Croom & G.L. Hasty. 1997. Phylogenetic relationships and adaptive shifts among major clades of Tetragnatha spiders (Araneae: Tetragnathidae) in Hawai‘i. Pacific Science 51:380–394.

Gillespie, R.G., H.B. Croom & S.R. Palumbi. 1994. Multiple origins of a spider radiation in Hawaii. Proceedings of the National Academy of Sciences 91:2290–2294.

Glor, R.E., M. E. Gifford, A. Larson, J. B. Losos, L. Rodriguez-Schettino, A. R. Chamizo-Lara, and T. R. Jackman. 2004. Partial island submergence and speciation in an adaptive radiation: a multilocus analysis of the Cuban green anoles. Proceedings of the Royal Society of London B 271:2257–2265.

Howard, D.J. & S.H. Berlocher. 1998. Endless
Forms: Species and Speciation. Oxford University Press, Oxford.
Huelsenbeck, J.P. 2000. MrBayes: Bayesian inference of phylogeny. University of Rochester.
Kaneshiro, K.Y. 1989. The dynamics of sexual selection and founder effects in species formation. Pp. 279–296. In Genetics, Speciation and the Founder Principle (L.V. Giddings, K.Y. Kaneshiro and W.W. Anderson, eds.). Oxford University Press, Oxford.
Losos, J.B., T.R. Jackman, A. Larson, K. de Queiroz & L. Rodriguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118.
Maddison, D. & W. Maddison. 2000. MacClade. Sinauer, Sunderland, Massachusetts.
Mayr, E. 1963. Animal Species and Evolution. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
Mendelson, T.C., & K.L. Shaw. 2005. Sexual behaviour: rapid speciation in an arthropod. Nature 433:375–376.
Palumbi, S.R. 1996. Nucleic acids II: The polymerase chain reaction. Pp. 205–247. In Molecular Systematics (D. Hillis, C. Moritz and B. Mable, eds.). Sinauer, Sunderland, Massachusetts.
Pons, J. & R.G. Gillespie. 2003. Common origin of the satellite DNAs of the Hawaiian spiders of the genus Tetragnatha: evolutionary constraints on the length and nucleotide composition of the repeats. Gene 313:169–177.
Pons, J., & R.G. Gillespie. 2004. Evolution of satellite DNAs in a radiation of endemic Hawaiian spiders: Does concerted evolution of highly repetitive sequences reflect evolutionary history? Journal of Molecular Evolution 59:632–641.
Posada, D. & K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.
Price, J.P. & D.A. Clague. 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. Proceedings of the Royal Society B 269:2429–2435.
Rees, D.J., B.C. Emerson, P. Oromi & G.M. Hewitt. 2001. Reconciling gene trees with organism history: the mtDNA phylogeography of three Neosotes species (Coleoptera: Tenebrionidae) on the western Canary Islands. Journal of Evolutionary Biology 14:139–147.
Roderick, G.K. & R.G. Gillespie. 1998. Speciation and phylogeography of Hawaiian terrestrial arthropods. Molecular Ecology 7:519–531.
Rokas, A., G. Melika, Y. Abe, J.L. Nieves-Aldrey, J.M. Cook & G.N. Stone. 2003. Lifecycle closure, lineage sorting, and hybridization revealed in a phylogenetic analysis of European oak gall wasps (Hymenoptera: Cynipidae: Cynipini) using mitochondrial sequence data. Molecular Phylogenetics and Evolution 26:36–45.
Ruber, L., E. Verheyen & A. Meyer. 1999. Replicated evolution of trophic specializations in an endemic cichlid fish lineage from Lake Tanganyika. Proceedings of the National Academy Science 96:10230–10235.
Schluter, D. 1998. Ecological causes of speciation. Pp. 114–129. In Endless forms: Species and speciation (D.J. Howard and S.H. Berlocher, eds.). Oxford University Press, Oxford, England.
Schluter, D. 2000. Ecological character displacement in adaptive radiation. American Naturalist 156:S4–S16.
Schluter, D. 2001. Ecology and the origin of species. Trends in Ecology & Evolution 16:372–380.
Schluter, D. & J.D. Mcphail. 1993. Character displacement and replicate adaptive radiation. Trends in Ecology & Evolution 8:197–200.
Seehausen, O. 2004. Hybridization and adaptive radiation. Trends in Ecology & Evolution 19:198–207.
Shaw, K.L. 2002. Conflict between nuclear and mitochondrial DNA phylogenies of a recent species radiation: What mtDNA reveals and conceals about modes of speciation in Hawaiian crickets. Proceedings of the National Academy of Sciences 99:16122–16127.
Shaw, K.L., & D. Herlihy. 2000. Acoustic preference functions and song variability in the Hawaiian cricket Laupala cerasina. Proceedings of the Royal Society of London B 267:577–584.
Simon, C. 1987. Hawaiian evolutionary biology: An introduction. Trends in Ecology and Evolution 2:175–178.
Swofford, D.L. 2000. PAUP*. Phylogenetic Analysis Using Parsimony (* and other methods). Sinauer, Sunderland, Massachusetts.
Thorpe, R.S., D.P. McGregor, A.M. Cumming & W. Jordan. 1994. DNA evolution and colonization sequence of island lizards in relation to geological history: mtDNA RFLP, cytochrome b, cytochrome oxidase, 12s rRNA sequence, and nuclear RAPD analysis. Evolution 48:230–240.
Thorpe, R.S., & A.G. Stenson. 2003. Phylogeny, paraphyly and ecological adaptation of the colour and pattern in the Anolis roquet complex on Martinique. Molecular Ecology 12:117–132.
Turelli, M., N.H. Barton & J.A. Coyne. 2001. Theory and speciation. Trends in Ecology and Evolution 16:330–343.
Wagner, W.L. & V. Funk. 1995. Hawaiian Biogeography: Evolution on a Hot Spot Archipelago. Smithsonian Institute Press, Washington, D.C.

Manuscript received 19 January 2005, revised 17 June 2005.