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

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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 conse-quence 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 sympatry, 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).
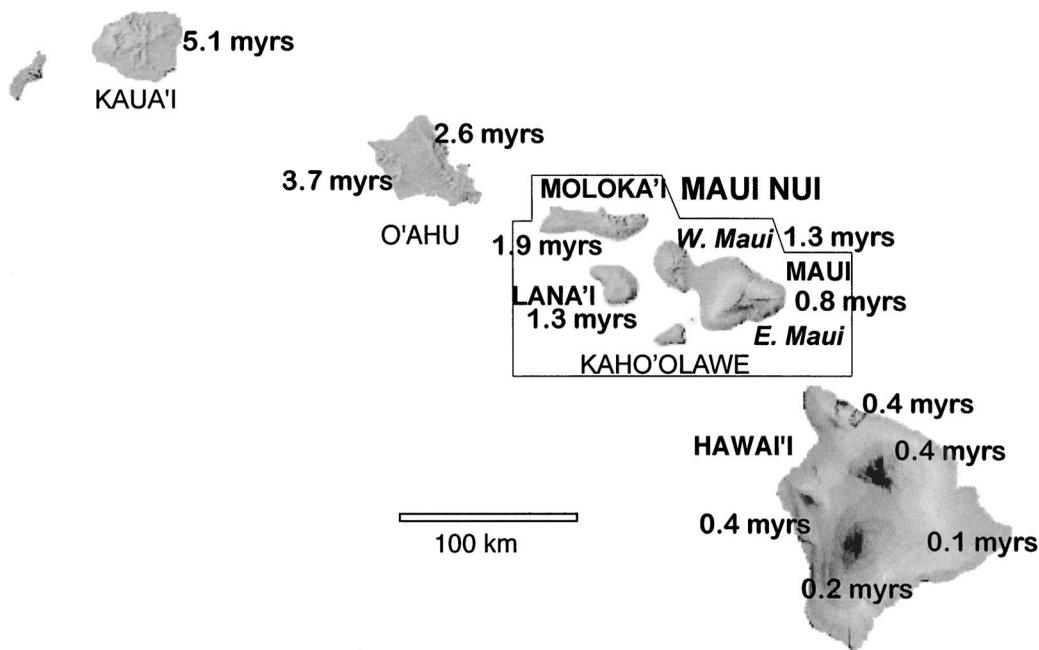
Figure 1.—Map of the Hawaiian Islands. Names in bold type indicate islands that were the focus of the current study. Ages of the different volcanoes are given (myrs = million years).

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 Makaala, 11 July 1994.

Phylogenetic Hypotheses.—An approximately 730 base pair piece of Cytochrome oxidase subunit I (COI) was amplified using primers LCO-1628 (ATAATGTAATTGT-TACTGCTCATGC) and HCO-2396 (ATTGT-AGCTGAGGTAAAATAAGCTCG) (Palumbi 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
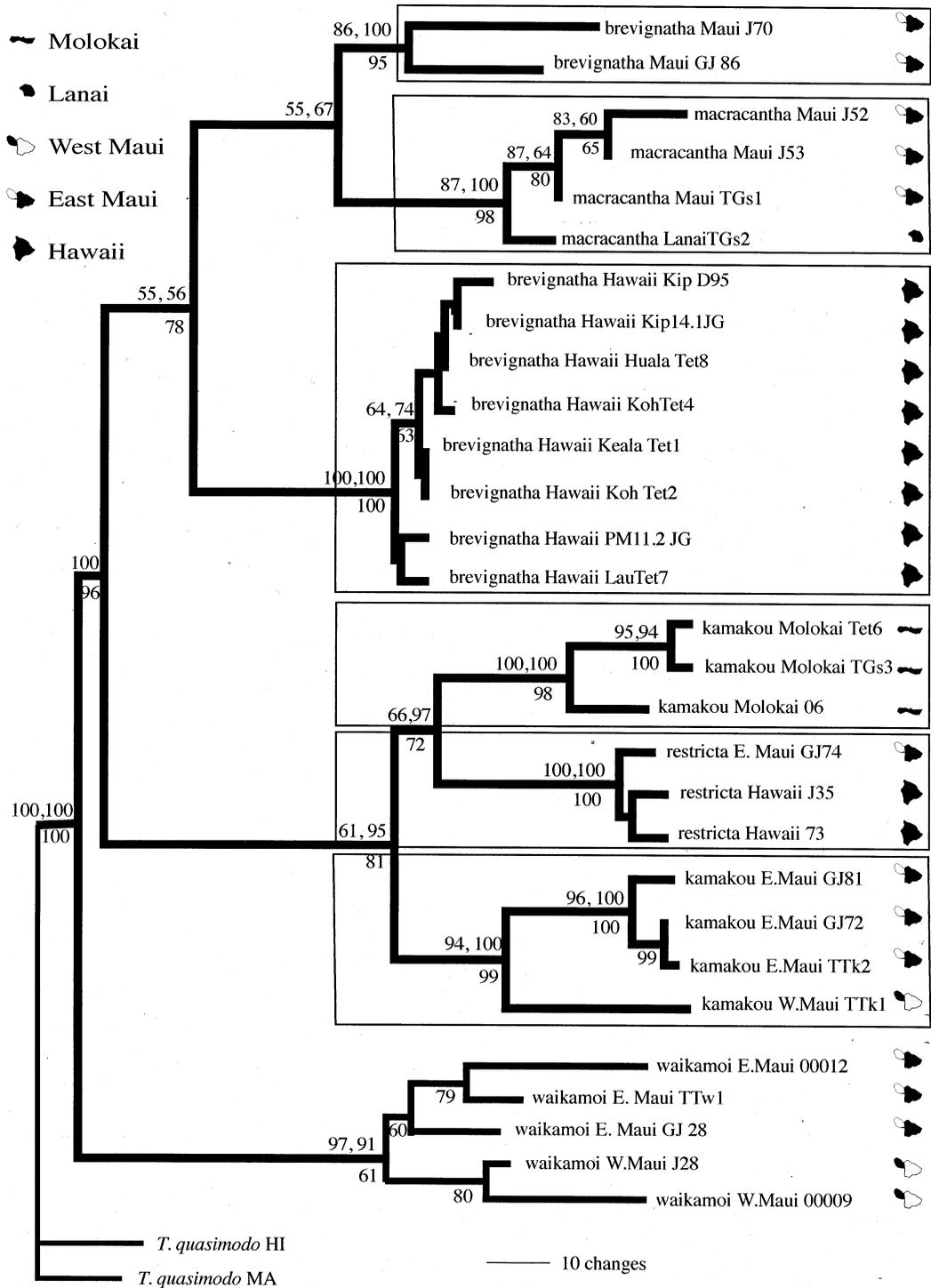
Figure 2.—Phylogenetic hypothesis based on DNA sequence of partial mitochondrial cytochrome oxidase I. Phylogeny reconstruction used Maximum Parsimony (tree length 523, Consistency index = 0.58, Retention index = 0.74), Maximum Likelihood (-Ln likelihood = 3376.47142), and Bayesian inference of likelihood, 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).
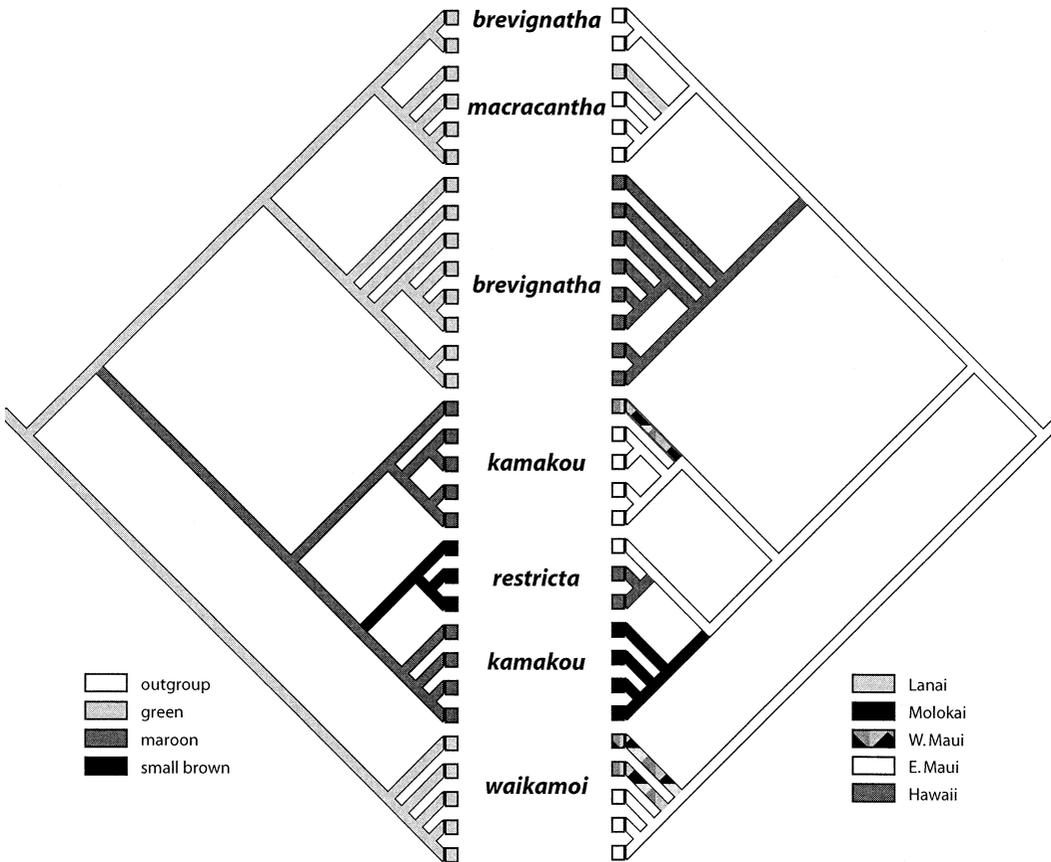
Figure 3.—Ancestral state reconstruction to infer transformations in ecomorph category and island (or volcano within island). Ecomorph category and island affiliation were mapped on to the molecular phylogeny using the accelerated transformation (ACCTRAN) optimization.

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. restrica* 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. brevignatha* 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 pa-

per 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 sympatry 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
		Kipukas	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	DQ178959
	Kilauea	Puu Makaala	4300ft	11 July 1994	GB	11.2JG	DQ182755
T. macracantha	E. Maui	Kipahulu	4000ft	15 May 1990	RG,AM	J52	DQ182765
		Kipahulu	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
		Puu Lua	3180ft	15 June 1999	CE, DP	Tet6	DQ182758
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	CE	TTw1	DQ182770
		Waikamoi Flume	4300ft	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 *T. restricta* has not been found on any island older than E. Maui. Further sampling of populations and genetic loci may help resolve this issue.

The results also indicate that both *T. brevignatha* and *T. kamakou* are paraphyletic when considering populations on the different volcanoes: *T. brevignatha* (E. Maui + Hawaii) with respect to *T. macracantha* (E. Maui + Lanai) and *T. kamakou* (W. Maui + E. Maui) with respect to *T. restricta* (E. Maui + Hawaii). Paraphyly at the species level is not uncommon (Funk & Omland 2003), and may even be expected under the scenario of ecological speciation. Among island radiations, the phenomenon has been clearly demonstrated in species of beetles (Rees et al. 2001) and lizards (Thorpe et al. 1994) in the Canary Islands and also a radiation of anole lizards in the Caribbean (Thorpe & Stenson 2003). In the current study, *T. restricta* has clearly emerged within *T. kamakou*: all extant allopatric populations of *T. kamakou* are very similar morphologically and do not warrant distinct species status.

One limitation of the current study is that it is based entirely on mitochondrial DNA sequences. Mitochondrial gene trees can frequently conflict with species trees, generally 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 (Kaneshiro 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 many other adaptive radiations, that allopatry, together with ecological divergence, 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

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