Dispersal and Vicariance in Hawaiian Platynine Carabid Beetles (Coleoptera)[1]

JAMES K. LIEBHERR[2]

ABSTRACT: The monophyletic, native Hawaiian Platynini have diversified on the Hawaiian Island chain through progressive colonization, mixed with vicariance on the various islands. Single-island endemism stands at 97% of the species, with the few widespread species exhibiting distributions largely congruent with the fundamental area cladogram found using cladistic biogeographic methods. The cost of accepting an ad hoc dispersal hypothesis for individual taxa that conflicts with the fundamental area cladogram is weighed against the savings in items of error when taxa are excluded from the biogeographic analysis. Based on this objective assessment, only one back-dispersal from Maui Nui to O'ahu is supported. Vicariance of Maui Nui, leading to the present-day islands of Moloka'i, Lāna'i, and Maui, has resulted in seven resolvable species triplets composed of single-island endemics occupying these areas. These seven triplets represent five biogeographic patterns, necessitating explanation by numerous ad hoc hypotheses of extinction to support a single hypothesis of area relationships. In six of the seven triplets, the cladistically basal species exhibits a higher minimum elevational limit of occupied habitat than either of the more apical sister species. This result is consistent with isolation of more persistent, peripheral populations at higher elevations, leading to speciation. Comparison of higher-elevation endemics to lower-elevation widespread species supports this interpretation. Such a finding affirms the importance of understanding geographic distribution on a scale appropriate to the action of vicariant mechanisms.

HISTORICAL BIOGEOGRAPHIC analysis has become more rigorous because of the development of the cladistic biogeographic method, in which phylogenetic relationships of taxa are used as the basis for hypothesizing historical relationships among areas of endemism defined by distributions of those taxa (Platnick and Nelson 1978, Rosen 1978, Nelson and Platnick 1981). Connecting the analysis of historical area relationships to historical relationships of taxa, coupled with adoption of objective means to hypothesize phylogenetic relationships (Hennig 1966, Farris et al. 1970) provided an objective basis to the discipline. Recent developments in

the use of Nelson and Platnick's (1981) concept of items of error to quantify the fit of one pattern to another (Page 1990, 1993, 1994) have allowed a more precise means to analyze congruence of biogeographic and coevolutionary patterns. Such methods have most often been aimed at illuminating patterns of vicariance, because the argument was made early on that dispersal patterns were essentially random (Rosen 1978). More recently, the interpretation that both dispersal and vicariance can explain biogeographic patterns, with such explanation dependent on a hypothesis of phylogenetic relationships (Minaka 1987), eliminates the dichotomy between dispersal and vicariance explanations in biogeography, and replaces it with the search for common patterns and causes, versus distinct patterns and causes.

The Hawaiian Islands are an ideal venue for exploration of such common and distinct patterns. Species-level diversity and endemicity are both extreme on the island chain, with as few

[2] Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0901; Research Associate, B. P. Bishop Museum, Honolulu, Hawai'i 96817-0916.

as 230 to 250 ancestors necessary as founders for the over 5000 native insects (Zimmerman 1948, Nishida 1992, Miller and Eldredge 1995). Single-island endemicity approaches 100% in numerous taxa (Nishida 1992): for example, Aglycyderidae, Cerambycidae, and Curculionidae (Coleoptera); Dolichopodidae and Drosophilidae (Diptera); Cixiidae and Delphacidae (Homoptera); Cosmopterygidae (Lepidoptera); Psocidae (Psocoptera). Because widespread distributions are anathema to cladistic biogeographic analysis (Nelson and Platnick 1981), these high levels of endemism permit derivation of area relationships from phylogenetic relationships in a relatively straightforward manner. That much of the biogeographic pattern in Hawai'i is based on overwater dispersal is indisputable given current knowledge of the geological history of the Islands (Clague and Dalrymple 1987, 1989). Nonetheless, the subsidence of Maui Nui affords the search for vicariant patterns among the resulting islands of Moloka'i, Lāna'i, and Maui.

This paper analyzes the biogeographic history for a group of Hawaiian carabid beetles: the native species of the tribe Platynini. This group composes one of only three tribes represented in the native carabid beetle fauna, the others being the tribe Bembidiini with 26 described species represented (Britton 1948a) and the genus *Mecyclothorax* Sharp of the tribe Psydrini (Britton 1948b) with about 165 native species now known (J.K.L. and E. C. Zimmerman, unpubl. data).

The phylogenetic relationships of the native Platynini were used to derive a general hypothesis of area relationships (Liebherr and Zimmerman, in press). Working from that general hypothesis, deviations including both dispersal-based and vicariance-based elements were investigated. Discordant dispersal is objectively identified by items of error criteria used to quantify the fit of observed cladograms to particular patterns. Deviations from a general vicariance hypothesis for Maui Nui are explained by the association of elevational shifts in peripheral populations with speciation. Investigation of explanatory mechanisms beyond vicariance is presented as a complementary approach to biogeographic analysis. Both methods require comprehensive field collections with precise data: a goal worthy of all research programs, but especially needed in Hawai'i because of the limited geographic ranges of species and degradation of native habitats due to invasion by exotics (Howarth 1985, Liebherr and Polhemus 1997).

Hawaiian Platynini

The carabid beetle tribe Platynini comprises over 2500 species in approximately 350 named genera, with an aggregate worldwide distribution. Species-level diversity and endemicity are greatest in tropical montane forests, with major radiations in Mexico, Central America, and the Antilles (Whitehead 1973, Liebherr 1986, 1992), South America (Moret 1990a,b, 1993, 1994), Madagascar (Jeannel 1948, Basilewsky 1985), Asia (e.g., Louwerens 1953), New Guinea (Darlington 1952), and the Hawaiian Islands (Sharp 1903). The restricted geographic ranges of montane endemic species are due primarily to the long-term duration of such habitats during climatic cycling, resulting in extensive adaptation of species to localized habitats (Southwood 1977). This adaptation is best exemplified by the evolution of reduced flight capacity, through the shortening of the metathoracic episterna and flight wings in taxa of most montane tropical radiations of the tribe (e.g., Sharp 1903, Darlington 1952, Liebherr 1988).

The Hawaiian Platynini represent a uniquely prolific level of diversification, with 128 species found within the 16,640 km^2 of the Islands (Table 1). In comparison, Japan supports 140 species (Habu 1978) within its area of 369,700 km^2, Madagascar houses 326 species (Basilew-

TABLE 1

SPECIES DIVERSITY AND PERCENTAGE SINGLE-ISLAND ENDEMISM FOR HAWAIIAN PLATYNINI

ISLAND	NO. SPECIES	NO. ENDEMICS	% ENDEMISM
Kaua'i	24	24	100
O'ahu	32	32	100
Moloka'i	21	17	81
Lāna'i	5	3	60
West Maui	17	13	76
East Maui	35	31	89
Hawai'i	6	4	67
Total	128	124	97

sky 1985) in 594,180 km^2, and New Guinea is home to 164 species (Darlington 1952, 1971) over 808,510 km^2. Species distributions of Hawaiian platynines are extremely limited, with only four species found on more than one island (Table 1), and two of these widespread species restricted to the islands that formerly were part of the superisland Maui Nui. Even within islands, known distributions may be limited to single ridges or valleys. On Kaua'i, two undescribed species ("atra" and "kahili") are known only from Mount Kāhili, a southern spur of the Kawaikini-Wai'ale'ale central uplands. On O'ahu, the 32 species include 8 restricted to the western Wai'anae range and 14 restricted to the eastern Ko'olau Mountains.

The extreme endemicity of the Hawaiian platynines makes them ideal candidates for cladistic biogeographic analysis (Platnick and Nelson 1978). Cladistic analysis of the Hawaiian Platynini (Liebherr and Zimmerman, in press), based on 206 morphological characters and including all native Hawaiian species plus 41 outgroup taxa, indicates that the Hawaiian platynine radiation is monophyletic, with the closest outgroup the genus *Lorostema* Motschulsky, distributed in India, Southeast Asia, New Guinea and northern Australia, and the Southwest Pacific as far as Tahiti (Figure 1). Therefore, biogeographic analysis of the Hawaiian platynines provides the opportunity to deduce

the history of a radiation resulting from colonization by a single common ancestor that has subsequently been played out on all the high islands. This not only adds another case study to the growing core of studies dealing with biogeographic relationships of Hawaiian endemic organisms (Wagner and Funk 1995), but because of the extreme endemicity and diversity of the group, also permits the search for repeated biogeographic patterns among the included taxa. Because cladistic biogeography attempts to summarize all area relationships in a single cladogram of areas, deviations from that summary can be investigated in light of various attributes of the attendant taxa. In this study, I first present the general biogeographic pattern exhibited by Hawaiian Platynini and then investigate concordant and discordant patterns of dispersal among the major islands, as well as the vicariant pattern among the fragments of the superisland Maui Nui.

Biogeographic Patterns

The cladistic analysis of native Hawaiian Platynini (Liebherr and Zimmerman, in press) was used as the basis for this biogeographic analysis. The strict consensus cladogram of 14,169 equally parsimonious cladograms—the number of trees stored was limited by computer memory and the NONA tree-finding program
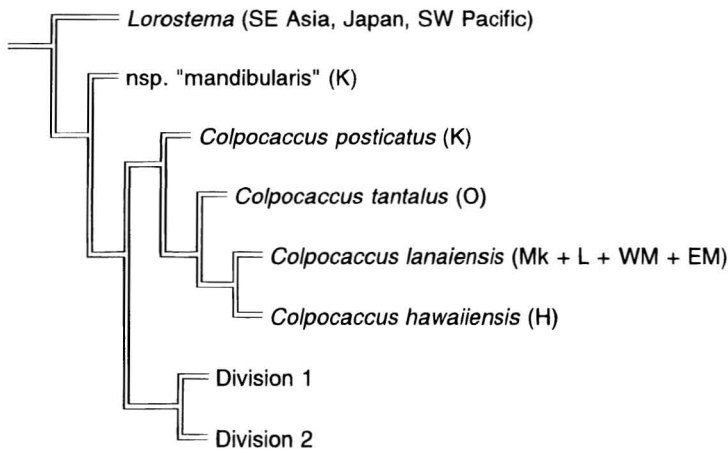

FIGURE 1. Cladistic relationships at base of Hawaiian platynine radiation and closest outgroup, *Lorostema* Motschulsky. Undescribed species name in quotation marks preceded by abbreviation "nsp." Area abbreviations are as follows: K, Kaua'i; O, O'ahu; Mk, Moloka'i; L, Lāna'i; WM, West Maui; EM, East Maui; H, Hawai'i (Big Island).

(Goloboff 1995)—showed that all discovered cladograms agreed on the monophyly of the group (Figure 1). Because the strict consensus cladogram (e.g., Figures 2, 3) retained a consistent and repeated pattern of area relationships among the major islands (Kaua'i, O'ahu, Maui, and the Big Island) and because the COMPONENT program of Page (1993) requires a fully resolved taxon-area cladogram, the first cladogram stored in memory was arbitrarily chosen for this analysis.

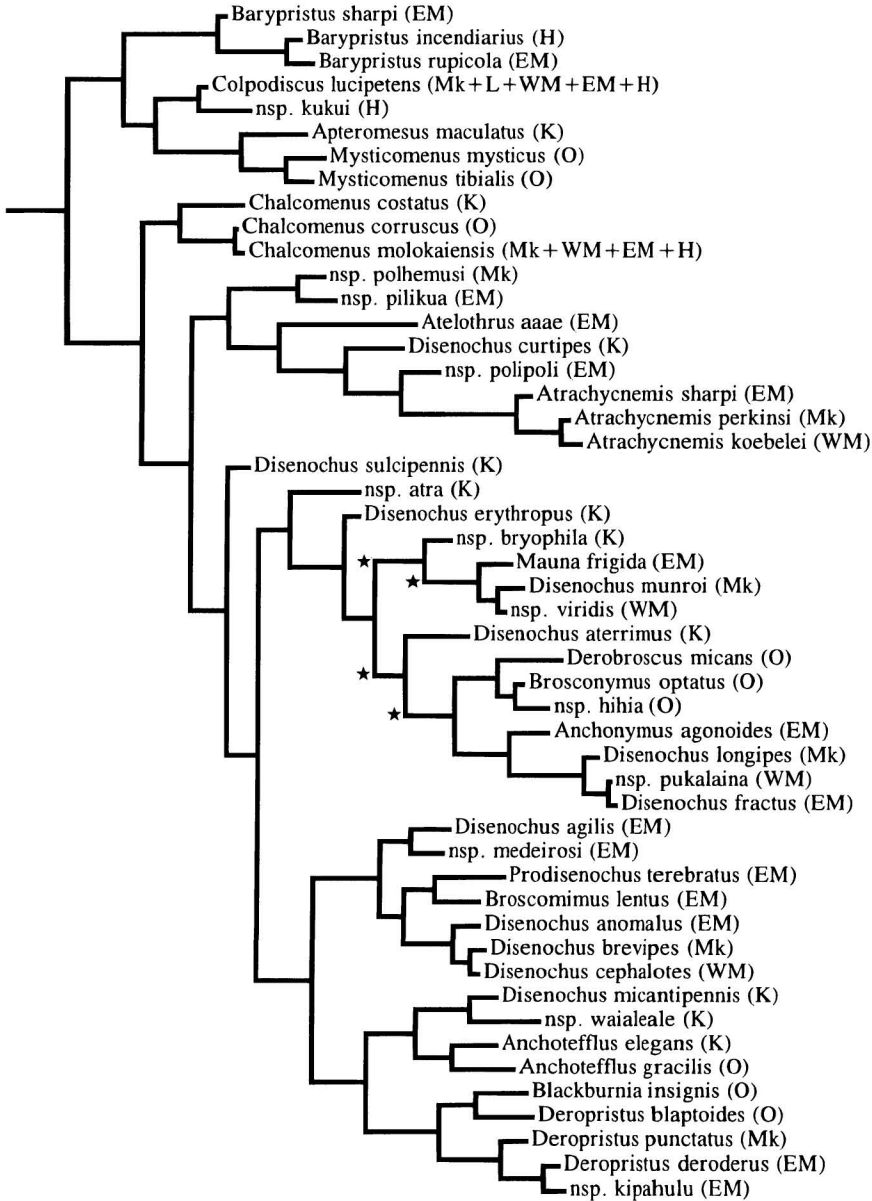When the resolved taxon cladogram was used

FIGURE 2. Resolved cladogram of division 1 used for biogeographic analysis. Internal cladogram nodes to the right of stars collapse on the strict consensus cladogram. Undescribed species names preceded by abbreviation "nsp." Area abbreviations as in Figure 1.

Metromenus aequalis (O)
Metromenus fraternus (O)
Metromenus limbatus (K)
Metromenus pavidus (K)
Metromenus cuneipennis (O)
Metromenus perpolitus (O)
Metromenus meticulosus (O)
Atelothrus fractistriatus (O)
nsp. fordi (O)
nsp. foveolata (EM)
Atelothrus metromenoides (O)
Metromenus hilaris (O)
Metromenus caliginosus (O)
Metromenus mutabilis (O)
Metromenus epicurus (O)
nsp. hakeakapa (Mk)
nsp. kauwa (WM)
nsp. fulgida (EM)
Atelothrus insociabilis (EM)
Metromenus fraudator (Mk)
Atelothrus filipes (L)
nsp. bartletti (WM)
Atelothrus gracilis (WM)
Atelothrus dyscoleus (EM)
Metromenus palmae (O)
Atelothrus platynoides (Mk)
Metromenus sphodriformis (Mk+WM+EM)
Atelothrus depressus (L)
Metromenus moerens (Mk)
Atelothrus longulus (WM)
Atelothrus constrictus (Mk)
Atelothrus erro (EM)
nsp. asquithi (K)
nsp. kahili (K)
nsp. huhula (O)
Mesothriscus muscicola (O)
nsp. paludicola (O)
Mesothriscus kauaiensis (K)
Atelothrus transiens (K)
Mesothriscus optimus (K)
Mesothriscus alternans (K)
Mesothriscus opacus (K)
Metromenus lentus (H)
Mesothriscus lanaiensis (L)
Mesothriscus vagans (Mk)
nsp. auana (WM)
Platynus ambiens (K)
Atelothrus howarthi (EM)
Platynus calathiformis (EM)
Atelothrus debilis (Mk)
nsp. kuiki (EM)
nsp. pauma (K)
nsp. ulaula (EM)
Mesothriscus tricolor (Mk)
Mesothriscus concolor (WM)
Mesosthriscus microps (WM)
Metromenus latifrons (Mk)
Mesothriscus abax (Mk)
nsp. kolukala (EM)
nsp. abaxoides (EM)
nsp. kuewa (EM)
Mecomenus putealis (EM)
Mecostomus perkinsi (EM)
Mecomenus koebelei (WM)
Metromenus audax (O)
nsp. lihau (WM)
Atelothrus cheloniceps (Mk)
Metromenus calathoides (EM)
nsp. paloloensis (O)
Metromenus bardus (O)
Metromenus oceanicus (O)
Metromenus fossipennis (O)
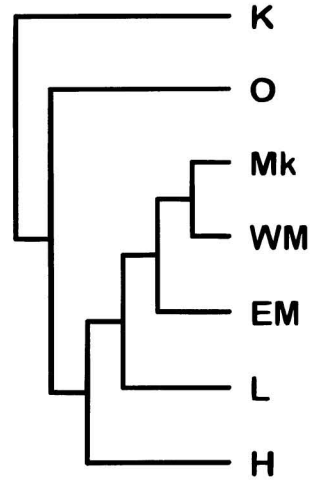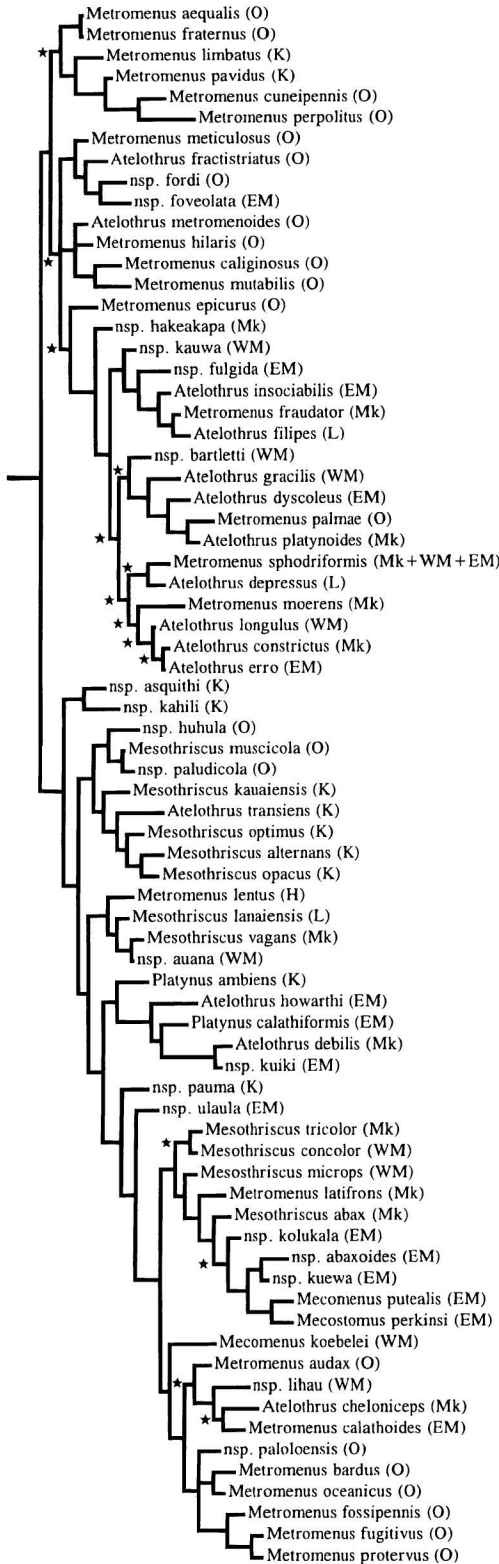Metromenus fugitivus (O)
Metromenus protervus (O)

FIGURE 4. Single fundamental area cladogram that best minimizes duplications, added leaves, and hypothesized losses (Page 1993) for Hawaiian platynine carabid taxa. Area abbreviations as in Figure 1.

as the basis for cladistic biogeographic analysis using items of error as implemented in COMPONENT 2.0 (Page 1990, 1993), a single fundamental area cladogram (Figure 4) exhibited the best combination of fewest duplications, fewest hypothesized losses, least items of error (Page 1993), and strongest underlying character support (Liebherr and Zimmerman, in press). This hypothesis recognizes the dominant pattern of area relationships exhibited by Hawaiian platynines to be progressive colonization from Kaua'i to the younger islands. This progressive pattern is at the level of superislands, as the Big Island is the sister area to the islands previously united as Maui Nui: Moloka'i, Lāna'i, and Maui. Therefore a vicariant pattern associated with the subsidence of Maui Nui (Clague and Dalrymple 1987) is overlain on a progressive dispersal pattern composing distinct oceanic islands. The predominant pattern of Maui Nui vicariance recognizes Moloka'i and West Maui as sister areas, with East Maui their sister area. Lāna'i is cladistically basal within Maui Nui. This general pattern is at odds with the presence of the Pailolo

FIGURE 3. Resolved cladogram of division 2 used for biogeographic analysis. Internal cladogram nodes to the right of stars collapse on the strict consensus cladogram. Undescribed species names preceded by abbreviation "nsp." Area abbreviations as in Figure 1.

Channel between Moloka'i and Maui, and the presence of an isthmus joining West and East Maui. Under a strictly vicariant scenario, this implies that mechanisms other than sea level inundation are responsible for fragmentation of platynine habitats on Maui Nui; that is, vicariant patterns were established before final subsidence of Maui Nui resulted in establishment of the Pailolo Channel.

Dispersal Patterns: Big Island Colonization

Based on the geologic history of the Islands and the pattern of area relationships summarized from all species, the most recent colonizations are likely to have occurred during the population of the Big Island. Based on the taxon-area cladogram, the six Big Island species have been derived from at least five colonization events (Table 2). Two of these involve sister species on Maui Nui: the sister pairs *Colpocaccus hawaiiensis* Sharp and *C. lanaiensis* Sharp, and *Barypristus incendiarius* (Blackburn) and *B. rupicola* (Blackburn). In a third case, the Maui Nui sister group comprises three species restricted to various islands, with *Metromenus lentus* Sharp now occurring on the Big Island. Thus, colonization of the Big Island by *M. lentus* predates the origin of the three distinct species on Lāna'i, Moloka'i, and West Maui.

One Big Island species, *Chalcomenus molokaiensis* Sharp, is widespread also on Maui Nui. On the Big Island, *C. molokaiensis* is restricted to the Kohala Mountains, the northernmost and oldest volcano composing the Big Island. The species is a streamside resident on Moloka'i and Maui, suggesting that erosional aspects of the Kohala Range may provide ecological requirements necessary for this species' existence there.

The final two species—*Colpodiscus lucipetens* (Blackburn) and undescribed species "kukui"—are sisters and most parsimoniously may be hypothesized to have been derived via allopatric speciation within the Big Island after colonization of the Big Island by a common ancestor. *Colpodiscus lucipetens* is distributed across the island and on Maui Nui, whereas the undescribed species has been collected only in windward forest on the Big Island from Hilo to Kīlauea. The undescribed species is much less common than *C. lucipetens,* and its known restricted range may represent inadequate collections from areas outside the historical collecting axis along the Hilo-Kīlauea Road (Manning 1986). Continued sampling of these taxa is required to adequately assess their area of sympatry.

Based on the variety of divergence levels exemplified by colonization events among Big Island Platynini, the inescapable conclusion is that the fauna of this island is being built by accretion of individually successful colonizing taxa. Major geologic events, such as massive failures of older islands (Moore et al. 1989) may contribute to such colonizations, but synchronous colonization does not appear to be the norm. Three of the five colonizing episodes involve species currently widespread across islands that composed Maui Nui—*Colpocaccus hawaiiensis* and *C. lanaiensis, Chalcomenus molokaiensis,* and *Colpodiscus lucipetens*. Ecological requirements for these species are poorly

TABLE 2

FLIGHT WING CONFIGURATION, SISTER TAXON, AND SISTER TAXON PROVENANCE OF SPECIES FOUND ON HAWAI'I (BIG ISLAND)

SPECIES	WINGS	SISTER TAXON	PROVENANCE
Colpocaccus hawaiiensis	+ +	*Colpocaccus lanaiensis*	Maui Nui
Barypristus incendiarius	−	*Barypristus rupicola*	East Maui
Colpodiscus lucipetens	+ +	Undescribed sp. "kukui"	Big Island
Undescribed sp. "kukui"	+ +	*Colpodiscus lucipetens*	Big Island
Chalcomenus molokaiensis	+	*Chalcomenus molokaiensis*	Maui Nui
Metromenus lentus	−	*Mesothriscus lanaiensis* + *M. vagans* + undescribed sp. "auana"	Maui Nui

NOTE: Macropterous metathoracic wings with wing ratio 3.0–5.0 (+ +), macropterous wings with wing ratio 1.7–2.3 (+), vestigial wings (−).

understood, but the association of the majority of colonizations with widespread species parallels the widespread distributions of colonists on Krakatau (Thornton et al. 1990).

Successful Big Island colonization has occurred in both macropterous and brachypterous lineages (Table 2). Of the minimum five colonization events possible, three involve fully winged colonists and two involve vestigially winged colonists. The flight-wing configuration of the winged colonists varies. Both *Colpocaccus hawaiiensis* and *Colpodiscus lucipetens* possess metathoracic wings 3.0–4.3 times the length of the elytra (Liebherr and Zimmerman, in press), the length hypothesized to be plesiomorphic for the Platynini. Records for these species include captures on a window and in a windowpane trap, respectively, suggesting that active flight occurs in these species. *Chalcomenus molokaiensis* individuals possess flight wings with full venation; however the alar surface is only 1.7–2.3 times the elytral length. All ecological information associated with this species involves collection in streamside habitats, under rocks, in litter, or on *Cyanea* plants. Though winged, flight is therefore not proven for this species. Both vestigially winged Big Island taxa (*Barypristus incendiarius* and *Metromenus lentus*) are sister to other vestigially winged taxa, indicating that their differentiation on the Big Island occurred in the absence of serviceable flight wings. Successful colonization in the above cases therefore may occur by active flight, but as often by means not requiring flight, such as transport on floating trees or other occupied plant parts.

Older Dispersal Patterns

Hennig (1966) advanced the progression rule to permit determination of historical dispersal pathways. By this rule, taxa possessing the most derived character states are reasoned to occupy the most recently colonized areas. Distributions of common ancestors are determined by the distribution of the patristically closest terminal taxa. He used the concept of rassenkreisen (sequences of subspecific taxa) to exemplify the progression rule. Thus, a pectinate cladogram of infraspecific taxa inhabiting areas in the relationship $(A(B(C(D,E))))$ indicates dispersal of the entire lineage from area A to area E leaving descendants in the intermediate areas. Such an approach is seriously deficient, because the pattern can also be explained by successive vicariance of a primordial distribution composed of all areas. Moreover, the simple example of five taxa in five areas with the relationship $((A,B)(C(D,E)))$ precludes the ability to assign a single unambiguous dispersal path connecting the taxa in their areas.

Items of error analysis (Page 1990, 1994) permits use of an objective criterion to evaluate how well a particular set of taxa adheres to a particular pattern of area relationships. In items of error analysis, an observed tree is modified through the addition of hypothetical terms so that its overall pattern of relationships is congruent with a particular general pattern. The hypothetical terms are called added leaves (Page 1993); the total number of leaves corresponds to the number of terminals in the modified observed tree. Items of error are the difference in total cladogram edges between the modified observed tree and the original observed tree. Because cladogram edges are two times the number of terminals in a dichotomous cladogram, added leaves $\times$ 2 = items of error.

As an example, the *Colpocaccus* clade (Figure 1) is perfectly congruent with the fundamental area cladogram found for the entire platynine radiation (Figure 4). *Colpocaccus* cannot resolve the Maui Nui areas, because *C. lanaiensis* is widespread across Moloka'i, Lāna'i, West Maui, and East Maui; however this lack of resolution cannot conflict with the overall pattern. Other parts of the resolved taxon-area cladogram fit less well. For example, the clade basally defined by *Disenochus aterrimus* Sharp (Figure 2) defines the area relationships (K(O(EM(Mk(WM, EM))))). To make this pattern congruent with the fundamental area cladogram (Figure 4), several leaves must be added: (1) Hawai'i must be included as a sister area to Maui Nui, resulting in the addition of one leaf or two items of error; (2) the redundant distribution of East Maui requires the addition of two duplications and five leaves so that the apical four taxa (in **bold**) are present in three replications of an identical subpattern—((**EM**(Mk,**WM**)), ((EM(**Mk**,WM)), (**EM**(Mk,**WM**))))—resulting in addition of five more terms or 10 items of error; and (3) the

missing area Lāna'i must be inserted as sister to the other Maui Nui areas, resulting in yet one more term (i.e., two more items of error). Thus, for the *Disenochus aterrimus* clade to fit the fundamental area cladogram (Figure 4) requires a total of seven additional leaves or 14 items of error. However, if we were to accept a hypothesis that dispersal by the ancestor of *D. fractus* Sharp into East Maui from West Maui occurred subsequent to vicariant events congruent with the fundamental area cladogram, we could eliminate the need for the five added leaves required under point 2 above. This ad hoc assumption of dispersal can be viewed as equivalent to five added leaves, or 10 items of error.

To assess the cost of assuming that relationships of each of the various taxa represent the general hypothesis of area relationships (Figure 4), each taxon was excluded sequentially from calculation of duplications, leaves added, and losses based on the other taxa. The resultant totals were then compared with the totals based on all taxa (Table 3). The savings in fit criteria were considered the decrease in duplications, leaves, and losses relative to those of the entire data set. These values were evaluated in the context of savings accrued for all taxon exclusions; only the greatest relative savings merit acceptance of an explanatory ad hoc dispersal hypothesis. In like manner, if a certain savings in the criteria merit acceptance of dispersal for one particular taxon, then taxon exclusions resulting in greater savings must also merit acceptance of dispersal.

Before the analysis was conducted, monophyletic groups of taxa were condensed into sin-

gle terminals. This resulted in a total of 100 terminals across the entire taxon-area cladogram (Figures 1–3), a total within the capacity of the COMPONENT program (Page 1993).

Exclusion of 37 of the 100 terminals resulted in no change in duplications, and exclusion of 61 others resulted in reduction by one duplication. A decrease of two duplications to a total of 58 was observed for only two terminals (Table 3). Duplications can be viewed as speciation events undiscoverable because of the scale of the areas of endemism. Thus the speciation event might be considered "sympatric" at the level of resolution of the areas of endemism, with both resultant taxa the common ancestors of their own subsequently evolving lineage. Pectinately redundant taxa (e.g., undescribed species "atra" and *Disenochus erythropus* Sharp [Figure 2]) are one example of such a pattern. In the case of these two taxa, their redundancy requires insertion of leaves representing the other six areas as sister to each species' representation. Thus a taxon exclusion resulting in only one fewer duplication is always associated with redundancy in the cladogram.

Exclusion of *Metromenus palmae* (Blackburn) results in reduction by two duplications (Table 3). Strong conflict with the fundamental area cladogram explains this reduction (Figures 3, 4). *Metromenus palmae* is the only O'ahu taxon within an entire clade of Maui Nui species. The cladistically closest O'ahu species is *Metromenus epicurus* (Blackburn), eight nodes away. Assuming that *M. palmae* is the result of back-dispersal from Maui Nui to O'ahu saves 23 added leaves, equivalent to 46 items of error. Those 23 added leaves are distributed in 18 monophyletic sets, as indicated by the saving of 18 losses. No other taxon exclusion is even close in such reductions of leaves added and losses (Figures 5, 6). Therefore, if we assume that the origin of *M. palmae* involved dispersal of a colonizing propagule from the Moloka'i portion of Maui Nui (Figure 3), we can reduce the leaves added by nearly 10% at a cost of one ad hoc hypothesis of dispersal.

Excluding *Disenochus fractus* also results in reduction by two duplications, and elimination of five added leaves and four losses (Table 3). This amount of reduction in leaves added is less than or equal to that observed because of

TABLE 3

Fit Criteria Maximized in Items of Error Analysis for Entire Taxon-Area Cladogram and for Cladograms Derived after Exclusion of Four Species

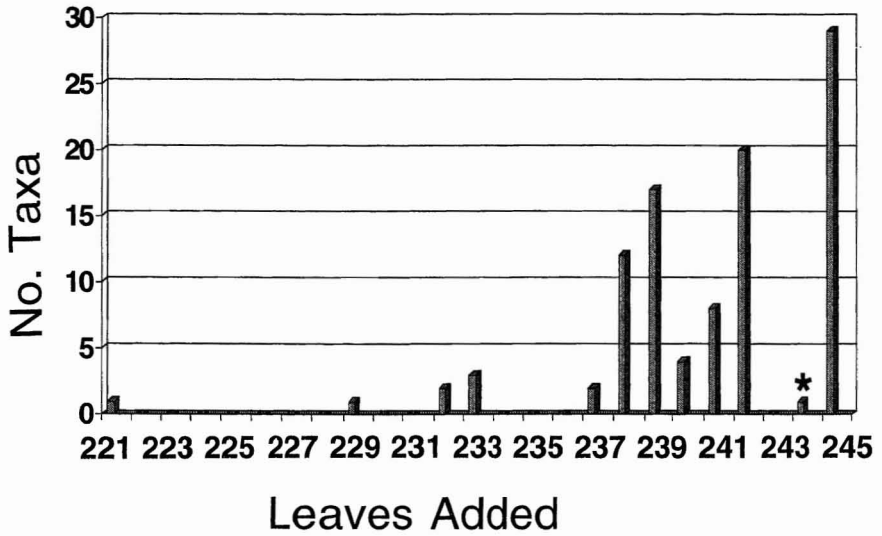| CLADOGRAM	DUPLICATIONS	LEAVES ADDED	LOSSES
All species	60	244	140
Metromenus palmae	58	221	122
Disenochus fractus	58	239	136
Undescribed sp. "foveolata"	60	229	135
Disenochus curtipes	60	237	133

FIGURE 5. Distribution of numbers of leaves added for taxon exclusion trials. Analysis of all 100 terms of taxon-area cladogram requires 244 added leaves (*, see Table 3).

exclusion of 38 other terminals (Figure 5); for losses the value is less than or equal to that observed by exclusion of 14 other terminals (Figure 6). Therefore, savings in items of error are less than for numerous other taxa, and for us to invoke an ad hoc hypothesis of dispersal in this case would call into question whether we should consider it for the numerous other taxa

associated with larger savings in items of error. We will return to this example when vicariant patterns of Maui Nui are investigated later in the paper.

It is important to analyze the cladistic relationships and distributions of taxa when evaluating the total reductions in items of error in such an analysis. For example, exclusion of the unde-
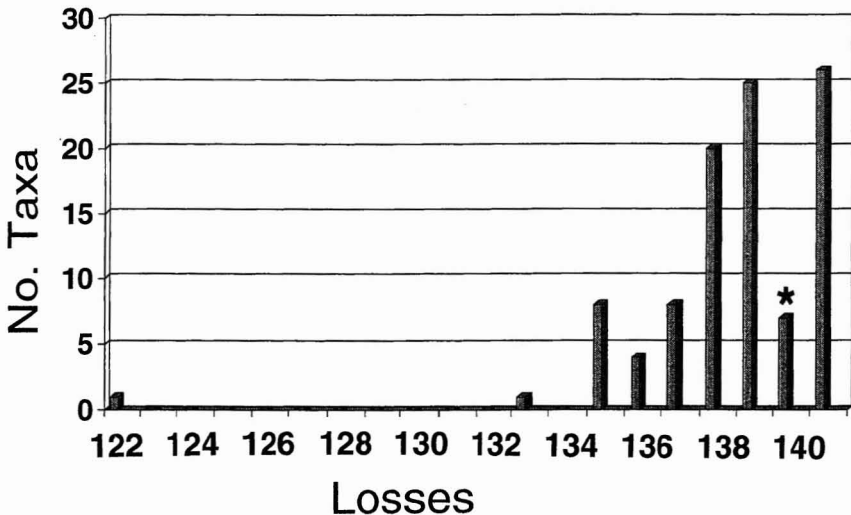
FIGURE 6. Distribution of losses for taxon exclusion trials. Analysis of all 100 terms of taxon-area cladogram requires 140 losses (*, see Table 3).

scribed species "foveolata" saves 15 added leaves accounted for by five losses (Table 3), the first value falling well below the values of 98 other terminals (Figure 5). However, inspection of the taxon-area cladogram indicates that this savings reflects paraphyletic redundancy of three taxa on Oʻahu that are successive sister groups of the new species (Figure 3). In fact, the pattern expressed is congruent with the fundamental area cladogram in that a Maui Nui taxon is related to those on Oʻahu.

Disenochus curtipes Sharp and its four relatives are hypothesized to be the sister group of the East Maui cave species *Atelothrus aaae* Samuelson & Liebherr (Figure 2). This relationship is supported by three characters: (1) reduced outer curvature of the eyes, (2) sparsely pubescent third antennomere, (3) elytral striae evenly punctured throughout length (Liebherr and Zimmerman, in press). The first and second traits are features often observed in cave species (Barr 1983), and the third is reversed from the derived condition wherein punctations are stronger on the base of the elytra than near the apex. Based on the weak character support for its current placement, and biogeographic relationships of *D. curtipes* and its sister group, it seems unlikely that the current cladistic hypothesis is correct. Be that as it may, the exclusion of *D. curtipes* results in the second fewest losses (Figure 6), but no reduction in duplications and only seven fewer leaves added, a value equal to or less than that for eight other terminals. Therefore, acceptance of an ad hoc dispersal hypothesis whereby *D. curtipes* colonized Kauaʻi from Maui is not called for in this instance.

Taking the fundamental area cladogram (Figure 4) as the template, the taxon-area cladogram was scanned and island transformations (i.e., colonization events) noted (Figure 7). The single back-dispersal event involving *Metromenus palmae* is the lone exception to progressive colonization from older to younger islands. The 10 colonization events linking Kauaʻi and Maui Nui may very well represent colonizations of Oʻahu, with subsequent extinction of the Oʻahu species on that highly eroded island. Currently, platynines are restricted to above 700 m on Oʻahu, reducing the Koʻolaus to an extremely thin strip of suitable habitat. In the Waiʻanaes, Mount Kaʻala represents the only substantial

portion of extant suitable habitat for these species.

Viewing the five colonization events of the Big Island in this more global (albeit islandic) context, it appears that this youngest island has received about 25% of the number of colonizing lineages observed for Maui Nui and those possible for Oʻahu. The isolation of Kauaʻi is profound, because it has witnessed the emigration of propagules to Oʻahu and/or Maui Nui, but has not yet delivered evidence of receiving a colonist from one of the younger islands.

Maui Nui Vicariance

One of the central tenets of cladistic biogeography is the assumption of a single history of areas decipherable from phylogenetic information held in common among a variety of taxa (Platnick and Nelson 1978). That there is a single history is tautological. That it is decipherable remains a challenge, with numerous techniques advanced that provide different hypotheses of area relationships given the same input of data (Morrone and Carpenter 1994). The approach taken here is slightly different. Rather than compare methods of analysis, the fundamental area cladogram (Figure 4) is used to identify patterns for taxa that conform and conflict with the general pattern of vicariance for Maui Nui. The goal is to find distributional attributes other than geographic range that might explain why a particular taxon deviates from the general pattern, which is simply the predominant pattern in the taxon-area cladogram.

Six three-taxon triplets involving areas composing Maui Nui (Figure 8B–G) are implicit in the strict consensus cladogram (Liebherr and Zimmerman, in press). A seventh triplet is composed of *Disenochus munroi* Perkins and undescribed species "viridis," sister taxa on the strict consensus (Figure 2), and *Mauna frigida* (Blackburn), sister group to these taxa in one class of most parsimonious cladograms, but only patristically closest in the second arrangement of these species. In the second arrangement, *M. frigida* composes the outgroup to the resolved *Anchonymus agonoides* Sharp clade (Figure 2). The monophyletic interpretation of *M. frigida, D. munroi,* and the undescribed species is illustrated
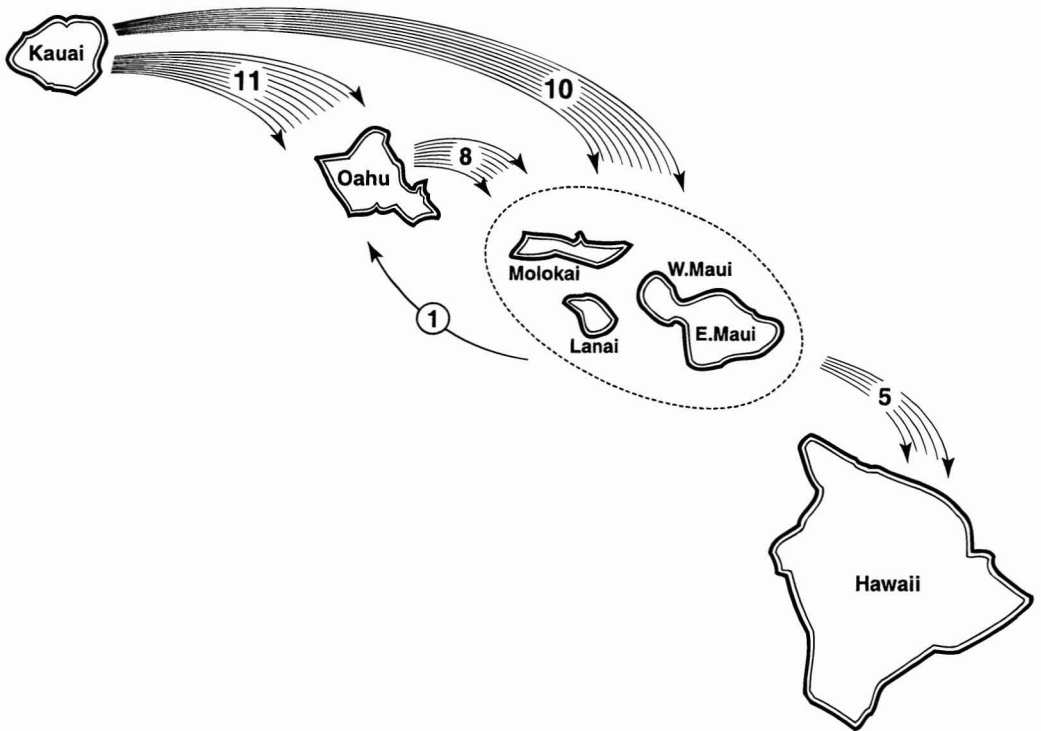
FIGURE 7. Dispersal pathways derived from taxon-area cladogram using the fundamental area cladogram (Figure 4) as a template. Dispersals from Kaua'i to Maui Nui (area inside dashed lines) hypothesized to include colonization of O'ahu based on general area relationships of fundamental area cladogram. Back-dispersal from Maui Nui to O'ahu supported by savings in items of error through taxon exclusion trials.

for this analysis (Figure 8A), with interpretation under the alternate topology also discussed later.

Three of these triplets (Figure 8A–C) are congruent with the fundamental area cladogram without addition of any leaves. Four others require added leaves to gain congruence, because of sister-area relationships hypothesized for Moloka'i and East Maui (Figure 8D), Moloka'i and Lāna'i (Figure 8E), West and East Maui (Figure 8F), and Moloka'i and West Maui but lacking East Maui (Figure 8G). Therefore, among these seven triplets, five biogeographic patterns are represented.

A single unifying distributional attribute is predominant among the seven triplets. In six of the seven (Figure 8A–F), the basal species of the triplet has its lower elevational limit of habitat at equal or higher elevation than either of the sister species. In the case of *Mauna frigida,* this basal species occurs above timberline in open scrubland, whereas the Moloka'i *D. munroi* and

West Maui undescribed species are found in closed canopy to fragmented 'ōhi'a forest at lower elevations. From what we know of the habitat preferences for the other species, all are associated with mesic to wet 'ōhi'a forest. The members of the *Mesothriscus lanaiensis-vagans*-undescribed species "auana" triplet (Figure 8G) comprise streamside species; however they have been collected along streams in 'ōhi'a forest.

The *M. lanaiensis-vagans*-undescribed species "auana" triplet is also the single exception to the elevational generalization that more basal groups are restricted to habitats at higher elevation. The basal species of this triplet, *Mesothriscus lanaiensis* Sharp, is known from only two specimens collected by Perkins at the 2000-foot elevation on Lāna'ihale in 1894 (Perkins 1894, Sharp 1903), most likely in a streamside situation. More collections of species in this triplet, and especially determination of whether the
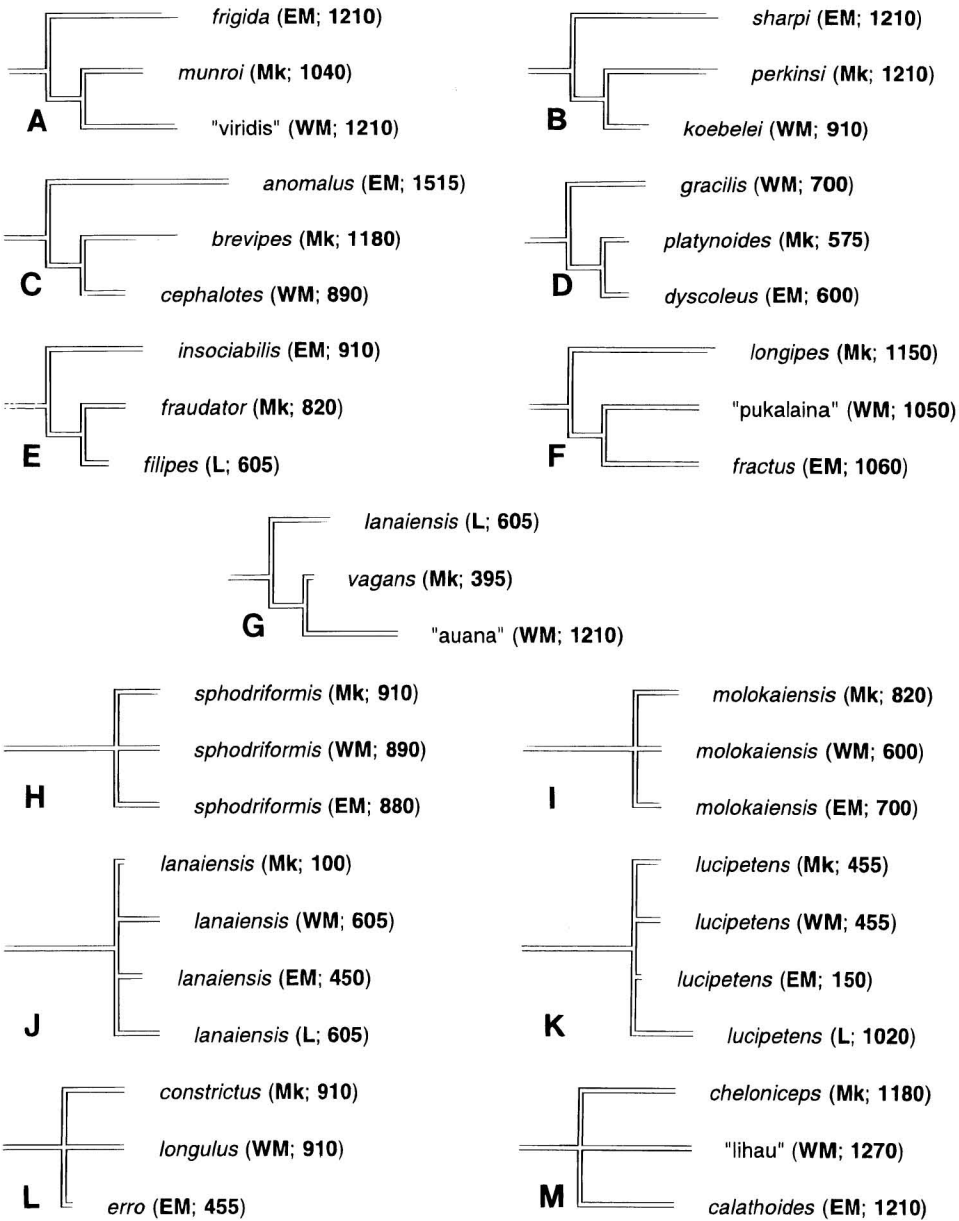
FIGURE 8. *A–G.* Resolved triplets of single-island Maui Nui endemic species. Area abbreviations as in Figure 1; lower elevational limit of known habitat in meters following area abbreviations; branch lengths for apical stems on cladogram proportional to minimum elevational habitat limit. *H–K.* Lower elevational limits for widespread species on volcanoes composing the former Maui Nui. *L–M.* Lower elevational limits for ambiguous triplets of single-island Maui Nui endemic species. Undescribed species names in quotation marks.

West Maui undescribed species is found at elevations equivalent to those of *M. vagans* Sharp of Moloka'i, is the means to test the current elevational hypothesis.

Given the alternate topology for the *Mauna frigida* triplet (Figure 8*A*), wherein *Anchonymus agonoides* is the root of a clade sister to *M. frigida*, the elevational generalization for this triplet still holds. *Anchonymus agonoides* has been found no lower than 1210 m elevation, a lower limit identical to that of *M. frigida*. Therefore, no closely related species outside the *D. munroi*–undescribed species "viridis" sister pair exhibits a lower elevational limit than either sister species.

This pattern is consistent with speciation via peripheral isolation (Mayr 1963). Those peripheral isolates that occupy higher elevations are the ones that persist longer as independent entities and thereby are able to speciate. Isolated populations at more climatically variable lower elevations: (1) have more opportunity to reestablish connections with other adjacent populations, thus delaying speciation, or (2) have undergone a higher rate of extinction with or without speciation. By this scenario, speciation is the means by which morphological distinctiveness is fixed (Futuyma 1989).

If higher-elevation populations are the ones isolated on various volcanoes, widespread species composing conspecific populations across these same volcanoes should exhibit lower elevational limits. In general this is so (Figure 8*H–K*). Of the four widespread species, *Colpocaccus lanaiensis* and *Colpodiscus lucipetens* both occur as low as 100 to 150 m elevation at some sites. *Colpodiscus lucipetens* is known from a single Lāna'i specimen collected atop Lāna'ihale (Figure 8*K*). Documenting permanent habitation of Lāna'i by this winged species requires subsequent collections. *Chalcomenus molokaiensis* occurs along streams and may have had a larger distribution with lower elevational limits before the advent of human introductions and deforestation (e.g., Asquith and Messing 1993). One might investigate infraspecific patterns of relationship in this case, predicting that Moloka'i populations would be less closely related relative to populations on West and East Maui (Figure 8*I*).

Two triplets are composed of single-island endemics whose relationships were ambiguous based on the strict consensus (Figure 8*L, M*). Unlike the other resolved triplets (Figure 8*A–G*), in these cases no single sister-species pair was represented in all most parsimonious cladograms. However, based on the elevational generalization for the resolved triplets, it might be predicted that *Atelothrus constrictus* Sharp or *A. longulus* Sharp (Figure 8*L*) and undescribed species "lihau" (Figure 8*M*) will be the cladistically basal species in these two triplets after more data are brought to bear.

The failure to find a single vicariant pattern for Maui Nui that fits all repetitions of areas across the taxon-area cladogram should not be construed as a weakness of the cladistic biogeographic method. Without a cladistic hypothesis of taxon relationships, no tests of any kind are possible. Moreover, the presentation of a single general pattern permits the search for deviants. Extinction, quantified by items of error, can account for disparities in how clades adhere to the general pattern. The means to test this sort of hypothesis include (1) showing that hypothesized "extinctions" really represent undiscovered taxa, and (2) generating more detailed distributional data that might allow us to recast our definition of areas of endemism at a scale appropriate to vicariant mechanisms. As shown above, extensive deviation from the general pattern costs numerous items of error, which can be objectively mitigated through adoption of an ad hoc dispersal hypothesis.

Changing the scale of areas of endemism will cause us to define different numbers of widespread species and change the number of times particular areas are redundantly represented on the taxon-area cladogram. For example, the West Maui mountains include the isolated block called Līhau that is topped with a forest no more than 0.65 km^2 in area. This isolated forest is home to seven species of Platynini, one of which is known only from this summit. Based on the definition of Platnick and Nelson (1978), this patch of forest could be defined as an area of endemism. Recognizing Līhau in an analysis would result in its placement seven times on the taxon-area cladogram, but the 10 other West Maui species would lack this area. Thus Līhau's relationships would be based on phylogenetic relationships of less than half the known West

Maui fauna. Moreover, the six Līhau species found at other sites would be treated as widespread species: some distributed over discordant sets of sampled localities on the volcano (e.g., Hanaʻula, Puʻu Kukui, and ʻEke Crater). To date, a comparative approach whereby the scale of endemism is modulated in repeated analyses of the same aggregate area has not been done. Given comprehensive sampling of Maui Nui localities, the rampant endemism of platynine carabids could allow such an attempt. The goal would be to find an optimal mix of precise areas and informative endemism. Moreover, the stability of hypotheses of area relationship throughout such modulation should be investigated.

Corroborating elevational habitat shifts as the overriding factor in the isolation and persistence of peripheral populations also requires a greater understanding of the distributional aspects of all species. This scenario assumes that populational processes operating at the level of individual demes work to produce shifts in occupied habitat. Extinction of only a portion of species' populations may be the cause of discordant vicariance. Therefore, a sound understanding of how selection and limited effective population size can influence these species is essential.

Bringing more character data to bear can improve our confidence in the phylogenetic relationships of the species, thereby eliminating mistakes in homology or polarity assessment as possible causes for disparate patterns. Corroboration using infraspecific divergence data eliminates the problem of extinct taxa, though it can never overcome the possibility that repeated bouts of gene exchange have replaced older patterns of area relationship with newer ones. Finally, addition of information from other taxa endemic to the volcanoes of Maui Nui can test both the general hypothesis of area relationships and the elevational generalization made here.

Conclusions

The diverse Hawaiian platynine species swarm provides abundant information for generating a general biogeographic hypothesis and then testing repeated congruent and discordant patterns. Contrary to older arguments about the random nature of dispersal (e.g., Rosen 1978), in this study the dispersal patterns across the Island chain are more congruent than the vicariant patterns on Maui Nui. This is in part because of the high cost established (i.e., relatively large numbers of items of error) for the adoption of an ad hoc dispersal hypothesis. Also, the areas of endemism used to test dispersal are of greater scale than the component volcanoes of Maui Nui used in the vicariance analysis.

The establishment of a biogeographic research program that distinguishes common and distinct patterns followed by a search for common and distinct causation (Minaka 1987) is an advance over other methods that attempt to restrict causation before identifying patterns. Items of error analysis provides an objective means to accomplish this, permitting the integration of dispersal and vicariance, a goal propounded by a variety of biogeographers (Croizat 1962, Thornton 1983, Stace 1989, Grehan 1990, Briggs 1991). Nonetheless, a common dispersal pattern may still be based on independent dispersal events, as shown for Big Island colonization by platynine carabids. Conversely, a common vicariant history of areas may be experienced differently by resident taxa facing populational extinction and habitat alterations operating on a fine geographic scale.

constructive reviews that helped improve the manuscript.

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