SPECIATION IN HAWAIIAN ANGIOSPERM LINEAGES: CAUSE, CONSEQUENCE, AND MODE

JONATHAN P. PRICE[1] AND WARREN L. WAGNER

Department of Botany, MRC-166, National Museum of Natural History, Smithsonian Institution, P.O. Box 37102,
Washington, D.C. 20013-7012
[1]*E-mail: price.jonathan@nmnh.si.edu*

Abstract.—The biota of Hawaiian Islands is derived entirely from long distance dispersal, often followed by in situ speciation. Species descended from each colonist constitute monophyletic lineages that have diverged to varying degrees under similar spatial and temporal constraints. We partitioned the Hawaiian angiosperm flora into lineages and assessed morphological, ecological, and biogeographic characteristics to examine their relationships to variation in species number (*S*). Lineages with external bird dispersal (through adhesion) were significantly more species-rich than those with abiotic dispersal, but only weakly more species-rich than lineages with internal bird dispersal (involving fleshy fruits). Pollination mode and growth form (woody vs. herbaceous) had no significant effect on *S,* in contrast to studies of angiosperm families. *S* relates positively to the geographic and ecological range size of whole lineages, but negatively to local abundance and mean range sizes of constituent species. Species-rich lineages represent a large proportion of major adaptive shifts, although this appears to be an artifact of having more species. Examination of 52 sister species pairs in numerous lineages provides evidence for allopatric (including peripheral isolates) and parapatric (ecological) modes, with 15 cases of each. Although postspeciational dispersal may obscure these modes in many of the remaining cases, instances of sympatric and hybrid speciation are also discussed. Because speciation is both a consequence and a cause of ecological and biogeographic traits, speciation mode may be integral to relationships between traits. We discuss the role of speciation in shaping the regional species pool.

Key words.—Adaptive radiation, dispersal, Hawaii, pollination, speciation.

Received September 2, 2003.   Accepted July 22, 2004.

In fact, the evolution theory could hardly find a more favorable field for observation than an isolated island-group in mid-ocean, large enough to have produced a number of original forms and at the same time so diversified in conditions of temperature, humidity, and atmospheric currents as to admit an extraordinary development in nearly every direction of vegetable morphology, uninfluenced by intercrossing with foreign elements.
(Hillebrand 1888, p. xxix)

Variation in the degree of diversification, the net balance of speciation and extinction, among groups of organisms has generated considerable interest because it forges a crucial bond between evolutionary processes and biodiversity. The striking diversity of angiosperms has been attributed to the development of a suite of characters putatively responsible for elevating speciation rates or depressing extinction rates (Stebbins 1981; Burger 1981). Animal-mediated dispersal and pollination presumably allow plants to establish scattered populations favorable to speciation (Regal 1977; Burger 1981; Crepet 1984) and to maintain gene flow in such populations, reducing the probability of extinction (Raven 1977). Initial tests of these hypotheses were equivocal: some downplayed reproductive mutualisms (Herrera 1989; Midgely and Bond 1991) and others maintained their importance (Fleming 1990). Herbaceous growth form may also promote rapid evolution through short generation times (Tiffney 1986) and the ability to specialize in a variety of ephemeral environments (Levin 1984; Niklas et al. 1985). Comparisons of angiosperm families have concentrated on dispersal mode (abiotic vs. biotic), pollination mode (abiotic vs. biotic), and growth form (woody vs. herbaceous) as explaining variation in species number (*S*) or rate of diversification (*R*), defined by Stanley (1979) as the net rate of increase in the number of species.

Eriksson and Bremer (1992) calculated *R* for angiosperm families based on ages from the fossil record and found that it was higher among animal-pollinated and herbaceous families, but not among animal-dispersed families. After establishing that estimates of *R* may have been unreliable, Ricklefs and Renner (1994) found that animal pollination and herbaceous growth form were associated with higher *S,* but that animal dispersal was not. However, Tiffney and Mazer (1995) found that animal dispersal associated strongly with greater *S* in woody plant families, and hypothesized that diversification was achieved through lower extinction rates, rather than through elevated speciation rates. Examining only independent monophyletic groups of angiosperms (rather than potentially paraphyletic or polyphyletic groups), Dodd et al. (1999) also found support for an association of high *S* with animal pollination and herbaceous growth form, but not animal dispersal.

Significant obstacles to studies linking species-level characteristics and diversification remain. Because the groups analyzed in such studies are broadly delimited (e.g. families), general classifications of species traits are treated as ''typical'' or ''dominant'' within the group, without a quantitative assessment of the constituent species of individual lineages. Analyzing intensively studied monophyletic groups permits a more quantitative approach that incorporates more specific categorization of individual species. Despite consideration of monophyletic groups in examining variation in *S* (Dodd et al. 1999), some uncertainties remain in identifying relationships among clades at the broadest scale within the angiosperms (Soltis et al. 1997, 2000; APG II 2003). Perhaps most importantly, the causes and consequences of speciation can be difficult to distinguish from each other in these studies. Ricklefs and Renner (1994) attributed greater *S* to ''evolu-
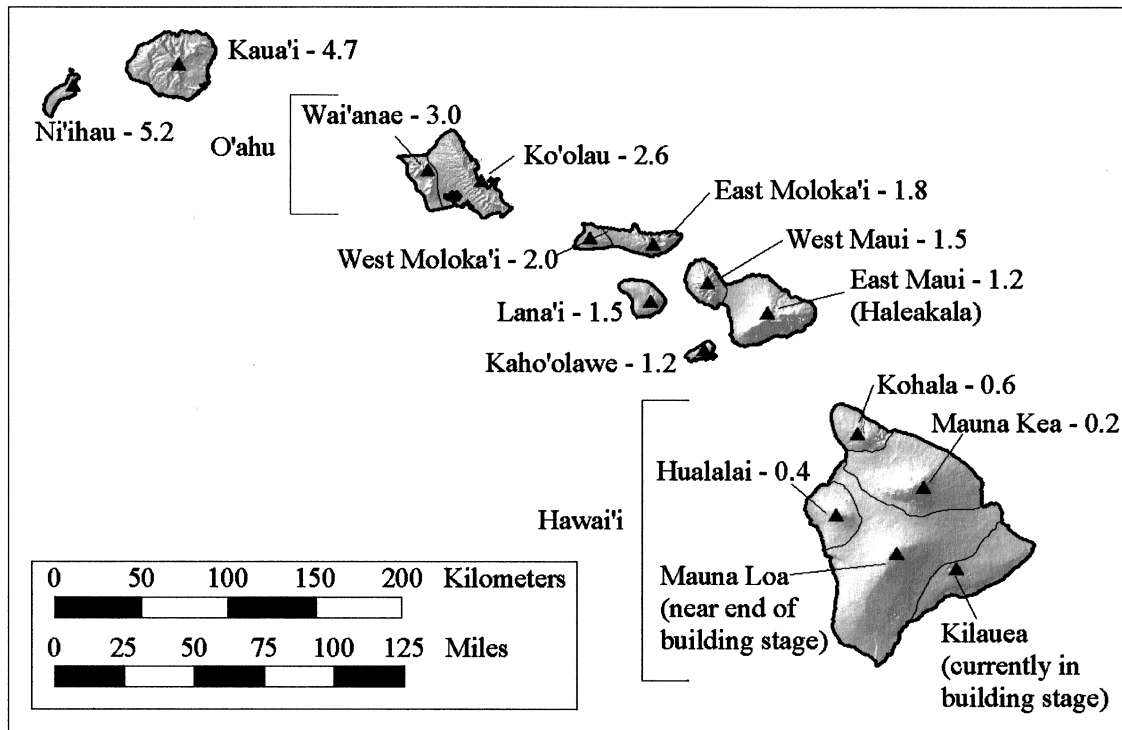
FIG. 1. Map of main Hawaiian Islands. Individual volcanoes are shown in shaded relief and boundaries are demarcated. Ages of volcanoes given in millions of years are from Clague (1996).

tionary flexibility'' whereby the possession of variable traits led to the generation of more species than the possession of a single trait. However, whether this was the actual cause of the diversification or a probabilistic consequence of having more species was not testable with their data. Dodd et al. (1999), in a test of this hypothesis, found no support for a causal relationship and considered variable traits in large families a consequence of diversification. Other potential consequences of diversification would be difficult to assess for angiosperm families. For example, geographic range size, which has been negatively associated with both S and R in mollusks (Jablonski and Roy 2003), would be difficult to examine in angiosperm families due to the lack of availability of such data for very large numbers of species. Finally, modes of speciation (allopatric, parapatric, or sympatric) have not been explicitly examined and are likely variable even within angiosperm families, thus their contribution to general patterns remains unclear.

The Hawaiian angiosperm flora exhibits conditions that permit a comprehensive exploration of species proliferation in monophyletic groups. Because the islands arose de novo in the mid-Pacific (Fig. 1), they have always been isolated from potential source areas and therefore have a flora derived entirely from colonization followed by in situ speciation (Fosberg 1948). The geologic youth of the current high islands of the archipelago places limits on the time available for diversification (Price and Clague 2002). The descendants of each colonization event therefore constitute monophyletic lineages that evolved under similar spatial and temporal constraints. The angiosperm flora is the best-studied major group of Hawaiian organisms, and ecological, morphological, and

biogeographic traits can be assessed for virtually all species (Carlquist 1974; Sakai et al. 1995a,b, 2002; Wagner et al. 1999). We examine relationships between traits of these colonist lineages and variation in S in more detail than has been possible in studies of angiosperm families. Specifically, we address the influence of multiple types of pollination and dispersal mode, woody verses herbaceous growth form, population structure, and the evolution of major morphological change on species proliferation. Additionally we examine the relationship between proliferation and the geographic and ecological range size of whole lineages and constituent species, respectively. We also examine sister species pairs across lineages to identify important modes of speciation. Although these analyses are restricted to a single geographic region of modest diversity, the interrelationships of traits associated with speciation explored here may also apply more broadly.

METHODS

Grouping Species into Lineages

Fosberg's (1948) assessment of the origins, relationships, and number of colonization events that gave rise to the Hawaiian flora was followed by studies of dispersal mechanisms and evolutionary trends (Carlquist 1974). A recent flora (Wagner et al. 1990) and an updated edition with supplement (Wagner et al. 1999) present a species concept using uniform taxonomic criteria across the whole flora. Additional evolutionary biogeographic studies (Wagner and Funk 1995) and a revised assessment of colonization events (Sakai et al. 1995a) provide further synthesis of phylogenetic affiliations. This series of studies has grouped species into lineages de-

TABLE 1. Published phylogenies for Hawaiian plant lineages. Ages representing time of diversification of Hawaiian lineages and given in millions of years (Ma) are from external phylogenies. If a range of ages was given, median values were used for analysis. External phylogeny indicates examination of relationships of Hawaiian taxa to outgroups. Internal phylogenies indicate examination of relationships among most Hawaiian taxa.

Lineage	Family	S	Age (Ma)	Reference for external phylogeny	Reference for internal phylogeny
Lobelioideae	Campanulaceae	125	16	Givnish et al. 1996	Givnish et al. 1995, 1996
Hawaiian mints	Lamiaceae	57	5.0	Lindqvist and Albert 2002	Lindqvist et al. 2003
Schiedea	Caryophyllaceae	32	—	Nepokroeff et al. 2004	Nepokroeff et al. 2004; Soltis et al. 1996
Silversword alliance	Asteraceae	30	5.1	Baldwin and Sanderson 1998	Baldwin and Robichaux 1995; B.G. Baldwin, unpubl. data
Hedyotis	Rubiaceae	20	—	—	Motley et al. 1998
Bidens	Asteraceae	19	—	Ganders et al. 2000	—
Labordia	Loganiaceae	16	—	Motley and Carr 1998	—
Psychotria	Rubiaceae	11	—	Nepokroeff et al. 2003	Nepokroeff et al. 2003
Tetramolopium	Asteraceae	11	0.65	Lowrey 1995	Lowrey 1995
Pittosporum	Pittosporaceae	10	—	Gemmill et al. 2002	—
Munroidendron, Tetraplasandra, Reynoldsia	Araliaceae	9	—	Costello and Motley 2001	Costello and Motley 2001
Hibiscadelphus	Malvaceae	7	—	—	Funk and Wagner 1995
Scaevola (3 lineages)	Goodeniaceae	6,1,1	—	Howarth et al. 2003	D.G. Howarth and D.A. Baum, unpubl. ms.
Viola	Violaceae	6	3.7	Ballard and Sytsma 2000	Ballard and Sytsma 2000
Metrosideros	Myrtaceae	5	1.0	Wright et al. 2001	—
Geranium	Geraniaceae	5	2	Pax et al. 1997	Pax et al. 1997; Funk and Wagner 1995
Korthalsella	Viscaceae	5	—	Molvray et al. 1999	Molvray et al. 1999
Cheirodendron	Araliaceae	5	—	Plunkett and Lowry 2001	—
Kokia	Malvaceae	4	3	Seelanan et al. 1997	Funk and Wagner 1995
Hesperomannia	Asteraceae	3	3.36	Kim et al. 1998	Funk and Wagner 1995
Remya	Asteraceae	3	—	—	Funk and Wagner 1995
Vaccineum	Ericaceae	3	—	Powell and Kron 2002	—
Gunnera	Gunneraceae	2	—	Wanntorp and Wanntorp 2003	—
Rubus (2 lineages)	Rosaceae	1,1	—	Howarth et al. 1998; Alice and Campbell 1999	—
Kanaloa	Fabaceae	1	—	Hughes et al. 2003	—
Hillebrandia	Begoniaceae	1	—	Clement et al. 2004	—
Euphorbia	Euphorbiaceae	1	—	Steinmann and Porter 2002	—
Broussaissia	Hydrangeaceae	1	—	Hufford et al. 2001	—

scended from each putative colonist ancestor by identifying shared morphological traits unique to taxa in the Hawaiian Islands, and in many cases relationships are confirmed by phylogenetic studies. Lineages range in taxonomic scale from containing a single species to encompassing multiple genera. Twenty-eight lineages have been verified as monophyletic groups in phylogenetic analyses that include outgroups, and 18 have undergone detailed phylogenetic analysis within the Hawaiian Islands (see Table 1). It is possible that some lineages have descended from two or more colonization events followed by reticulate evolution within the Hawaiian Islands, however to date no cases have been analyzed in detail to support this.

Despite the development of alternative species concepts based on phylogenetic tree topology (Wiley 1981; Mishler and Donoghue 1982; Cracraft 1989), species described from morphology represent a more consistent concept for ecological and biogeographic analyses, make use of more types of data, and apply to a much wider array of taxa (Kelt and Brown 2000). Nonetheless, in cases where phylogenetic data are available (see Table 1), phylogenetic and morphological species concepts have usually proven to be congruent. We there-

fore follow previous studies of diversification in using species number (S) as the measure of diversity with which to compare lineages. As currently delimited (Wagner et al. 1999, 2001), the native angiosperm flora of the eight main Hawaiian Islands consists of 1004 species in 263 presumed lineages. Lineages range in S from one to 125; of the 172 single-species lineages, 88 consist of indigenous nonendemic species (with extra-Hawaiian ranges) that have not evolved strictly within the Hawaiian Islands. We therefore omitted these from consideration, focusing on the 175 lineages that have evolved in situ.

We assessed traits that characterize all members of a lineage, its colonist ancestor, or the most common derived trait of its constituent species. For most variables, all species in a lineage shared a given trait with the presumed colonist ancestor. In other lineages, however, some species have traits other than that of the presumed colonist ancestor, indicating a character shift. In such cases, if the trait associated with the shift is that most frequent in the lineage, we presume that this trait is more closely associated with speciation events than was the trait of the colonist ancestor. We therefore used the most frequent trait among constituent species in order to

characterize the lineage as a whole. This differs from analyses of Ricklefs and Renner (1994), which included a category for plant families with variable traits. We treat lineages with multiple traits and those that differ from presumed ancestors in the section on adaptive shifts, drawing as much as possible from available phylogenies. For continuous variables that measure traits of species, we calculated the mean for all species in each lineage. A brief summary of each variable follows, including methods of classification or measurement, and sources of data. Separating traits that may drive speciation from those that may result from it is not straightforward (Chown 1997), and therefore we consider both possibilities when assessing potential relationships of traits to diversification.

Classification Variables

Dispersal mode

Considering that speciation in the Hawaiian Islands may frequently be initiated as founder events between islands (Carson 1983), it is best to view dispersability as it pertains to water barriers. Because birds are the sole animal fruit dispersers in the Hawaiian Islands, a limited and comparable set of potential dispersers exists. Higher dispersability associated with bird dispersal might increase the frequency of founder events, facilitating diversification (Stebbins 1981). However, if frugivorous birds are reluctant to cross such barriers (Diamond 1973; Yumoto 1999) then fleshy-fruited plants might be expected to have lower dispersability and gene flow (Eriksson and Bremer 1992; Givnish et al. 1995; Givnish 1998), leading to allopatric speciation (Mayr 1963). Smith (2001) found support for greater species diversity of fleshy-fruited clades compared with related dry-fruited clades. However, many plants lacking fleshy fruit colonized the Hawaiian Islands and presumably dispersed between them via transport by external adhesion to birds (Carlquist 1970), thus bird behavior may influence lineages with this type of dispersal as well.

Carlquist (1974) and Sakai et al. (1995a) hypothesized the mode of dispersal for the ancestors of each lineage to colonize the Hawaiian Islands. Although detailed dispersal studies are available for relatively few Hawaiian plants, the modest size of the flora and the detail in which species are known permits a more specific categorization of dispersal mode than those used in other studies. All species were categorized according to three major dispersal modes following Sakai et al. (1995a) with modification: abiotic dispersal, internal bird dispersal, and external bird dispersal. Abiotic dispersal in most cases refers to oceanic drift either with floating diaspores or attached to branches, although it also includes five cases of wind dispersal. Internal bird dispersal (endozoochory) includes species with fleshy fruits or accessory tissues that are actively sought by birds. Four lineages (*Korthalsella* [Viscaceae] and three lineages of *Cyrtandra* [Gesneriaceae]) have fruits with fleshy tissue that serves as an adhesive rather than as a food source that is actively sought by birds, and are therefore classified in the external bird dispersal mode. Although granivorous birds may move the seeds of some species (dyszoochory), these are typically large seeds unlikely to be ingested without damage. Because we assume that such seeds

are moved only short distances and cross water barriers via abiotic means (typically oceanic drift), they are not included in the internal mode. External bird dispersal (epizoochory) includes species with seeds having mucilage, barbs, or other attaching mechanisms, or with small seeds likely to embed in mud on birds' feet. We made the distinction between internal and external bird dispersal to examine whether these modes differ in dispersability. In species where more than one mode may be possible, we chose the mode we considered to occur most commonly based on morphological characters. The most frequent dispersal mode for species was then attributed to each lineage.

Pollination mode

Biotic pollination promotes a population structure favorable to fine-scale niche partitioning and scattered populations favoring speciation (Crepet 1984). Differences between bird and insect pollination are worthy of examination, because bird pollination, especially by endemic Hawaiian honeycreepers and formerly Hawaiian honeyeaters (now extinct), has been attributed to diversification of Hawaiian plant lineages (Carlquist 1974; Givnish et al. 1995; Givnish 1998; Lindqvist et al. 2003).

We categorized species according to the most likely pollination mode based on floral morphology, and lineages were categorized according to the most frequent pollination mode of constituent species (modified from Sakai et al. 1995a). In species where more than one mode is possible, the most likely mode was chosen. In most cases, all species in a lineage share the same pollination mode; the implications of lineages that include species with different modes are discussed in the section on adaptive shifts. Unlike previous studies comparing abiotic to biotic pollination (Eriksson and Bremer 1992; Ricklefs and Renner 1994; Dodd et al. 1999), a detailed species-level assessment here permits recognition of three pollination modes: insect, bird, and abiotic (wind- and self-pollination). Facultative autogamy occurs in many species of Hawaiian plants, including lobelioids (Carlquist 1974), and others may be cryptically self-pollinating. However, obligate autogamy, as far as known, is not the predominant pollination mode of any lineage.

Growth form

Herbaceous taxa may exhibit higher speciation rates due to short generation times (Tiffney 1986) and specialization in ephemeral habitats (Levin 1984; Niklas et al. 1985). We assessed whether species were herbaceous or woody following Sakai et al. (2002) and categorized lineages according to the status of the majority of constituent species. One hundred and five lineages were considered primarily woody, and 70 were considered primarily herbaceous. It is worth noting that only 19 Hawaiian species are strictly annuals, and that perennial herbaceous species may be long-lived. We address the proposition that several lineages evolved a woody habit after colonizing the Hawaiian Islands (Carlquist 1970) in the section dealing with adaptive shifts.

Population density

Population structure has long been linked to speciation processes in several ways. Mayr (1963) and Stanley (1979) argued that species with poor dispersability, and consequently narrow geographic distribution and sparse populations, should have higher speciation rates than highly dispersable species with broad distributions and dense populations. Stanley (1986) linked local ecological condition to speciation by hypothesizing that species whose population density is driven down by ecological interactions are prone to speciation in what he dubbed the ''fission effect.'' Gavrilets et al. (2000) provide theoretical support for a scenario in which sparse populations, between which propagule dispersal probabilities are low, cannot maintain gene flow across a geographic range, thus favoring speciation. However, some species may have pollen dispersal that is effective enough to sustain gene flow even in scattered or sparse populations where propagules disperse infrequently.

Unfortunately, acquiring data on the local population density of all species at various locations within their ranges would prove extraordinarily difficult, particularly given the degraded and modified status of many Hawaiian ecosystems (Kirch 1982; Cuddihy and Stone 1990). In addition, most quantitative vegetation analyses have only dealt with mesic and wet forest communities and have quantified cover rather than population density of species. As a simple way to assess local population density, we determined 123 species considered common, dominant, abundant, or important by Gagné and Cuddihy (1990) as having dense populations and the remaining species as having sparse populations. Species with dense populations include a variety of growth forms representing different vegetation layers, and not simply canopy tree species. Thirty-five of those with dense populations were among the 88 native species not restricted in distribution to the Hawaiian Islands and therefore not analyzed here. We then characterized lineages as having typically dense populations if at least half of their species categorized as such. We classified 28 endemic lineages as typically having dense populations and the remaining 147 as having comparatively sparse populations.

Adaptive shifts

There are several ways to view adaptive shifts with respect to proliferation. Ricklefs and Renner (1994) found that plant families with variable dispersal mode, pollination mode, or degree of woodiness have more species than those that are not variable, which they interpreted as ''evolutionary flexibility,'' promoting high rates of speciation. Dodd et al. (1999), however, in a more direct test of whether multiple character states within a phylogenetic group were a cause or consequence of speciation, found no support for the hypothesis of evolutionary flexibility. It is more probable that lineages with more species are statistically more likely to experience a change in one of these traits. Another view of the relationship between speciation (cladogenesis) and directional evolution (anagenesis) is available from Eldredge and Gould's (1972) idea that many evolutionary novelties originate suddenly in association with speciation events, in what they dubbed ''punctuated equilibrium.''

Several types of shift in ecological, reproductive, and morphological character states have occurred in Hawaiian angiosperm lineages (Carlquist 1974; Wagner and Funk 1995). We determined a lineage to exhibit an adaptive shift either if it contains species with different morphological characteristics associated with habit, pollination biology, or dispersal mode, or if its species differ in such characteristics from the presumed colonist ancestor or closest relative following Sakai et al. (1995a) with adjustments based on recent phylogenetic studies.

A prominent type of adaptive shift on oceanic islands is that from herbaceous to woody habit (Carlquist 1970). We determined that ten lineages have experienced a shift from a presumably herbaceous ancestor toward a woody habit, and another two toward a herbaceous habit from a woody ancestor. Seven of these are confirmed by phylogenetic analyses (Lowrey 1995; Pax et al. 1997; Baldwin and Sanderson 1998; Ganders et al. 2000; Ballard and Sytsma 2000; Lindqvist and Albert 2002; Nepokroeff et al. 2004), and the rest were assessed from comparison to putative colonist ancestors (Sakai et. al 1995a). Studies of four lineages (Givnish et al. 1995; Givnish 1998; Lindqvist et al. 2003; Motley et al. 1998; Nepokroeff et al. 2004) have documented shifts from external to internal bird dispersal through the autochthonous evolution of fleshy fruit. In addition, some members of the silversword alliance have an expanded pappus adapted for wind dispersal, and some species of *Bidens* have seeds with greatly reduced barbs compared to ancestral forms (Carlquist 1970). These modifications constitute shifts toward abiotic dispersal from external bird dispersal. Carlquist (1970) noted an evolutionary trend toward bird pollination in several Hawaiian groups. Fourteen lineages experienced a shift in pollination syndrome from the presumed ancestral state: 11 from insect to bird pollination (Givnish et al. 1996; Pax et al. 1997; Seelanan et al. 1997; Lindqvist et al. 2003), one from bird to abiotic (self) pollination, one from bird to insect pollination, and one lineage, *Schiedea*, has experienced insect-to-bird and insect-to-abiotic shifts (Nepokroeff et al. 2004). In total, 22 lineages have experienced some kind of shift, four of these (*Geranium*, silversword alliance, Hawaiian mints, and Lobelioidae) with two types of shift, and three (*Bidens*, *Hedyotis*, and *Schiedea*) with all three types. In some cases, species resulting from a shift make up small proportions of a given lineage, and thus their trait does not characterize it.

Continuous Variables

Range size of species

Because geographic speciation typically results in range subdivision (Glazier 1987), and provided this speciation mode occurs comparatively frequently, species-rich lineages should have species with smaller range sizes. Supporting this prediction, Jablonski and Roy (2003) established a negative relationship between range size and both speciation rate and net species production in mollusk lineages.

We used a database of the geographic and ecological distributions of Hawaiian angiosperm species (Price 2004) to determine the ranges of all species for which data were available. We measured geographic range size as the number of volcanic mountains on which the species is present. The fif-

teen volcanoes of the eight high islands have distinct geologic and geomorphologic boundaries (Fig. 1), and the presence of species within these was determined from herbarium specimens, published records, fieldwork, and other sources; although there is variation in available habitat among islands and volcanoes, most volcanoes have a range of habitats (Price 2004). For each lineage, the mean geographic range size of constituent species characterized the lineage. Four extinct species for which volcano distribution could not be determined due to poor collecting information were not included when calculating means.

Another outcome of some types of speciation may be greater levels of ecological specialization among species in certain lineages. If parapatric speciation resulting from divergent selection along a habitat gradient were important in lineage diversification, we expect that species in large lineages should have narrow ecological ranges. We also might expect that speciation caused by divergence of a peripheral isolate from the main population (Mayr 1963) may result in numerous habitat-restricted species. Sympatric speciation (particularly the result of localized polyploidy or hybridization) may also generate species with narrow habitat ranges.

The Hawaiian Islands include a startling range of habitats varying greatly in temperature and mean annual precipitation (MAP). The aforementioned database also indicates in which of five major habitat zones each species has been recorded. These zones as determined from Gagné and Cuddihy (1990) include coastal, dry (<1200 mm MAP), mesic (1200–2500 mm MAP), wet (>2500 mm MAP), and subalpine/alpine (where frequent frost may occur). We determined the habitat range size of each species as the number of major habitat types within which it has been recorded. For each lineage, the mean habitat range size of constituent species characterized the lineage. Twelve extinct species for which habitat distribution could not be determined due to poor collecting information were not included when calculating these means.

The range of elevation occupied by a species is another measure of its degree of specialization. The Hawaiian Islands range from sea level to over 4000 m elevation, with six islands and 11 volcanoes exceeding 1000 m elevation. We determined the elevational range size of each species as the difference between its upper and lower limit (in meters) from the previously described data (Price 2004). For each lineage, the mean elevational range size of constituent species characterized the lineage. Thirty-six extinct species collected at unknown elevation were not included when calculating means.

Range size of lineage

In contrast with the range sizes of individual species, the geographic range size of a lineage as a whole may relate to speciation differently, reflecting both dispersal ability and ecological tolerances. If dispersability is a limiting factor, lineages with larger geographic ranges and better developed dispersal ability may be more likely to speciate because they are more likely to form isolated populations and their ranges are more likely to be interrupted by a barrier (Snow 1981; Vermeij 1987; Bleiweiss 1990; Brooks and McLennan 1993). Alternatively, wide-ranging lineages may possess dispersa-

bility that also leads to a high level of gene flow that suppresses speciation.

Presumably, after a founder colonizes an island in the archipelago, its progeny disperse to other islands, sometimes with speciation occurring in the process. In many cases, a given lineage is present only in a subset of available islands. This may occur when there is not appropriate habitat for the lineage on some islands, as is the case, for example, for subalpine taxa that are restricted to the higher, younger islands of Maui and Hawai'i. Alternatively, a lineage may not have had sufficient time since colonization to disperse to all islands, particularly if it has limited dispersal ability. These two possibilities are not mutually exclusive: a taxon could colonize the archipelago and be restricted to habitats available only on some islands, but may require time to evolve traits necessary to colonize other islands. Although all lineages operate under the temporal and spatial constraints of the archipelago as a whole, they respond to further limitations on an individual basis. Lineages that are less widespread are thus restricted by either dispersal or habitat limitation. Using the ranges of constituent species, we compiled the overall geographic range size of each lineage as a whole.

The range of climatic habitats a lineage inhabits may also relate to the degree to which it diversifies. When a plant lineage occupies a wider range of environments, it may be more likely to diversify (Ricklefs and Renner 1994). On the other hand, parapatric (ecological) speciation associated with differentiation along a habitat gradient (Endler 1977), and particularly adaptive radiation associated with divergent selection (Schluter 2000), may permit newly forming species to adapt to habitats not available to parent species. In such cases, the speciation process may widen the overall ecological range of the whole lineage. Species habitat ranges were compiled to measure the habitat range size of each lineage. Another measure of the ecological range of a species is the breadth of elevations at which it exists. We compiled the elevational range size of each lineage from species data.

Lineage age

Lineages of long standing in the Hawaiian Islands may be expected to contain more species if speciation rates are similar to those of younger lineages (Simon 1987; Carson and Clague 1995). Islands suitable for angiosperm colonization have been available continuously for about 30 million years (Clague 1996). However, a period with relatively small and widely spaced islands immediately preceded the formation of the present eight high islands, thus limiting transfer of biota from older islands (to the northwest) and confining most colonization from extra-Hawaiian sources and subsequent radiation of lineages to the past five million years (Price and Clague 2002). Because the Hawaiian Islands have been the focus of considerable evolutionary research, numerous age estimates are available for a variety of taxa and confirm this hypothesis. We used age estimates (all but one of which are molecular) for nine plant lineages (included in Table 1) to test whether lineage age correlates positively with the number of species. For a detailed discussion of the methods and assumptions of age estimates, see Price and Clague (2002). We

also calculated R as specified by Stanley (1979) for comparison.

Associations between Classification Variables

We investigated potential associations between pairs of five classification variables (dispersal mode, pollination mode, growth form, population density, adaptive shift) using two-way tables to establish whether traits were independently distributed. Because some cells in several tests had fewer than five lineages, we tested for homogeneity using a Monte Carlo contingency table test (Engels 1988) using 100,000 randomizations, rather than chi-squared tests. Several two-way combinations of classification variables exhibited nonindependent distributions. External bird dispersal, abiotic pollination, herbaceous growth form, and the absence of an adaptive shift were all positively associated. The 16 lineages in the grass family (Poaceae) and the 13 lineages in the sedge family (Cyperaceae) together made up the majority of each two-way combination of these traits. Despite their independence within the Hawaiian Islands, this consistent set of traits is clearly the result of phylogenetic relationships at the family level predating arrival to the Hawaiian Islands, making these lineages arguably nonindependent. Other families include large numbers of lineages: Asteraceae (11), Fabaceae (10), Malvaceae (8), and Rubiaceae (8). All of these families, however, contain lineages with different traits in at least two of three morphological categories (dispersal mode, pollination mode, growth form), so the relationship between their traits is at least partially independent. Because the Poaceae and Cyperaceae weight analyses with traits that were not derived independently, we performed all further analyses without the lineages from these two families ($N = 146$). We re-analyzed all two-way combinations of classification variables to determine which combinations were nonindependently distributed.

Correlation of Continuous Variables

Several continuous variables were not distributed normally. After removal of the Poaceae and Cyperaceae, 65 of 146 lineages contained a single species, and S was thus strongly right-skewed. We therefore log-transformed these values; however, the resulting distribution was still skewed, albeit less strongly. Similarly, all three measures of mean species range size were right-skewed with most lineages typified by species with narrow geographic and ecological ranges; after log-transformation of species range sizes, mean values more closely approximated normal distributions. Measures of geographic and habitat ranges of whole lineages approximated normal distributions without log transformation. We subjected some combinations of continuous variables to correlation analysis in the program SYSTAT version 10.2 (SYSTAT Software, Richmond, CA 2002). S was examined against all measures of range size. For monotypic lineages, the mean of each species range size measure was the same as the corresponding whole lineage measure. We therefore did not examine measures of species means against measures of whole lineages because relationships between these variables are not always independent. We did, however, examine means of the three different measures against each other, and whole lineage measures against each other to determine the relationships between biogeographic and ecological characteristics of species and whole lineages, respectively.

Analysis of Variance of Continuous Variables

For each of the five classification variables (dispersal mode, pollination mode, growth form, population density, adaptive shift), we used one-way analysis of variance (ANOVA) in the program SYSTAT version 10.2 (SYSTAT Software, 2002) to examine variation in each of the six range size measures (lineage geographic, lineage habitat, lineage elevation, species geographic, species habitat, species elevation). We used the range size measure of whole lineages and the log-transformed mean of the range size measure of each species as dependent variables. This resulted in a total of 30 one-way ANOVAs. We performed a post-hoc Scheffé test to examine significant differences in range size among lineages with different traits.

We carried out a more detailed analysis for variation in S. We performed a two-way ANOVA in the program SAS (SAS Institute, Cary, NC, 2002) using $\log(S)$ as the dependent variable using each of the 10 two-way combinations of classification variables. Factors were treated as random. Because there were no significant interactions, we used one-way ANOVAs in the program SYSTAT version 10.2 (SYSTAT software, Inc. 2002) to examine the relationship of each classification variable to species number. We performed Scheffé tests to examine significant differences in means of $\log(S)$ between lineages with different traits.

Although ANOVA can determine whether lineages exhibiting an adaptive shift contain more species on average, it cannot determine whether this is due to some intrinsic trait of the lineage or is a statistical artifact of larger lineages containing more species, or more chances a novelty will emerge. Therefore, in addition to ANOVA, lineages were ranked from largest to smallest and divided into two groups representing approximately equal numbers of species. Thus, the two groups have equal probabilities per species of generating adaptive shifts. If there is some aspect of speciation within diverse lineages that relates to anagenetic change, then we expect that the group consisting of species-rich lineages should include more adaptive shifts than the group consisting of species-poor lineages.

Mode of Speciation

Studies of the geographic ranges of sister species have offered insights into the prevalence of different modes of speciation. Lynch (1989) determined that vicariant speciation was the most common mode among 66 vertebrate taxa using the geographic ranges of sister species. Chesser and Zink (1994), using Lynch's method, found an inordinately high rate of sympatric speciation in 44 bird lineages, and concluded that postspeciational dispersal (due to high vagility of avian taxa) brought species that had likely diverged allopatrically into sympatry. Barraclough and Vogler (2000) determined the predominant mode of speciation was allopatric from peripheral isolates, but that postspeciational dispersal clouded the pattern, particularly with older speciation events.

TABLE 2. Relationships among classification variables. Numbers of lineages with each two-way combination of traits are given. Probabilities from Monte Carlo randomizations are given for each combination. Bonferroni-adjusted significance levels denoted by asterisks ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$). $N = 146$ (Poaceae and Cyperaceae excluded).

		Pollination mode			Growth form		Population density		Adaptive shift	
		Abiotic	Insect	Bird	Herbaceous	Woody	Sparse	Dense	No shift	Shift
Dispersal mode:	Abiotic	1	24	9	10	24	26	8	32	2
	Bird-external	9	38	1	23	25	44	4	37	11
	Bird-internal	7	51	6	8	56	53	11	55	9
			$P = 0.005$			$P < 0.001**$		$P = 0.178$		$P = 0.106$
Adaptive shift:	No shift	15	100	9	38	86	102	22		
	Shift	2	13	7	3	19	21	1		
			$P = 0.011$			$P = 0.125$		$P = 0.130$		
Population density:	Sparse	14	97	12	38	3				
	Dense	3	16	4	3	20				
			$P = 0.590$			$P = 0.086$				
Growth form:	Herbaceous	4	36	1						
	Woody	13	77	15						
			$P = 0.073$							

Twenty-six Hawaiian plant lineages contain exactly two species. An additional 26 pairs of sister species were determined from phylogenetic analyses including seven pairs in the Madiinae, or silversword alliance (Baldwin and Robichaux 1995; B.G. Baldwin, unpubl. data), six in *Schiedea* (Nepokroeff et al. 2004), two in one lineage of *Scaevola* (D. G. Howarth and D. A. Baum, unpubl. ms,), two in *Tetramolopium* (Lowery 1995), two in *Psychotria* (Nepokroeff et al. 2003), two in one lineage of the Araliaceae (Costello and Motley 2001), two in *Platydesma*, and one pair each in *Hesperomannia*, *Remya*, and *Kokia* (Wagner and Funk 1995). We examined three characteristics of all 53 sister species pairs that may suggest the mode of speciation. First, we calculated the degree of sympatry as the percentage of the range of the more restricted species that overlaps the range of the other species. Overlap in this case is the number of volcanoes on which both species are found divided by the range size (number of volcanoes occupied) of the smaller species. Following Lynch (1989), we considered species allopatric if overlap was less than 20% and sympatric if greater than that. However, if species co-exist on a given volcanic mountain, they may not be fully sympatric if they inhabit mostly or completely separate habitat types. We therefore calculated two similar indexes for the degree of overlap of habitat and elevation

range and considered ecological ranges dissimilar if either overlap index was less than 20%, and similar if both were greater than 20%. If sister species occupy different habitat types or elevations within the same volcano or set of volcanoes, this may suggest parapatric speciation through divergence along some gradient as detailed by Endler (1977). Finally, we determined the degree of range size symmetry. The criteria of Lynch (1989), which considered species ranges asymmetric if one species' range was less than 5% of that of the other, could not be applied because it was not possible to detect such a fine-scale difference with the coarse measure of range size used here. Using the criteria suggested by Chesser and Zink (1994), we considered range sizes asymmetric if one species' range was less than 25% of that of the other. This degree of asymmetry may be indicative of speciation in which one species is recently derived from a peripheral isolate. We examined numbers of lineages in each combination of possibilities with respect to degree of sympatry, habitat range similarity, and range size symmetry.

RESULTS

Associations between Classification Variables

Numbers of lineages sharing each possible two-way combination of traits (after removing grass and sedge lineages) are shown in Table 2. Only one combination of classification variables, dispersal mode and growth form, had significantly nonrandom distributions, with internal bird dispersal associating strongly with woody growth form.

Correlation of Continuous Variables

Geographic, habitat, and elevational range were significantly correlated with each other, for species and for lineages; $\log(S)$ was significantly positively correlated with the three range sizes for lineages and significantly negatively correlated with the three range sizes for species (Table 3). For the nine lineages with age estimates, there was a positive correlation between $\log(S)$ and age ($r = 0.79$, $P < 0.05$). Rate of diversification (R) varied between 0.41 for *Hesperomannia*

TABLE 3. Correlation matrix of continuous variables. Pearson's correlation coefficients are given with Bonferroni probabilities denoted by asterisks ($* P < 0.05$, $** P < 0.01$, $*** P < 0.001$). $N = 146$ (Poaceae and Cyperaceae excluded). (A) Relationships of $\log(S)$ and means of measures of species range size. (B) Relationships of $\log(S)$ and measures of whole lineage range size.

Geographic	Habitat	Elevation	
A. Means of species range sizes			
−0.643***	−0.370***	−0.265*	$\log(S)$
	0.581***	0.453***	geographic
		0.496***	habitat
B. Whole-lineage range sizes			
0.376***	0.563***	0.492***	$\log(S)$
	0.529***	0.547***	geographic
		0.702***	habitat

(Asteraceae) and 3.70 for *Tetramolopium* (Asteraceae). There was no significant correlation between log(S) and R.

Analysis of Variance of Continuous Variables

Measures of range size exhibited significant differences among certain classification variables (Table 4). Whole-lineage geographic range size was significantly larger in insect-pollinated lineages compared with bird-pollinated lineages, and in those with dense populations. Whole-lineage habitat and elevational range size were larger for lineages with both modes of bird dispersal compared with abiotic dispersal, and for lineages exhibiting an adaptive shift. All three measures of range size for species were greater in lineages with internal bird dispersal compared with external bird and abiotic dispersal. Lineages with dense populations also exhibited larger mean geographic and habitat range size for species. Finally, lineages exhibiting a shift had larger mean geographic range sizes for species.

Results of one-way ANOVA for each classification variable (Table 4) indicate several traits related to elevated species richness. Dispersal mode alone exhibits a significant effect, with log(S) being greater in lineages with external bird dispersal than in those with abiotic dispersal. There was no significance of pollination mode or growth form on log(S). Log(S) was larger for lineages with dense populations and those that experienced some sort of adaptive shift (Table 4). However, shifts were not distributed in large lineages disproportionate to their number of species: the most species-rich lineages (more than 16 species) had 16 shifts in 424 species, whereas smaller lineages (16 or fewer species) had 16 shifts in 427 species. Thus, the probability per species of an adaptive shift is not greater in larger lineages.

Mode of Speciation

Frequencies of different characteristics among the 52 sister species pairs are summarized in Figure 2. Fifteen were allopatric (mostly found on different volcanoes), of which only four had asymmetric ranges suggesting speciation from a peripheral isolate. Of the 15 allopatric species pairs, 13 were in similar habitats, whereas only two were in different habitats. Of sister species pairs mostly co-existing on the same volcanoes, 15 were mostly in nonoverlapping habitats, suggesting parapatric speciation. The remaining 22 lineages, those co-existing mostly on the same volcanoes and in the same habitats, are considered sympatric (not necessarily resulting from sympatric speciation). In all, 39 of the 52 species pairs had symmetric range sizes, according to the criteria. There were no notable differences in the frequencies of putative speciation modes between two-species and multi-species lineages, or between lineages with more or less than 10 species.

DISCUSSION

Relationships between characters may illuminate ecological processes, and the complex nature of dispersal in particular may inform the ecological context in which speciation occurs. Species in lineages with internal bird dispersal had larger geographic, habitat, and elevational range sizes than

those in lineages with other dispersal modes. The fact that birds actively seek out fleshy fruits may result in comparatively greater frequencies and distances of seed transport for species with this trait. This is bolstered by the proposition that frequency of colonization is positively related to dispersability. Dispersal modes in order of increasing dispersability would then be abiotic (34 colonists), external bird (50 colonists), and internal bird (62 colonists). Furthermore, if whole-lineage geographic range size is at least partly indicative of dispersability, then range size suggests the same order of increasing dispersability (although differences are not statistically significant). Because a large majority of lineages are primarily bird dispersed, the behavior of bird species, the size and nature of fruits and seeds, and other characteristics not examined here may result in considerable variation in dispersability among lineages with internal and external bird dispersal.

Lineages typified by dense populations have species with comparatively large geographic and habitat range size. This frequently observed positive relationship between population density and range size has been attributed to several potential causes. First, a sampling effect may exist in which species with sparse populations are less likely to be sampled throughout their range, giving the false appearance of a smaller range (Hanski et al. 1993). Brown (1984) asserted that species with larger geographic ranges were ecological generalists that could occupy a wide range of regional and local habitats. Hanski et al. (1993) provided a third hypothesis suggesting that the pattern is due to metapopulation dynamics in which species with greater dispersal ability are able to maintain dense local populations (Hanski 1991) and extend sink populations on the edges of their range. The latter two hypotheses are not mutually exclusive, and both may contribute to the relationship between population and biogeographic traits in the Hawaiian flora.

Lineages with external bird dispersal exhibited the highest species numbers. We propose that the tendency toward proliferation is due to the putative intermediate dispersability of such lineages. Species-rich lineages may have moderate dispersability that is effective enough to extend the geographic range of whole lineages, yet infrequent enough to depress levels of gene flow, the combination of which promotes frequent speciation (Vermeij 1987; Bleiweiss 1990). Thus, dispersability that is sufficient to colonize all major islands but not so much as to dampen diversification may explain the higher S seen in lineages with this mode.

Lineages that exhibit biotically mediated pollination were not significantly larger than those that do not, in disagreement with studies of angiosperm families that established a clear effect of pollination mode (Eriksson and Bremer 1992; Ricklefs and Renner 1994; Dodd et al. 1999). In fact, abiotically pollinated lineages exhibit considerable diversification compared with biotically pollinated lineages. Eight of the 17 abiotically pollinated lineages (47%) have more than one species compared with 57% for biotically pollinated lineages, and one wind-pollinated lineage of *Coprosma* (Rubiaceae) has radiated into 12 species.

In contrast to previous studies (Eriksson and Bremer 1992; Ricklefs and Renner 1994; Tiffney and Mazer 1995; Dodd et al. 1999), predominant growth form exhibited no clear

TABLE 4. ANOVA of continuous variables by classification variable. Columns indicate continuous (dependent) variables, rows indicate classification variables (factors). Degrees of freedom (df), sum of squares (SS), F-ratio (F), probabilities (P), and means are given for each analysis. Means of log-transformed variables have been back-transformed for comparison. Asterisk indicates traits associated with a greater value (for the continuous variable) than at least one other trait according to a post-hoc Scheffé test (P < 0.05). Poaceae and Cyperaceae excluded.

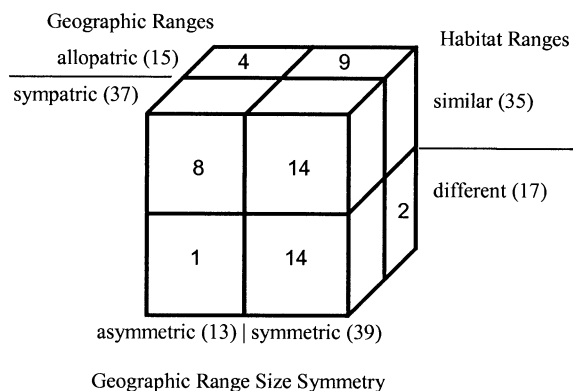| Classification variable	N	Lineage as a whole			Mean of species in lineage			
		Geographic range size	Habitat range size	Elevational range size	Geographic range size	Habitat range sizeq	Elevational range size	Species richness (S)
Dispersal mode:		df = 2; SS = 47.1; F = 1.8; P = 0.173	df = 2; SS = 14.3; F = 6.5; P = 0.002	df = 2; SS = 1.2e + 7; F = 10.1; P < 0.001	df = 2; SS = 0.9; F = 4.2; P = 0.017	df = 2; SS = 0.2; F = 6.1; P = 0.003	df = 2; SS = 3.6; F = 8.7; P < 0.001	df = 2; SS = 2.5; F = 5.9; P = 0.003
Abiotic	34	8.4	2.1	917	4.5	1.6	338.8	1.6
Bird-external	48	9.2	2.9*	1635*	3.1	1.6	476.4	3.7*
Bird-internal	64	9.9	2.9*	1563*	4.7*	2.0*	820.4*	2.4
Pollination mode:		df = 2; SS = 98.0; F = 6.5; P = 0.025	df = 2; SS = 1.5; F = 0.6; P = 0.523	df = 2; SS = 3 × 10⁶; F = 2.3; P = 0.108	df = 2; SS = 0.4; F = 1.9; P = 0.158	df = 2; SS = 0.01; F = 0.2; P = 0.786	df = 2; SS = 0.3; F = 0.7; P = 0.502	df = 2; SS = 0.5; F = 1.0; P = 0.366
Abiotic	17	9.0	2.6	1468	4.7	1.7	622.3	1.8
Bird	16	7.1	2.4	1029	2.9	1.7	415.0	2.4
Insect	113	9.7*	2.8	1490	4.2	1.8	574.1	2.7
Growth form:		df = 1; SS = 0.3; F = 0.02; P = 0.884	df = 1; SS = 2.9; F = 2.4; P = 0.120	df = 1; SS = 7 × 10⁵; F = 1.1; P = 0.287	df = 1; SS = 0.1; F = 1.3; P = 0.263	df = 1; SS = 0.04; F = 1.6; P = 0.203	df = 1; SS = 0.7; F = 3.2; P = 0.074	df = 1; SS = 0.3; F = 1.2; P = 0.272
Herbaceous	41	9.2	2.5	1321	4.6	1.7	430.5	2.2
Woody	105	9.3	2.8	1482	3.9	1.8	618.0	2.7
Population density:		df = 1; SS = 81.6; F = 6.3; P = 0.013	df = 1; SS = 0.02; F = 0.02; P = 0.898	df = 1; SS = 32,251; F = 0.05; P = 0.828	df = 1; SS = 2.3; F = 23.1; P < 0.001	df = 1; ss = 0.3; F = 14.8; P < 0.001	df = 1; SS = 0.7; F = 3.2; P = 0.074	df = 1; SS = 1.7; F = 7.6; P = 0.007
Dense	23	11.0*	2.7	1471	8.0*	2.3*	812.8	1.4
Sparse	123	9.0	2.7	1430	3.6	1.7	521.2	2.8*
Adaptive shift:		df = 1; SS = 6.4; F = 0.5; P = 0.491	df = 1; SS = 8.1; F = 7.2; P = 0.008	df = 1; SS = 3.5 × 10⁶; F = 5.4; P = 0.021	df = 1; SS = 1.6; F = 14.6; P < 0.001	df = 1; SS = 0.04; F = 1.8; P = 0.178	df = 1; SS = 0.1; F = 0.5; P = 0.483	df = 1; SS = 4.2; F = 20.8; P < 0.001
No shift	124	9.4	2.6	1371.1	4.5*	1.8	574.1	2.2
Shift	22	8.8	3.3*	1806	2.3	1.6	479.7	6.4*

FIG. 2. Comparison of ranges of sister species pairs. Octants of the cube indicate numbers of sister species pairs for a given combination of characteristics; back-lower-left octant has a zero value.

relationship to species number and presumed diversification rate. However, three of the 10 largest woody lineages in the Hawaiian Islands were derived from herbaceous ancestors (Baldwin and Sanderson 1998; Ganders et al. 2000; Lindqvist and Albert 2002), and many have anomalous or poorly sclerified wood (Carlquist 1974). We speculate that these may have some of the characteristics of herbaceous plants (such as short generation time and specialization in ephemeral habitats) favorable to diversification.

Our analysis provisionally indicates a negative relationship between population density and speciation potential, or at least indicates that the highest population densities are typically accompanied by low S. The fact that ecosystem dominants make up 35 of the 88 (40%) native species not confined to the Hawaiian Islands and therefore not examined in the analysis of lineages suggests that the inferred high dispersability of nonendemic species is directly related both to their inability to speciate and to their local abundance. A more detailed study, perhaps including population densities of many species across several islands and habitat types, might better quantify typical population structure within lineages.

The positive correlation of species number with age might suggest that species-rich lineages are simply older than those with few species. However, only nine lineages have age estimates and they represent comparatively species-rich lineages, making it difficult to draw conclusions. Although more than half of all lineages contain a single species, no monotypic lineage has an age estimate. While it may require time for divergent lineages to speciate, some monotypic lineages may also be quite old. Possible examples include three distinctive monotypic endemic genera with phylogenetic studies suggesting a long residence in the Hawaiian Islands and therefore a very low (effectively zero) diversification rate (R): *Broussaisia arguta* Gaud. (Hufford et al. 2001), *Hillebrandia sandwicensis* Oliver (Clement et al. 2004), and *Kanaloa kahoolawensis* Lorence and Wood (Hughes et al. 2003). Of nine R values we calculated, two (*Tetramolopium* and *Metrosideros*) greatly exceeded the highest diversification rates reported by Eriksson and Bremer (1992). However, age estimates for these lineages were less than one million years, arguably imprecise considering the likely margin of error. Nonetheless, in comparing R between Hawaiian and non-

Hawaiian sister taxa, Baldwin and Sanderson (1998) found a higher rate in Hawaiian taxa, confirming the notion of increased evolutionary rates on islands. We qualify this, however, by suggesting that high diversification rates are restricted to a small number of lineages.

Why do some lineages contain so many morphologically distinct species and why do so many contain only one? Despite the significance of external bird-dispersal and sparse populations, no species-level trait appears responsible for initiating diversification, and it is likely that a unique combination of intrinsic and extrinsic factors plays a role in the most species-rich lineages. By contrast, a given lineage may have failed to speciate for any one or a combination of reasons. The high frequency of monotypic lineages is perhaps best explained by the long-distance dispersal required to colonize the Hawaiian Islands, which favors highly dispersable and consequently nonproliferating taxa.

The negative relationships between log(S) and geographic and habitat range size for species suggest that both allopatric and parapatric (ecological) speciation are important. Considering the positive relationship of log(S) to habitat range size for whole lineages, species-rich lineages usually span a wide range of habitats but contain narrowly adapted species. We can therefore infer that individual species must occupy different parts of the overall range of the lineage. Many of such lineages can be considered adaptive radiations in the strictest sense by exhibiting rapid speciation with species that are sufficiently differentiated and specialized (Schluter 2000). The finding that species-rich lineages contain high proportions of narrowly adapted species (with small geographic and habitat range sizes and sparse populations) is consistent with the conclusions of Sakai et al. (2002) that such lineages include disproportionate numbers of species threatened with extinction.

The positive relationship between log(S) and the presence of an adaptive shift suggests a link between speciation events (cladogenesis) and the evolution of novel traits (anagenesis). This does not explicitly point to punctuated equilibrium, which would predict that the two events occur simultaneously. Because the evolution of novelty on a per-species basis is roughly equivalent in large and small lineages, proliferation appears to increase the probability that a novel trait will emerge. The ability of a lineage to speciate extensively has apparently permitted the progeny of a small number of colonists to produce a majority of evolutionary novelties. Some shifts may not be simply byproducts of diversification, but may contribute to it. A hint at the importance of ecological interactions comes from the two largest lineages, one including six genera of lobelioids (Givnish et al 1995; Givnish 1998) and one including three genera in the Lamiaceae (Lindqvist et al. 2003). These two lineages, which collectively make up nearly 20% of the angiosperm flora, exert a strong influence on the regional species pool. In both cases, clades defined by autochthonously derived fleshy fruit make up the majority of species in the lineage. In the former case, a clade defined by bird pollination makes up a majority of species in the lineage, and the latter contains a large bird-pollinated clade, with both instances having been derived autochthonously. Therefore, at least in these two cases, pro-

gression toward new ecological relationships with birds may constitute a key innovation driving diversification.

Speciation mode further resolves relationships among ecological and biogeographic traits. In sum, we presume 29% of the sister species pairs examined to be products of allopatric speciation (including 8% as peripheral isolates), 29% from parapatric speciation, and the remaining 42% considered indeterminable. Our assessment of parapatric speciation events may be conservative, and with more precise measures of habitat affinity, more species pairs might prove to inhabit largely separate habitats. The low frequency of clear peripheral isolates indicates either that such speciation is rare or that peripheral isolates quickly expand their ranges to be similarly sized to those of their sister species, as has been suggested for other taxa (Jablonski 1987; Webb and Gaston 2000). It is also possible that related plant species have similar range sizes due to the conservation of niche breadth as a trait of species (Ricklefs and Latham 1992). Speciation via peripheral isolation may be more common in the Hawaiian Islands than is suggested by our data, particularly considering the probable frequency of founder events establishing populations on newly colonized islands. Furthermore, in 13 cases both sister species are single-volcano endemics and thus their ranges are equivalent in our measure. A finer-scale examination might elicit a disparity in range sizes; however, a cursory examination of within-volcano distributions suggests similar range size for most species pairs. Interestingly, 12 of the 13 cases in which both sister species are single-volcano endemics occur in lineages with more than 10 species, again highlighting the negative association between lineage size and range size.

Whereas many patterns in which sister species exhibit overlapping geographic and habitat ranges probably result from dispersal following allopatric speciation, some may be attributable to sympatric speciation. For example, the bird-pollinated species *Abutilon menziesii* Seem. probably gave rise to the self-pollinated species *A. eremitopetalum* Caum, which is easily distinguished by its greatly reduced corolla (Bates 1990). Presumably, an autogamous mutant arose, immediately severing gene flow with the parent population; subsequently, in the absence of selection needed to maintain large, showy flowers, the corolla was reduced, resulting in a conspicuous morphological difference. Other lineages may exhibit similar types of reduction of gene flow independent of geography or ecology through hybridization, polyploidy, or some other means. For example, two species of *Scaevola* (Goodeniaceae) appear to be of hybrid origin (D. G. Howarth and D. A. Baum, unpubl. ms,). Additional genetic studies point to the possibility that reticulation within certain lineages may be important in generating new species while confounding phylogenies (Baldwin 1997; Lindqvist et al. 2003). However, polyploid speciation events do not appear to be more frequent in the Hawaiian Islands than in continental areas (Carr 1998).

Overall, our analysis of speciation mode is consistent with an examination of numerous phylogenies of Hawaiian organisms that indicated that speciation events were one-third interisland and two-thirds intraisland (Funk and Wagner 1995). It is also consistent with the conclusions of Stuessy et al. (1998) who found evidence for both geographic and ecological isolation between species pairs in the Juan Fernandez Islands. Although the proportion they reported for geographic isolation (70%) is higher than ours (30%), they included speciation events between monotypic lineages and their purported outside relatives, whereas we did not. When considering only speciation events within the Juan Fernandez Islands, the relative proportion (37%) is comparable to our result. It is interesting to note that in both our study and that of Stuessy et al. (1998) geographically isolated sister species strongly tended to occur in similar habitats, suggesting that the geographic mode of speciation is largely distinct from the ecological (parapatric) mode.

Phylogenetic data provide an opportunity to examine the role of the evolutionary process in relationships of species traits that might otherwise be viewed in strictly ecological terms. This analysis presents an opportunity to revisit the positive relationship between population density and geographic range size, and explore how it relates to dispersal, niche breadth, and speciation. In addition to previously discussed ecological explanations for the pattern, Gaston et al. (1997) proposed that the relationship may be an artifact of phylogeny, whereby traits co-vary according to the degree of phylogenetic relatedness. However, Gaston et al. (1997) and Thompson et al. (1999) rejected this hypothesis, by demonstrating that the relationship holds true within phylogenetic groups. While we did not compare traits *within* phylogenetic groups, we observed clear differences *between* them, in qualified support of the hypothesis. Our data support the positive relationship between local population density and geographic range size as typical traits of lineages (Sakai et al. 2002) and indicate that low population density relates to frequent allopatric or parapatric speciation, which results in reduced geographic or habitat range size, respectively. However, dispersal ability may influence both population density and range size independently of speciation. A more realistic view may be one of a complex interplay whereby species-level traits influence range size directly through population processes and indirectly through speciation (Fig. 3).

A unique aspect of these analyses is that they represent the entire angiosperm flora of a distinct biogeographic region divided into putatively monophyletic lineages (Sakai et al. 1995a,b, 2002). As a regional process, speciation influences species composition at multiple scales (Ricklefs and Schluter 1993; Rosenzweig 1995; Webb et al. 2002). The unified neutral theory of biodiversity and biogeography (Hubbell 2001) outlines testable predictions about speciation in regional species pools. First, the theory predicts that rare and narrowly distributed species are recent in origin, whereas widespread abundant species are older. The data presented here cannot address this assertion because virtually no lineages consisting of widespread and abundant species have age estimates. A second prediction of the neutral theory is that the relative frequency of two extreme modes of speciation (termed ''random fission'' and ''point mutation'') should determine relative species abundances (Hubbell 2001). The random fission mode is defined as the random parsing of the range of the parent species into the ranges of the daughter species, while point mutation mode is defined as the sudden localized appearance of a new species; predominance of the former produces a more even distribution of range size and abundance
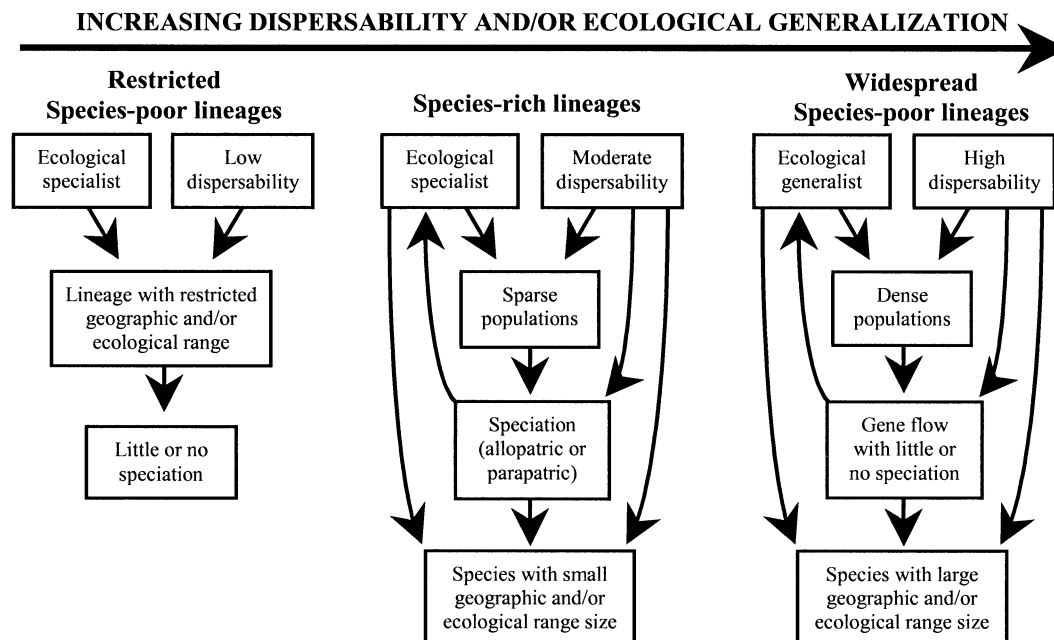
INCREASING DISPERSABILITY AND/OR ECOLOGICAL GENERALIZATION

Restricted Species-poor lineages   **Species-rich lineages**   **Widespread Species-poor lineages**

Ecological specialist	Low dispersability

Lineage with restricted geographic and/or ecological range

Little or no speciation

Ecological specialist	Moderate dispersability

Sparse populations

Speciation (allopatric or parapatric)

Species with small geographic and/or ecological range size

Ecological generalist	High dispersability

Dense populations

Gene flow with little or no speciation

Species with large geographic and/or ecological range size

Fig. 3. The role of speciation in relationships between species-level traits. Typical ecological, population, and evolutionary characteristics for species-rich and species-poor lineages are contrasted. Ecological characteristics of species (such as dispersability and degree of ecological specialization) shape whole-lineage range size and population density, both of which may influence speciation. Dispersability may also affect the potential for speciation directly by regulating gene flow among populations. The frequency of speciation influences range size and potentially the degree of ecological specialization. Dispersal ability and the degree of ecological specialization may also affect range size directly. The speciation process is therefore one component of a complex interplay of species characteristics. Although many potential pathways of influence among characteristics are shown, the importance of each will vary by lineage. The heritability of ecological characteristics reinforces the chain of cause and effect over time, ultimately resulting in lineages with very different species numbers.

than the latter. The predominant modes of speciation in Hawaiian angiosperm lineages (where discernable) appear to be allopatric and parapatric, resulting in sister species with similar range sizes. Although this pattern may more closely fit the random fission mode, it is far from random: most speciation events occur in a small number of lineages in which species rarely attain large range size. When such narrow ranges are subdivided through allopatric or parapatric speciation, the result may be a very high proportion of rare species, more typical of the point mutation mode.

The neutral theory's central assumption of neutrality (Hubbell 2001), by circumventing differences in immigration, extinction, and speciation rates among species, serves the purpose of creating a null model of processes within broad regions. As shown by our analyses, however, much of the deviation from this null assumption can be explained by the likelihood that dispersability, abundance, degree of specialization, and ultimately the tendency to diverge differ according to phylogenetic affinity. A small number of species-rich lineages are responsible for disproportionate numbers of species, ecological specialists, and evolutionary novelties, yet most of their species consist of sparse and geographically limited populations. A large number of species-poor lineages include disproportionate numbers of wide-ranging and ecologically dominant species, yet contribute little to species diversity or evolutionary innovation. Variation in species proliferation among lineages thus appears to produce a paradox: the relative contribution of an evolutionary lineage to ecosystem function (through ecological dominance and geo-

graphic expanse) is inversely proportional to its contribution to species diversity and ecological novelty within the region.

LITERATURE CITED

Alice, L. A., and C. S. Campbell. 1999. Phylogeny of *Rubus* (Rosaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. Am. J. Bot. 86:81–97.

Angiosperm Phylogeny Group (APG) II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. Biol. J. Linn. Soc. 141:399–436.

Baldwin, B. G. 1997. Adaptive radiation of the Hawaiian silversword alliance: congruence and conflict of phylogenetic evidence from molecular and non-molecular investigations. Pp. 104–128 *in* T. J. Givnish and K. J. Sytsma, eds. Molecular evolution and adaptive radiation. Cambridge Univ. Press, New York.

Baldwin, B. G., and R. H. Robichaux. 1995. Historical biogeography and ecology of the Hawaiian silversword alliance (Asteraceae). New molecular phylogenetic perspectives. Pp. 259–287 *in* W. L. Wagner and V. A. Funk, eds. Hawaiian biogeography: evolution on a hotspot archipelago. Smithsonian Institution Press, Washington, DC.

Baldwin, B. G., and M. J. Sanderson. 1998. Age and rate of di-

versification of the Hawaiian silversword alliance (Compositae). Proc. Natl. Acad. Sci. USA 95:9402–9406.

Ballard, H. E., and K. J. Sytsma. 2000. Evolution and biogeography of the woody Hawaiian violets (*Viola*, Violaceae): Arctic origins, herbaceous ancestry and bird dispersal. Evolution 54: 1521–1532.

Barraclough, T. G., and A. P. Vogler. 2000. Detecting the geographic pattern of speciation from species-level phylogenies. Am. Nat. 155:419–434.

Bates, D. M. 1990. Malvaceae. Pp. 868–903 *in* W. L. Wagner, D. R. Herbst, and S. H. Sohmer. Manual of the flowering plants of Hawai'i. Vol. 1. Univ. of Hawai'i and Bishop Museum Press, Honolulu.

Bleiweiss, R. 1990. Ecological causes of clade diversity in hummingbirds: a neontological perspective on the generation of diversity. Pp. 354–380 *in* R. M. Ross and W. R. Allmon, eds. Causes of evolution: a paleontological perspective. Univ. of Chicago Press, Chicago.

Brooks, D. R., and D. A. McLennan. 1993. Phylogeny, ecology and behavior. A research program in comparative biology. Univ. of Chicago Press, Chicago.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124:255–279.

Burger, W. C. 1981. Why are there so many kinds of flowering plants? Bioscience 31:572–581.

Carlquist, S. 1970. Hawaii: a natural history. Natural History Press, New York.

———. 1974. Island biology. Columbia Univ. Press, New York.

Carr, G. D. 1998. Chromosome evolution and speciation in Hawaiian flowering plants. Pp. 5–47 *in* T. F. Stuessy and M. Ono, eds. Evolution and speciation of island plants. Cambridge Univ. Press, New York.

Carson, H. L. 1983. Chromosomal sequences and interisland colonizations in Hawaiian *Drosophila*. Genetics 103:465–482.

Carson, H. L., and D. A. Clague. 1995. Geology and biogeography. Pp. 14–29 *in* W. L. Wagner and V. A. Funk, eds. Hawaiian biogeography: evolution on a hotspot archipelago. Smithsonian Institution Press, Washington, DC.

Chesser, R. T., and R. M. Zink. 1994. Modes of speciation in birds: a test of Lynch's method. Evolution 48:490–497.

Chown, S. L. 1997. Speciation and rarity: separating cause from consequence. Pp. 91–109 *in* W. E. Kunin and K. J. Gaston, eds. The biology of rarity. Chapman and Hall, London.

Clague, D. A. 1996. The growth and subsidence of the Hawaiian-Emperor volcanic chain. Pp. 35–50 *in* A. Keast and S. E. Miller, eds. The origin and evolution of Pacific island biotas, New Guinea to Eastern Polynesia: patterns and processes. SPB Academic Publishing, Amsterdam.

Clement, W. L., M. C. Tebbitt, L. L. Forrest, J. E. Blaire, L. Brouillet, T. Eriksson, and S. M. Swensen. 2004. Phylogenetic position and biogeography of *Hillebrandia sandwicensis* (Begoniaceae): a rare Hawaiian relict. Am. J. Bot. 91:905–917.

Costello, A., and T. J. Motley. 2001. Molecular systematics of *Tetraplasandra*, *Munroidendron* and *Reynoldsia sandwicensis* (Araliaceae) and the evolution of superior ovaries in Tetraplasandra. Edinb. J. Bot. 58:229–242.

Cracraft, J. 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 27–59 *in* D. Otte and J. A. Endler, eds. Speciation and its consequences. Sinauer Associates, Sunderland, MA.

Crepet, W. L. 1984. Advanced (constant) insect pollination mechanisms: patterns of evolution and implications vis-à-vis angiosperm diversity. Ann. Mo. Bot. Gard. 71:607–630.

Cuddihy, L. W., and C. P. Stone. 1990. Alteration of native Hawaiian vegetation: effects of humans, their activities and introductions. Cooperative National Park Resources Studies Unit, Univ. of Hawai'i, at Manoa, Honolulu.

Diamond, J. M. 1973. Distributional ecology of New Guinea birds. Science 179:759–769.

Dodd, M. E., J. Silvertown, and M. W. Chase. 1999. Phylogenetic analysis of trait evolution and species diversity variation among angiosperm families. Evolution 53:732–744.

Eldredge, N., and S. J. Gould. 1972. Punctuated equilibrium: an alternative to phyletic gradualism. Pp. 82–115 *in* T. J. M. Schopf, ed. Models in paleobiology. Freeman Cooper and Company, San Francisco, CA.

Endler, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, NJ.

Engels, B. 1988. Monte Carlo R × C contingency table test. Ver. 2.0. University of Wisconsin, Madison, WI.

Eriksson, O., and B. Bremer. 1992. Pollination systems, dispersal modes, life forms, and diversification rates in angiosperm families. Evolution 46:258–266.

Fleming, T. H. 1990. Fruiting plant-frugivore mutualism: the evolutionary theater and the ecological play. Pp. 119–144 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, eds. Plant-animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley and Sons, New York.

Fosberg, F. R. 1948. Derivation of the flora of the Hawaiian Islands. Pp. 107–119 *in* E. C. Zimmerman. Insects of Hawai'i. Vol. 1. Univ. of Hawai'i Press, Honolulu.

Funk, V. A., and W. L. Wagner. 1995. Biogeography of seven ancient Hawaiian plant lineages. Pp. 160–194 *in* W. L. Wagner and V. A. Funk, eds. Hawaiian biogeography: evolution on a hotspot archipelago. Smithsonian Institution Press, Washington, DC.

Gagné, W. C., and L. W. Cuddihy. 1990. Vegetation. Pp. 45–114 *in* W. L. Wagner, D. R. Herbst, and S. H. Sohmer. Manual of the flowering plants of Hawai'i. Vol. 1. Univ. of Hawai'i and Bishop Museum Press, Honolulu.

Ganders, F. R., M. Berbee, and M. Pirseyedi. 2000. ITS base sequence phylogeny in *Bidens* (Asteraceae): Evidence for the continental relatives of Hawaiian and Marquesan *Bidens*. Syst. Bot. 25:122–133.

Gaston, K. J., T. M. Blackburn, and R. D. Gregory. 1997. Interspecific abundance-range size relationships: range position and phylogeny. Ecography 20:390–399.

Gavrilets, S., H. Li, and M. D. Vose. 2000. Patterns of parapatric speciation. Evolution 54:1126–1134.

Gemmill, C. E. C., G. J. Allan, W. L. Wagner, and E. A. Zimmer. 2002. Evolution of insular Pacific *Pittosporum* (Pittosporaceae): origin of the Hawaiian radiation. Mol. Phylogenet. Evol. 22: 31–42.

Givnish, T. J. 1998. Adaptive plant evolution on islands: classical patterns, molecular data, new insights. Pp. 281–304 *in* P. R. Grant, ed. Evolution on islands. Oxford Univ. Press, New York.

Givnish, T. J., K. J. Sytsma, J. F. Smith, and W. J. Hahn. 1995. Molecular evolution, adaptive radiation, and geographic speciation in *Cyanea* (Capanulaceae, Lobelioideae). Pp. 288–337 *in* W. L. Wagner and V.A. Funk, eds. Hawaiian biogeography: evolution on a hotspot archipelago. Smithsonian Institution Press, Washington, DC.

Givnish, T. J., K. J. Sytsma, T. A. Patterson, and J. R. Hapeman. 1996. Comparison of patterns of geographic speciation and adaptive radiation in *Cyanea* and *Clermontia* (Campanulaceae) based on a cladistic analysis of DNA sequence and restriction-site data. Am. J. Bot. 83(Suppl.):159.

Glazier, D. S. 1987. Toward a predictive theory of speciation: the ecology of isolate selection. J. Theor. Biol. 126:323–333.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biol. J. Linn. Soc. 42:17–38.

Hanski, I., J. Kouki, and A. Halkka. 1993. Three explanations of the positive relationship between distribution and abundance of species. Pp.108–116 *in* R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities: historical and geographic perspectives. Univ. of Chicago Press, Chicago.

Herrera, C. M. 1989. Seed dispersal by animals: a role in angiosperm diversification? Am. Nat. 133:309–322.

Hillebrand, W. 1888. Flora of the Hawaiian Islands: a description of their phanerogams and vascular cryptogams. Hafner Publishing, New York.

Howarth, D. G., D. E. Gardner, and C. W. Morden. 1998. Phylogeny of *Rubus* subgenus *Idaeobatus* (Rosaceae) and its implications toward colonization of the Hawaiian Islands. Syst. Bot. 22: 433–441.

Howarth, D. G., M. H. G. Gustafsson, D. A. Baum, and T. J. Motley. 2003. Phylogenetics of the genus *Scaevola* (Goodeniaceae): implications for dispersal patterns across the Pacific basin and colonization of the Hawaiian Islands. Am. J. Bot. 90:915–923.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in Population Biology 32. Princeton Univ. Press, Princeton, NJ.

Hufford, L., M. L. Moody, and D. E. Soltis. 2001. A phylogenetic analysis of Hydrangeaceae based on sequences of the plastid gene *matK* and their combination with *rbcL* and morphological data. Int. J. Plant Sci. 162:835–846.

Hughes, C. E., D. E. Bailey, S. Krosnick, and M. A. Luckow. 2003. Relationships among genera of the informal *Dichrostachys* and *Leucaena* groups (Mimosoidae) inferred from nuclear ribosomal ITS sequences. Pp. 221–238 *in* B. B. Klitgaard and A. Bruneau, eds. Advances in legume systematics. Part 10, Higher level systematics. Royal Botanic Gardens, Kew, U.K.

Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. Science 238: 360–363.

Jablonski, D., and K. Roy. 2003. Geographic range and speciation in fossil and living mollusks. Proc. R. Soc. Lond. B 270: 401–406.

Kelt, D. A., and J. H. Brown. 2000. Species as units of analysis in ecology and biogeography: Are the blind leading the blind? Glob. Ecol. Biogeogr. 9:213–217.

Kim, H. G., S. C. Keeley, P. S. Vroom, and R. K. Jansen. 1998. Molecular evidence for an African origin of the Hawaiian endemic *Hesperomannia* (Asteraceae). Proc. Natl. Acad. Sci. USA 95:15440–15445.

Kirch, P. V. 1982. The impact of prehistoric Polynesians on the Hawaiian ecosystem. Pac. Sci. 36:1–14.

Levin, D. A. 1984. Immigration in plants: an exercise in the subjunctive. Pp. 242–260 *in* R. Dirzo and J. Sarukhan, eds. Perspectives on plant population ecology. Sinauer Associates, Sunderland, MA.

Lindqvist, C., and V. A. Albert. 2002. Origin of the endemic Hawaiian mints within North American *Stachys* (Lamiaceae). Am. J. Bot. 89:1709–1724.

Lindqvist, C., T. J. Motley, J. J. Jeffrey, and V. A. Albert. 2003. Cladogenesis and reticulation in the endemic Hawaiian mints (Lamiaceae). Cladistics 19:480–495.

Lowrey, T. K. 1995. Phylogeny, adaptive radiation, and biogeography of Hawaiian *Tetramolopium* (Asteraceae, Astereae). Pp. 195–220 *in* W. L. Wagner and V. A. Funk, eds. Hawaiian biogeography: evolution on a hotspot archipelago. Smithsonian Institution Press, Washington, DC.

Lynch, J. D. 1989. The gauge of speciation: on the frequency of modes of speciation. Pp. 527–553 *in* D. Otte and J. A. Endler, eds. Speciation and its consequences. Sinauer Associates, Sunderland, MA.

Mayr, E. 1963. Animal species and evolution. Belknap Press of Harvard Univ., Cambridge, MA.

Midgely, J. J., and W. J. Bond. 1991. Ecological aspects of the rise of the angiosperms: a challenge to the reproductive superiority hypothesis. Biol. J. Linn. Soc. 44:81–92.

Mishler, B. D., and D. J. Donoghue. 1982. Species concepts: a case for pluralism. Syst. Zool. 31:491–503.

Molvray, M., P. J. Kores, and M. W. Chase. 1999. Phylogenetic relationships within *Korthalsella* (Viscaceae) based on nuclear ITS and plastid trnL-F sequence data. Am. J. Bot. 86:249–260.

Motley, T. J., and G. D. Carr. 1998. Artificial hybridization in the endemic Hawaiian genus *Labordia* (Loganiaceae). Am. J. Bot. 85:654–660.

Motley, T. J., L. Struwe, and V. A. Albert. 1998. Molecular systematics of Hawaiian *Hedyotis* (Rubiaceae). Am. J. Bot. 85(Suppl.):146.

Nepokroeff, M., K. J. Sytsma, W. L. Wagner, and E. A. Zimmer. 2003. Reconstructing ancestral patterns of colonization and dispersal in the Hawaiian understory shrub genus *Psychotria* (Rubiaceae): a comparison of parsimony and likelihood approaches. Syst. Biol. 52:820–838.

Nepokroeff, M., W. L. Wagner, P. S. Soltis, S. G. Weller, D. E.

Soltis, A. K. Sakai, and E. A. Zimmer. 2004. Phylogeny. *In* W. L. Wagner, S. G. Weller, and A. K. Sakai. Monograph of *Schiedea* (Caryophyllaceae subfam. Alsinoideae). Syst. Bot. Monogr. No. 72. *In press.*

Niklas, K. J., B. H. Tiffney, and A. H. Knoll. 1985. Patterns in vascular plant diversification: an analysis at the species level. Pp.97–128 *in* J. W. Valentine, ed. Phanerozoic diversity patterns. Profiles in macroevolution. Princeton Univ. Press, Princeton, NJ.

Pax, D. L., R. A. Price, and H. J. Michaels. 1997. Phylogenetic position of the Hawaiian geraniums based on *rbcL* sequences. Am. J. Bot. 84:72–78.

Plunkett, G. M., and P. P. Lowry, II. 2001. Relationships among ''ancient araliads'' and their significance for the systematics of apiales. Mol. Phylogenet. Evol. 19:259–276.

Powell, E. A., and K. A. Kron. 2002. Hawaiian blueberries and their relatives—a phylogenetic analysis of *Vaccinium* sections *Macropelma*, *Myrtillus*, and *Hemimyrtillus* (Ericaceae). Syst. Bot. 27:768–779.

Price, J. P. 2004. Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. J. Biogeogr. 31:487–500.

Price, J. P., and D. A. Clague. 2002. How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. Proc. R. Soc. Lond. B 269:2429–2435.

Raven, P. H. 1977. A suggestion concerning the Cretaceous rise to dominance of the angiosperms. Evolution 31:451–452.

Regal, P. J. 1977. Ecology and evolution of flowering plant dominance. Science 196:622–629.

Ricklefs, R. E., and R. E. Latham. 1992. Intercontinental correlation of geographic ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. Am. Nat. 139:1305–1321.

Ricklefs, R. E., and S. S. Renner. 1994. Species richness within families of flowering plants. Evolution 48:1619–1636.

Ricklefs, R. E., and D. Schluter. 1993. Species diversity in biological communities: historical and geographic perspectives. Univ. of Chicago Press, Chicago.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge Univ. Press, Cambridge, U.K.

Sakai, A. K., W. L. Wagner, D. M. Ferguson, and D. R. Herbst. 1995a. The origin of dioecy in the Hawaiian flora. Ecology 76: 2517–2529.

Sakai, A. K., W. L. Wagner, D. M. Ferguson, and D. R. Herbst. 1995b. Biogeographical and ecological correlates of dioecy in the Hawaiian flora. Ecology 76:2530–2543.

Sakai, A. K., W. L. Wagner, and L. A. Mehrhoff. 2002. Patterns of endangerment in the Hawaiian flora. Syst. Biol. 51:276–302.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford Univ. Press, Oxford, U.K.

Seelanan, T., A. Schnabel, and J. F. Wendel. 1997. Congruence and consensus in the cotton tribe (Malvaceae). Syst. Bot. 22: 259–290.

Simon, C. 1987. Hawaiian evolutionary biology: an introduction. Trends Ecol. Evol. 2:175–718.

Smith, J. F. 2001. High species diversity in fleshy-fruited tropical understory plants. Am. Nat. 157:646–653.

Snow, D. W. 1981. Tropical frugivorous birds and their food plants: a world survey. Biotropica 13:1–14.

Soltis, D. E., P. S. Soltis, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Swere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, S. M. Chaw, L. J. Gillespie, W. J. Kress, and K. J. Sytsma. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. Ann. Mo. Bot. Gard. 84:1–49.

Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, L. M. Prince, W. J. Kress, K. C. Nixon, and J. A. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, rbcL, and atpB sequences. Bot. J. Linn. Soc. 133:381–461.

Soltis, P. S., D. E. Soltis, S. G. Weller, A. K. Sakai, and W. L. Wagner. 1996. Molecular phylogenetic analysis of the Hawaiian endemics *Schiedea* and *Alsinidendron* (Caryophyllaceae). Syst. Bot. 21:365–379.

Stanley, S. M. 1979. Macroevolution: pattern and process. W. H. Freeman, San Francisco, CA.

———. 1986. Population size, extinction, and speciation: the fission effect in neogene Bivalvia. Paleobiology 12:89–110.

Stebbins, G. L. 1981. Why are there so many species of flowering plants? Bioscience 31:573–577.

Steinmann, V. W., and J. M. Porter. 2002. Phylogenetic relationships in Euphorbiae (Euphorbiaceae) based on ITS and *ndh*F sequence data. Ann. Mo. Bot. Gard. 89:453–490.

Stuessy, T. F., D. J. Crawford, C. Marticorena, and M. Silva. 1998. Isolating mechanisms and modes of speciation in endemic angiosperms of the Juan Fernandez Islands. Pp. 79–96 *in* T. F. Stuessy and M. Ono, eds. Evolution and speciation of island plants. Cambridge Univ. Press, New York.

Thompson, K., K. J. Gaston, and S. R. Band. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. Ecology 87:150–155.

Tiffney, B. H. 1986. Fruit and seed dispersal and evolution of the Hamamelidae. Ann. Mo. Bot. Gard. 73:394–416.

Tiffney, B. H., and S. J. Mazer. 1995. Angiosperm growth habit, dispersal and diversification reconsidered. Evol. Ecol. 9:93–117.

Vermeij, G. J. 1987. The dispersal barrier in the tropical Pacific: implications for molluscan speciation and extinction. Evolution 41:1046–1058.

Wagner, W. L. and V. A. Funk, eds. 1995. Hawaiian biogeography: evolution on a hotspot archipelago. Smithsonian Institution Press, Washington, DC.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1990. Manual of the flowering plants of Hawai'i. Univ. of Hawaii Press and Bishop Museum Press, Honolulu.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Manual of the flowering plants of Hawai'i, revised edition with supplement by W. L. Wagner and D. R. Herbst. Univ. of Hawaii Press, Honolulu.

Wagner, W. L., D. R. Herbst, and D. D. Palmer. 2001. Flora of the Hawaiian Islands. Available online at http://rathbun.si.edu/botany/pacificislandbiodiversity/hawaiianflora/index.htm. Accessed 1 May 2003.

Wanntorp, L., and H. E. Wanntorp. 2003. The biogeography of *Gunnera* L.: vicariance and dispersal. J. Biogeogr. 30:979–987.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Syst. 33:475–505.

Webb, T. J., and K. J. Gaston. 2000. Geographic range size and evolutionary age in birds. Proc. R. Soc. Lond. B 267:1843–1850.

Wiley, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. Wiley-Interscience, New York.

Wright, S. D., C. G. Yong, S. R. Wichman, J. W. Dawson, and R. C. Gardner. 2001. Stepping stones to Hawaii: a trans-equatorial dispersal pathway for *Metrosideros* (Myrtaceae) inferred from nrDNA (ITS + ETS). J. Biogeogr. 28:769–774.

Yumoto, T. 1999. Seed dispersal by Salvin's currasow, *Mitu salvini* (Cracidae), in a tropical forest of Colombia; direct measurement of dispersal distance. Biotropica 31:654–660.