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BIOGEOGRAPHICAL AND ECOLOGICAL CORRELATES OF DIOECY IN THE HAWAIIAN FLORA¹

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Abstract. The angiosperm flora of the Hawaiian Islands, with its high incidence of dioecy, has been central in development of hypotheses about the evolution of dioecy. Based on a recent taxonomic treatment of the Hawaiian angiosperm flora, we analyzed biogeographic patterns of dioecy as well as the association of dioecy with ecological traits potentially important in the evolution of dioecy for native current species and genera. We also analyzed patterns for presumed colonists of the flora to control better for phylogenetic patterns in these traits. Dioecy is associated with woodiness, especially trees; however, this pattern does not hold for gynodioecy. Within woody species, dimorphism (dioecy, gynodioecy, subdioecy, polygamodioecy) is associated with mesic habitats and occurs more frequently in species with lowland and lowland–montane distributions. In contrast, in the endemic Hawaiian Alsinoideae (*Schiedea* and *Alsinidendron*) and in *Bidens* (two groups with autochthonous evolution of dimorphism), dimorphism is associated with more xeric habitats, and for the former group, with wind pollination. For the entire angiosperm flora, dimorphic species are associated with flowers that are small and green. Woody dioecious species and genera are disproportionately associated with wind pollination; hermaphroditic species are disproportionately bird pollinated primarily because of one species-rich lineage in the Campanulaceae. There was no association of dimorphism and pollinator type for colonists. Because of a few species-rich lineages, dimorphism is associated with dry fruits at the specific level, but at the generic level and for colonists, dimorphism is associated with fleshy fruits.

Dioecious and gynodioecious species are found more often on older islands, a result of speciation of dimorphic colonists as well as autochthonous evolution of dimorphism. Single-island endemism is not associated with dioecy in the flora as a whole or with dimorphism within lineages evolving dimorphism autochthonously; thus Baker's law is not supported within the Hawaiian Islands. Because the Hawaiian angiosperm flora originated from a minimum of only 291 colonists, many of the associations of dimorphism with ecological traits occur because of the influence of only a few species-rich lineages. Better knowledge of phylogenetic patterns and further ecological studies, particularly within those groups evolving dioecy autochthonously, are needed to determine causality.

Key words: *angiosperms; biogeography of plant breeding systems; breeding systems; dioecy; ecological correlates of dioecy; endemism; evolution of plant breeding systems; gynodioecy; Hawaiian Islands; island biogeography; islands; long-distance dispersal of plants; sexual dimorphism of flowers.*

INTRODUCTION

Selective forces promoting the evolution of dioecy have been debated intensely in recent years. The classic argument suggests that dioecy has resulted from se-

lection for outcrossing to avoid the consequences of inbreeding depression (Mather 1940, Lewis 1942, Baker 1959, 1967, Charlesworth and Charlesworth 1978, Thomson and Barrett 1981). More recently, others have placed emphasis on the importance of resource allocation, sexual selection, and ecological factors in the evolution of separate sexes (reviewed in Bawa 1980, Thomson and Brunet 1990).

Surveys of floras have shown associations between ecological factors and dioecy at various taxonomic levels. Dioecy has been associated with fleshy fruits and

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animal dispersal (Bawa 1980, Givnish 1980, 1982, Flores and Schemske 1984, Muenchow 1987), entomophily (Bawa and Opler 1975, Bawa 1980, Bawa and Beach 1981, Beach 1981) and anemophily (Conn et al. 1980, Freeman et al. 1980), woodiness and longer life-spans (Baker 1959, Gilmartin 1968, Bawa and Opler 1975, Croat 1979, Bawa 1980, Conn et al. 1980, Freeman et al. 1980, Flores and Schemske 1984, Fox 1985), various moisture conditions (Conn et al. 1980, Freeman et al. 1980, Weller and Sakai 1990), and tropical and island floras (Baker 1959, Carlquist 1974, Bawa 1980, Baker and Cox 1984).

Many different hypotheses have been proposed to explain how these associations may indicate causal factors in the evolution of dioecy (e.g., Charnov 1979, 1982, Willson 1979, 1982, Bawa 1980, Lemen 1980, Cox 1981, 1982, Lloyd 1982, Charlesworth 1993). At the same time discussions have included concerns over how useful correlations of dioecy and various ecological traits are in general to determine causal factors of dioecy. Several of the more recent surveys (Fox 1985, Muenchow 1987, Steiner 1988) have pointed out the problems of analyzing characters that are correlated and the difficulty of explaining why these correlations may occur. An ecological character may be associated with dioecy because of a direct association with dioecy, or because of indirect associations with other ecological or morphological characters that are related to dioecy.

More recently, others have questioned whether correlations in extant species can be used at all to infer causal agents in the evolution of dioecy (e.g., Felsenstein 1985, Donoghue 1989, Thomson and Brunet 1990). A primary problem is the constraints imposed by phylogeny, and the fact that each species (or taxon at other levels) may not represent an independent event in the evolution of dioecy. Ideally, one would like to know the number of times dioecy arose independently and whether the ecological conditions of concern were present before, during, or after the breeding system change (Donoghue 1989). Unfortunately, these data are often very difficult to obtain, and the accuracy of the analysis depends not only upon the accuracy of the ecological data but also upon the accuracy of the phylogeny. For these reasons, we know of no analyses of the incidence of dioecy for an entire flora of a geographical region that incorporates the phylogenetic component.

The angiosperm flora of the Hawaiian Islands is an important flora for such an analysis because it has been known for its high incidence of dioecy. Although worldwide, only $\approx 4\%$ of flowering plant species are dioecious (Yampolsky and Yampolsky 1922), Carlquist (1974) estimated that 27.7% of the Hawaiian flora was dioecious. Based on more recent taxonomic data, 14.7% of the 971 native species are dioecious and 20.7% are dimorphic (dioecious, gynodioecious, or subdioecious, polygamodioecious; Sakai et al. 1995).

Although lower than previous estimates, the Hawaiian flora still has the highest incidence of dioecy of any flora surveyed, including that of New Zealand (12–13%; Godley 1979). The Hawaiian angiosperm flora has been especially important in the development of some of these theories and associated ideas about dioecy (Baker 1967, Carlquist 1974, Bawa 1980, 1982, Givnish 1980, 1982, Thomson and Barrett 1981, Baker and Cox 1984, Donoghue 1989). The high levels of dioecy and the assumed absence of self-incompatibility in virtually all Hawaiian species were important in the argument for dioecy as an outcrossing mechanism (e.g., Thomson and Barrett 1981, Bawa 1982). Baker (1967) used the high incidence of dioecy in the Hawaiian Islands to support "Baker's law." He argued that most colonists arrived and established as self-compatible hermaphrodites, and subsequent selection for outcrossing led to high levels of dioecy, since this mechanism was particularly easy to evolve. More recently, Baker and Cox (1984) cited elements of the Hawaiian flora that may have established from dioecious colonists, and suggested that breeding systems of island floras reflect those of the source floras. They gave several factors that may facilitate dispersal of dioecious taxa, including "leakage" in the dioecious breeding system, bird dispersal of multiple seeds as a unit, vegetative propagation and longevity of perennials, and pollination by wind or unspecialized insects.

The Hawaiian Islands vary in age from $<0.5 \times 10^6$ yr to 7.5×10^6 yr for existing larger islands (Hawai'i to Nihoa), with monotonically increasing age toward the northwest and with older ages for once large islands now submerged (MacDonald et al. 1983). This pattern of island age suggests specific predictions about dioecy. If dioecy has arisen within the archipelago, and if rates of speciation are similar for hermaphroditic and dioecious lineages (Sakai et al. 1995), then a higher incidence of dioecy is expected in endemic species (found naturally only in the Hawaiian Islands) than in indigenous species (native to the Hawaiian Islands as well as elsewhere; Baker 1967). Assuming that it takes some time for dioecy to evolve and that Baker's (1967) law is true within the Hawaiian Islands, i.e., that self-compatible hermaphroditic species are better colonists than dioecious species because they are less likely to be constrained by lack of mates, then a higher incidence of dioecy is expected in endemic species on older islands than on younger islands. If these assumptions hold, then higher incidence of single-island endemism within the Hawaiian Islands is expected for dioecious taxa than for hermaphroditic taxa.

Our approach with the Hawaiian angiosperm flora uses current hypotheses about the original plant colonists and their lineages to examine several associations of ecological traits with dioecy in colonists as well as current genera and species. The Hawaiian flora (971 native species) was founded by only a small number of colonists (291) and lineages of only a few colonists

resulted in a large proportion of current species (89% of native angiosperm species are endemic to the Hawaiian Islands; Wagner et al. 1990, Sakai et al. 1995). Because of this, it is especially important to take the evolutionary history of the Hawaiian flora into account. Ideally, explicit phylogenies of lineages would be used to infer causal factors in the evolution of dioecy; lacking phylogenetic hypotheses for many Hawaiian groups, we have used the descendant lineages of each presumed successful colonization as a first approximation. Explicit phylogenetic hypotheses for a number of species-rich Hawaiian lineages have been developed only recently (e.g., Wagner and Funk 1995, Weller et al. 1995). We have presented the data on species and genera to allow comparison to other floras as well as to demonstrate the importance of controlling for independent origins of traits.

The high incidence of dioecy in the Hawaiian Islands has resulted from successful colonization and radiation of lineages with dioecious breeding systems as well as from evolution of dioecy in situ from hermaphroditic colonists (Sakai et al. 1995). In at least 12 cases, monomorphic colonists evolved dimorphism autochthonously in the Hawaiian Islands (Sakai et al. 1995). Knowledge of the ecological conditions associated with dioecious species in these lineages may be especially relevant for ascertaining causal factors in the evolution of dioecy.

We used information from the *Manual of the Flowering Plants of Hawai'i* (Wagner et al. 1990) with some additional data to address the following questions: (1) Do endemic species show a higher proportion of dioecy than nonendemic indigenous species? (2) Do dioecious species in the Hawaiian flora show greater single-island endemism than hermaphroditic species? (3) Are dioecious species more common on older islands? (4) Is there an association of dioecy with habit, habitat, pollination syndrome, or fruit type? We analyzed these associations for (a) known (extant and recently extinct) species and genera, (b) presumed colonists (for pollination or fruit type only), and (c) four lineages with large numbers of both monomorphic and dimorphic species [(*Bidens* (Asteraceae), the endemic Hawaiian Alsinoideae (Caryophyllaceae), *Myrsine* (Myrsinaceae), and *Hedyotis* (Rubiaceae)].

MATERIALS AND METHODS

Taxa.—Data were extracted from the *Manual of the Flowering Plants of Hawai'i* (Wagner et al. 1990; referred to hereafter as the *Manual*). All native (endemic and indigenous) species listed in the *Manual* were included. Endemic species refer to species found naturally only in the Hawaiian Islands, and included those listed in the *Manual* as endemic ($N = 849$) or questionably endemic ($N = 1$). Indigenous species refer to species found naturally in the Hawaiian Islands as well as elsewhere and included species listed in the *Manual* as indigenous ($N = 88$), questionably indigenous ($N =$

19), questionably introduced by colonizing Polynesians ($N = 3$), and questionably naturalized ($N = 11$). Species known to be naturalized or of certain introduction by Polynesians (a total of 861 species treated in Wagner et al. 1990) were excluded except as noted above. Ninety angiosperm families, 229 genera, and 971 species were included. Species listed as possibly or certainly extinct in the *Manual* were included, although missing information on breeding system, habitat, and other ecological information precluded their use in some analyses. Intraspecific taxa were not included in analyses because there was no variability in breeding system within species noted in the *Manual*. Our analysis of the flora without consideration of infraspecific taxa is in contrast to Carlquist's (1974) earlier work on Hawaiian breeding systems, which was based on estimates of the number of species as well as infraspecific taxa.

Our database reflected a few post-1990 changes in the taxonomy and number of species in the *Manual*. We included 16 species more than the native species included in the *Manual*. The majority of these (*Caesalpinia major*, *Cardiospermum halicacabum*, *Daucus pusillus*, *Dioclea wilsonii*, *Garnotia acutigluma*, *Hydrocotyle verticillata*, *Ipomoea cairica*, *Lemna perpusilla*, *Merremia aegyptia*, *Polygonum glabrum*, *Spirodela polyrhiza*) were treated as questionably naturalized species in the *Manual*. The dates of introduction to the Hawaiian Islands were very early for these species, and there is a chance they may have dispersed naturally to the islands. Likewise, *Ludwigia octovalvis*, *Oxalis corniculata*, and *Rorippa sarmentosa* may have been introduced by the Polynesians, but are about as likely to have naturally dispersed to the Hawaiian Islands, and are therefore included. Finally, *Mucuna sloanei*, misidentified in the *Manual*, is included here, as is the taxonomic segregate, *Stenogyne kealiae* (Wagner and Weller 1991).

We also updated the taxonomy from that in the *Manual* in another two cases. We followed the taxonomic incorporation of *Pelea* (Rutaceae) into the Pacific genus *Melicope* (Hartley and Stone 1989); *Gahnia gahniiiformis* (Cyperaceae) is treated as a member of the ditypic genus *Morelotia* (St. John 1958, Blake 1969). Our database did not reflect new species discovered since 1990 nor additional species that will be resurrected from inclusion in more widespread species. The only analyses to include very recent information in the Hawaiian Alsinoideae (Wagner et al. 1995) were those done for biogeographical and ecological correlates within the lineage.

Breeding systems.—A complete listing of data on the breeding system and lineages of colonists is given in Sakai et al. (1995). Terminology follows that given in the *Manual* (see also Sakai et al. 1995). Following Lloyd (1980), we also use the term sexually dimorphic to refer collectively to taxa with dioecious, subdioecious, polygamodioecious, or gynodioecious systems; monomorphic refers to taxa with hermaphroditic, mon-

oecious, andromonoecious, gynomonoecious, or polygamomonoecious systems. These more general terms of dimorphism and monomorphism were used to avoid small sample sizes and to include species where breeding systems could not be categorized more specifically. Breeding systems were generally taken as those listed in the *Manual*. If data on breeding systems in the *Manual* were ambiguous, specimens (BISH, US) were re-examined or authorities for those taxa were consulted when possible (*Schiedea*, A. Sakai and S. Weller; *Wikstroemia*, S. Mayer; *Bidens*, F. Ganders). Five species were omitted from analyses because their breeding systems were unknown; *Poa* also was excluded from the generic-level analysis because the breeding systems of the native species are not known.

Most genera were easily classified with respect to breeding system because species within them all had the same breeding system or at least were all monomorphic or all dimorphic. Genera composed of species with both dimorphic and monomorphic breeding systems were classified as mixed.

Flower and fruit classifications.—Characters extracted from the *Manual* included flower color, shortest and longest petal length, flower shape, presence of nectaries or other potential attractants, and any notation of known pollinators. If flowers were apetalous, then the petaloid part of the flower (sepals, tepals, glumes, etc.) was used for the above characters. In the Asteraceae, characters were determined on the ray florets. No attempt was made to estimate inflorescence size or overall attractiveness of the inflorescence to pollinators. Additional information on flower and fruit traits was taken from photographs in Sohmer and Gustafson (1987). Flowers were designated as small (<7 mm) or large (≥ 7 mm) based on the length of the longest petal or petaloid part.

We also recorded the presumed pollinators, based on information on pollinators noted in the *Flora* as well as our own anecdotal field observations and inferences from floral traits such as shape, size, color, and presence of nectaries. In the absence of additional information, species with large flowers of various colors, but usually zygomorphic and curved with nectar were classified as bird pollinated [presumably by Hawaiian honeycreepers (Drepanididae) and honeyeaters (Meliphagidae)]; species with generally small flowers, usually white or green, with nectar and/or abundant pollen were classified as insect pollinated (bees, flies, butterflies, and moths); and species with usually small flowers with easily dislodged pollen or well-exposed anthers (e.g., *Coprosma*) and little or no nectar were classified as wind pollinated. Species with two or more pollination modes ($N = 22$), with water pollination ($N = 5$), complete selfing ($N = 4$), or with unknown pollination mode ($N = 3$) were excluded from analyses involving pollination modes. Genera were assigned the pollination syndrome present in >50% of the species of that genus. Presumed pollinators of colonists were inferred

from floral morphology of the closest outgroup if known; otherwise, the generalized condition in extra-Hawaiian species (or genera in the case of endemic Hawaiian genera) was used (see Appendix of Sakai et al. 1995).

Technical fruit types were taken from the *Manual* and further classified as fleshy or dry to allow comparisons to previous studies. Genera were classified as dry or fleshy based on the category of >50% of their species. Colonists' fruit types also were classified as fleshy or dry. For colonists, we also used Carlquist's (1974) assessments (with slight modifications) of modes of long distance dispersal to the islands (see Appendix of Sakai et al. 1995). Categories included dispersal by birds internally, by birds externally (barbs, in mud, etc.), by birds (when it was ambiguous whether dispersal occurred internally or externally), or abiotically (oceanic drift or air flotation).

Habit and habitat.—Descriptions of plant habit were taken from the *Manual*; species were classified as trees, shrubs, subshrubs (woody at the base), herbs, vines, or lianas (woody vines). These descriptions were further categorized as woody (tree, shrub, liana, and some subshrubs) or herbaceous (herb, vine, and some subshrubs). Species were also classified as annual or perennial (where perennial included those species listed as both annual and perennial). Many genera are composed of both shrubs and trees. Because it was difficult to distinguish these two woody categories for genera, genera were classified only as woody or herbaceous (based upon the state of >50% of the species within the genus). Colonists also were classified as only woody or herbaceous.

Moisture regime, elevation, and plant community type were used to describe habitat. We used four moisture categories derived from information in the *Manual* (wet, mesic, dry, or widespread for species occurring in the first three categories) for statistical analyses. Many species occur in two moisture categories; for these, we classified the species based on the moisture conditions where it most commonly occurs. When possible, we took into account the specific microhabitat preferences of species within these habitats, although in most cases this was unknown. Five elevational categories were used based on a combination of elevation and aspect [coastal (0–300 m), lowland (15–2000 m), montane (500–2700 m), subalpine-alpine (>1700 m), and unknown]. Eight categories for plant communities were used (coastal–strand, cliff, bog, shrubland, grassland–pasture, forest, both forest and montane bog, both shrubland and forest; species with aquatic–semiaquatic ($N = 17$) or unknown habitats ($N = 16$) were omitted from these analyses). In some cases, species now occur only in disturbed areas dominated by alien vegetation, and habitat was inferred based on the presumed previous vegetation type (usually dry forest or dry shrubland) or based on morphology and habitat of closely related species. The habitat of many extinct species was

unknown. Associations of breeding system and habitat were analyzed only at the specific level because genera usually included species in several different habitats.

Biogeography.—Distributions of species were analyzed to determine single-island endemism, where the following groups were each considered a single island: Northwestern Hawaiian Islands (Kure Atoll, Midway Island, Pearl and Hermes Reef, Lisianski Island, Laysan Island, Gardner Island, French Frigate Shoals, Necker Island), Nihoa, Ni'ihau, Kaua'i, O'ahu, Maui Nui complex (Maui, Moloka'i, Lana'i, and Kaho'olawe), and the island of Hawai'i. Although the extremely long chain of the Northwestern Hawaiian Islands was once a series of islands comparable to the current eight large Hawaiian Islands with a diversity of habitats (MacDonald et al. 1983), we considered them a single island primarily because they are now all low islands or atolls with coastal habitat largely inhabited by widespread strand species. The Maui Nui complex was designated as a single island because the four islands forming it were connected during the Pleistocene (MacDonald et al. 1983). The four major islands (or island groups) based on size and used in analyses are Kaua'i, O'ahu, the Maui Nui complex, and Hawai'i.

Data analysis.—The database was manipulated using PARADOX 3.0 (Borland 1988). Two-way and three-way contingency analyses were performed using PROC FREQ in SAS (1990). These analyses assume a hypergeometric distribution and fixed marginals. Marginal values were considered fixed because the entire flora was surveyed, but joint probabilities of cell frequencies were considered open to hypothesis. The hypothesis tested was that there was no association among variables. The general association statistic used (Q_{CMH} ; Landis et al. 1978, SAS 1990) is equivalent to the Pearson chi-square statistic (χ^2) when there is only one stratum and is a stratum-adjusted Pearson chi-square statistic if more strata are involved. Unlike the Pearson chi-square statistic, it requires only a large overall sample size, rather than a large sample size in each stratum. Tests of association with dioecy as well as dimorphism both at the specific and generic level are presented for clarity, although they are not independent of one another, and thus marginal significance levels should be interpreted with caution.

RESULTS

Flora—Biogeography, endemism, and breeding systems.—Dioecy and dimorphism are significantly associated with endemism [test for independence of breeding system (dioecy [or dimorphism]/other breeding systems) vs. origin (endemic/indigenous), $\chi^2 = 6.62$ for dioecy and 8.38 for dimorphism, respectively, $df = 1$, $P < 0.01$ for both]. For endemic species with known breeding systems ($N = 846$), 16.1% are dioecious and 22.6% are dimorphic. In contrast, for indigenous species ($N = 106$), only 6.6% are dioecious and 10.4% are dimorphic.

A very high proportion of native Hawaiian angiosperm species is endemic to the archipelago (89%, 846/952 with known breeding systems), and many of these endemic species occur on only one of the Hawaiian Islands, i.e., are single-island endemics (Fig. 1). The older islands of Kaua'i and O'ahu have significantly more native species than the youngest island of Hawai'i. The older major islands also have a larger number and proportion of single-island endemics (single-island endemic/multi-island endemic vs. four major islands, $\chi^2 = 24.7$, $df = 3$, $P < 0.001$). Almost half of endemic species on Kaua'i occur only on that island (163/350, 46.6%). In contrast, only about one-quarter of endemic species are single-island endemics (79/286, 27.6%) on the youngest island of Hawai'i, even though that island has a much larger land mass constituting slightly over 60% of the total area of the archipelago. This suggests that the island of Hawai'i has a greater proportion of species that evolved on another island and then colonized the island of Hawai'i and that the colonization process is at a much earlier stage (Fig. 1).

Among all endemic species, dioecious species are no more likely than species with other breeding systems to occur on a single island (single-island endemic/multi-island vs. dioecy/not, $\chi^2 = 0.92$ for dioecy, 0.0012 for dimorphism, $df = 1$, NS at $P = 0.05$). Overall, 16.9% of single-island species (90/532) and 14.2% of multi-island endemic species (44/310) are dioecious [for dimorphism: 22.4% of single-island endemics (119/532) and 22.3% of multi-island endemic species (69/310)]. This lack of association of breeding systems with single-island endemism is also true for each major island, although on Kaua'i there is a trend for association of dioecy and single-island endemics (for Kaua'i, $\chi^2 = 2.9$ for dioecy, $df = 1$, $0.05 < P < 0.10$).

Considering only single-island endemic species, the oldest major island (Kaua'i) has the greatest number and proportion of single-island species that are dioecious, and the younger islands of the Maui Nui complex and Hawai'i have the fewest single-island species that are dioecious (Fig. 1). This pattern of increasing dimorphism with greater island age also holds for gynodioecious species [6.1% (10/163) of single-island endemic species on Kaua'i, 4.8% (6/124) on O'ahu, 1.9% (3/158) on the Maui Nui complex and 1.3% (1/79) on Hawai'i are gynodioecious].

Flora—Breeding systems and habit.—Woody species comprise two-thirds of the native Hawaiian flora (65.1%), and five genera alone [*Labordia* (Loganiaceae), *Coprosma* (Rubiaceae) and *Psychotria* (Rubiaceae), *Melicope* (Rutaceae), and *Wikstroemia* (Thymelaeaceae)] account for 63% of the 138 woody dioecious species. Annual species are all monomorphic ($N = 30$) and comprise only 3.1% of the total native flora, and over half of these annuals are in either the genus *Sicyos* (Cucurbitaceae) or grasses. Islands also vary in the proportion of the flora that is woody (Kaua'i: 81%, O'ahu: 86%, Maui Nui: 71%, and Ha-

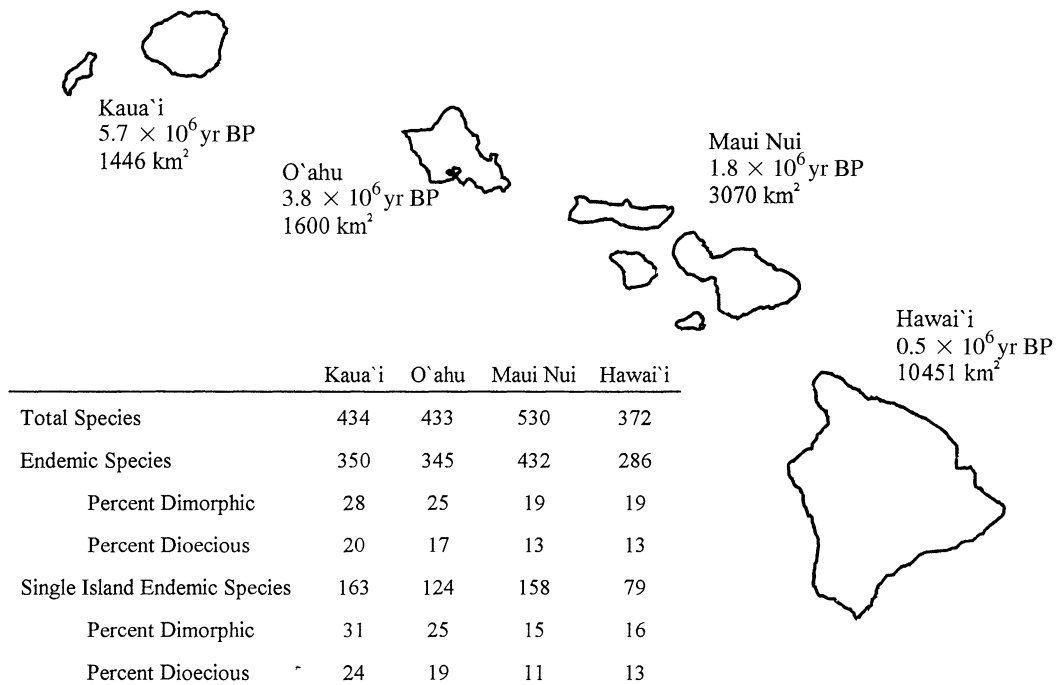


FIG. 1. Biogeography of plant breeding systems of endemic and indigenous species. Total species on each island include both indigenous and endemic species. Endemic species are those that occur only in the Hawaiian Islands, but may occur on one or more islands of the archipelago. Single-island endemic species are those that occur only on one island (or island group as in Maui Nui) within the Hawaiian Islands. Dimorphic and dioecious percentages are relative to the endemic (or single-island endemic) species found on each island. Island ages and sizes are taken from MacDonald et al. (1983) and the *Atlas of Hawaii* (Armstrong 1983). Species that were possibly naturalized, possibly introduced by colonizing Polynesians, or with unknown breeding systems were excluded from this analysis.

wai'i: 75% for single-island endemic species; $N = 527$, $\chi^2 = 10.92$, $df = 3$, $P < 0.025$), adding additional complexity to associations.

Dioecy is significantly associated with woodiness and hermaphroditism is associated with a herbaceous

habit, although gynodioecious species do not show this association (Table 1). Woody genera also are significantly associated with dimorphism ($N = 217$, $\chi^2 = 14.8$, $df = 1$, $P < 0.001$).

Using the three life forms with the most numbers of

TABLE 1. Association of breeding system with habit.*

	Dimorphic			Monomorphic			
	Dioec.	Gynod.	Pd.-sd.	Androm.	Gynom.	Herm.	Monoec.
A) Woodiness							
Herbac.	5/48	8/12	2/7	32/15	25/13	217/202	32/25
Woody	139/96	29/25	18/13	12/29	13/25	389/404	42/49
B) Habit							
Herb	4/42	9/9	1/6	32/13	25/11	157/157	26/17
Shrub	58/57	14/13	7/8	3/18	10/14	228/212	24/22
Tree	78/41	8/9	11/6	8/12	0/10	134/150	5/16
C) Moisture-woody species only							
Dry	19/31	6/5	8	4	7	89/85	16/9
Mesic	77/58	14/10	1	2	3	135/160	19/16
Wet	38/46	4/8	6	5	3	148/126	3/13

* Breeding systems: androm. = andromonoecy, dioec. = dioecy, gynod. = gynodioecy, gynom. = gynomonoecy, herm. = hermaphroditism, monoec. = monoecy, pd = polygamodioecy, sd = subdioecy. Observed or observed/expected values for each breeding system are shown in each cell. Woodiness and breeding system: $N = 963$, $df = 6$, $\chi^2 = 118.6$, $P < 0.001$; woodiness and dimorphism: $N = 966$, $df = 1$, $\chi^2 = 77.1$, $P < 0.001$. Habit and breeding system: $N = 844$, $df = 12$, $\chi^2 = 167.6$, $P < 0.001$; habit and dimorphism: $N = 845$, $df = 2$, $\chi^2 = 84.5$, $P < 0.001$. Moisture and breeding system for woody species only: $N = 568$, $df = 6$, $\chi^2 = 37.6$, $P < 0.001$ using only dioecious, gynodioecious, hermaphroditic, and monoecious species because of sample size; moisture and dimorphism for woody species: $N = 608$, $df = 2$, $\chi^2 = 15.2$, $P < 0.001$.

TABLE 2. Association of breeding system with vegetation type and elevation of woody species.*

	Dimorphism	Monomorphism
A) Vegetation type		
Cliff face	3/6	18/15
Coastal	1/4	13/10
Grassland	1/1	3/3
Shrubland	8/11	30/27
Shrubland-forest	9/9	21/21
Forest	145/136	325/334
Forest-bog	14/12	28/30
Bog	4/5	14/13
B) Elevation		
Coast	0/5	16/11
Coast-lowland	3/6	17/14
Lowland	74/71	168/171
Lowland-montane	21/15	31/37
Montane	78/79	192/191
Montane-subalpine	3/6	19/16
Widespread	6/3	4/7

* Observed/expected shown in each cell. Dimorphism and vegetation type: $N = 637$, $df = 7$, $\chi^2 = 8.2$, $P = 0.31$. Dimorphism and elevation: $N = 632$, $df = 6$, $\chi^2 = 19.1$, $P = 0.004$. Note that in four cells, expected values are < 5 and thus results should be interpreted with some caution.

species (tree, shrub, and herb), there is a significant association of dioecy with trees. One-third (32.0%) of the trees are dioecious, in contrast to only 16.9% of shrubs and 1.6% of herbs. A disproportionate number of gynodioecious species are herbaceous ($N = 25$, Table 1), primarily because of 19 species of *Lipochaeta* (Asteraceae).

Flora—Breeding system and habitat.—Not surprisingly, coastal, grassland, and shrubland vegetation contain proportionately more herbaceous species, with woody species predominating in the forest vegetation ($N = 938$, $\chi^2 = 93.9$, $df = 7$, $P < 0.001$). Woodiness is associated with lowland and montane elevations and herbaceous species are associated with coastal and coastal-lowland vegetation as well as montane-subalpine vegetation and widespread elevational distributions ($N = 947$, $\chi^2 = 98.4$, $df = 6$, $P < 0.001$). Woodiness is strongly associated with more mesic conditions while dry habitats have proportionately more herbaceous species, including several grass and composite species ($N = 959$, $\chi^2 = 34.2$, $df = 3$, $P \leq 0.001$). Because of these associations, we controlled for woodiness when using these measures of habitat.

In a three-way analysis controlling for woodiness, breeding system (dimorphism/monomorphism) is significantly associated with moisture (general test of association $Q_{CMH} = 18.9$, $df = 3$, $P < 0.001$; see Table 1), primarily because of woody species. Among woody species, dimorphism is significantly associated with mesic habitats and under-represented in dry and wet habitats ($N = 638$, $\chi^2 = 16.0$, $df = 3$, $P < 0.001$). Among herbaceous species, only 15 are dimorphic, and dimorphism is not associated with any particular moisture category ($N = 305$, $\chi^2 = 1.1$, $df = 2$, $P = 0.58$).

Among woody species, dioecious and gynodioecious species exhibit similar patterns and both are over-represented in mesic habitats relative to hermaphroditic species, primarily because of the large numbers of dimorphic species of *Melicope* (Rutaceae), *Psychotria* (Rubiaceae), *Coprosma* (Rubiaceae), and *Labordia* (Loganiaceae) occurring in mesic habitats. Relative to woody hermaphroditic species, there are more woody monoecious species in dry habitats and fewer in wet habitats than expected. About half (7/16 species) of these monoecious woody species in dry habitats are in the genus *Chamaesyce* (Euphorbiaceae).

Among woody species, there is no association of dimorphism with vegetation type (forest, shrubland, coastal vegetation, etc.; Table 2A). Woody species do show an association of dimorphism with elevation, with greater than expected proportions of dimorphic species having lowland and lowland-montane distributions (Table 2B).

We also examined the association of dimorphism with moisture (dry/mesic/wet) within lowland and montane forests (Table 3). The overall test of general association is significant, with lowland forests showing an association of dimorphism with mesic conditions and under-representation of dimorphism in wet conditions. For montane forests, there is no association of dimorphism and moisture.

Flora—Breeding system and pollination.—Because only 15 herbaceous species are dimorphic, we analyzed only woody species for the association of dimorphism, color, and flower length (Table 4). Dioecy and more generally, dimorphism, are most strongly associated with flowers that are small and green; the association of green flowers and dioecy (dimorphism) is true regardless of size (both small and large flowers, $P < 0.001$ for each size; Table 4). When green and white flowers are combined into an “inconspicuous” color category, dioecy (or dimorphism) is associated with “inconspicuous” small flowers ($P < 0.001$), but not for flowers that are large ($P = 0.10$; overall test of general association $Q_{CMH} = 10.9$, $N = 597$, $df = 1$, $P = 0.001$).

TABLE 3. Association of breeding system with moisture in lowland and montane forests.*

	Dimorphism	Monomorphism
A) Lowland forest		
Dry	12/14	39/37
Mesic	47/38	89/98
Wet	6/13	41/34
B) Montane forest		
Dry	5/4	15/16
Mesic	31/26	85/90
Wet	25/31	112/106

* Observed/expected shown for each cell. Overall test of general association: $N = 507$, $df = 2$, $Q_{CMH} = 9.8$, $P = 0.007$. Lowland forest: $N = 234$, $df = 2$, $\chi^2 = 8.8$, $P = 0.012$. Montane forests: $N = 273$, $df = 2$, $\chi^2 = 2.7$, $P = 0.26$.

TABLE 4. Association of breeding system with flower color and flower size for woody species.*

	Dioecious	Dimorphic	Monomorphic
A) Long flowers			
Green	29	38/14	26/50
Brown	0	0	1
White	14	20	143
Yellow	13	21	40
Orange	3	3	2
Pink-purple-red	2	2	72
Blue	1	1	6
Total not green	33	47/70	264/241
B) Short flowers			
Green	48	59/43	42/58
Brown	1	5	4
White	16	18	36
Yellow	4	4	22
Orange	2	3	8
Pink-purple-red	4	6	15
Blue	0	0	0
Total not green	27	36/52	85/69

* Observed or observed/expected shown. Although species are listed by flower color, the overall test of general association was of long/short flowers \times dimorphism/monomorphism \times green/not green flowers: $N = 597$, $df = 1$, $Q_{CMH} = 68.3$, $P < 0.001$. The overall test of general association for long/short flowers \times dioecy/not dioecy \times green/not green: $N = 602$, $df = 1$, $Q_{CMH} = 53.5$, $P < 0.001$.

In a related analysis, we examined the relationship of breeding system and inferred pollinator. Most (13/15) dimorphic herbaceous species and all four dimorphic herbaceous genera are insect pollinated. The great majority of woody hermaphroditic species are either pollinated by insects or birds. In contrast, among dimorphic species there is virtually no bird pollination, and most pollination occurs by insects, with some pollination by wind (Table 5). Although wind pollination is relatively uncommon in the native Hawaiian flora ($N = 36$), dioecy is significantly associated with wind pollination in woody species, in part because of the 13 wind-pollinated species of *Coprosma* (Rubiaceae), but this association also is true at the generic level (Table 5). Hermaphroditic species are disproportionately pollinated by birds (149 species; Table 5), primarily because of the 108 bird-pollinated species in the Campanulaceae (species of *Clermontia*, *Cyanea*, *Lobelia*, *Delissea*, *Rollandia*, *Trematolobelia*) descended from only three colonists (Sakai et al. 1995).

Flora—Breeding system and fruit dispersal.—Patterns of association of fruit type and breeding system depend upon the taxonomic level of analysis. Herbaceous species show no association of breeding system and fruit type, but among woody species, monomorphic breeding systems (particularly hermaphroditism) are strongly associated with fleshy fruits, and dimorphic breeding systems (both dioecy and gynodioecy) are associated with dry fruits (Table 6). This association is the result of a few species-rich genera. Four genera *Schiedea* (Caryophyllaceae), *Labordia* (Loganiaceae),

Pittosporum (Pittosporaceae), and *Melicope* (Rutaceae)] with a total of 71 species account for 60% of the woody dimorphic species with dry fruits. Five genera [*Pritchardia* (Arecaceae), *Clermontia* and *Cyanea* (Campanulaceae), *Cyrtandra* (Gesneriaceae), and *Myrsine* (Myrsinaceae)] with 156 species account for 60% of the woody monomorphic species with fleshy fruits. In fact, when associations are examined at the generic level, the direction of association reverses. For woody genera, there is a significant association of dimorphism with fleshy fruit (Table 6).

Colonists.—With respect to pollination, there is no association of breeding systems of colonists and presumed pollinators (dimorphic/monomorphic vs. insect/wind/birds; Table 7). With respect to dispersal, colonists with dimorphic breeding systems and strictly dimorphic lineages show significant association with fleshy fruit and dispersal internally by birds rather than dispersal externally by birds or by abiotic dispersal (Table 7). Eight of the 12 colonists that had autochthonous evolution of dimorphism also have fleshy fruit.

Lineages.—The four largest lineages with significant numbers of both monomorphic and dimorphic species [*Bidens* (Asteraceae), the endemic Hawaiian Alsinoideae (Caryophyllaceae), *Hedyotis* (Rubiaceae) and *Myrsine* (Myrsinaceae)] were examined in more detail for associations of ecological traits with breeding systems in current taxa. The endemic Hawaiian Alsinoideae is the only group among the four analyzed to show an association of breeding system with woodiness or pollination vector—dimorphic species are associated with woodiness and wind pollination while hermaphroditic species are more often herbaceous and insect pollinated

TABLE 5. Association of breeding system with inferred pollinator for woody species only.*

	Dioecy	Gynodioecy	Herm.	Monoecy
A) Herbaceous species				
Bird pollinated	0	0	0	0
Insect pollinated	4	8	157	2
Wind pollinated	0	0	56	14
B) Woody species				
Bird pollinated	1/34	0/7	149/98	0/11
Insect pollinated	110/90	22/19	228/262	40/29
Wind pollinated	21/8	6/2	7/24	2/3
	Dimorphic	Monomorphic		
C) Woody genera				
Bird pollinated	2	16		
Insect pollinated	18	64		
Wind pollinated	6	6		

* Observed/expected shown for each cell for woody species. For woody species, pollinator \times dioecy/gynodioecy/hermaphroditism/monoecy: $N = 586$, $df = 6$, $\chi^2 = 132.6$, $P < 0.001$. For woody genera, pollinator \times dimorphic/monomorphic: $N = 112$; $df = 2$, $\chi^2 = 6.4$, $P = 0.041$. Note that in two cells expected values are < 5 and thus results should be interpreted with some caution.

TABLE 6. Association of breeding system with fruit type.*

	Dimorph.	Monomorph.	Dioec.	Gynod.	Herm.	Monoec.
A) Herbaceous species						
Dry fruit	9/11	219/217
Fleshy fruit	6/4	88/90
B) Woody species						
Dry fruit	117/91	195/221	83/66	24/14	142/184	34/20
Fleshy fruit	70/96	262/236	56/73	5/15	247/205	8/22
C) Herbaceous genera						
Dry fruit	0	81
Fleshy fruit	2	11
D) Woody genera						
Dry fruit	8/14	46/40
Fleshy fruit	21/15	40/46

* Observed or observed/expected shown. For woody/herbaceous species \times dry/fleshy fruit \times monomorphic/dimorphic test of general association: $N = 966$, $df = 1$, $Q_{CMH} = 17.0$, $P < 0.001$. For herbaceous species, dry/fleshy fruit \times monomorphic/dimorphic: $N = 322$, $df = 1$, $\chi^2 = 0.89$, $P = 0.35$; for woody species: $N = 644$, $df = 1$, $\chi^2 = 21.0$, $P < 0.001$. For woody species, dry/fleshy fruit \times dioecy/gynodioecy/hermaphroditism/monoecy: $N = 599$, $df = 3$, $\chi^2 = 60.5$, $P < 0.001$. For woody genera: $N = 115$, $df = 1$, $\chi^2 = 5.84$, $P = 0.016$. Ellipses indicate data not calculated.

or self-pollinating (Table 8). In the endemic Hawaiian Alsinoideae as well as *Bidens*, dimorphism is also associated with dry habitat.

These lineages were also examined for biogeographical patterns (island age and single-island endemism; Table 8). *Bidens* and the endemic Hawaiian Alsinoideae show no association of either breeding system with single-island endemism or of breeding system with island age. Most species of *Myrsine*, regardless of breeding system, occur on the older islands and are single-island endemics. In *Hedyotis*, a greater proportion of species occurring on older islands are gynodioecious. All three of the latter lineages are under-represented on the youngest island of Hawai'i.

DISCUSSION

Biogeographical patterns. Sexual dimorphism of angiosperms in the Hawaiian Islands is the result of both colonization by dimorphic colonists as well as autochthonous evolution of dioecy (Sakai et al. 1995). The

biogeographical patterns within the Hawaiian Islands analyzed here are consistent with this interpretation. If dioecy evolves in situ, we would expect higher levels of dimorphism in endemic than indigenous species, and a higher incidence of dimorphism on older islands. These predictions hold for the flora as a whole—dioecy and gynodioecy are significantly associated with endemism and are more common on older islands. This association of increasing island age and dimorphism is complicated by the association of island age and woodiness, and woodiness and dimorphism. This pattern is a result of autochthonous evolution of dimorphism in several woody lineages (e.g., *Myrsine*) as well as greater numbers of species from strictly dimorphic lineages on older islands than younger islands [e.g., *Labordia* (Loganiaceae), *Psychotria* (Rubiaceae), and *Melicope* (Rubiaceae)]. Among the four species-rich lineages examined, *Myrsine* and *Hedyotis* both have more species on older islands, suggesting an origin on older islands for these lineages. Both dimorphic and monomorphic

TABLE 7. Presumed pollinators, fruit type, and dispersal agents of colonists. Observed/expected shown for each cell. Note that in three cells, expected values are <5 and thus results should be interpreted with some caution.

	Breeding system		
	Dimorphic	Monomorphic	
A) Pollinator			
Insect	20/18	137/139	
Wind	7/9	76/74	
Bird	1/1	10/10	$\chi^2 = 1.1$, $df = 2$, $P = 0.59$
B) Fruit type			
Fleshy	21/9	60/72	
Dry	9/21	179/167	$\chi^2 = 25.5$, $df = 1$, $P < 0.001$
C) Dispersal agent			
Bird—internal	23/9	55/69	
Bird—external	2/9	79/72	
Bird—internal or external	1/4	35/32	
Abiotic	4/7	62/58	$\chi^2 = 35.7$, $df = 3$, $P < 0.001$

TABLE 8. Ecological characteristics, biogeography, and breeding systems of current species from colonists of the Hawaiian Alsinoideae (*Schiedea* and *Alsiniidendron*, Caryophyllaceae), *Bidens* (Asteraceae), *Hedyotis* (Rubiaceae), and *Myrsine* (Myrsinaceae). Analysis of the Hawaiian Alsinoideae includes recent data on two species not included in other analyses. All *Myrsine* were woody, and all but one species of *Myrsine* and of *Hedyotis* were in mesic to wet environments. All but one *Bidens*, all but one *Hedyotis*, and all *Myrsine* are insect pollinated. Ni = Nihoa, K = Kaua'i, O = O'ahu, M = Maui Nui, Hi = the island of Hawai'i.

		Taxon		Dimorphic		Mono-morphic	
A) Woodiness	woody	Hawaiian Alsinoideae		9		9	
	herbaceous			1		8	
	woody	<i>Bidens</i>		6		6	
	herbaceous			4		3	
	woody	<i>Hedyotis</i>		10		4	
	herbaceous			4		2	
B) Moisture	dry	Hawaiian Alsinoideae		10		3	
	mesic/wet			0		14	
	dry	<i>Bidens</i>		5		1	
	mesic/wet			3		8	
	wide			2		1	
C) Pollinators	insect	Hawaiian Alsinoideae		0		11	
	wind			10		0	
	self			0		4	
	bird			0		1	
D) Biogeography		Ni	K	O	M	Hi	Total
Endemic Hawaiian Alsinoideae							
Single-island endemics							
Dimorphic		0	2	4	3	0	9
Monomorphic		1	7	4	3	0	15
• All species							
Dimorphic		0	2	5	4	0	10
Monomorphic		1	7	6	5	1	18
<i>Bidens</i>							
Single-island endemics							
Dimorphic		0	1	4	0	1	6
Monomorphic		0	2	1	3	0	6
All species							
Dimorphic		0	3	6	2	3	10
Monomorphic		0	2	3	5	2	9
<i>Hedyotis</i>							
Single-island endemics							
Dimorphic		0	3	2	2	0	7
Monomorphic		0	1	0	1	0	2
All species							
Dimorphic		0	10	8	7	4	14
Monomorphic		0	2	3	5	3	6
<i>Myrsine</i>							
Single-island endemics							
Dimorphic		0	3	2	0	0	5
Monomorphic		0	7	0	1	0	8
All species							
Dimorphic		0	4	4	2	1	7
Monomorphic		0	9	4	4	2	12

species occur on older islands, however, so neither lineage shows an association of breeding system and island age. *Bidens* and the endemic Hawaiian Alsinoideae also show no association of island age and dimorphism, although the latter group is under-represented on the island of Hawai'i. This contradicts earlier work on the endemic Hawaiian Alsinoideae, which suggested a stronger association of dimorphism with older islands (Weller et al. 1990), and occurs because of new

information on the group, including new species and reinterpretations of others (Wagner et al. 1995). Most lineages in the Hawaiian flora have not been well studied, and as more detailed studies of other taxa become available, other changes will undoubtedly improve our interpretation of evolution of breeding systems in the archipelago.

If Baker's (1967) law is true with the Hawaiian Islands, we would expect a greater proportion of dioe-

cious species to be single-island endemics, since hermaphrodites would be expected to be the better colonists. In contrast, if Bawa's (1982) prediction that dioecious species are more readily dispersed because of an association with bird dispersal is true, then a greater proportion of hermaphroditic species would be predicted to be single-island endemics. We found no association of single-island endemism and breeding system for the angiosperm flora as a whole nor within lineages with autochthonous evolution of dimorphism. Further tests of this hypothesis await better resolution of phylogenies of these groups. In *Bidens*, gynodioecy appears to have evolved only once (F. Ganders, unpublished manuscript), and thus the distribution of gynodioecious species on all the major islands suggests that the breeding system has not severely limited colonization. Similarly, in *Wikstroemia*, the autochthonous evolution of dioecy at least twice (Mayer and Charlesworth 1992) does not appear to have hindered colonization. In the endemic Hawaiian Alsinoideae, dimorphism is most likely to have evolved independently 2–6 times (Wagner et al. 1995, Weller et al. 1995). In general, dispersal has been limited in this group, regardless of breeding system, with only four species occurring on more than one main island.

Habit.—The Hawaiian angiosperm flora has a high proportion (65.1%) of woody species, and secondarily woody species have evolved on a number of occasions (Carlquist 1974). The Hawaiian flora has a strong association of dioecy and woodiness, although it is interesting to note that there is no association of woodiness and dioecy in *Bidens* and *Hedyotis*. The association of woodiness and dioecy has also been noted in many other floras (Bawa and Opler 1975, Croat 1979, Conn et al. 1980, Freeman et al. 1980, Sobrevila and Kalin Arroyo 1982, Flores and Schemske 1984, Bullock 1985, Fox 1985, Steiner 1988). The percentages of dioecy for Hawaiian shrubs (16.9%) and herbs (1.6%) are similar to values found in North Carolina (Conn et al. 1980) and Panama (Croat 1979), but are much greater for Hawaiian trees (32%) than trees elsewhere [North Carolina 12% (Conn et al. 1980), Panama 21% (Croat 1979), Puerto Rico 18% (Flores and Schemske 1984)].

The association of woodiness and dioecy generally has been attributed to strong selection for outcrossing in large long-lived plants that might otherwise self through geitonogamy (reviewed in Bawa 1980; see also Steiner 1988). Muenchow (1987) attributed that association in the northeast United States to pollination of shrubs by small insects abundant in the understory. Baker and Cox (1984) suggested that in the Hawaiian Islands, with the limited opportunities for long-distance dispersal, the longer life-spans of woody plants and potential for vegetative propagation permitted establishment of populations through sequential colonizations within the lifetime of a plant, rather than necessarily requiring potential mates to arrive simulta-

neously. The limited number of native annual species is consistent with the idea that availability of mates may have been a limiting factor for colonists, regardless of breeding system, but other factors (e.g., a nearly aseasonal subtropical climate) may also influence the proportion of annual species in the flora. With the great isolation of the Hawaiian Islands, the chances of sequential colonizations within the life-span and space of even a long-lived plant seem limited. Simultaneous arrival through clumped dispersal from ingestion by birds seems more likely (see *Discussion: Fruit dispersal* below).

Unlike other studies that have shown higher levels of dioecy within certain community types (Bawa and Opler 1975, Freeman et al. 1980, Steiner 1988), our analysis of breeding system and community type does not show any patterns of association. Flores and Schemske (1984) also found little variation in the frequency of dioecy among life zones in Puerto Rico. Better field observations are needed in the Hawaiian Islands, however, since often only limited information on communities is available from herbarium specimens and collectors have used many different classification schemes of habitats. In addition, some species [e.g., *Styphelia* (Epacridaceae), *Metrosideros* (Myrtaceae)] in the Hawaiian Islands occur across a broad distribution of community types and elevations. Unfortunately, detailed studies may not be possible because plant communities in Hawai'i continue to disappear at an alarming rate due to habitat loss and alteration. Those remaining are becoming increasingly disturbed or eliminated because of the invasion of alien plant species and activities of alien animals such as feral goats, pigs, and insects or other invertebrates (Cuddihy and Stone 1990, Wagner et al. 1990).

Habitat. Analyses of habitat (moisture and elevational distributions) of dimorphic species are very heavily biased by a few species-rich genera [*Melicope* (Rutaceae), *Psychotria* and *Coprosma* (Rubiaceae), *Labordia* (Loganiaceae)], and as a consequence, dimorphic species are associated with mesic habitats and lowland and lowland–montane distributions in the flora as a whole. In contrast, dimorphism is associated with more xeric habitat within both *Bidens* and the Hawaiian Alsinoideae. In the Alsinoideae, the shift to dry habitat may precede the change in breeding system, as evidenced by the occurrence of dry-site hermaphroditic species but the absence of wet site dimorphic species (Weller and Sakai 1990). Freeman et al. (1980) suggested that wind pollination in combination with disruptive selection for spatial segregation of the sexes based on moisture requirements has promoted the evolution of dioecy in some arid areas. Interestingly, spatial segregation of the sexes (with females in more mesic microhabitats) has been reported in the one wind-pollinated subdioecious species of *Schiedea* (Sakai and Weller 1991), although further work is needed to determine whether this is adaptive.

Pollination.—The Hawaiian angiosperm flora has an abundance of small green or white flowers, colors presumably associated with pollination by wind or unspecialized insects. Potential insect pollinators of the small-flowered groups include many species of small native moths and flies; their disproportionate representation in the native fauna reflects the better long-distance dispersal ability of the smaller insects (Howarth and Mull 1992). Carlquist (1974) suggested that the lack of specialized pollinators in the Hawaiian Islands limits the number of specialized flowers, and Bawa (1980) suggested that the absence of specialized pollinators is correlated with the high incidence of dioecy in the Hawaiian Islands. Specifically, he hypothesized that the association of generalist pollinators with dioecy allows dioecious species to establish more readily than hermaphroditic species requiring specialist pollinators [Bawa 1982 although see Renner and Feil (1993) for a contrasting viewpoint]. Charlesworth (1993) also suggested that dioecy may evolve more easily if pollination mechanisms (such as wind or small insects) cannot discriminate female flowers from hermaphroditic flowers with pollen rewards. In the Hawaiian Islands there are only a few large Lepidoptera (only two species of butterflies) and no bumble bees, although there are six native species of hawk moths (Howarth and Mull 1992), but none are abundant. In general, the fauna in the Hawaiian Islands is depauperate, with only one native terrestrial mammal (a bat), and with only $\approx 50\%$ of known orders and only 15% of known families of insects (Howarth and Mull 1992). Unfortunately, because of the many and continuing extinctions of native fauna, it may become increasingly difficult to identify precisely and to assess the importance of native pollinators of native plants.

Within the Hawaiian flora, most dimorphic woody species and genera have small green flowers and are pollinated by wind and small insects, with virtually no bird pollination. In contrast, there is an association of hermaphroditism and bird pollination at the specific level because of a few species-rich lineages in the Campanulaceae. There is a significant association of dioecy with wind pollination at both the specific and generic level in the native Hawaiian flora. Other surveys have also shown an association of dimorphism with wind pollination (western North America, Freeman et al. 1980; northeast U.S., Meuncho 1987; Cape flora of South Africa, Steiner 1988), although others show dioecy associated with unspecialized insect pollination (temperate flora of Great Britain, McComb 1966; tropical forests, Bawa 1980; New Zealand, Lloyd 1985; reviewed in Thomson and Brunet 1990). The disproportionate association of anemophily and dioecy or dimorphism at the specific and generic level is contrary to earlier observations of dimorphism associated with entomophily at the species level in the Hawaiian Islands (Carlquist 1974, Bawa 1980). Most dimorphic species are insect pollinated, but most of the flora is

also insect pollinated. We find that insect pollination is actually under-represented in dimorphic and dioecious species and genera, and that wind pollination is over-represented. The association of dimorphism with wind pollination is also evident within the endemic Hawaiian Alsinoideae, and is correlated with a shift to drier habitats and potential loss of pollinators (Wagner et al. 1995, Weller et al. 1995). The association of anemophily and dimorphism does not hold for *Bidens*, *Myrsine*, and *Hedyotis*.

Unlike analyses at the specific and generic level, analysis of colonists shows no pattern of association of pollinators and breeding systems. The contrasting results for species, genera, and colonists suggest how difficult it may be to show meaningful correlation (much less causation) of dioecy with pollinators for the flora as a whole because of phylogenetic considerations. Steiner (1988), in an analysis of the Cape flora of South Africa, also found that associations of pollination system and breeding system were heavily influenced by species-rich taxa and shifted with the taxonomic level of analysis.

Fruit dispersal.—Analysis of associations of breeding system and dispersal mode also show the importance of phylogenetic considerations. For example, one hermaphroditic colonist with fleshy fruit has given rise to 91 species in the Campanulaceae, 15% of all hermaphroditic species in the flora. The colonist of *Melicope* (Rutaceae) was probably functionally dioecious with dry fruit and gave rise to 47 species, 45 of which are dimorphic with dry fruit and account for 22% of the 202 dimorphic species in the flora. As a result of these taxa, at the specific level dimorphism is associated with dry fruits and hermaphroditism with fleshy fruits, even when woodiness is controlled. At the generic level, however, dimorphism is associated with fleshy fruits for woody taxa.

The association of fleshy fruits and dimorphism in current genera is related to the very strong association in colonists of dimorphism and presumed dispersal of propagules through ingestion by birds. Both Bawa (1980) and Lloyd (1985) suggested that there are disproportionate numbers of dimorphic colonists on remote islands because most long-distance dispersal of immigrants occurred through bird dispersal, and dimorphism is often associated with bird dispersal. Carlquist (1974) also suggested that most long-distance dispersal to the Hawaiian Islands was by birds, either internally or externally. Our analysis supports this idea. In addition, while monomorphic colonists arrived both internally and externally on birds, almost all dimorphic colonists arrived through presumed ingestion of propagules. Carlquist (1974) noted that, in general, ingestion and consequent clumped dispersal of propagules facilitates colonization. Clumped dispersal may be especially important for dimorphic (and especially dioecious) colonists that cannot reproduce without other plants. The association of dimorphism in colonists

and dispersal by avian frugivores in the Hawaiian Islands may be a reflection of source floras that have a disproportionate number of dioecious taxa relative to hermaphroditic taxa that are dispersed by frugivores (Bawa 1982, see also Baker and Cox 1984). This association may also occur because the only dimorphic taxa that could establish in the islands were those with clumped dispersal resulting from internal bird dispersal. The association of dimorphism and fleshy fruit in woody genera and colonists is consistent with Bawa's (1980) and Givnish's (1980) correlation of dioecy and animal dispersal of fleshy fruits. The correlation may be evident, not so much because a greater proportion of fruits are dispersed in dioecious species, but primarily because of the importance of clumped dispersal associated with these long-distance dispersal events.

In groups where dimorphism evolved within the Hawaiian Islands, changes in seed dispersal patterns were not correlated with changes in breeding system. Within the Hawaiian Alsinoideae (*Alsinidendron*), fleshy calyces evolved in species that also evolved facultative or obligate selfing, but the species have few fruits and the dispersal agent is unknown, although it is assumed to reflect bird dispersal. There is no evidence that dispersal of fleshy fruits by specialist frugivores drives the evolution of dioecy because of accelerating fitness gains for females with large fruit crops (Bawa 1980, Givnish 1980). In *Bidens*, dispersal shifted from external bird dispersal to wind dispersal, but again with no obvious correspondence to breeding system. It may be that for dioecious species, the clumped pattern of disseminules possible with bird dispersal is not as important for dispersal within archipelagos as in long-distance dispersal because dispersal events within archipelagos are more frequent.

The Hawaiian flora has the highest known incidence of dioecy of any area in the world, a result of both colonization by dimorphic species as well as evolution of dioecy in situ (Sakai et al. 1995). Dimorphism appears to be associated with woodiness, small green flowers, and fleshy fruits, although particular care must be taken in interpreting these associations because of the limited number of colonists and small size of the flora. The limited number of lineages comprising the Hawaiian flora also creates a unique opportunity for detailed study of each independent origin of dioecy and its associated traits. We know that in some cases, the use of the colonist's breeding system coupled with an assumption of parsimony in evolution of dimorphism in situ, rather than use of an explicit phylogeny, may lead to underestimates of the evolution of dioecy, as shown by more detailed studies of groups [e.g., dioecy evolved at least twice in *Wikstroemia* (Mayer and Charlesworth 1992) and 2–6 times in *Schiedea* (Wagner et al. 1995, Weller et al. 1995)]. We also know that use of species-level and genus-level analyses of ecological correlates may be misleading in some cases, as shown in the contrast of those analyses with those controlling

for lineage. Better knowledge of phylogenetic patterns and further ecological studies, particularly within those groups evolving dioecy autochthonously, are needed to determine causality.

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