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Patterns of Endangerment in the Hawaiian Flora

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Abstract.—The Hawaiian flora, because of its great isolation, high levels of endemism, known lineages, and high rates of endangerment, offers unique opportunities to explore patterns of endangerment related to phylogeny, ecological and life history traits, and geographic patterns. Nine percent of the native flora of 1159 taxa are already extinct, and 52.5% are at risk (extinct, endangered, vulnerable, or rare). Risk is strongly associated with limited geographic distribution at several scales: endemic taxa (native only to the Hawaiian Islands) are at far greater risk than indigenous taxa (with both Hawaiian and extra-Hawaiian ranges); single-island endemics are more at risk than multi-island endemics; small islands have the highest proportion of endemic taxa at risk; and endemics with more limited habitat distributions (elevation, community type) are more at risk. Historic population density is a strong predictor of risk, and taxa with low historic population densities are at greatest risk with rapid anthropogenic changes. Among the major islands, Maui Nui has the highest percent of taxa that are extinct. Kaua'i has the lowest percent of extinct taxa and the highest proportion of single-island endemic taxa that are rare. Endemic taxa at risk are associated with distributions in shrublands, forests, bogs, and cliff habitats. Endemic taxa with distributions in low elevation dry habitats have the highest proportion of taxa at risk, but the greatest absolute numbers of taxa at risk have distributions in mesic lowland and montane forests, and in wet montane forests. The life history patterns associated with risk are complicated, and inclusion of the effects of evolutionary relationships (lineages) changes some of these patterns. Species level analyses without respect to lineage shows risk associated with monomorphic (hermaphroditic) breeding systems and bird pollination because of the large number of hermaphroditic, bird-pollinated species in the Campanulaceae. Analyses incorporating the effect of lineage greatly reduce the impact of large lineages and result in an association of risk with insect pollination, and no effect of breeding system. There is no association of lineage size and the percent of taxa at risk within the lineage; endemic taxa from lineages with large radiations are at no greater risk than endemic single-taxon lineages. The percentages of taxa at risk at the family level in the Hawaiian Islands and worldwide (excluding Hawaiian taxa) are positively correlated, although flowering plant families in the Hawaiian Islands have a much greater proportion of taxa at risk. Some of the approaches described here may be useful to predict geographical and biological patterns of endangerment in island and island-like ecosystems under increasing pressures of endangerment and extinction. [Angiosperms; biogeography; conservation planning; endangered plants; endemism; extinction; Hawaiian Islands; rarity.]

Island ecosystems, including the Hawaiian Islands, are well known for the insights they have provided about speciation and endemism and, more recently, about extinction (e.g., Carlquist, 1974; Wagner and Funk, 1995; Craddock, 2000; Myers, 2000). More than half of the 25 biodiversity hotspots (defined as areas where exceptional concentrations of endemic species are undergoing exceptional loss of habitat) are islands or island groups (e.g., New Caledonia, New Zealand, Madagascar, the Philippines) or ecological islands (e.g., Cape Floristic Province, southwestern Australia, Caucasus [Myers et al., 2000]). The Polynesia/Micronesia hotspot includes the Hawaiian Islands and ranks fourth in the world for the number of endemic plant species per area (after only the eastern arc and coastal forests of Tanzania/Kenya, the Philippines, and New Caledonia). Less than a quarter of the original area of primary vegetation of Polynesia/Micronesia remains (Myers et al., 2000). Within the USA, the state of Hawaii has the greatest number of extinct plant and animal species (Stein et al., 2000), and all four Hawaiian counties rank in the top five counties nationally for numbers of threatened or endangered federally listed plant and animal species (Rutledge et al., 2001).

Many of the factors associated with distinctive evolutionary patterns in the native Hawaiian biota may also be related to the vulnerability of the flora. The islands contain a high diversity of habitats over a small geographical area, with isolation limiting colonization and leading to a high proportion of endemism. Volcanic in origin,

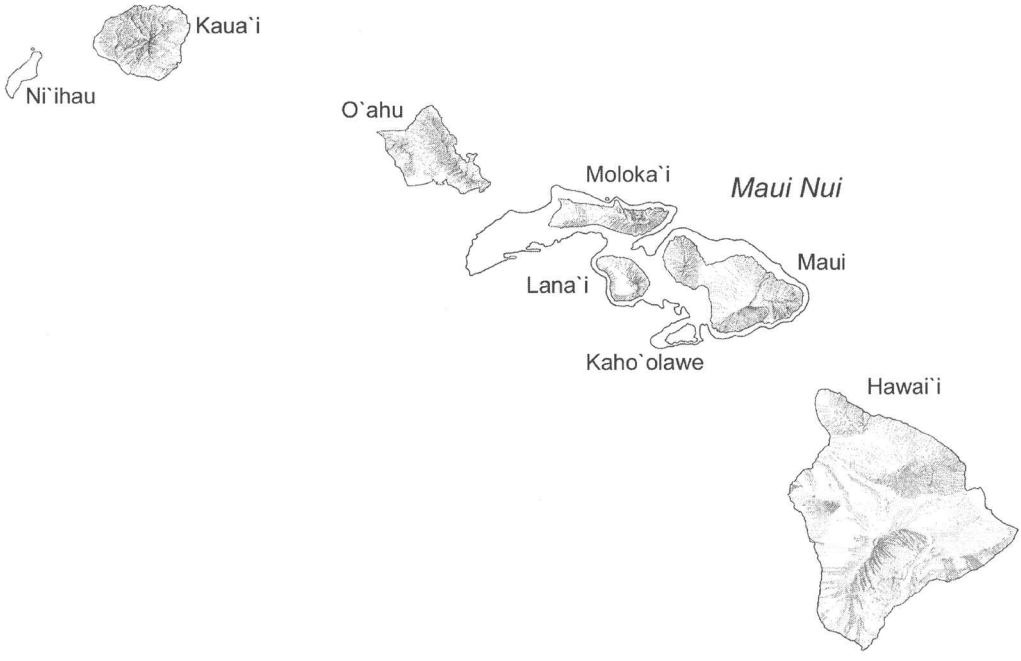

FIGURE 1. Map of the Hawaiian Islands (redrawn from Macdonald et al., 1983: Fig. 20.1), showing the current main Hawaiian Islands as well as the 180-m submarine contour of Maui Nui. The Northwest Hawaiian Islands, extending to the northwest, are not shown. During the formation and early history of the current main islands, various connections have led to formation of larger islands (Carson and Clague, 1995). Kaua'i and Ni'ihau formed as two separate islands that coalesced as Kaua'i grew, but later become separate islands once again as the growth subsided. A wide and deep channel separates Kaua'i and the Wai'anae volcano on O'ahu. In contrast, subsequent volcanoes after Wai'anae and until Haleakala on Maui have each coalesced with the previously formed volcano. Similarly, each of the volcanoes that make up the Maui Nui complex (east and west Maui, eastern and western Moloka'i, Lana'i, and Kaho'olawe), were at one time joined by land bridges with elevations as much as 1,300 m above sea level. The Maui Nui complex first became two islands, one consisting of Moloka'i and Lana'i, the second consisting of Maui and Kaho'olawe, <300,000–400,000 years ago. Kaho'olawe separated from Maui, and finally Lana'i separated from Moloka'i, both within the past 100,000–200,000 years. The channel between Haleakala (Maui) and Kohala (Hawai'i) volcanoes is 1,890 m deep and subsidence on the south side of Maui has been on the order of only 1,000 m. Consequently, Maui and Hawai'i have never had a land bridge between them.

the Hawaiian Islands were formed by a stationary hot spot as the Pacific tectonic plate moved in a northwesterly direction. This geologic hot spot has been actively producing islands for ~85 million years (my) (Clague, 1996). The Northwest (NW) Islands are a series of low, older islands and atolls (29 my old, 8 sq km). The eight larger islands range in age from Kaua'i (5.1 my old, 1,430 sq km) to the youngest island of Hawai'i (<0.5 my old, 10,433 sq km) with elevations as high as 4,205 m on Mauna Kea (Fig. 1) (Carson and Clague, 1995; Clague, 1996). The taller mountains create distinct rainshadows, resulting in steep elevation and moisture gradients and corresponding shifts in communities. The islands create natural boundaries associated with patterns of endemism and rarity, and this correspondence between political boundaries, natural habitats, and island distributions makes identification of patterns of endemism and rarity easier than in other areas. Risk can be determined not only locally on an island, but also within the state, and globally for endemic taxa.

Most of the flora is endemic, with distributions restricted only to the Hawaiian Islands. Only a small proportion (10%) of the native Hawaiian flora is indigenous (with Hawaiian and extra-Hawaiian distributions) and has range distributions comparable with those of many continental species (Wagner et al., 1999a). As a consequence, the patterns of risk described for endemic taxa are at a much finer scale within the Hawaiian Islands than in many other areas.

Few plants and animals have been able to successfully cross the Pacific Ocean (3,200 km from the nearest continent of North America), colonize, and establish reproducing populations in the islands. Because native plant species have evolved in the absence of large grazing or browsing mammals and many plant competitors, they have been particularly susceptible to extinction after the introduction of alien species by the Polynesians ~1,600 years ago and by Europeans beginning ~200 years ago (Wagner et al., 1985). Unique adaptations such as secondary woodiness (Carlquist, 1974) can evolve in island habitats (e.g., Ballard and Sytsma, 2000), but these adaptations also may result in species that cannot compete well in highly perturbed systems, especially with large introduced mammals.

The small size of the flora has allowed identification of colonists and assessments of their descendent lineages. The Hawaiian Islands, along with the Cape Floristic Region in South Africa (Cowling and Pressey, 2001), are among the few areas in the world with high levels of endemism, high risk to the flora, and enough information on evolutionary processes of diversification (lineages) to incorporate this information in conservation decisions. The native Hawaiian flora is composed of 1,029 species from only ~293 successful presumed colonists (Sakai et al., 1995a,b; Wagner et al., 1999a). Most of the colonists gave rise to new endemic species, but about one-third of the colonists were more widespread indigenous species that did not radiate (Sakai et al., 1995a; Wagner et al., 1999a). Specific phylogenetic hypotheses have been proposed for only a few lineages (e.g., Hawaiian silversword alliance (Asteraceae): Baldwin and Robichaux, 1995; Baldwin, 1997; Baldwin and Sanderson, 1998; *Bidens* (Asteraceae): Ganders et al., 2000; *Schiedea* (Caryophyllaceae): Weller et al., 1995; Wagner et al., 1995; Sakai et al., 1997; *Pittosporum* (Pittosporaceae): Gemmill et al., 2002; *Rubus* (Rosaceae): Alice & Campbell, 1999; and *Viola* (Violaceae): Ballard & Sytsma, 2000).

In this study we combine knowledge of the geology, ecology, biogeography, and the evolutionary history of angiosperm taxa (lineages) in the Hawaiian Islands to examine patterns of endangerment with respect to several factors. These factors include (1) the number and proportion of taxa at risk at different taxonomic levels (taxa at minimum recognized rank, species, genus, family); (2) endemism (endemic vs. indigenous to the Hawaiian Islands); (3) island age and island distributions (single- vs. multi-island distributions) of taxa; (4) habitat (elevation, moisture, physiognomy) and life history characteristics (habit, breeding system, flower size and color, presumed pollinators, fruit type, population size, and density) of taxa; (5) phylogenetic patterns, including ecological characteristics of lineages and lineage size (number of taxa per colonist); and (6) patterns of rarity, based on geographical range (island distributions), habitat specificity, and local population density.

Taxonomic levels.—Listings of endangered taxa from the World Conservation Union (IUCN), the Nature Conservancy Heritage Program database, and the US Fish and Wildlife Service are usually at the minimum taxonomic rank recognized (infraspecific taxa or species; Wagner et al., 1999b). If species vary greatly in the number of infraspecific taxa recognized, and if these infraspecific taxa share characteristics that make them endangered, then concerns over endangerment at the lowest taxonomic level may emphasize particular species and genera at the expense of more diverse taxa. Knowledge of how these taxonomic patterns influence endangerment is critical if decisions about conservation priorities are to reflect not only the number of taxa but also their biological distinctness (Soltis and Gitzendanner, 1999). To the extent that familial relationships reflect a common evolutionary history, family-level comparisons may show patterns of biodiversity and endangerment across broader geographical regions (Edwards, 1998).

Endemism and geographic distributions.—Geographic distributions will undoubtedly affect patterns of risk. Indigenous taxa, with broader global distributions than endemic taxa, also may have life history traits that result in greater geographic distribution within the Hawaiian Islands, and thus indigenous taxa may be less at risk than endemic taxa. Endemic taxa occurring only on single islands within the chain (single-island endemics; SIEs) may be more at risk than those with multi-island distributions (multi-island endemics). Geographic distributions may also provide indirect evidence for the vulnerability of older versus more recently

evolved taxa. Older islands have greater numbers of SIE taxa (Sakai et al., 1995b). If the mean age of SIE taxa is older on older islands, and if more recently evolved taxa are more susceptible to extinction, then younger islands should have a greater proportion of SIE taxa at risk. Alternatively, older islands with steeper valleys and ridges may have more dissected and smaller patches of habitat than larger, younger islands, thus increasing the risk to SIE taxa on older islands.

Ecological and life history traits.—In recent years, several studies have tried to identity habitat and life history characteristics that distinguish rare from common species, in part because rare species are often species at risk (e.g., Harper, 1979; Lahti et al., 1991; Kunin and Gaston, 1997; Kunin and Shmida, 1997; Medail and Verlaque, 1997; Cowling and McDonald, 1998; Hegde and Ellstrand, 1999; Duncan and Young, 2000; Gitzendannner and Soltis, 2000). Unfortunately, different traits have been measured in many of these comparisons, making it harder to discern more general patterns (Bevill and Louda, 1999).

Phylogenetic patterns.—When taxa are closely related to each other, they are not independent samples, and these relationships confound statistical analysis of patterns of endangerment (e.g., Cotgreave and Pagel, 1997; Kunin and Smida, 1997). Several methods consider taxonomic and phylogenetic relationships in these analyses (reviewed in Cotgreave and Pagel, 1997), although most taxa in lack morphological or molecular phylogenies. In the absence of more detailed phylogenies, in the Hawaiian Islands lineages can be identified consisting of current species descended from a presumed common colonist. Comparison of these lineages, although not as refined as phylogenetic analyses, allows assessment of endangerment with some consideration of phylogeny and can take more evolutionary history into account than simple species-level analyses of endangerment. Life history characteristics and habitat preferences may be conserved within lineages, and these traits may make some lineages more prone than others to rarity and endangerment (Edwards, 1998).

Lineage size may also affect patterns of endangerment. In the Hawaiian Islands, large endemic lineages are the result of extensive radiation and probably have a larger proportion of recently evolved taxa. If greater radiation is associated with increasing differentiation and potentially greater specialization with narrower habitat specificity, then taxa in these large lineages may be more prone to extinction. In addition, the ability to analyze ecological traits such as habitat, moisture, and elevation at both the species level and lineage level may be one way to indicate functional groups as well as the uniqueness and value of particular species in maintaining ecosystem functions (M. Bruegmann, pers. comm.).

Rarity.—Rarity and the risk of endangerment and extinction are often, but not always, linked. Characteristics associated with rare taxa may be the traits that make them prone to extinction, or alternatively, may be the traits that allow them to persist as rare species (Fiedler and Ahouse, 1992; Kunin and Gaston, 1997). Interpretation of the effects of rarity on the risk of endangerment may be difficult because historically rare species may differ significantly in life history traits from historically common species recently made rare, and these two kinds of histories may be difficult, if not impossible, to distinguish. Rabinowitz (1981) described seven types of rarity, based on combinations of geographic range (broad, narrow), habitat range (wide, narrow), and local population density (common, sparse). Although this classification does not distinguish causes and effects of rarity, it remains a useful descriptive tool. In general, common taxa (with wide geographic distributions, broad habitat ranges, and dense populations) are not expected to be at risk, whereas classic rare species (with narrow geographic distributions, narrow habitat specifications, and sparse populations) are predicted to be at greatest risk.

METHODS

Taxonomy and lineages.—Taxonomy follows the *Manual of Flowering Plants of Hawai'i*, revised edition (Wagner et al., 1999a), including updates in the supplement to this edition. Each taxon was placed in a hypothesized lineage composed of current taxa arising from the same colonist as described in Sakai et al. (1995a,b; based on Wagner et al. [1990] with modifications). The lineages were updated to reflect recent taxonomic revisions (Wagner

et al., 1999a) and phylogenetic studies published since 1990.

Biogeography, endemism, and ecological traits.—Only native (endemic and indigenous) taxa were included in this analysis. Data on endemism and the geographical distribution of taxa were taken from Wagner et al. (1999a). Species and lineages were classified as endemic, indigenous, or both (i.e., with both endemic and indigenous infraspecific taxa or species). Endemic taxa and lineages were classified as SIEs if they occurred naturally only on a single major Hawaiian island, or as multi-island endemics if they occurred naturally on more than one major Hawaiian island. The NW Islands (Kure Atoll, Midway Atoll, Pearl and Hermes Reef, Lisianski, Laysan, Gardner Pinnacles, French Frigate Shoals, Necker, and Nihoa) were pooled and considered as one island because of their current small surface area and similar coastal habitats. In some analyses, the Pleistocene island of Maui Nui (including the current islands of Moloka'i, Lana'i, Maui, and Kaho'olawe) was considered as one biogeographic island because of connections in the recent geologic past (Fig. 1) (Carson and Clague, 1995; Clague, 1996).

Ecological traits of species and lineages followed the descriptions of character states and data given in Sakai et al. (1995b), with updates to reflect taxonomic changes from Wagner et al. (1999a). Life history and ecological traits included data on flower size (small [<7 mm] or large [7 mm or longer]) and flower color. The breeding system was described as one of eight states (hermaphroditic, monoecious, andromonoecious, gynomonoecious, gynodioecious, subdioecious, polygamodioecious, or dioecious) or alternatively, as sexually monomorphic (pooling the first four breeding systems) or dimorphic (pooling the latter four breeding systems). The presumed pollinator (bird, insect, wind), fruit type (fleshy or dry), lifespan (annual or perennial), and habit (tree, shrub, subshrub [woody at the base], herbs, vines, or lianas [woody vines]) were also described. Habitat characteristics included four moisture categories (wet, mesic, dry, and widespread for species regularly occurring in more than one of the first three categories), seven elevation categories (coastal, both coastal and lowland, lowland, both lowland and montane, montane, montane–subalpine, wide), and eight community types (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. For species occurring now only in disturbed areas, habitat was inferred on the basis of the presumed previous vegetation type. Lineages were characterized by endemism (with taxa that were indigenous, endemic, or both endemic and indigenous). The breeding system of the lineage (dimorphic, monomorphic, or both) was determined by the breeding systems of current taxa or by comparison with the breeding system of species presumed to be related. The presumed pollinator (bird, insect, wind), fruit type (fleshy, dry), and presumed mode of long-distance dispersal (dispersal by birds internally, by birds externally [barbs, mud, etc.], by birds [ambiguous if it was internal or external bird dispersal], or abiotically [oceanic drift, rafting, or air flotation]) also were inferred from traits of current taxa and by comparison to presumed related species.

Conservation status.—Categories used to indicate degrees of threat to native species for conservation status were based on those in Wagner et al. (1999b), which in turn were adopted from the *IUCN Plant Red Data Book* (Lucas and Synge, 1978), with modifications. The definitions provided here are similar to those used in the earlier assessment by Wagner et al. (1990). Extinct taxa (EX) are those for which evidence indicates that plants are no longer extant in the wild, although some species currently in this category (particularly taxa with very restricted distributions) will likely be rediscovered. Also included as extinct are taxa that have not been collected for decades or for which known occurrences are no longer extant but recent or specific information is lacking (EX?) and indigenous taxa with no known extant Hawaiian populations remaining (EXH). Endangered taxa include endemic taxa in danger of becoming extinct throughout all or a substantial portion of their range unless the threats jeopardizing their survival are alleviated (E), and indigenous taxa that are endangered throughout all or a substantial portion of their range in the Hawaiian Islands (EH). Vulnerable taxa are endemic taxa likely to become endangered in the near

future unless the threats to their survival are removed or reduced (V), and indigenous taxa that have imminent threats to populations in the Hawaiian Islands (VH). Rare taxa are endemic (R) or indigenous (RH) taxa occurring in small, localized populations that are not believed to be endangered or vulnerable at present but that could be considered at risk. This category does not distinguish between taxa that historically occur naturally in small populations and those that have been reduced in population size because of anthropogenic changes. In several analyses, taxa were pooled further into two categories of risk: "at risk" (taxa classified as EX, E, V, R) and "apparently secure" (AS; taxa not included in one of those four categories). These risk assessments for the native flowering plants of the Hawaiian Islands were recently compared with those of the U.S. Fish and Wildlife Service and those of the Hawai'i Natural Heritage Program of The Nature Conservancy of Hawai'i and are largely overlapping (Wagner et al., 1999b). We have used the Wagner et al. (1999b) assessment because it is the most current and comprehensive system available. The risk level of lineages was calculated as the proportion of taxa that were at risk within that lineage. In some analyses, lineages were classified as at risk if half or more of the taxa comprising the lineage were at risk.

Population number and population size.—The number of presumed populations and estimated total number of individuals for each taxon were taken in part from data refined and updated by the US Fish and Wildlife Service, based on the Center for Plant Conservation annual meetings in Honolulu in 1997. At those meetings, field botanists working in the Hawaiian Islands meet to tabulate these statistics and the threats for all the Hawaiian taxa of conservation concern. We updated data on several taxa by contacting Hawaiian botanists with direct field knowledge of current population status and by using data from research on particular genera (e.g., *Phyllostegia* [Wagner, 1999], *Schiedea* and *Alsinidendron* [Weller, Sakai, and Wagner, unpubl.]).

Rarity.—We constructed categories (geographic range, habitat specificity, and local population size) corresponding to those of Rabinowitz (1981) for use in the Hawaiian Islands. The geographic range or distribution of a taxon was classified as large if taxa occurred on more than one island (multi-island) and small if a taxon occurred on only one island (single-island). Habitat specificity was classified as narrow if a taxon occurred most commonly in only one community type (coastal, cliff, bog, shrubland, grassland, or forest) or classified as broad if it commonly occurred in more than one community (combinations of two or more of any of the previous categories).

Local abundance was estimated by using three categories (high, medium, low) of historic population density (within a population, the relative number of plants of that taxon/area at a majority of sites). Historical population density is intended to be an estimate of prehuman (pre-Polynesian) population densities. To estimate historic density, we used information from published floras (e.g., Hillebrand, 1888; Rock, 1913; Wagner et al., 1990). We also used information from field observations of Wagner and several field botanists in Hawai'i (T. Flynn, D. Herbst, J. Lau, D. Lorence, T. Motley, S. Perlman, and K. Wood) to obtain more quantitative data. High-density taxa are common (c) and often dominant or codominant elements of the canopy, subcanopy, or understory. Medium-density taxa are uncommon overall (u) but usually relatively frequent in a particular area. Low-density taxa are rare (r), with infrequent and scattered individuals. Differences in densities within an island were averaged to create one value. When population densities varied greatly within taxa from island to island, taxa were classified with a combination of categories. These categorizations are extrapolations from knowledge of population densities in current relatively intact habitat. Unfortunately, because so much of the natural habitat in the Hawaiian Islands is radically changed from the prehuman landscape (Juvik and Juvik, 1998), these categorizations will tend to underestimate historic population densities.

Statistics.—Contingency table analyses were used for initial examination of the relationship of single traits and endemism or risk for lineages and for the lowest taxonomic levels (species or infraspecific taxa). Results at the lowest taxonomic level without correction for their lineages should be interpreted with caution because of the lack of independence of related taxa. The impact of combinations of traits on endemism or on risk was assessed using logistic regression

(Proc Genmod in SAS version 6.12; SAS, 1997). For analysis of lineages, either endemism (endemic/indigenous) or risk (at risk/secure) was used as the dichotomous dependent variable, with combinations of life history and habitat traits as independent variables. For analyses of cases at the lowest taxonomic level, generalized estimating equations (GEE with Proc Genmod) were used, and lineage was used to cluster cases to partially correct for the lack of independence because of shared evolutionary history. This method assumes that observations are correlated within clusters and independent between clusters (Allison, 1999). A significance level of $P = 0.05$ was used to test if the values of trait coefficients were significantly different from 0.

RESULTS

Taxonomic Patterns of Risk

The native Hawaiian flowering plants include a total of 1,159 taxa (species + infraspecific taxa), 1,029 species, 226 genera, and 89 families (Table 1). These taxa are presumed to have originated from only 293 colonists. Most Hawaiian species (91.25%) are not further subdivided into infraspecific taxa or are represented in the Hawaiian Islands by a single infraspecific taxon; 64 species have two infraspecific taxa, and 24 species have three or four native infraspecific taxa. Only two species, *Chamaesyce celastroides* (Euphorbiaceae) and *Metrosideros polymorpha* (Myrtaceae), have eight infraspecific taxa.

A high proportion of the native Hawaiian flowering plants is already extinct or at risk. Nine percent ($N = 104$) of the flora is already extinct in the wild, and several taxa (for example, *Hibiscadelphus giffardianus* and *H. hualalaiensis* (Malvaceae), *Kokia cookei* (Malvaceae), *Clermontia peleana* ssp. *peleana* (Campanulaceae), and *Silene perlmanii* (Caryophyllaceae)) are now known only in cultivation. About one-quarter of the taxa (24.6%) has <100 remaining individuals (Table 2), and 16.9% is extinct or known only from a single population. One-quarter of the flora is endangered, and more than half (52.5%) of the native Hawaiian flowering plant taxa are at risk (extinct, endangered, vulnerable, or rare; see Table 2).

TABLE 1. Summary of the native Hawaiian angiosperm flora and numbers of taxa at risk.

	Lowest taxonomic level recognized	Species	Genera	Families	Lineages
1. Total native (indigenous + endemic)	1,159	1,029	226	89	293
2. Only indigenous taxa in HI	114	112	58	17	103
3. Only endemic taxa in HI	1,045	916[a]	142	43	180
(% of line 1)	(90.2)	(89.0)	(62.8)	(48.3)	(61.4)
4. Both indigenous and endemic taxa in HI	—	1[b]	31	29	10[c]
(% of line 1)		(0.1)	(13.7)	(32.6)	(3.4)
5. Taxa endemic to HI	1,045	908[a]	28	none	—
(% of line 1)	(90.2)	(88.2)	(12.4)		
6. Indigenous taxa at risk	4[d]	4	4	4	4
(% of [line 2 + line 4])	(3.5)	(3.55)	(4.8)	(8.7)	(3.5)
7. Endemic taxa at risk	605	557	121	53	129
(% of [line 3 + line 4])	(57.9)	(60.7)	(72.0)	(73.6)	(67.9)
8. Extinct endemic taxa	102	102	33	20	30
(% of [line 3 + line 4])	(9.8)	(11.1)	(19.6)	(27.8)	(15.8)
9. Taxa at risk (indigenous or endemic)	609	561	123	54	133
(% of line 1)	(52.5)	(54.5)	(54.4)	(60.7)	(45.4)

[a] Eight species are indigenous to the Hawaiian Islands at the species level, but Hawaiian populations are classified as endemic at the infraspecific level: *Heliotropium anomalum* var. *argenteum* (Boraginaceae; AS), *Lepidium bidentatum* var. *o-waihiense* (Brassicaceae, V), *Jacquemontia ovalifolia* subsp. *sandwicensis* (Convolvulaceae, AS), *Gahnia aspera* subsp. *globosa* (Cyperaceae, AS), *Gahnia vitiensis* subsp. *kauaiensis* (Cyperaceae, AS), *Machaerina mariscoides* subsp. *meyenii* (Cyperaceae, AS), *Joinvillea ascendens* subsp. *ascendens* (Joinvilleaceae, RH), and *Fragaria chiloensis* subsp. *sandwicensis* (Rosaceae, V). AS = apparently secure, RH = rare in Hawai'i, and V = vulnerable.

[b] *Mucuna sloanei* (Fabaceae) has both an indigenous variety not at risk and an endemic variety that is endangered.

[c] All 10 lineages had one indigenous taxon plus endemic taxa: *Boerhavia* (Nyctaginaceae, 1 end), *Cyperus* (Cyperaceae, 2 end), *Eugenia* (Myrtaceae, 1 end), 2 lineages of *Korthalsella* (Viscaceae, each with 1 end), *Mucuna* (Fabaceae, 1 end), *Myoporum* (Myoporaceae, 1 end), *Peperomia* (Piperaceae, 19 end), *Pisonia* (Nyctaginaceae, 2 end), and *Portulaca* (Portulacaceae, 1 end).

[d] Indigenous taxa at risk are *Cleome spinosa* (Capparaceae, extinct in HI; last seen 1864), *Cyperus odoratus* (Cyperaceae; newly rediscovered; previously last seen in HI in 1939), *Nesoluma polynesicum* (Sapotaceae), and *Vigna adenantha* (Fabaceae, extinct in HI; last seen 1851).

TABLE 2. Conservation status, number of individuals, and number of populations remaining in the wild for taxa of the native flowering plants of Hawai'i. Extinct taxa include EX? (18) and EXH (2) taxa. Rare taxa include RH (2), and vulnerable taxa include VH (1). Five taxa are extinct in the wild and have no natural populations, but individuals are in cultivation. For further explanation of categories, see Methods.

Conservation status	No. of taxa	% of taxa
Apparently secure	550	47.5
Extinct (EX, EX?, or EXH)	104	9.0
Endangered	290	25.0
Vulnerable (V or VH)	65	5.6
Rare (R or RH)	150	13.0
Total at risk (extinct, endangered, vulnerable, rare)	609	52.5
No. of individuals		
0	99	8.5
1	11	0.9
2–10	52	4.5
11–20	25	2.2
21–50	46	4.0
51–100	51	4.4
101–300	100	8.6
301–500	51	4.4
501–1,000	43	3.7
1,001–5,000	69	6.0
No. of natural populations		
0	104	9.0
1	91	7.9
2–5	187	16.1
6–10	79	6.8
11–20	51	4.4

Taxa at risk are found throughout the flora. Because there are so few infraspecific taxa, the percentages of the flora at risk are similar at the species level (54.5%) and at the lowest taxonomic level recognized (52.5%). Only 24 species (2.3% of native species) had infraspecific taxa that differed in risk (at risk vs. secure). At least one taxon is at risk in more than half of the genera (54.4%) and families (60.7%) and in slightly less than half (45.4%) of the lineages. Half or more taxa within each group are at risk for 53.5% of the species, 42.2% of the genera, and 30.3% of the families (Table 1). Families vary considerably in the proportion of taxa at risk. Among the larger families in the Hawaiian Islands ($N \geq 20$ or more taxa), the percent of taxa at risk ranges from 13% in the Piperaceae to 98% in the Caryophyllaceae (Table 3). The three largest families (Campanulaceae, Asteraceae, Lamiaceae) have the largest absolute numbers of taxa at risk and together account for almost one-fifth (19.8%) of all taxa at risk. The Caryophyllaceae also contribute a large number of taxa at risk. Large families on average have taxa at much greater risk in the Hawaiian Islands (58%) than elsewhere (16%). Despite the coarseness of the worldwide data, the percent of species in a family that are threatened worldwide (excluding Hawaiian taxa) and the percent of endemic taxa at risk within a family in the Hawaiian Islands are significantly correlated (Table 3; Fig. 2).

Endemism and Patterns of Endangerment

The native flowering plants of the Hawaiian Islands have the greatest percentage of endemism in the world (90% of all taxa at the specific and infraspecific level and 89% of species: Table 1). Twelve percent of genera are unique to the Hawaiian Islands, and almost two-thirds of the genera (62.8%) are represented in the Hawaiian Islands by only endemic taxa. Although the islands' great isolation and geological history have permitted many endemic species and some endemic genera to evolve, no flowering plant families are unique to the Hawaiian Islands.

Endemic taxa are far more likely to be at risk than indigenous taxa. More than half (57.9%) of endemic taxa (605/1045) but only 3.5% of indigenous taxa (4/114) are at risk (Tables 1 and 4a). The four indigenous taxa at risk (*Cleome spinosa* (Capparaceae), *Cyperus odoratus* (Cyperaceae), *Nesoluma polynesicum* (Sapotaceae), and *Vigna adenantha* (Fabaceae)) all occur in drier habitats (*Cyperus* in locally wet sites within dry regions) at lower elevations, areas that have suffered substantial habitat loss.

Endemic taxa also differ from indigenous taxa in most life history and habitat traits and in biogeographic patterns, even within the Hawaiian Islands (Table 4a). Most families ($N = 29$) have only a single indigenous taxon, but the grasses (Poaceae) and Fabaceae each have 9 indigenous taxa and the sedges (Cyperaceae) have 25 indigenous taxa. Partially because of the dominance of grasses and sedges (30% of indigenous taxa), when single traits are examined at the taxon level, indigenous taxa (relative to endemic taxa) are more likely to be monocots; herbaceous (rather than woody); with dry fruits, monomorphic breeding systems (significant for taxa, not for lineage-level analysis), small brown flowers, and with proportionately more wind pollination and less bird pollination (significant for taxa, not lineages;

TABLE 3. Families with 10 or more taxa (species or infraspecific taxa) of native flowering plants in the Hawaiian Islands, with number of species, number of lineages, and percent of taxa at risk in the Hawaiian Islands. Data on the total number of taxa per family worldwide, and the percent of the family threatened worldwide are taken from Walter and Gillett (1998). The last column was calculated from data in Walter and Gillett (1998), omitting Hawaiian taxa.

Family	No. of taxa		No. of species in Hawai'i	No. of lineages in Hawai'i	Endemic taxa at risk in Hawai'i		% family (−HI) threatened worldwide
	Worldwide	In Hawai'i (total/endemic)			*N*	%	
Campanulaceae	2,000	145/145	127	1	110	75.9	17.1
Asteraceae	20,000	127/126	94	11	74	58.7	12.5
Lamiaceae	3,200	64/62	60	3	46	74.2	21.9
Rubiaceae	6,500	62/60	55	11	23	38.3	17.0
Gesneriaceae	2,500	60/60	58	3	36	60.0	9.4
Rutaceae	1,500	58/58	56	4	36	62.1	24.1
Cyperaceae	4,000	52/27	45	37	9	33.3	6.8
Poaceae	8,000	51/42	48	25	19	45.2	9.5
Caryophyllaceae	2,000	41/41	40	3	40	97.6	24.5
Euphorbiaceae	7,500	34/34	22	6	20	58.8	12.2
Malvaceae	1,250	31/26	25	13	23	88.5	17.2
Fabaceae	13,100	26/17	25	19	11	64.7	16.7
Piperaceae	1,700	25/23	25	4	3	13.0	9.5
Arecaceae	3,000	22/22	22	1	15	68.2	28.7
Myrsinaceae	1,000	20/20	20	2	6	30.0	18.9
Loganiaceae	500	18/18	16	1	9	50.0	5.8
Araliaceae	700	16/16	14	4	5	31.3	14.9
Myrtaceae	3,000	16/15	8	3	1	6.7	25.0
Urticaceae	700	16/15	15	8	6	40.0	16.2
Amaranthaceae	900	15/15	12	4	8	53.3	4.1
Cucurbitaceae	700	14/14	14	1	7	50.0	9.8
Primulaceae	1,000	14/13	14	2	9	69.2	10.4
Thymelaeaceae	500	14/14	12	1	4	28.6	14.0
Violaceae	800	14/14	11	2	9	64.3	12.9
Pittosporaceae	200	11/11	11	1	4	36.4	16.9
Santalaceae	400	10/10	7	3	3	30.0	8.2
Goodeniaceae	300	10/9	10	4	3	33.3	10.3

Tables 4a and b). Indigenous taxa are also more likely to occur in aquatic habitats or coastal areas in drier habitats, rather than in forest or montane–subalpine areas.

Using logistic regression with lineages as clusters, and moisture, elevation, and habitat type as independent variables, relative to those with wide distributions, the coefficients of these traits are all significant. The estimated odds of endemism are 2.6 times greater for taxa with lowland distributions, 2.5 times greater for lowland–montane distributions, 2.8 times greater for montane distributions, and 3.1 times greater for montane–subalpine distributions. The odds of endemism are significantly higher for taxa in dry (1.7 times), mesic (1.8 times), and wet (1.6 times) conditions than in wide-ranging moisture conditions. Relative to taxa in bog habitats, indigenous taxa are 3.3 times more likely to occur in coastal habitats, 2.0 times more likely in grassland, and 1.5 times more likely in shrubland, whereas the odds of endemism are similar to each other for cliff habitats, forests, and bogs. When habitat range, population density, and island range are considered together, habitat range is not significant, and the odds of endemism are greatest for taxa with single-island distributions (1.3 times that of multi-island distributions) and the lowest population density. The odds of endemism are 24 times greater for trees relative to herbs when the joint effects of class (dicot/monocot), habit, and fruit type are considered, but class and fruit type are not significant.

Lineages with only indigenous taxa and those with only endemic taxa differ greatly in size. All indigenous lineages have only one taxon (except for one colonist of *Fimbristylis cymosa* (Cyperaceae), which has two infraspecific taxa). Although many endemic lineages are composed of only one taxon, ~10% of the endemic lineages have more than eight taxa and some are quite large (e.g., native Campanulaceae with 145 taxa). Ten

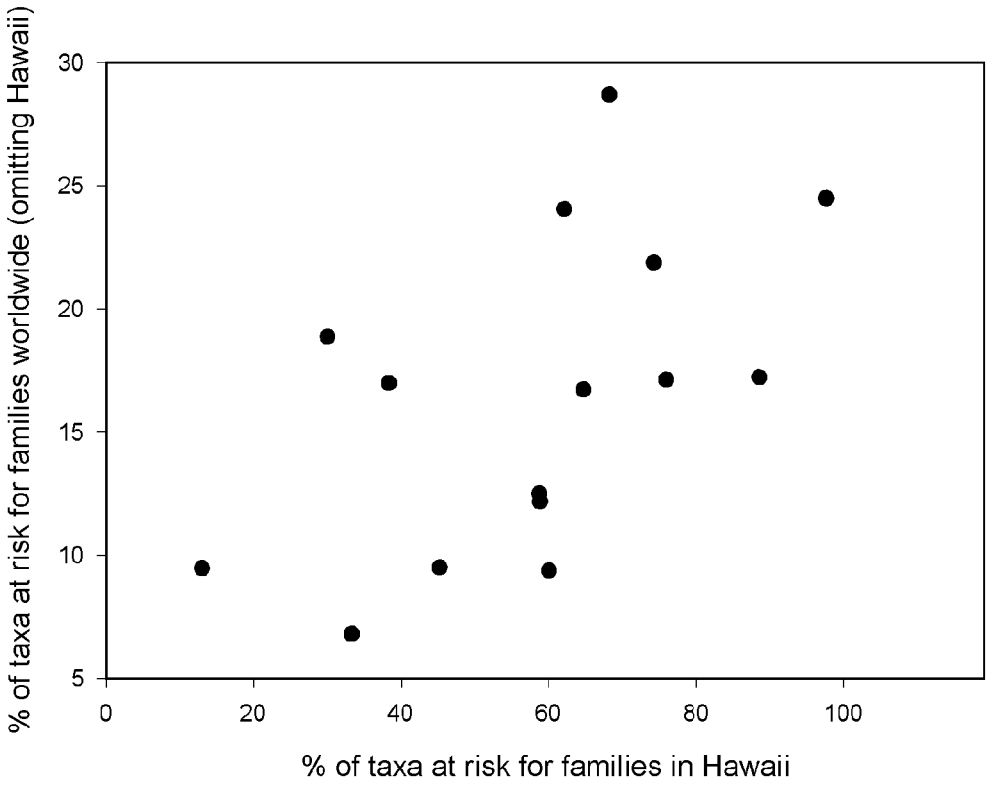

FIGURE 2. Percent of taxa at risk for families worldwide (omitting Hawaiian taxa) vs. percent of taxa at risk for families in Hawai'i. There is a significant correlation between taxa at risk for families worldwide and taxa at risk in the Hawaiian Islands ($N = 15$ [all families with 20 or more taxa], $r = 0.557$, SE = 0.23, $p = 0.0311$).

lineages have both endemic and indigenous taxa.

Island Age and Island Distributions with Patterns of Endangerment

Indigenous and endemic taxa show different patterns of distribution among the main Hawaiian Islands. The dispersal abilities of the indigenous taxa have permitted relatively even colonization of all the main islands, despite differences in the size and age of the islands (N = 90–104 indigenous taxa per island for Kaua'i, O'ahu, Maui Nui, and the island of Hawai'i (referred to as the Big Island), Table 5). In contrast, patterns of endemic taxa, and particularly single-island endemic taxa (endemic to a single island within the Hawaiian Islands), show greater association with island age. The oldest large island of Kaua'i has more endemic taxa (430) as well as single-island endemic taxa (SIE, 225) than O'ahu (393 endemic, 155 SIE), and both of these have more endemic taxa and single-island endemic taxa than the larger but younger Big Island (323 endemic, 104 SIE). Maui Nui, with about twice the area as O'ahu, has the most endemic taxa (509) of the main islands, and almost as many SIE taxa (215) as Kaua'i. In contrast, patterns of endemic taxa, particularly SIE taxa (those endemic to a single island within the Hawaiian Islands), show greater association with island age. The oldest large island of Kaua'i has more endemic taxa (430) and SIE taxa (225) than O'ahu (393 endemic, 155 SIE), and both of these have more endemic taxa and SIE taxa than the larger but younger Big Island (323 endemic, 104 SIE). Maui Nui, with about twice the area as O'ahu, has the most endemic taxa (509) of the main islands, and almost as many SIE taxa (215) as Kaua'i.

Islands also differ in patterns of endangerment for endemic and SIE taxa. Endemic taxa with single-island distributions are more at risk than those with multi-island distributions ($N = 1052$, $G = 101.911$, df = 1, $P = 0.001$). All SIE taxa are

TABLE 4A. Traits of endemic versus indigenous taxa. *N* and percentages of each row are given.

Endemism vs. trait	*N*	%								
Taxa at risk		No	Yes							
Endemic	1,045	42.1	57.9							
Indigenous	114	96.5	3.5							
($N = 1{,}159$, $G = 146.538$, df = 1, $P = 0.001$)										
Class		Dicot	Monocot							
Endemic	1,045	89.5	10.5							
Indigenous	114	60.5	39.5							
($N = 1{,}159$, $G = 55.742$, df = 1, $P = 0.001$)										
Island range		Multi	Single							
Endemic	1,045	32.1	67.9							
Indigenous	114	94.7	5.3							
($N = 1{,}159$, $G = 183.730$, df = 1, $P = 0.001$)										
Historical density		High	Medium	Low						
Endemic	1,033	12.7	44.5	42.8						
Indigenous	103	47.6	39.8	12.6						
($N = 1{,}136$, $G = 78.250$, df = 2, $P = 0.001$)										
Habitat range		Narrow	Wide							
Endemic	1,045	77.5	22.5							
Indigenous	114	64.0	36.0							
($N = 1{,}159$, $G = 9.465$, df = 1, $P = 0.002$)										
Habitat		Aquatic	Bog	Cliff	Coast	Forest	Forest-bog	Grass	Shrub-forest	Shrub
Endemic	1,030	0.2	3.1	4.7	2.7	69.9	5.0	1.3	4.4	8.7
Indigenous	113	15.9	1.8	0	24.8	26.6	6.2	5.3	7.1	12.4
($N = 1{,}143$, $G = 185.815$, df = 8, $P = 0.001$)										
Elevation		Coastal	Coast-low	Lowland	Low-montane	Montane-subalpine	Wide			
Endemic	1,023	4.5	3.6	36.4	9.6	45.0	1.0			
Indigenous	114	30.7	16.7	29.0	4.4	11.4	7.9			
($N = 1{,}137$, $G = 143.920$, df = 5, $P = 0.001$)										
Moisture		Dry	Mesic	Wet	Wide					
Endemic	1,036	25.9	38.0	33.6	2.5					
Indigenous	113	45.1	13.3	31.9	9.7					
($N = 1{,}149$, $G = 45.686$, df = 3, $P = 0.001$)										
Habit		Herb	Liana	Shrub	Subshrub	Tree	Vine			
Endemic	1,039	21.7	1.1	39.9	5.5	27.2	4.7			
Indigenous	114	60.5	5.3	12.3	4.4	10.5	7.0			
($N = 1{,}153$, $G = 96.790$, df = 5, $P = 0.001$)[a]										
Fruit type		Dry	Fleshy							
Endemic	1,045	55.5	44.5							
Indigenous	114	78.1	21.9							
($N = 1{,}159$, $G = 23.030$, df = 1, $P = 0.001$)										
Flower size		Long	Short							
Endemic	1,019	55.9	44.1							
Indigenous	109	33.0	67.0							
($N = 1{,}128$, $G = 20.954$, df = 1, $P = 0.001$)										
Flower color		Blue	Brown	Green	OPR[b]	White	Yello			
Endemic	1,029	1.0	3.5	29.7	16.3	32.3	17.2			
Indigenous	114	2.6	19.3	28.1	9.7	28.1	12.3			
($N = 1{,}143$, $G = 39.537$, df = 5, $P = 0.001$)										
Presumed pollinator		Wind/insect	Bird	Insect	Wind					
Endemic	1,033	1.9	19.2	66.7	12.2					
Indigenous	114	0.9	0.9	61.7	36.4					
($N = 1{,}139$, $G = 61.097$, df = 3, $P = 0.001$)										
Breeding system		Dimorphic	Monomorphic							
Endemic	1,041	21.0	79.0							
Indigenous	113	8.9	91.1							
($N = 1{,}154$, $G = 11.246$, df = 1, $P = 0.001$)										

[a] $N = 1150$, $G = 81.322$, df = 1, $P = 0.001$ for herbaceous vs. woody.
[b] Orange–pink–red.

TABLE 4B. Traits of endemic and indigenous lineages. *N* and percentages of each row are given.

Lineages	*N*	%			
Risk		Secure	At risk		
Endemic	180	43.9	56.1		
Indigenous	103	96.1	3.9		
($N = 283$, $G = 92.609$, df = 1, $P = 0.001$)					
Class		Dicot	Monocot		
Endemic	180	77.8	22.2		
Indigenous	103	58.2	41.8		
($N = 283$, $G = 11.805$, df = 1, $P = 0.001$)					
Fruit type		Dry	Fleshy		
Endemic	180	62.8	37.2		
Indigenous	103	80.6	19.4		
($N = 283$, $G = 10.191$, df = 1, $P = 0.001$)					
Breeding system		Dimorphic	Mono-morphic		
Endemic	159	12.6	87.4		
Indigenous	102	8.8	91.2		
($N = 261$, $G = 0.911$, df = 1, $P = 0.340$)					
Presumed pollinator		Bird	Insect	Wind	
Endemic	172	4.1	68.6	27.3	
Indigenous	91	2.2	57.1	40.7	
($N = 263$, $G = 5.088$, df = 1, $P = 0.079$)					
Presumed dispersal		Bird	Ocean drift/raft		
Endemic	176	83.0	17.0		
Indigenous	103	68.0	32.0		
($N = 279$, $G = 8.140$, df = 1, $P = 0.004$)					
Lineage size (no.)		1 taxon	2 taxa	3–4 taxa	>4 taxa
Endemic	180	87	20	31	42
Indigenous	103	102	1	0	0
Both end. and ind.	10	0	7	2	1

at risk on the four smallest islands (NW Islands, Ni'ihau, Lana'i, and Kaho'olawe), although the absolute number of taxa involved is low. These islands also have the least variation in habitat (elevation, moisture, community type). Within Maui Nui, all of the SIE taxa on the smaller islands of Lana'i and Kaho'olawe are at risk, and about three-fourths of the SIE taxa are at risk on Maui (73%) and Moloka'i (84%). Comparisons of the major separate islands (Kaua'i, Lana'i, Maui, Moloka'i, O'ahu, and the Big Island) show significant differences because the islands of Lana'i and Moloka'i have a high proportion of SIE taxa at risk ($N = 635$, $G = 21.006$, df = 5, $P = 0.001$). The island of Maui is particularly high in the proportion of SIE taxa that are extinct (risk (AS, E, Ex, R, V) × island (Hawai'i, Kaua'i, Lana'i, Maui, Moloka'i, O'ahu), $N = 649$, $G = 68.75$, df = 20, $P = 0.001$). When the islands of Maui Nui are pooled, SIE taxa do not show significant differences by island in the proportion of taxa at risk (Kaua'i, 64%; O'ahu, 73%; Maui Nui, 73%; Big Island, 62% ($N = 699$, $G = 5.881$, df = 3, $P = 0.118$)).

Although the total proportion of endemic taxa at risk is similar for the four main islands, Kaua'i has only half the percentage of extinct taxa of other islands and has a higher proportion of SIE species that are rare relative to the larger islands (islands (Hawai'i, Kaua'i, Maui Nui, NW Islands, O'ahu) × risk (AS, E, EX, R, V), $N = 707$, $G = 45.74$, df = 16, $P = 0.001$), Table 5). The total percentage of SIE taxa at risk (pooling Ex + E + V + R) is only slightly lower on Kaua'i than the other islands.

Habitat and Life History Patterns of Endangerment in Endemic Taxa

To better understand more subtle patterns of risk, we focused only on endemic taxa for several life history traits and habitat characteristics (Table 6a). Fifty-three families have endemic taxa at risk (45 dicot families, 8 monocot families), and 9 families have 20 or more endemic taxa at risk, including the Campanulaceae (110 taxa at risk), Asteraceae (74), Lamiaceae (46), and Caryophyllaceae (40) (Table 3).

TABLE 5. Patterns of endangerment of the Hawaiian flowering plants by island. Island areas and age taken from Juvik and Juvik (1998). Total native taxa = number of indigenous taxa + number of endemic taxa. Single-island endemic (SIE) = taxon endemic to the Hawaiian Islands and found on only one island or group of islands (Maui Nui or NW Islands). Within each endangerment category—extinct, endangered, vulnerable, rare, total at risk (=extinct + endangered + vulnerable + rare), apparently secure—% SIE is the percentage of SIE taxa for that island that are in that risk category. % endem. is the percentage of the endemic taxa found on that island (including both SIE taxa and other taxa endemic to the Hawaiian Islands) in that risk category. Data are given for both Maui Nui and the individual islands Maui Nui comprises (Lana'i, Maui, Moloka'i, Kaho'olawe).

	NW Isles	Ni'ihau	Kaua'i	O'ahu	Maui Nui	Moloka'i	Lana'i	Maui	Kaho'olawe	Hawai'i	Overall
Area (sq km)	8.0	179.9	1,430.5	1,546.5	3,036.7	673.5	364.0	1,883.7	115.5	10,433.1	16,634.7
Maximum age ($\times 10^6$ BP)	27.7	4.9	5.1	3.7	1.8	1.8	1.3	1.3	1.0	0.43	
Total native taxa (no.)	49	97	520	490	613	385	268	518	63	417	1,159
Indigenous	23	49	90	97	104	87	59	96	24	94	114
Endemic	26	48	430	393	509	298	209	422	39	323	1,045
SIE (no.)	8	3	225	155	215	38	14	99	3	104	710/649[a]
Extinct											
% SIE	37.50	66.67	6.67	12.26	20.93	21.05	42.86	27.27	33.33	13.46	13.80/14.64[a]
% endem.	11.54	4.17	3.72	5.34	9.63	3.69	4.31	8.06	2.56	5.26	9.76
Endangered											
% SIE	50.00	33.33	30.67	39.35	28.84	42.11	35.71	24.24	33.33	29.81	32.11/32.66[a]
% endem.	62.50	18.75	23.49	25.95	21.61	17.79	18.18	18.72	12.82	19.50	27.75
Vulnerable											
% SIE	0	0	4.00	6.45	8.84	5.26	21.43	9.09	0	4.81	6.06/5.86[a]
% endem.	19.23	10.42	5.12	6.87	7.66	6.71	7.66	7.58	10.26	5.57	6.12
Rare											
% SIE	12.50	0	23.11	12.90	14.42	15.79	0	14.14	33.33	14.42	16.76/16.80[a]
% endem.	3.85	4.17	15.58	10.18	11.39	10.74	6.70	10.66	7.69	11.15	14.26
Total at risk											
% SIE	100.0	100.0	64.44	72.97	73.02	84.21	100.0	74.75	100.0	62.50	68.73/69.95[a]
% endem.	53.85	37.50	47.91	48.35	50.29	38.93	36.84	45.02	33.33	41.49	57.89
Apparently secure											
% SIE	0	0	35.56	27.03	26.98	15.79	0	25.25	0	37.50	31.27/30.05[a]
% endem.	46.15	62.50	52.09	51.65	49.71	61.07	63.16	54.98	66.67	58.51	42.11

[a]The ratio between that number (or percentage) of SIEs for Maui Nui and the number (or percentage) of SIEs found on the separate islands of Maui Nui.

TABLE 6A. Comparison of traits of endemic taxa in different risk categories. Island range (single-island vs. multi-island distribution analysis includes the use of Maui Nui and the NW islands). Taxa with narrow habitats occur in only one type of habitat; taxa with wide habitats occur in more than one habitat (e.g., forest and bog, shrubland and forest). For breeding systems, Am = andromonoecious, D = dioecious, Gd = gynodioecious, Gm = gynomonoecious, H = hermaphroditic, M = monoecious, Poly = polygamodioecious, N = number of taxa in row. Values in cells represent the percent of the row in that column.

Endemic taxa vs. risk	N	%							
Class		Dicot	Monocot						
Apparently secure	440	86.8	13.2						
Endangered	290	91.4	8.6						
Extinct	102	91.4	8.6						
Rare	149	87.9	12.1						
Vulnerable	64	95.3	4.7						
Total at risk (E, Ex, R, V)	605	91.4	8.6						
($N = 1{,}045$, $G = 10.219$, df = 4, $P = 0.037$ for 5 risk cat; $N = 1{,}045$, $G = 5.616$, df = 1, $P = 0.018$ for apparently secure vs. at risk)									
Island range		Single	Multi						
Apparently secure	440	50.5	49.5						
At risk	605	80.7	19.3						
($N = 1{,}045$, $G = 106.90$, df = 1, $P = 0.001$)									
Historical density		High	Medium	Low					
Apparently secure	440	25.45	64.1	10.5					
At risk	605	3.5	29.8	66.8					
($N = 1{,}045$, $G = 391.79$, df = 2, $P = 0.001$)									
Habitat range		Narrow	Wide						
Apparently secure	440	67.7	32.3						
At risk	605	84.6	15.4						
($N = 1{,}045$, $G = 41.3$, df = 1, $P = 0.001$)									
Habitat		Bog	Cliff	Coast	Forest-bog	Forest	Grass	Shrub-forest	Shrub
Apparently secure	439	3.0	2.0	2.0	8.7	68.3	1.6	6.4	8.0
At risk	589	3.2	6.6	3.2	2.4	71.3	1.0	2.9	9.3
($N = 1{,}028$, $G = 41.9$, df = 7, $P = 0.001$)									
Elevation		Coastal	Coast-lowland	Lowland	Lowland-montane	Montane	Mont-subalp	Wide	
Apparently secure	440	2.7	5.0	33.2	12.7	38.4	5.9	2.0	
At risk	583	5.8	2.6	38.8	7.2	42.4	3.1	0.2	
($N = 1{,}023$, $G = 35.12$, df = 6, $P = 0.001$; $N = 834$, $G = 3.860$, df = 2, $P = 0.145$ for coast, lowland, montane only)									
Moisture		Dry	Mesic	Wet	Wide				
Apparently secure	440	23.6	35.7	36.1	4.6				
At risk	596	27.5	39.8	31.7	1.0				
($N = 1{,}036$, $G = 16.867$, df = 3, $P = 0.001$; $N = 1{,}010$, $G = 3.743$, df = 2, $P = 0.154$ for dry, mesic, wet only)									

TABLE 6A. Continued.

Endemic taxa vs. risk	*N*	%								
Habit		Herb	Liana	Shrub	Subshrub	Tree	Vine			
Apparently secure	440	24.3	0.9	33.9	4.6	32.0	4.3			
At risk	599	19.7	1.2	44.2	6.2	23.7	5.0			
($N = 1{,}039$, $G = 17.523$, df $= 5$, $P = 0.004$)										
Lifespan		Annual	Peren							
Apparently secure	440	3.0	97.0							
At risk	605	1.5	98.5							
($N = 1{,}045$, $G = 2.617$, df $= 1$, $P = 0.106$)										
Woodiness		Herb	Woody							
Apparently secure	440	28.2	71.8							
At risk	605	26.3	73.7							
($N = 1{,}045$, $G = 0.465$, df $= 1$, $P = 0.495$)										
Fruit type		Dry	Fleshy							
Apparently secure	440	52.5	47.5							
At risk	605	57.7	42.3							
($N = 1{,}045$, $G = 2.77$, df $= 1$, $P = 0.096$)										
Presumed pollinator		Wind/insect	Bird	Insect	Wind					
Apparently secure	438	1.8	13.5	67.8	16.9					
At risk	594	2.0	23.4	65.8	8.8					
($N = 1{,}032$, $G = 27.14$, df $= 3$, $P = 0.001$)										
Flower color		Blue	Brown	Green	Orange	Pink	Purple	Red	White	Yellow
Apparently secure	440	1.1	5.7	35.0	2.3	1.8	4.6	6.1	25.2	18.2
At risk	589	0.9	1.9	25.8	1.5	2.9	8.0	5.1	37.5	16.5
($N = 1{,}029$, $G = 37.45$, df $= 8$, $P = 0.001$)										
Dimorphism		Dimorphic	Monomorphic							
Apparently secure	440	28.0	72.0							
At risk	601	16.0	84.0							
($N = 1{,}041$, $G = 21.717$, df $= 1$, $P = 0.001$)										
Breeding system		Am	D	Gd	Gm	H	M	Poly		
Apparently secure	452	5.3	19.7	6.2	4.4	52.9	7.3	4.2		
At risk	588	3.2	10.7	3.2	5.1	70.6	7.1	0		
($N = 1{,}040$, $G = 66.34$, df $= 6$, $P = 0.001$)										

TABLE 6B. Comparison of risk for lineages comprising endemic taxa only and lineages with both endemic and indigenous taxa. For dispersal, bb = bird dispersed, with barbs; bi = bird dispersed (internal); bm = bird dispersed (mud); bv = bird dispersed (viscid propagules); d = drift. Values in cells for traits represent the percentage of the row that is in that column.

Lineages	*N*	%					
Class		Dicot	Monocot				
Apparently secure	83	73.5	26.5				
At risk	107	82.2	17.8				
($N = 190$, $G = 2.10$, df = 1, $P = 0.147$)							
Breeding system		Dimorphic	Monomorphic				
Apparently secure	78	14.1	76.9				
At risk	103	9.7	85.4				
($N = 181$, $G = 2.25$, df = 2, $P = 0.325$)							
Presumed pollinator		Bird	Insect	Wind			
Apparently secure	82	3.7	61.0	35.4			
At risk	107	3.7	77.6	18.7			
($N = 189$, $G = 6.76$, df = 2, $P = 0.034$; $N = 182$, $G = 6.76$, df = 1, $P = 0.009$ for insect and wind only)							
Fruit type		Dry	Fleshy				
Apparently secure	83	53.0	47.0				
At risk	107	69.2	30.8				
($N = 190$, $G = 5.17$, df = 1, $P = 0.023$)							
Presumed dispersal		bb	bi	bibm	bm	bv	d
Apparently secure	72	13.9	52.8	6.9	5.6	11.1	9.7
At risk	95	20.0	31.6	10.5	9.5	4.2	24.2
($N = 167$, $G = 14.63$, df = 5, $P = 0.012$; $N = 181$, $G = 6.716$, df = 1, $P = 0.010$ for only bird vs. drift)							
Lineage size		1 taxon	2–3 taxa	4–10 taxa	>10 taxa		
Apparently secure	83	50.6	24.1	14.5	10.8		
At risk	107	42.1	26.2	16.8	15.0		
($N = 190$, $G = 1.60$, df = 3, $P = 0.66$)							

When single traits are considered, endemic taxa at risk grow in more narrow ranges of moisture (not widespread) and elevation (less often occurring in two categories such as coastal–lowland, lowland–montane, montane–subalpine, or wide) (Table 6a); community type is also significant (Table 6a). Risk is not associated with moisture conditions when single categories (dry, mesic, wet) are considered or when only coastal, lowland, or montane elevations are compared. A logistic regression with moisture, elevation, and community type as independent variables, risk as the dependent variable and with clustering by lineage generally supports these patterns. Taxa with distributions in dry, mesic, and wet habitats all have greater odds of endemism than taxa with widespread moisture distributions, but none of these odds is significant. Taxa with distributions in single elevational categories (coastal, lowland, montane) have significantly greater odds of being at risk than taxa with more widespread elevational distributions. Taxa with distributions over two categories (coastal–lowland, lowland–montane, montane–subalpine) have odds of risk that do not differ from those of widespread taxa. Relative to taxa with coastal distributions, taxa with distributions on cliffs, in shrubland, in forests, and in bogs have much greater odds of being at risk (8.5 times greater for cliffs, 3.7 times for shrubland, 3.2 times for forest, and 3.7 times for bogs).

When taxa with distributions in the most common habitats characterized by elevation, moisture, and community type are considered, taxa at risk are again associated with more narrow categories (Table 7). The greatest number of total endemic taxa and the greatest number of endemic taxa at risk have distributions in mesic lowland forest, wet montane forest, and mesic montane forest. In contrast, the greatest proportion of taxa at risk have dry lowland shrubland, dry lowland forest, and dry coastal distributions. About one-fifth of the taxa with dry lowland shrubland and dry montane forest distributions are extinct (Table 7). Taxa with mesic lowland–montane forest distributions

TABLE 7. Endemic taxa at risk (*N* and % of taxa with that habitat distribution at risk) and endemic taxa extinct (EX, EX?), combining habitat categories of moisture, community type, and elevation, with 10 or more taxa. Test of independence of risk versus habitat: For all categories, $N = 823$, $G = 42.835$, df = 14, $P = 0.001$; for only first 10 categories (taxa without wider distributions), $N = 693$, $G = 15.537$, df = 9, $P = 0.077$.

Moisture	Elevation	Community	N taxa	N taxa at risk	% at risk	% EX
Dry	Coastal	Coastal	26	18	69.23	15.38
Dry	Lowland	Forest	50	35	70.00	2.00
Dry	Montane	Forest	20	12	60.00	20.00
Dry	Lowland	Shrubland	26	22	84.62	19.23
Dry	Montane	Shrubland	14	9	64.29	0
Mesic	Lowland	Forest	180	101	56.11	11.67
Mesic	Montane	Forest	122	80	65.57	12.30
Wet	Lowland	Forest	60	30	50.00	8.33
Wet	Montane	Forest	164	99	60.37	7.92
Wet	Montane	Bog	31	18	58.06	0
Dry	Coast-lowland	Shrubland	14	5	35.71	0
Dry	Mont-subalpine	Shrubland	17	7	41.18	5.88
Mesic	Lowland-montane	Forest	43	29	67.44	9.30
Wet	Lowland-montane	Forest	21	5	23.81	4.76
Wet	Montane	Forest-bog	35	12	34.29	0

also have a high proportion of taxa at risk (Table 7). If only taxa with distributions in forest habitat are analyzed in a logistic regression, with lineage used for clustering, there is no significant effect of moisture, elevation, or their interactions on risk. Taxa with dry forest (59.2% at risk), mesic forest (58.2% at risk), and wet forest (54.7% at risk) distributions have similar proportions of taxa at risk.

Life history characteristics have more complicated patterns with risk, depending on whether taxa or lineages are considered, and whether traits are considered singly or in combination (Table 6a). When single traits are considered for taxa without respect to lineage, endemic taxa at risk are more likely to be shrubs than trees. Although taxa at risk are associated with monomorphic and hermaphroditic breeding systems, lineages at risk show no significant association with breeding system. Analysis at the taxon level suggests that endemic taxa at risk are more likely to be bird-pollinated, have longer flowers, and be associated with white rather than brown or green flowers, but lineages with endemic taxa at risk are disproportionately insect-pollinated.

Endemic taxa at risk and those apparently secure are not significantly different in lifespan (annual, perennial), woodiness (herbaceous, woody), or fruit type (dry, fleshy). In contrast, lineages at risk are more likely to be associated with dry rather than fleshy fruit (Table 6b). Lineages at risk are disproportionately dispersed abiotically (drift, rafting, flotation) rather than by birds.

In contrast to analysis of single traits, when the traits of breeding system (monomorphism/dimorphism), flower color, and flower size are used in a logistic regression with clusters by lineage, monomorphic taxa are at significantly greater risk, but flower color and flower size are not significant. Woodiness, fruit type, and habit are also not significant factors for risk in similar analyses.

Most indigenous lineages are single-taxon lineages and are not at risk. As a result, there is a strong association of risk and lineage size if all indigenous and endemic lineages are considered (Table 4b). If only lineages with endemic taxa are considered, however, there is no association of risk with lineage size (Table 6b).

Patterns of Rarity and Risk

In general, Rabinowitz's (1981) classification for rarity also works well to identify taxa at risk (Table 7). Endemic taxa at risk (relative to those that are apparently secure) are significantly more likely to have single-island distributions, low historic density, and more restricted habitat distributions in only one community type. In a logistic regression with risk as a dependent variable and habitat range, historical density, and island range as independent variables, all three have significant effects. Taxa are 1.7 times more likely to be at risk with narrow habitat ranges than with wider habitat range and are 2.9 times more likely to be at risk with single-island

TABLE 8. Classification of endemic taxa ($N = 1,045$) by geographic range (multi-island vs. single island), habitat (narrow [1 habitat] vs. wide [>1 habitat]), and historic population density (high, medium, low). Number of taxa are given (and percentage of the total of secure taxa + at-risk taxa) in each of the 12 categories. The percentage of the total taxa at risk occurring in each category is also given for each cell.

Historic populn. density	Endangerment	Multi-island range		Single-island range	
		Wide	Narrow	Wide	Narrow
High	Secure	32	32	9	39
	At risk (% in cell)	3 (8.6%)	4 (11.1%)	2 (18.2%)	12 (23.5%)
	% total taxa at risk	(3.4%)	(3.4%)	(1.0%)	(4.9%)
Medium	Secure	50	84	42	106
	At risk (% in cell)	7 (12.3%)	38 (31.1%)	27 (39.1%)	108 (50.5%)
	% total taxa at risk	(5.5%)	(11.7%)	(6.6%)	(20.5%)
Low	Secure	6	14	3	23
	At risk (% in cell)	17 (73.9%)	48 (77.4%)	37 (92.5%)	302 (92.9%)
	% total taxa at risk	(2.2%)	(5.9%)	(3.8%)	(31.1%)
Total *N*		115	220	120	590

rather than multi-island distributions. The most critical factor appears to be historic population density; taxa with low historic population density are 28.6 times more likely to be at risk than taxa with high density. Combinations of these traits also are associated with taxa at risk, with especially strong effects of population density and island range. Thirty-five taxa are common (wide habitat, multi-island distribution, and high local density). For example, *Wikstroemia oahuensis* var. *oahuensis* (Thymelaeaceae) and *Metrosideros polymorpha* var. *glaberrima* (Myrtaceae) both are dominant elements of several vegetation types, and *Oreobolus furcatus* (Cyperaceae) is a common component of montane bogs. Only three common taxa (*Chamaesyce skottsbergii* var. *skottsbergii* (Euphorbiaceae), *Sesbania tomentosa* (Fabaceae), and *Hibiscus brackenridgei* var. *mokuleianus* (Malvaceae)) are at risk.

Some combinations of traits are uncommon, such as sparse taxa in low density but with wide habitat range and geographic distribution ($N = 23$). Most sparse species are at risk. Taxa in high density and with wide habitat range but occurring only on one island are also uncommon ($N = 11$).

Most taxa are naturally rare, occurring on a single island, in a narrow habitat type, with either low or medium population density. In some cases, estimates of historic population size have probably not totally corrected for anthropogenic influences, and these local densities may be underestimated. A very high proportion (92.9%) of endemics that occur in low density ($N = 325$) are at risk.

DISCUSSION

The Hawaiian flora, because of its great isolation, high levels of endemism, known lineages, and high rates of endangerment, offers unique opportunities to explore general patterns of endangerment that may be shared by many islands or habitats that are ecological islands. Some patterns are not surprising, such as the association of indigenous taxa with broader distributions within the Hawaiian Islands and lower risk. Other analyses, particularly for life history traits, demonstrate how evolutionary relationships confound patterns, as indicated by differences in results of analyses of taxa with and without consideration of lineage.

Taxonomic Patterns

Most Hawaiian species (91%) are not further subdivided and thus the high proportion of taxa at risk in the Hawaiian Islands is not an artifact of large numbers of infraspecific taxa in a few endangered species. Use of infraspecific taxa, rather than species, slightly decreases the proportion of the flora at risk. Taxa at risk are spread widely across the flora, with > half the species, ~40% of the genera, > one-third of the lineages, and ~ one-third of the families with ≥50% of taxa within the group at risk. If the effects of lineage are not considered, characteristics of taxa in the largest families (Campanulaceae, Asteraceae, Lamiaceae) have a disproportionate effect on species-level analyses of endangerment, life history, and ecological traits.

Families in the Hawaiian Islands differ in their proportion of taxa at risk. For example, almost all of the native Caryophyllaceae are at risk, and many are from a single lineage that has given rise to two genera (*Schiedea* and *Alsinidendron*). This lineage shows remarkable radiation in habit and habitat, including wet rainforest lianas, mesic forest herbs, dry shrubland shrubs, and subalpine as well as coastal herbs. Many of these are SIE species and have low population densities (Weller et al., 1990; Wagner et al., 1995). In contrast, taxa in the Piperaceae, a family with only 13% of the taxa endangered, probably represent four lineages that have given rise to a total of 25 taxa, with most having multi-island distributions. Geographic distribution (single- or multi-island) is a critical factor in determining patterns of endangerment.

Despite the divergence in morphology between many endemic Hawaiian taxa and their closely related extra-Hawaiian relatives, families with a higher proportion of taxa at risk in the Hawaiian Islands are also at greater risk on a worldwide basis (excluding Hawaiian taxa). These similarities of families in patterns of endangerment in different geographic areas may be the result of selection to maintain a suite of characters. Alternatively, these similarities may result from genetic constraints on the evolution of traits within families. Edwards (1998), studying whether family-based levels of rarity reflected generic levels of rarity, found that the occurrence of rarity was consistent between families and genera. This suggests that studies at the family level could be used to estimate patterns of rarity within a flora. Studies within lineages, if known, may show even stronger patterns. In later work, Edwards and Westoby (2000) report that families with the greatest proportions of rare species are not consistent between floras. Our results showing correspondence between patterns of risk worldwide and in the Hawaiian Islands suggest that the Hawaiian species retain general family attributes that are relevant to risk worldwide. Representatives of the Piperaceae, a family with low proportions of taxa at risk in the Hawaiian Islands and worldwide, are mostly herbaceous and grow in shady habitats worldwide, and many species have wide distributions both in the Hawaiian Islands and elsewhere.

In contrast, some taxa that have diversified in the Hawaiian Islands and elsewhere may differ in risk. The Hawaiian Myrtaceae are woody plants that tend to have multi-island distributions and to be a dominant of vegetation communities. Other geographic areas, such as Australia, have had numerous radiations of Myrtaceae, resulting in the evolution of many narrow endemics. The Hawaiian Myrtaceae have wider distributions and therefore may have a lower risk than Myrtaceae in other geographic areas. At the other extreme, the Hawaiian Malvaceae have a very high level of risk relative to the rest of the family. In this case, the family attributes have remained the same in the Hawaiian Islands, but the lowland dry to mesic habitats typical of the family have been greatly disturbed or completely eliminated in the islands.

At the species and infraspecific level, monocots are less at risk in the Hawaiian flora than dicots for both endemic and indigenous taxa. In a long-term study of extinction and rarity in New Zealand, Duncan and Young (2000) also found that monocots were less likely to be at risk than dicots. However, analyses with consideration of lineages in the Hawaiian flora show no difference in risk between monocot and dicot lineages. This difference in pattern between species-level and lineage-level analyses occurs because of the large number of taxa at risk in dicot lineages that have undergone large radiations. In the most spectacular example, one lineage in the Campanulaceae has given rise to 145 taxa, 110 of which are endangered and account for 18% of all endemic taxa at risk in the Hawaiian Islands. Taxa that share traits in these large lineages can dominate patterns of risk if lineages are not taken into account.

Endemism

Indigenous taxa are only a small proportion of the flora, but very few are at risk. As a result, indigenous taxa are a significant proportion (20%) of the taxa that are apparently secure. Indigenous taxa share many ecological and life history traits and thus have a large effect on interpretation of patterns of endangerment. This effect is true not only at the species level, but particularly at the lineage level, where indigenous lineages are about one-third of all lineages. For example, almost all indigenous lineages consist

of a single taxon. When endemic and indigenous lineages are pooled, single-taxon lineages are more likely to be secure than larger lineages. If only lineages with endemic taxa are considered, however, there is no association of lineage size and risk. The majority of lineages were bird-dispersed, but indigenous lineages were disproportionately dispersed by drifting or rafting. Many indigenous taxa are typical strand plants (e.g., *Scaevola taccada* (Goodeniaceae)) in coastal or aquatic habitats. Several indigenous species may have been dispersed by migrating waterfowl (e.g., *Cyperus polystachyos* (Cyperaceae), *C. laevigatus*, and *Lemna aequinoctialis* (Lemnaceae)); *Drosera anglica* (Droseraceae) was probably dispersed by the Pacific golden plover.

Other indigenous taxa such as *Cocculus orbiculatus* (Menispermaceae) or *Dodonaea viscosa* (Sapindaceae) may have low risk because they have broader ecological niches with respect to community type, elevation, and moisture ranges, and have greater historic densities than endemic taxa. Life history traits of indigenous taxa (herbaceous monocots with small brown flowers) reflect the large proportion (30%) of indigenous grasses and sedges. Many characteristics of indigenous taxa (good dispersal, broad ecological range, multiple populations on different islands, higher population densities) also are traits that make them less likely to be at risk.

Island Age and Geographic Ranges (Single- vs. Multi-Island Distributions)

Most indigenous taxa in the Hawaiian Islands have good long-distance dispersal capabilities and good dispersal within the Hawaiian Islands. All of the major islands, including the Big Island (<0.43 my old), have existed long enough for indigenous taxa to spread so that all the major islands have similar numbers of indigenous taxa. The maintenance of lineages with a single taxon and the lack of differentiation among populations of indigenous taxa are consistent with good dispersal of these taxa, continuing gene flow among populations, or alternatively, their recent introduction.

There is no consistent pattern in the number of endemic taxa per island, a function of both island age and area. Maui Nui has the highest number of endemics, perhaps because it is young enough to have great size and ecological diversity and because it developed during a period of major climatic fluctuation. At the same time, Maui Nui is old enough for radiations of lineages to have occurred. The Big Island is the youngest island and has the fewest endemic and SIE taxa, despite its larger size. As islands age, their area and elevation generally decrease from erosion, subsidence, and catastrophic landslides; the topography and habitats become more dissected, with deeper valleys and other local topographic features (Macdonald et al., 1983; Moore et al., 1994; Carson and Clague, 1995). Greater fragmentation of habitats may create greater isolation and opportunities for speciation. These simultaneous changes in age and habitat make it difficult to determine whether the greater number of endemics on older islands is simply a result of having enough time to evolve new endemic taxa, or whether the changing availability of habitats and changes in communities are also involved.

Patterns of endangerment of endemic taxa with island size and distribution (multi- vs. single-island) are consistent with expectations. SIEs are more at risk than multi-island endemics, and small islands have the greatest percentage of taxa at risk. The smaller, older islands (e.g., NW Hawaiian Islands, Ni'ihau) are remnants of much larger islands that had a large variety of habitats. In many cases, these islands are now only low atolls. The homogeneity of habitat and small size of these islands make the endemic taxa on these islands especially vulnerable. One example is the release of the European hare on Laysan Island in the NW Islands in 1903; by 1923, the island was essentially devoid of vegetation (Ely and Clapp, 1973). Soon afterward, the remaining hares starved. Several species, such as the flightless Laysan Rail, became extinct, and the population size of *Cyperus pennatiformis* var. *bryanii* (Cyperaceae) is still unstable and subject to extinction.

Patterns of endangerment vary among islands. When all taxa at risk are pooled (extinct, endangered, vulnerable, and rare), the main islands do not differ in the proportion of SIEs at risk. This is not consistent with the hypothesis that SIE taxa that have evolved on older islands could be at greater risk. Habitat losses may have been so extensive on all of the islands that more subtle patterns have been swamped out. The

loss of natural communities after human contact has been tremendous, ranging from 41% lost on the Big Island to ~83% lost on Oahu and Maui (USFW and Hawaii Natural Heritage Program 2001, unpublished). When taxa at risk are subdivided more finely, they show different geographic patterns. Among the larger islands, Maui Nui has the greatest proportion of extinct endemics and SIEs. This extinction rate may be particularly high because Maui Nui, once a Pleistocene island of ~26,000 sq km, fragmented into several islands beginning ~300,000–400,000 years ago (Carson and Clague, 1995). The smaller islands of Lana'i and Kaho'olawe, which are part of Maui Nui, have much higher extinction rates of SIE species than Maui Nui as a whole. The total percentage of taxa at risk is similar for Kaua'i and other islands, but the proportion of extinct SIE taxa on Kaua'i is about half of that of Oah'u and the Big Island. At the same time, the percentage of SIE taxa that are rare on Kaua'i is higher than expected. The lower number of extinct species on Kaua'i may reflect the fact that a relatively greater proportion of habitat is intact than on other islands (Juvik and Juvik, 1998). On Kauai, ~38% of natural communities remain intact on Kaua'i relative to 17% on Oah'u, 30% on Maui, 16% on Moloka'i, 22% on Lana'i and on Kaho'olawe, and 59% on the Big Island (Hawaii Natural Heritage Program 2001, unpubl.). Alternatively, the lower percentages of extinct taxa and higher percentages of rare taxa may reflect the intensive field work by botanists on Kaua'i (e.g., J. Lau, S. Perlman, K. Wood) that has led to rediscoveries of species presumed to be extinct. Many areas of the Hawaiian Islands remain understudied and still lack historical and current data on taxa.

Ecological and Life History Traits of Taxa and Lineages

Endemic Hawaiian taxa at risk have many traits often used to define rare species. They are associated with narrow geographic range (single-island rather than multi-island distributions); narrow habitat specificity in moisture, community type, and elevation, and have much lower historic densities. Endemic taxa at risk are disproportionately associated with cliffs, shrubland, forest, and bog habitats. In many cases, taxa with these cliff distributions may be the remnants of species that were once more widespread. Feral animals (goats, pigs, deer) and cows are a major threat to the flora, and these cliff habitats may serve as refugia that are inaccessible to these animals. For example, the recently discovered *Hibiscadelphus woodii* (Malvaceae) and *Nototrichium divaricatum* (Amaranthaceae) are known from very steep slopes in Kalalau Valley, Kaua'i. They may always have been restricted to this narrow habitat, or they may have had wider distributions before the introduction of goats.

In the Hawaiian Islands, taxa at risk do not have broad elevational ranges but they are not associated with any particular elevational range. In studies of endemic plants from southeast France and Corsica, Medail and Verlaque (1997) found that threatened plants were more likely to occur at lower elevations, particularly in coastal areas, rocky grasslands, and damp ecosystems. Rare plants were also more common at lower elevations in California (Hegde and Ellstrand, 1999). In the Hawaiian Islands, the greatest number of endemic taxa as well as endemic taxa at risk occur in mesic lowland forest, wet montane forest, and mesic montane forest. Although involving fewer taxa, the greatest proportion of taxa at risk have dry coastal, dry lowland scrubland, and dry lowland forest distributions.

Although >90% of the area of dry forest, ~60% of mesic forest area, and ~40% of wet forest area have been lost (Juvik and Juvik, 1998), these differences in habitat destruction are not reflected in significantly different proportions of taxa at risk in dry, mesic, or wet forest. In all these habitats, more than half of the taxa are at risk, and destruction of habitat may have been so significant that more subtle patterns are lost. Less than 1% of the area of lowland dry forest and shrubland remains on O'ahu, Moloka'i, and Lana'i and <2% remains on Maui. On the Big Island, 17% of the area once in dry forest and shrubland remains (Hawaii Natural Heritage Program 2001, unpubl.). Alternatively, taxa in different habitats may have different patterns of habitat degradation or may respond differently to habitat loss. These conclusions about forests differ from those of Mehrhoff (1996), who found a correlation of plant extinction and endangerment with dry, mesic, and wet Hawaiian habitats. The discrepancy may be due to the more restricted habitats used here (forests) as well as use

of all taxa at risk rather than only federally listed species.

Several studies have examined the relationship between risk and life history traits. In a study of rare vascular plant species of Utah, Colorado, and California, Harper (1979) found that herbs were more likely to be endangered than woody plants and that rare species were more likely to be insect-pollinated. In a more recent study of rare species of California and the British Isles, Hegde and Ellstrand (1999) found that rare species were more likely to be woody, shorter in stature (for nonwoody species, but not within woody species), and with many-seeded fruits (in California only). They found no association of rarity with fruit dispersal.

Hawaiian taxa at risk differ from secure taxa in life history traits, although these patterns are heavily influenced by lineages with a large number of taxa. Very few taxa are herbaceous, and many genera that are herbaceous in continental areas have evolved secondary woodiness in endemic taxa such as *Chamaesyce* (Euphorbiaceae), which in Hawai'i are shrubs and trees as tall as 9 m. Taxa at risk are more likely to be shrubs than trees. Future work distinguishing between taxa that are members of woody lineages compared with those that have evolved insular (secondary) woodiness from essentially an herbaceous ancestry (such as *Schiedea* (Caryophyllaceae); Carlquist, 1995) or the silversword alliance (Asteraceae; Carlquist, 1974) may show clearer patterns.

Analyses at the taxon level are useful because the concerns of conservation practitioners in the field are often focused on particular species or taxa, and official listings of the status of endangered species are reported at this level (Wagner et al., 1999a). At the same time, these analyses of associations of traits and levels of endangerment at the taxon level must be interpreted with considerable caution because consideration of lineages may change relationships. For taxon-level analyses, taxa at risk are more likely to be monomorphic, bird-pollinated, and with longer flowers that are more often white than brown or green. These traits are characteristic of the Campanulaceae and Lamiaceae, both families with large numbers of taxa at risk.

In contrast, analyses that control for lineages reduce the effects of these large families, and show no association of risk with breeding system. They suggest an association with insect pollination rather than bird pollination. The extinction of many native birds in the Hawaiian Islands (Juvik and Juvik, 1998) may particularly affect lineages such as the native Campanulaceae with its many bird-pollinated species. Although analyses of species show no association of risk with fruit type (fleshy, dry), lineage-level analyses show an association of lineages at risk with dry fruit types. Lineages at risk also have a greater association with long-distance dispersal by drift rather than by birds. In contrast, studies of dispersal mechanisms in California and the British Isles (Hedge and Ellstrand, 1999) as well as those of long-distance dispersal mechanisms in New Zealand, another isolated flora (Duncan and Young, 2000), found no association of dispersal type with risk.

Lineage Size

Very few plants managed to survive long-distance dispersal and successfully establish naturally in the Hawaiian Islands. With only 293 presumed flowering plant colonists, successful lineages established at a rate of once every 17,400 years (beginning with Kaua'i 5.1 my ago [Ma]) or once every 99,000 years (beginning with Kure in the NW Islands 29 Ma). Between 48 Ma and 29 Ma, older islands subsided, volcanic activity slowed, and no islands higher than 1,000 m were formed (Carson and Clague, 1995; Clague, 1996). The absence of high islands limited opportunities for inter-island colonizations within the Hawaiian Islands during this time. A rate of successful colonization once every 99,000 years seems more realistic.

The Hawaiian Islands are well known for the spectacular radiation of some lineages (e.g., the silverswords, lobelioids, and *Schiedea*; Wagner and Funk, 1995). In many cases, taxa in large lineages are more isolated and may be SIEs or even be restricted to a small part of an island, often in more specialized habitats with lower historic population densities. These species may be more at risk with introduction of alien herbivores, alien weedy competitors, and habitat loss.

Most lineages in the Hawaiian Islands did not speciate (Wagner, 1991), and almost all indigenous lineages and about half of lineages with endemic taxa are single-taxon lineages.

For endemic lineages, lineage size is not associated with taxa at risk, and large endemic lineages are no more at risk than small lineages. Given this pattern, taxa in lineages that have undergone extensive radiation do not appear to be at greater risk. Rather than being more recently evolved and therefore at greater risk (Fenner et al., 1997), taxa in larger lineages may actually be older than taxa in smaller lineages that have not yet evolved distinct species.

The number of taxa in a lineage may vary for a number of reasons. In some cases, hybridization may prevent extensive speciation (e.g., *Metrosideros* (Myrtaceae), *Pittosporum* (Pittosporaceae)). In other cases, lineages may not have had sufficient time to differentiate into a large number of taxa, particularly on younger islands. For example, *Stenogyne* (Lamiaceae) species on the older islands of O'ahu and Kaua'i are more clearly defined than the more polymorphic species found on the younger Big Island (Weller and Sakai, 1990; Wagner and Weller, 1999). Greater polymorphism within species on the younger islands also occurs in *Cyrtandra* (Gesneriaceae), *Labordia* (Loganiaceae), *Lysimachia* (Primulaceae), *Melicope* (Rutaceae), *Myrsine* (Myrsinaceae), and *Phyllostegia* (Lamiaceae). Species on older islands may be easier to delimit because of extinction of intermediate forms and evolution of novel forms with increasing isolation resulting from erosion and dissection of habitats.

Rarity

Rabinowitz's (1981) classification of rarity based on geographic range, habitat specificity, and local abundance is still used today, in large part because of its simplicity and the ease in obtaining the necessary data. Although other systems have been proposed that take the evolutionary history of organisms into account and address causal factors (e.g., Fiedler and Ahouse, 1992), they have been difficult to apply because of the lack of phylogenetic information (Kunin and Gaston, 1997).

In this analysis, we examined the relationship of rarity and risk by adapting our measures of geographic range (single- vs. multi-island), habitat range (across more than one community vs. only in one community), and historic population density (large, medium, and small) to create categories similar to those of Rabinowitz. We used historic population density rather than current population size to remove some of the well-known immediate effects of anthropogenic disturbance. Taxa may be rare because they are naturally scarce or because they have lost range as a result of anthropogenic activity. The response of these two types of taxa to habitat change may differ dramatically. Although we attempted to estimate pre-Polynesian population sizes, even these "historic" population estimates are probably influenced by pre-European contact, Hawaiian land use practices, and the nonnative species that accompanied them. The effects of the Polynesians on land birds and vegetation were extensive; ~50% of Hawaii's endemic land birds were extirpated (Juvik and Juvik, 1998) and marked changes occurred in vegetation communities (Cuddihy and Stone, 1990). The effects of human colonization on plant population densities and species extinctions were also significant, although only a few studies have clearly shown declines in plant population densities that may be attributed to human colonization (Athens, 1997).

As expected, risk and rarity show a strong association. Taxa that occur on more than one island, with broad habitat tolerances, and in dense populations are rarely at risk. Species such as the common forest dominant *Acacia koa* (Fabaceae) with broad moisture and elevation ranges, although less common today, still occurs on most of the main islands and is not currently at risk. A few formerly common taxa are not secure, primarily because of tremendous habitat loss throughout the Hawaiian Islands, particularly in low-elevation dry forest. *Hibiscus brackenridgei* subsp. *mokuleianus* (Malvaceae) has multiple threats (habitat degradation; possible herbivory by pigs, goats, axis deer, and cattle; competition with alien plant species; fire; road construction; and stochastic extinction (Canfield et al., 1994)). *Sesbania tomentosa* (Fabaceae) and *Chamaesyce skottsbergii* (Euphorbiaceae) have been adversely affected by habitat loss and their brittle wood with trailing stems makes them extremely vulnerable to damage by alien ungulates. Based on fossil pollen records, *Kanaloa kahoolawensis* (Fabaceae) was once abundant in lowland Kaua'i, O'ahu, Kaho'olawe, and Maui. After human settlement, *Kanaloa* became

increasingly scarce and disappeared almost completely ~800 years ago. Recently, two individuals were discovered still clinging to existence on Kaho'olawe (Lorence and Wood, 1994).

At the other extreme, the vast majority of the endemic taxa of Hawaii are classic "rare" taxa, with single-island distributions and narrow habitat range. These taxa are also disproportionately at risk. As habitat specialists, these taxa are particularly vulnerable to habitat degradation and destruction. Those taxa not at risk tend to have mesic and wet lowland and montane forest distributions. Taxa in Hawaii are found in all the Rabinowitz (1981) rarity categories and show patterns of abundance similar to those in other studies (e.g., Rabinowitz et al., 1986). In a study of the British flora, Rabinowitz et al. (1986) found no plants with narrow range (single-island) and small populations but with broad habitat specificity. In our study, despite the broad habitat specificity, >90% of these taxa are at risk. Sparse species (multiple-island, wide habitat, but low density) are infrequent and 74% of those taxa are at risk or extinct. Some species that are apparently secure in this category are adapted to dry, open, often disturbed areas (*Argemone glauca* var. *glauca* (Papaveraceae), *Panicum konense* (Poaceae)) or occur in wet forest, a habitat with relatively less destruction (*Dubautia laxa* subsp. *laxa* (Asteraceae)).

The most infrequent rarity category in the Hawaiian Islands has wide habitat, high local population density, but a single-island distribution. Only 2 of these 11 taxa are at risk, both species of *Chamaesyce* (Euphorbiaceae). *Chamaesyce celastroides* var. *lorifolia* is vulnerable because of rat predation on seeds and because alien kikuyu grass (*Pennisetum clandestinum*) prevents establishment of seedlings. More detailed analyses of factors associated with these different types of rarity as well as better categorization of habitat range may provide more clues to patterns of rarity and potential causes and consequences of endangerment.

Conclusions

The Hawaiian Islands are one of several island ecosystems that are biodiversity hotspots, with both exceptional concentrations of endemic species and ongoing major loss of habitat (Myers et al., 2000). Understanding patterns of local endemism and extinction in these areas is critical to understand more global extinction patterns and to better manage these areas. For example, the Cape Floristic Region is similar in some ways to the Hawaiian Islands, with rapid diversification of many plant lineages, a high proportion of endemic species, and high rates of endangerment. Patterns of endemism and endangerment have been explored in detail in this region to develop conservation planning for the preservation of biodiversity and of ecological and evolutionary processes that generate new taxa (e.g., McDonald et al., 1995; McDonald and Cowling, 1995; Trinder-Smith et al., 1996; Cowling and McDonald, 1998; Cowling and Pressey, 2001).

Comparisons of endemic and indigenous taxa as well as study of patterns of risk among endemic taxa of the native Hawaiian flowering plants stress the importance of several well-known patterns (Pimm et al., 1995) and identify other patterns. First, data at three different scales suggest that biogeographic range is critical, and species with more restricted ranges are more likely to be at risk. Species are far more likely to be at risk if they are (a) endemic to the Hawaiian Islands without extra-Hawaiian distributions; (b) single-island endemics without wider distribution within the islands; and (c) restricted to a narrow habitat (defined particularly by elevation and community type). Species with distributions on cliffs, in shrublands, forests, and bogs of the Hawaiian Islands have far greater odds of being at risk than those in coastal habitats. Restricted range confers great risk, given the magnitude of habitat destruction.

Second, population density is also a critical factor. Species with historically low numbers of individuals in populations are more likely to be at risk than those with greater densities. The life history traits associated with historically low population densities may make these taxa more susceptible to the pressures of rapid anthropogenic changes, including introduced ungulates and other alien, invasive species.

Third, the life history patterns associated with risk are complicated, and consideration of the effect of evolutionary relationships (lineages) changes some of these pattern. For example, in the Hawaiian Islands, the largest lineage is in the Campanulaceae. As a result, species-level analyses without

respect to lineage shows risk associated with a monomorphic (hermaphroditic) breeding system and bird pollination. Analyses incorporating the effect of lineage greatly reduce the impact of these taxa, resulting in an association of taxa at risk with insect pollination and no effect of breeding system. The effect of lineage points out how more general decisions remain to be made about the relative importance of preserving lineages that have radiated and shown great evolutionary potential vs. lineages that have not radiated but collectively exhibit greater biodiversity.

Fourth, patterns in the Hawaiian Islands may be a model for worldwide patterns. The native Hawaiian flora has a much higher proportion of taxa at risk than worldwide, and families with higher proportions of taxa at risk in the Hawaiian Islands also have a higher proportion of taxa at risk worldwide. Some of the approaches described here may be useful to predict patterns of endangerment in other island and island-like ecosystems under increasing pressures of endangerment and extinction.

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