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Extrafloral Nectaries on Plants in Communities without Ants: Hawaii

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Since the Hawaiian Islands lack native ants, it was hypothesized that extrafloral nectaries, an ant-related mutualistic trait, should be lacking on native species. Presence of extrafloral nectaries (EFNs) on plants was determined by direct observation and related to vegetation structure and floral composition. Frequency of plants with EFNs was low by all possible comparisons. However, several endemic species had functional EFNs. The hypotheses to explain these anomalies are (1) phylogenetic inertia or (2) mutualism with some other organism than ants.

1. Introduction

The question is: Are extrafloral nectaries present on endemic and indigenous plant populations on islands lacking ants? Extrafloral nectaries are plant glands, found on virtually all aboveground plant parts, which attract on virtually all aboveground plant parts, which attract numerous nectar-feeding insects (but generally not the numerous nectar-feeding insects (but generally not the pollinators). The interaction of plants with their nectarfeeders has been shown to be a mutualistic antiherbivore defense: ants exclude or prey upon herbivores while visiting extrafloral nectaries (e.g. Bentley 1977, Tilman 1978, Inouye and Taylor 1979, Keeler 1980b, Schemske 1980, Beckmann and Stucky 1981, Stephenson 1982, but see also O'Dowd and Catchpole 1983, and Tempel 1983 for counter-examples).

The expectation was that plants either lose or do not evolve EFNs in the absence of ants; the null hypothesis is that there is no relationship between presence of ants and presence of extrafloral nectaries. A third alternative is that phylogenetic inertia maintains extrafloral nectaries in the island flora.

A site to test this hypothesis is Hawaii. The Hawaiian Islands have the most complex set of ecosystems in the world with no native ants (Wilson and Taylor 1967). The existing high islands are 4.5-5.6 Myr old, the oldest atoll of the chain perhaps 11.3 Myr, and the island chain as a whole 25 Myr old. At no time were the islands connected to a continent (Mueller-Dombois 1981). Ants are present now, but only because they were recently introduced (Wilson and Taylor 1967). Consequently, the flora of Hawaii (1440 native angiosperm species, derived from an estimated 272 immigrants (Fosberg 1948)), has evolved in the absence of ants and thus the ant-plant mutualism.

This paper reports the abundance of plants with extrafloral nectaries in Hawaii. The question was asked in two ways. First, what is the relative abundance or cover of plants with extrafloral nectaries in natural Hawaiian ecosystems? This allowed comparison with other studies (Bentley 1976, Keeler 1979a, 1980a, 1981b, Keeler and Death unpubl.). Second, what is the proportion of species with extrafloral nectaries among endemics as compared with introduced plants in the flora?

2. Materials and Methods

Little exists in the literature on which plants in Hawaii have extrafloral nectaries. Since EFNs are often small and only rarely preserve unambiguously on dried materials, they have frequently gone unreported. Consequently, it was important to observe plants under natural conditions, preferably with active ants, to determine the presence of EFNs. The method employed here was to search

live plants for EFNs. I determined that a plant had EFNs based on as many of the following types of evidence as possible: 1) production of nectar, 2) presence of a nectary, 3) nectar-gathering, stereotyped behavior by ants or other nectar-feeders, and 4) a published report of the presence of an EFN (e.g., Zimmermann 1932, Schnell et al. 1963, Napp-Zinn 1973, Fahn 1979, Elias 1983). This approach was greatly aided by the introduced ants of Hawaii, although the dominant ant of the Big Island, *Anoplolepis longipes*, is a relatively poor nectar-gatherer. With this information, information from vegetational studies and floras could be interpreted in terms of the frequency of plants with EFNs.

The rare endemic species presented a particular problem. Every attempt was made to see them alive, i.e., in gardens. For this purpose, I visited: Maui County Botanical Garden, Kahului; Pacific Tropical Botanic Garden, Lawai; Nani Mau Garden, Hilo, the Orchidarium Hilo; Foster Botanical Garden, Honolulu; Waimea Arboretum, Haleiwa; and the Lyon Arboretum of the University of Hawaii. Also ornamental plantings were observed wherever they occurred (e.g. at the visitor centers in Hawaii Volcanoes National Park; HVNP).

Extrafloral nectaries are defined ecologically for the purposes of this paper. That is, an extrafloral nectary is a plant gland which produces nectar that attracts non-pollinating nectar-seeking insects, whether or not there is a recognizable structure. In this usage, the postfloral nectaries of *Morinda citrifolia* L. (Rubiaceae) are included. They begin as floral nectaries attracting pollinators but continue to function while the fruit is developing. Their function has not been studied, but is presumably for protectionist mutualism (Keeler 1981a, Guerrant and Fiedler 1981: Figure 3).

It is unlikely that plants without EFNs were determined to have EFNs, because for each species several lines of evidence were used on several individuals. Failure to recognize a plant with extrafloral nectaries as having EFNs is more likely. In some cases, EFNs lack structure (Frey-Wyssling and Hausermann 1960, Tilman 1978, Elias 1983), some function only for a very short time (e.g., nectaries on fruit, Elias and Prance 1978) and they may be missing from poorly developed leaves (Keeler 1977). Six species for which a high chance of error exists were omitted from the analysis of the HVNP flora. All belong to genera for which EFNs are reported, but where nothing is known of the species, and I did not see them. Five are exotics (*Agave* cf. *sasalana* (Amaryllidaceae), *Centaurea melitensis* (Asteraceae), *Jatropha curcas* (Euphorbiaceae), *Plumbago zeylandica* (Plumbaginaceae) and *Sambucus mexicana* (Caprifoliaceae). One, *Pleomele aurea* (H. Mann) N.E. Br. (= *Dracaena hawaiiensis* Deg & Deg), is endemic; if present, extrafloral nectaries would be close to the base of the calyx.

If any subspecies had EFNs, the whole species was designated "having EFNs." However, in three species, Hawaiian plants lacked EFNs although the species had been reliably reported to have EFNs. These cases are discussed individually below, and in the analysis they appear as "lacking EFNs."

The categories "endemic," "indigenous," "Polynesian introduced," and "exotic" are taken from St. John (1973), modified in some cases by more recent information. These are hierarchical categories, arranged in the order listed: if a plant can be classed in the earlier category, it goes there. Therefore, endemics may be indigenous but no indigenous species are endemic. Most species classified as indigenous are tropical beach and strand taxa which may interbreed beyond Hawaii.

Vegetation analysis was taken from Newell (1968). She analyzed sixty-five plots by cover class by species, using the method of Mueller-Dombois (1964). Plot size was determined based on the diversity of the community: most plots were 500 m², but the smallest was 6 m² and the largest, in the Ka'u Desert, 10,000 m². Species lists with cover class by species were presented and the plots combined by community type. To determine cover of plants with extrafloral nectaries, I scored each plot for presence of plants with EFNs and summed their contribution to total cover. The plot summaries were averaged over all the plots from the same plant alliance as determined by Newell (1968).

Newell (1968) recognized five major plant alliances. These correspond to the "environmental sections" of Mueller-Dombois and Bridges (1981), except that Newell combines their alpine and subalpine sections as a single alliance. There are slight differences between the two classifications schemes, perhaps due to the location of the particular plots studied. I used Newell's scheme since I used her data, but I have applied Mueller-Dombois and Bridges' (1981) terms for reference.

The sites studied were on the island of Hawaii, ranging from near sea level to above treeline on Mauna Loa. The island of Hawaii is the newest and largest of the islands, at 10,470 km² nearly the size of all the other islands combined. Native forest and shrubland remain mainly on the slopes of Mauna Loa (4146 m) and Kilauea (1190 m) in and adjacent to HVNP.

The five plant associations of HVNP (Newell 1968, Mueller-Dombois 1981, Mueller-Dombois and Bridges 1981) are as follows: 1) Coastal Lowland Section: defined by Newell as the *Waltheria indica* L.-*Chrysopogon aciculatus* (Retz.) Trin. alliance. This plant alliance was found from the coastal salt-spray zone (15 m a.s.l.) to dry slopes at 520 m (Hilina Pali). Annual rainfall ranged from 1100 to 1500 mm per year and mean annual temperature was 20 to 23°C. These plots were all highly disturbed: of the species censused, 47 of the 66

(71%) were exotics, 8 (12%) were endemic, 10 (15%) were indigenous and one a Polynesian introduction. 2) Submontane Seasonal Section: the *Andropogon glomeratus* (Walt.) BSP-*Conyza canadensis* (L.) Cronq. alliance. It ranged from the top of Hilina Pali at 640 m, a moderately xeric coastal area to very dry Ka'u Desert plots at 975 m and up to high (1340 m) dry plots on the slopes of Mauna Loa. Rainfall was between 100 and 1500 mm per year but strongly seasonal, and average annual temperature ranged from 23°C at the lower sites to 9.5°C at the upper sites. Of the 86 species in the plots, 25 (29%) were endemic, 11 (13%) indigenous, 49 (57%) exotic and one a Polynesian introduction. 3) Montane Rain Forest Section. This is Newell's (1968) *Ilex anomala* H. & A.-*Vaccinium calycinum* Sm. alliance. These sites received from 1500 to 2400 mm rainfall annually, while average annual temperatures were between 17 and 20°C. Elevations ranged from 730 to 1230 m. The community is visually dominated by *Metrosideros polymorpha* Gaud. and endemic tree ferns (*Cibotium* spp.). Sixty-seven (61%) of the 110 plants censused by Newell were endemic, 14 (13%) indigenous, and 29 (26%) exotic. 4) Montane Seasonal Forest Section: dominated by *Acacia koa* Rock-*Holcus lanatus* L. This is a mesic vegetation at middle elevations (1800-1900 m), best developed on kipukas (islands of older vegetation among newer lava flows). Rainfall is 1100 to 1300 mm per year; mean annual temperatures were approximately 14°C. While all of HVNP is geologically very young and has poorly developed soils, this alliance contained some of the oldest, best developed soils. Of the 76 species, 26 (34%) were endemic, 14 (19%) were indigenous, and 36 (47%) exotics. 5) The Alpine and Subalpine Sections: defined as *Vaccinium peleanum* Skotts.-*Tetramolopium humile* (Gray) Hdb. alliance. This is the uppermost community, beginning at 2030 m on the Mauna Loa Strip Road. Trees gradually dropped out about 2500 m, and shrubs dropped out by 3050 m. Mean annual temperatures ranged from 6 to 9.5°C with regular frost at the upper sites. Rainfall averaged 1000 to 1300 mm annually. Probably the four uppermost plots are "alpine" and the lower "subalpine" as defined by Mueller-Dombois and Bridges (1981) but there is no discontinuity in Newell's data to distinguish them. Of the 30 species, 19 (63%) were endemic, 7 (23%) indigenous and 4 (13%) exotic.

Proportion of plants with extrafloral nectaries among native (endemic and indigenous) species was compared with the proportion among nonnative (Polynesian-introduced and exotic) species. Lacking the distribution of extrafloral nectaries in any comparable flora, it was the best estimate I could make of whether there were "many" or "few" species with EFN's among Hawaiian native plants. This was done for both the well-known flora of HVNP and the Hawaiian flora as a whole.

3. Results

In Hawaii Volcanoes National Park, of the 636 vascular plant species present, 33 species in 11 families were found to have extrafloral nectaries (Table 1). This includes both those found in study plots and others outside the plots but reported for HVNP. Only one of the species with EFNs is considered endemic, *Acacia koa*. Six indigenous species have EFNs. These are pantropical coastal species, including *Ipomoea pes-caprae* (L.) R. Br., *Erythrina tahitensis* (until recently considered the endemic *E. sandwicensis* [Barneby and Krukoff 1982], and *Thespesia populnea* (L.) Soland. ex Correa. Plants introduced by Polynesian settlers (labelled P in Table 1) are rich in EFN-bearing species (Table 2). The other 22 species were more recently introduced to Hawaii.

Table 1. Species of vascular plants with extrafloral nectaries in Hawaii Volcanoes National Park. E = endemic, I = indigenous, P - introduced by Polynesians, X = exotic, naturalized. List according to Fosberg (1966). Nomenclature is according to St. John (1973). CL = coastal lowland section, SS = seasonal submontane section, MS = montane seasonal section, AS = alpine/subalpine section and MR = montane rainforest (see Table 3 and text for description of plant associations). HD = human disturbances, species found in HVNP in association with man disturbances, species found in HVNP in association with residence or disturbances and () indicates species was not residence or disturbances and () indicates species was not found in the study plots.

| | |
|-----------------------------------|---|
| Liliaceae | <i>Yucca filamentosa</i> L. X (HD) |
| Orchidaceae | <i>Arundina bambusaefolia</i> X CL MR |
| | <i>Spathoglottis plicata</i> X CL SS MR |
| | <i>Phaius tankervilleae</i> X MR |
| Dioscoraceae | <i>Dioscorea alata</i> L. P (HD) |
| Rosaceae | <i>Prunus persica</i> (L.) Batsch. X (HD) |
| Fabaceae | <i>Acacia koa</i> E MS |
| | <i>Caesalpinia bonduc</i> (L.) Roxb. I (CL) |
| | <i>Cassia bicapsularis</i> L. X CL |
| | <i>C. laevigata</i> Willd. X (HD) |
| | <i>C. leschenaultiana</i> X CL |
| | <i>C. occidentalis</i> L. X (CL/SS) |
| | <i>Crotalaria incana</i> L. X (CL) |
| | <i>C. mucronata</i> Desr. X (CL) |
| | <i>Dolichos lablab</i> L. X (HD) |
| | <i>Erythrina tahitensis</i> I (CL) (\approx <i>E. sandwicensis</i>) |
| | <i>Leuceana leucocephala</i> (Lam) DeWit X (SS) |
| | <i>Pithecellobium dulce</i> (Roxb.) Benth. X HD |
| | <i>Prosopis pallida</i> (Willd.) H.B.K. X (CL) |
| | <i>Vicia sativa</i> L. X (HD) |
| | Euphorbiaceae |
| <i>Ricinus communis</i> L. X (CL) | |
| Balsaminaceae | <i>Impatiens sultani</i> Hook f. X (HD) |
| Malvaceae | <i>Hibiscus rosa-sinensis</i> L. X (HD) |
| | <i>H. tiliaceus</i> L. I (CL) |
| | <i>Thespesia populnea</i> I (CL) |
| Passifloraceae | <i>Passiflora edulis</i> Sims X (MR) |
| | <i>P. ligularis</i> Just. X (HD) |
| Apocynaceae | <i>Plumeria rubra</i> L. X (CL) |
| Convolvulaceae | <i>Ipomoea batatas</i> (L.) Poir. P (HD) |
| | <i>I. pes-caprae</i> I (CL) |
| | <i>Stictocardia tiliaefolia</i> (Desr.) Hallier f. I (CL) |
| Rubiaceae | <i>Morinda citrifolia</i> (postfloral nectaries) P CL |

Endemic: 1; Indigenous: 6; Polynesian-introduced: 4; Exotic: 22; Total 33 species.

Three species which have EFNs elsewhere in the world lacked EFNs on plants in HVNP. These were *Passiflora foetida* L. (Passifloraceae) reported by Baker et al. (1978) to have extrafloral nectar, *Ipomoea indica* (Burm.) Merr. (= *I. congesta* R. Br. and *I. acuminata* (Vahl) R. & S. of some literature, Convolvulaceae) which Keeler and Kaul (1979) reported as having petiolar nectaries and *Pteridium aquilinum* (Polypodiaceae) whose foliar nectaries have been the subject of discussion for a century (Darwin 1897). I could find neither nectar glands nor nectar production on plants of these species growing in HVNP. In addition, they were not visited by nectar feeders in the field. Durkee et al. (1984) has confirmed anatomically that plants of *Passiflora foetida* from Hawaii lack extrafloral nectaries.

Cover of plants with extrafloral nectaries in the plant associations of HVNP is given in Table 3. Their cover was 3% for the coastal lowland section and less than one percent in submontane seasonal, alpine/subalpine, and montane rainforest sections. In these sections, none of the plants contributing to the cover by plants with EFNs were endemic (*Arundina bambusaefolia* Lindl., *Phaius tankervilleae* (Banks) Bl., *Spathoglottis plicata* Bl. (Orchidaceae), *Morinda citrifolia* (Rubiaceae) and *Cassia leschenaultiana* DC (Fabaceae)) (Table 3). In montane seasonal forest section, however, the cover by plants with EFNs averaged 21.2% with single plots as high as 66.5%. This was due to the variable abundance of *Acacia koa* (Fabaceae), a Hawaiian endemic and a dominant tree. There is no question that the nectaries of *A. koa*, located near the base of the phyllodes, produced nectar: introduced honey bees (*Apis mellifera*) foraged for nectar at these structures, going systematically from one to the next.

Of the 48 indigenous and 1394 endemic species of Hawaii, 7 indigenous and 11 endemic species from four vascular plant families have extrafloral nectaries (Table 4). A few members of genera with EFNs may be added upon subsequent study, but I believe this is

Table 2. Distribution of plants with extrafloral nectaries (EFNs) in Hawaii Volcanoes National Park. List of species based on HVNP Checklist (Fosberg 1966). Names of species with EFNs are given in Table 1. Differences between groups were tested using chi-square or Fisher's exact test; all were significantly different ($P < 0.01$) except indigenous vs. Polynesian-introduced ($P \approx 0.04$, Fisher's exact test) and indigenous vs. exotic ($\chi^2 = 0.44$, $df = 1$, not significant).

| Origin | No. of species | All species | Frequency of species with EFNs |
|-----------------------|----------------|-------------|--------------------------------|
| Endemic | 1 | 197 | 0.005 |
| Indigenous | 6 | 72 | 0.08 |
| Polynesian-introduced | 4 | 13 | 0.31 |
| Exotic | 22 | 354 | 0.06 |
| Total | 33 | 636 | 0.05 |

Table 3. Cover of plants with extrafloral nectaries in Hawaii Volcanoes National Park communities. Communities are those of Newell (1968), named according to Mueller-Dombois and Bridges (1981).

| Community | Mean cover plants with EFNs | Std. dev. | Mean number species with EFNs | Elev. (m) | Avg. annual rainfall (mm) | No. plots |
|---------------------|-----------------------------|-----------|-------------------------------|-----------|---------------------------|-----------|
| Coastal Lowland | 0.032 | 0.033 | 1.2 | 0-600 | 1100-1500 | 13 |
| Submontane Seasonal | <0.001 | <0.001 | 0.8 | 600-1400 | 1000-1500 | 12 |
| Montane Rainforest | 0.002 | 0.004 | 0.6 | 700-1300 | 1500-2400 | 17 |
| Montane Seasonal | 0.212 | 0.234 | 0.7 | 1800-1900 | 1100-1300 | 11 |
| Alpine/Subalpine | 0.000 | 0.000 | 0 | 2000-3100 | 1100-1300 | 9 |

Table 4. Endemic and indigenous Hawaiian species with extrafloral nectaries.

ENDEMIC

| |
|---|
| Convolvulaceae |
| <i>Ipomoea tuboides</i> |
| Fabaceae |
| <i>Acacia kauaiensis</i> Hbd. |
| <i>A. koa</i> |
| <i>A. koaia</i> Hbd. |
| Malvaceae |
| <i>Hibiscus arnottianus</i> Gray (var. <i>parviflorus</i> Skottsb.) |
| <i>H. brackenridgei</i> Gray |
| <i>H. immaculatus</i> Roe |
| <i>H. rockii</i> Deg. & Deg. (possibly indigenous) |
| <i>H. waimeae</i> Heller |
| <i>H. youngianus</i> Gaud. |
| <i>Kokia drynarioides</i> (Seem.) Lewt. |

INDIGENOUS

| |
|-----------------------------------|
| Convolvulaceae |
| <i>Ipomoea pes-caprae</i> |
| <i>Stictocardia tiliaceifolia</i> |
| Fabaceae |
| <i>Caesalpinia bonduc</i> |
| <i>Erythrina tahitensis</i> |
| Malvaceae |
| <i>Hibiscus tiliaceus</i> |
| <i>Thespesia populnea</i> |

Table 5. Distribution of plant species for Hawaii with extrafloral nectaries.

| Origin | Species with EFNs | Total | Frequency of species with EFNs |
|-----------------------|-------------------|-------|--------------------------------|
| Endemic | 11 | 1394 | 0.008 |
| Indigenous | 6 | 48 | 0.125 |
| Polynesian-introduced | 6 | 22 | 0.273 |
| Exotic | 218 | 4719 | 0.046 |
| Total | 241 | 6183 | 0.039 |

close to the complete figure. The distribution of plants with EFNs for the Hawaiian archipelago as a whole is summarized in Table 5.

Comparison of the frequency of plants with EFNs between groups of plants of different origins in HVNP (Table 2) gave statistically significant differences in

every case ($P < 0.05$, χ^2 or Fisher's exact test) except for indigenous versus exotic; these were not significantly different. Thus, there are significantly fewer species with EFNs among endemics than indigenous, Polynesian-introduced or exotic species. Similarly, if, for HVNP, plants with a long period of evolution in Hawaii (endemic and indigenous species) are compared with those which recently arrived (Polynesian-introduced and exotics) the former have significantly fewer species with EFNs ($\chi^2 = 6.74$, $P < 0.01$, $df = 1$). The distribution of plants with EFNs in Hawaii as a whole, as determined from the species list in St. John (1973), is much richer in introduced plants than HVNP (Tabs 2 and 5), but differences between native (endemic plus indigenous) and introduced (Polynesian-introduced plus exotic) for the flora of Hawaii as a whole are also significantly different ($\chi^2 = 37.1$, $P < 0.001$, $df = 1$); a lower proportion of native species had EFNs than did introduced species.

4. Discussion

4.1. Extrafloral Nectaries and Vegetation Patterns

Vegetation analysis of plant communities in Hawaii Volcanoes National Park found only one endemic species in one community to have EFNs (*Acacia koa*, in the montane seasonal forest section). However, three indigenous species with EFNs were present in some other associations (Tables 1, 3). Cover by species with EFNs in HVNP natural communities was lower than most other areas studied. Bentley (1976, 1981) studied the distribution of plants with EFNs in tropical dry forest in Costa Rica and found values between 20% and 80%, all distinctly higher than the 3.2% for HVNPs coastal lowland section. Similarly, Keeler (1979a) found cover by plants with EFNs to be 28% in lowland, disturbed sites in Jamaica; those communities were wetter than the sites studied in HVNP. In Jamaica, Keeler (1979a) also found 0% cover of plants with EFNs at 1310 m. This site was at approximately the elevation of the three higher-elevation communities in HVNP; the montane seasonal forest section of Hawaii had one species with EFNs (*Acacia koa*), while the montane site in Jamaica lacked them. Other values

for cover of plants with EFNs (summarized in Keeler 1981b) ranged from less than one percent (temperate grassland, chaparral, coniferous forest) to over 50% (Lower Sonoran zone desert, patches of aspen). The situation in montane seasonal forest in HVNP (*Acacia koa* transects) is very similar to Hudsonian zone forest in Arizona (Keeler 1981b), where cover by plants with EFNs was highly variable and almost entirely due to aspen (*Populus tremuloides* Michx., Salicaceae).

Undoubtedly, *Acacia koa* arrived on Hawaii with EFNs. Most other *Acacia* species have EFNs, including the Pacific species closely related to *A. koa* (Broughton 1981). Milton and Moll (1982) studying Australian acacias in Africa, report that bees use the foliar nectaries as floral nectaries, i.e., on pollinating trips. It is possible, therefore, that the function of petiolar nectaries in *Acacia*, in Hawaii and elsewhere, is "floral," rather than "extrafloral" (or nuptial rather than extranuptial, in the sense of Delpino (1886-9)). Alternatively, there is no question that the petiolar nectaries of New World ant-acacias function in an ant-plant protectionist mutualism (Janzen 1966). The actual function of the foliar nectaries of *Acacia koa* will have to be studied before this point can be settled, and, in the absence of an intact native insect fauna in Hawaii, it may never be fully resolved. The one native Hawaiian plant with EFNs making a measurable contribution to cover in natural communities in HVNP is therefore a doubtful case. I will discuss the other native plants with EFNs in HVNP after reviewing the results of the analysis of the flora.

4.2. Patterns of Extrafloral Nectaries in the Flora: HVNP

From the species list of HVNP (Fosberg 1966), 33 of the 636 species were found to have EFNs (Tables 1, 2). The majority of them (26) were exotic or Polynesian-introduced species, recently arrived in Hawaii. Only one (*Acacia koa*, discussed above) was endemic. The six remaining species are indigenous to Hawaii; all are coastal lowland species, widely distributed in the Pacific. They are also members of genera and families (Fabaceae, Malvaceae, Convolvulaceae) rich in plants with EFNs (Zimmermann 1932, Schnell et al. 1963, Elias 1983, Keeler unpubl.). It is probable that these species arrived in Hawaii with EFNs and have maintained them in their evolutionary history on the islands.

There are three indigenous species - *Passiflora foetida* (Passifloraceae), *Ipomoea indica* (Convolvulaceae) and *Pteridium aquilinum* (Polypodiaceae) - which lack EFNs in Hawaii, although they are reported to have them elsewhere in their range. *Passiflora foetida* is a weedy lowland plant for which Baker et al. (1978) published extrafloral nectary chemistry from Costa Rican material. Durkee et al. (1984) confirmed that the Hawaiian plants lack EFNs,

although she notes that the species may require major subdivision. *Ipomoea indica*, a highly variable pantropical species, is similarly in need of taxonomic revision (H. St. John pers. comm., D. F. Austin pers. comm.). In Hawaii *I. indica* is widespread and is found abundantly in well developed native forest (e.g., Kipuka Puauolu), associated with endemic *Drosophila* species (Montague and Kaneshira 1982). In neither case can the possibility of a founder effect (the founder lacked EFNs) be ruled out. Whether or not these taxa are truly single species, no EFNs occur on the Hawaiian members.

For *Pteridium aquilinum*, there is taxonomic evidence for evolutionary change since its arrival in Hawaii. The Hawaiian plants of this cosmopolitan fern are recognized as an endemic subspecies (Fosberg 1966). However, worldwide *P. aquilinum* is polymorphic. Darwin (1897) reports EFNs on *P. aquilinum* in England and M. Douglas (pers. comm.) on plants in Michigan, but they were lacking on California plants (I. Baker pers. comm., S. Hendrix pers. comm.).

4.3. Patterns in the Flora: Hawaiian Islands

Looking at the flora of Hawaii as a whole, only 11 endemic species (0.8%) have extrafloral nectaries (Tabs 4, 5). It is difficult to find values to which to compare that figure. No other tropical flora has been studied for the distribution of extrafloral nectaries and only a single temperate flora (Keeler 1979b). However, the 1.2% of the native (endemic plus indigenous) Hawaiian flora with EFNs is significantly less than the frequency of plants with EFNs in the flora of Nebraska (3.5%; $\chi^2 = 11.18$, $P < 0.001$, $df = 1$). Since the tropics are believed to be richer in species with EFNs than temperate areas (Gilbert in Orians 1974, Keeler and Kaul 1979, Keeler 1981b), this suggests that a typical tropical flora would be even more distinct from Hawaii in terms of abundance of plants with EFNs. It must be emphasized that the species list for Hawaii is a strange collection of native and introduced species and does not represent a natural assemblage of species. For example, St. John (1973) lists 1027 species of orchids, only four of which are native (and endemic). A typical tropical flora would be expected to include some orchids, but not as 16% of the flora.

The number of uncertain determinations in the figure for all of Hawaii is high. Among introduced species, genera in which species with extrafloral nectaries are known frequently include species for whom the presence (or absence) of EFNs is unknown. These were classified conservatively as lacking EFNs, since there is too much within-genus variation to do otherwise (c.f. Keeler and Kaul 1979). Thus the percent of species with EFNs in Hawaii is an underestimate. No similar percent error exists for endemic and indigenous species because I saw most of those. Improved information should only increase the contrast between the fre-

quency of plants with EFNs among Hawaiian native species to species native elsewhere in the world.

The species native to Hawaii with EFNs (Table 4) are all members of taxa in which EFNs are known. Thus, each case could be explained by phylogenetic inertia, specifically that selection against this plant character has not been strong enough to eliminate it in the time since the plant arrived in Hawaii. The species for which I find this argument the least compelling is *Acacia koa*, because it is a dominant tree with large population sizes; here selection pressure for loss of nonfunctional traits seems most likely. Furthermore, there has been enough time to evolve three endemic *Acacia* species. However, *koa* is a long-lived tree with significant vegetative reproduction; there may have been fewer generations since arrival in Hawaii than are needed to remove the nectaries. All three endemic *Acacia* species have nectaries on the phyllodes. Foliar nectaries are common if not universal in the genus *Acacia*; Elias (1983) suggests that all the Australian species have phyllodal nectaries and certainly a great many of them do (Keeler unpubl., O'Dowd pers. comm.). *Acacia* EFNs could certainly be explained by phylogenetic inertia.

Kokia drynarioides Lewt., one of three species of an endemic genus, has functional foliar nectaries, as do six endemic *Hibiscus* species. Again, in citing phylogenetic constraints for the EFNs of *Kokia*, one must argue for the retention of foliar nectaries in the face of evolution of a generic distinction. Fryxell (1978) reports them as absent from *K. drynarioides*: perhaps they are variable.

Extrafloral nectaries on endemic *Hibiscus* species can also be explained as retention of ancestral traits. In the case of *Hibiscus* spp., this is supported by the fact that of the eleven endemic species, only six have EFNs. In the species with EFNs, many individuals were not producing nectar, but whether this was due to poor growing conditions or lack of the trait is impossible to say. Of the endemic *Hibiscus* species, in six neither nectaries nor nectar production were ever seen; one species (*H. kahilii* Forbes) is unknown, because I never saw a specimen. Comparing those numbers with the introduced *Hibiscus* species of Hawaii, 25 have EFNs, 8 did not and 13 were not seen. On that basis, it seems likely that Hawaiian *Hibiscus* species have tended to lose EFNs. A similar pattern is seen in *Gossypium*, where most (47 of 50) species worldwide have three types of extrafloral nectaries as well as floral nectaries, while the Hawaiian endemic *Gossypium sandoicense* Parl. lacks all three types of EFNs but has retained the floral nectaries (Tyler 1908, Fryxell 1978).

The only other endemic species with EFNs is *Ipomoea tuboides* Deg. & van Ooststr., a large-flowered morning glory of the lowlands. This species is very like *Ipomoea muricata* (L.) Jacq. or *I. alba* L., both of which have similar nectaries: it is likely that there are relictual.

A possible alternative to explain the EFNs observed on Hawaiian plants is that mutualism was established with taxa other than ants. Alternate mutualisms at EFNs have been suggested with parasitic solitary wasps (Koptur 1982, Hespeneheide unpubl.), larger wasps and predaceous beetles (Keeler 1978, 1980b). Nothing is known of such interactions in Hawaiian communities. However, there has been widespread extinction of native Hawaiian insects and a rich fauna has been introduced (Zimmerman 1948, Sweezy 1954). Future work may be able to partition the factors responsible for the maintenance of extrafloral nectaries on Hawaiian native plants.

Generally, plants with EFNs tend to be woody and perennial (Tilman 1978, Keeler 1979b, Keeler and Kaul 1979) and since the introduced and widely naturalized species of Hawaii are generally not perennial or woody, it is likely that the difference between the percent with EFNs among natives as compared with introduced plants is an underestimate of the difference between the frequency of plants with EFNs in the Hawaiian flora as compared with a mainland tropical flora (i.e., with ants). Bentley (1981) found that vines had significantly more EFNs than a control group of plants of different habit. The native Hawaiian flora is poor in vines for a tropical flora, but two indigenous vines with EFNs elsewhere, *Passiflora foetida* and *Ipomoea indica*, lack extrafloral nectaries in Hawaii.

In summary, Hawaii was poor in species with extrafloral nectaries. 1) There are few species with EFNs in the natural communities of HVNP; they contribute little to total plant cover and most of the species with EFNs are non-native. 2) Species with EFNs are significantly fewer among native species (whether endemic or indigenous) than among non-natives (Polynesian introductions and European introductions (exotic)). 3) Frequency of native plants with EFNs are significantly fewer than in the other flora studied (Nebraska), despite the general tendency for tropical sites to be richer in plants with EFNs (Gilbert in Orians 1974, Keeler and Kaul 1979, Keeler 1981b). 4) Three indigenous species known to have EFNs elsewhere in their range lack them in Hawaii. No reverse effect, species with EFNs in Hawaii but not elsewhere, was observed. 5) The endemic species with EFNs are members of groups which include many species with EFNs. The explanation of EFNs in these taxa may be due to phylogenetic constraints. In many groups which generally have EFNs, endemic Hawaiian species lack them (e.g., *Gossypium*, *Hibiscus*). The extrafloral nectaries of the few endemic species which have them could either be relictual or maintained in a mutualism with something other than ants. The Hawaiian flora is poor in extrafloral nectaries, consistent with the view that extrafloral nectaries are part of a plant anti-herbivore defense system that does not function in the absence of ants.

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