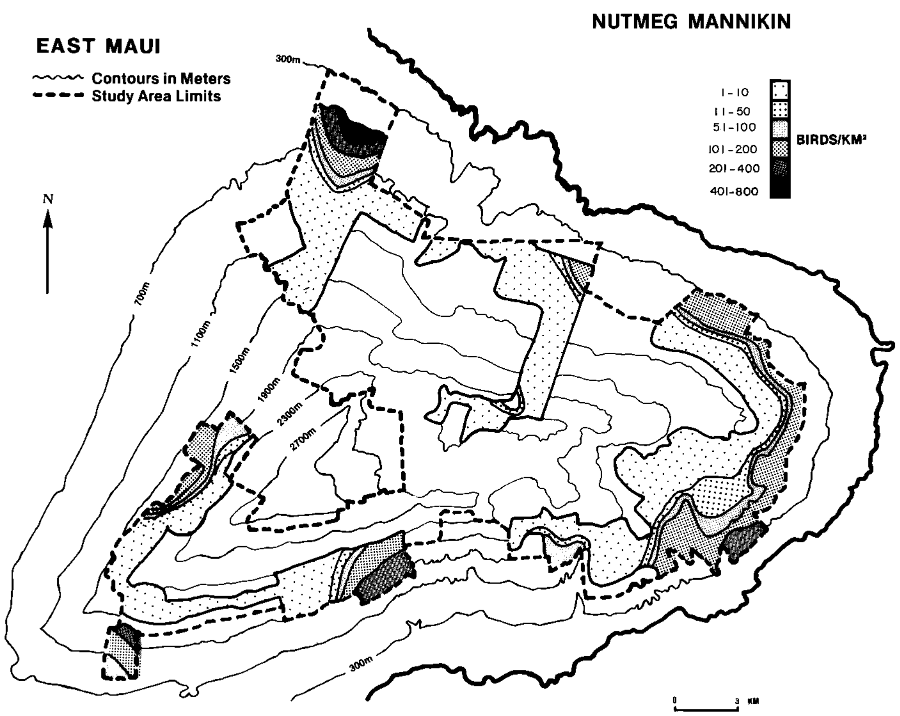

FIGURE 307. Distribution and abundance of the Nutmeg Mannikin in the East Maui study area.

in rainforest interiors (Fig. 310). The regression models (Table 65) show an association with introduced trees in low elevation areas. Other than these trends, the habitat response pattern appears to comprise a scattered, erratic series of relations to other variables. This is also seen in the high variance of the habitat response graphs, and reflects the flocking habit and highly erratic variation in seasonal and annual distribution across a broad span of habitats (see Berger 1981). Richardson and Bowles (1964) found that Nutmeg Mannikins occupy a diverse range of habitats on Kauai, from dry lowland to fairly wet montane sites.

In southeast Asia, Nutmeg Mannikins primarily occur at lower elevations in a range of open and semi-open habitats (Goodwin 1982). They feed almost entirely on seeds, and the positive response to introduced grasses in the Maui regression model may reflect attraction to grass seeds.

COMMUNITY ECOLOGY

SPECIES-AREA RELATIONSHIPS

Island area is a critical component of biogeographic theory (MacArthur and Wilson 1967; Diamond 1973, 1975; Slud 1976; Diamond and Mayr 1976). Distinctive habitats often have island-like relationships between their area and species composition, as noted for birds in deciduous forests surrounded by agricultural land (Bond 1957), in primary versus secondary tropical forest (Terborgh and Weske 1969), and in páramo habitats in the Andes (Vuilleumier 1970, Vuilleumier and Simberloff 1980). On the main Hawaiian Islands, rainforests tend to form distinctive habitat islands surrounded by agricultural land, introduced vegetation, and unforested areas. Although in a few cases boundaries are inexact (e.g., in windward and leeward Hawaii), 20 major rainforest islands may be distinguished (Fig. 311). The data from the HFBS and work on Oahu (Shallenberger and Vaughn 1978) and Kauai (Sincock et al. 1984) allowed us to examine the relationships between the area of these habitat islands, their maximum elevation, and the number of native land bird species present.

The classic species relationship, $S = cA^z$, where S = number of extant native species and A = area in km^2 (MacArthur and Wilson 1967), fits our data. The best fit ($R^2 = 0.41$, $P < 0.01$) is obtained when $z = 0.20$, a value toward the low end but within the range of typical examples for birds (MacArthur and Wilson 1967). A significantly better fit ($R^2 = 0.71$, $P < 10^{-4}$) occurs when elevation (E, in km) is included in the regression equation

$$S = -1.84 + 0.37E + 0.76 \log_e A;$$

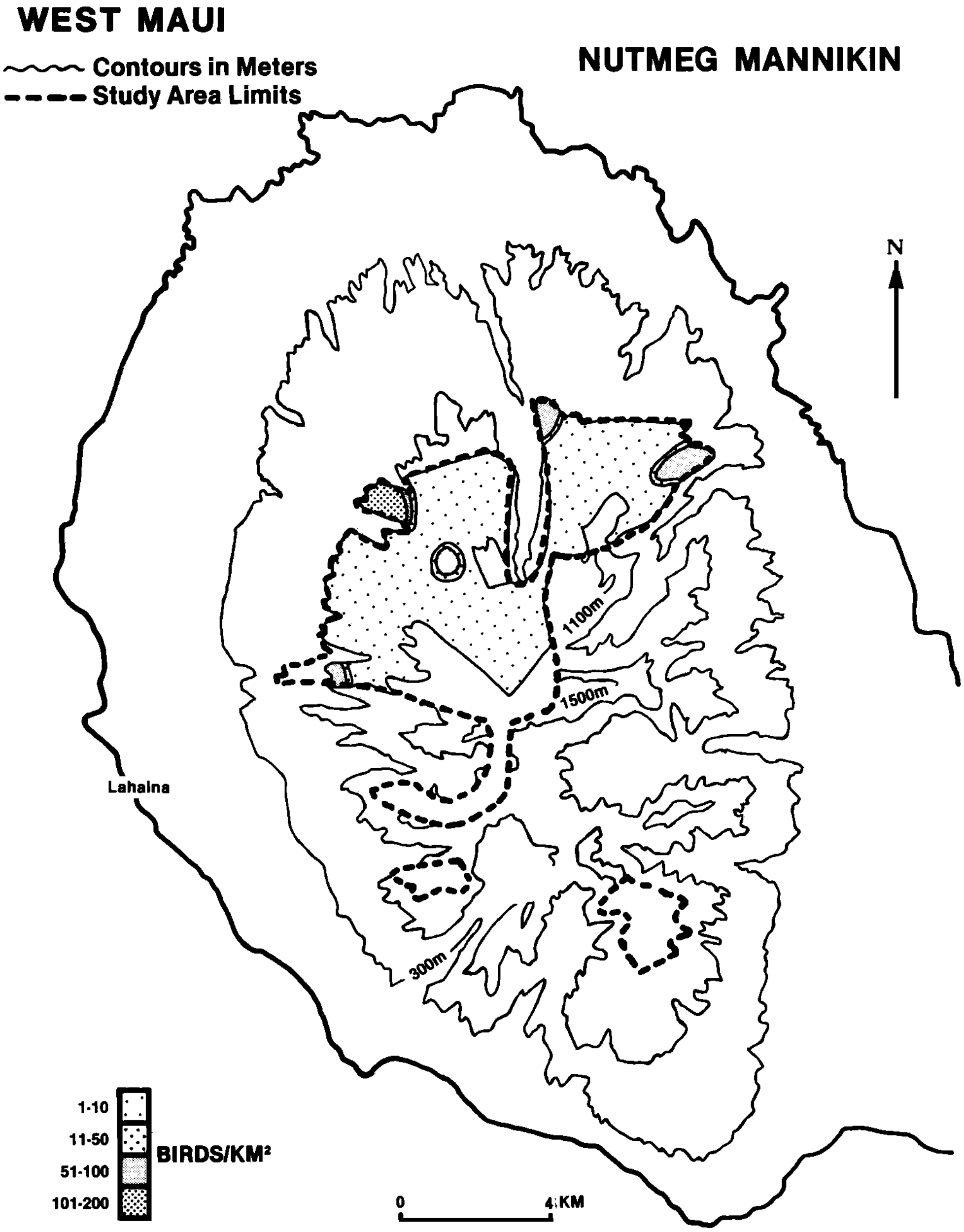

FIGURE 308. Distribution and abundance of the Nutmeg Mannikin in the West Maui study area.

the coefficients are significant at the 1% level. The relation between elevation and species number does not particularly reflect increased habitat diversity, because all species occurred in the most widespread habitat type (wet ohia forest), and the areas are rather similar in their general habitat aspect. In most habitat islands, the greatest number of species occurs near the highest elevations in the area.

The positive association between elevation and species richness reflects extensive extinctions and habitat destruction in the lowlands. Mayr and Diamond (1976) also found an association between elevation and species number in the montane avifauna of northern Melanesia, but this probably reflects the effect of isolation on geographical speciation. More typically, however, lowland areas have greater numbers of bird

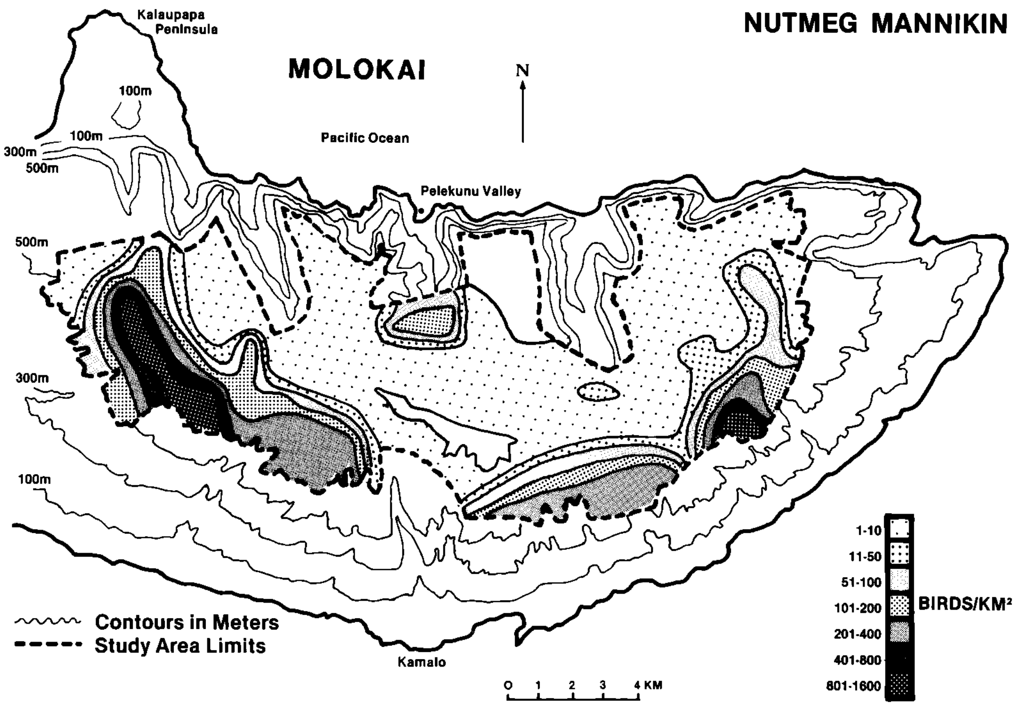

FIGURE 309. Distribution and abundance of the Nutmeg Mannikin in the Molokai study area.

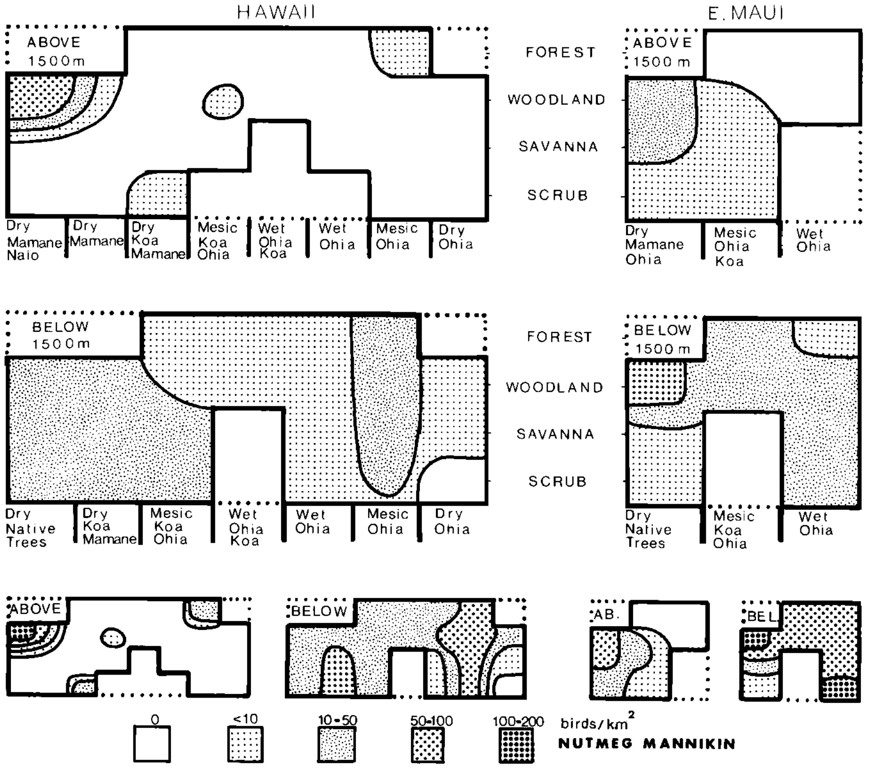

FIGURE 310. Habitat response graphs of the Nutmeg Mannikin. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

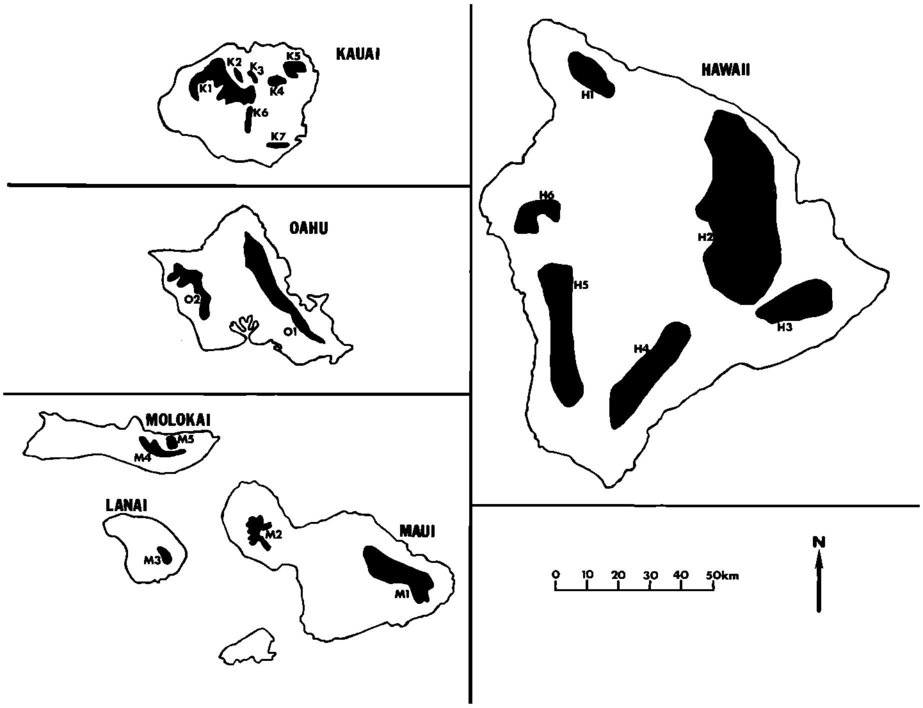

FIGURE 311. Location of "habitat islands" of montane rainforest in the Hawaiian Islands. (Codes: H1 = Kohala, H2 = Hamakua, H3 = Puna, H4 = Kau, H5 = South Kona, H6 = Hualalai; K1 = Alakai, K2 = Laau, K3 = Namolokama, K4 = Makaleha, K5 = Anahola, K6 = Kapalaoa, K7 = Hoary Head; M1 = East Maui, M2 = West Maui, M3 = Lanaihale, M4 = Kamakou, M5 = Olokui; O1 = Koolau, O2 = Waianae.)

species than montane areas, as in the West Indies (Kepler and Kepler 1970, Lack 1976), the Galápagos Islands (Harris 1973), the Solomon Islands (Greenslade 1968), New Guinea (Diamond 1972), and in temperate (Miller 1951, Able and Noon 1976, Sabo 1980, Sabo and Holmes 1983) and tropical (Moreau 1966; Terborgh 1971, 1977; Haffer 1974; Pearson and Ralph 1978) continental areas.

A scatter plot of richness, elevation, and area in the 20 rainforest habitat islands (Fig. 312) shows that several habitat islands deviate substantially from the number of species predicted by the regression. The Alakai Swamp (K1 in the figures), and to a lesser extent the other high habitat islands on Kauai, have more species than predicted. This may reflect the low incidence of mosquitoes in the Alakai, and possibly the proximity of Laau Ridge (K2), Namolokama Mountain (K3), and other peaks to the Alakai. On the other hand, our data show that the native Kauai birds have declined precipitously in the last decade. From an equilibrium standpoint, the Kauai habitat islands may be "oversaturated" with species because of the environmental changes that have occurred since Western contact, and imminent extinction of several species may reflect biogeographical "relaxation" of the fauna. The West Maui forest (M2) has the highest negative deviation (3 species instead of 7 predicted), and this in part reflects the small area at high elevations and extensive area of unforested bogs. Here it would be instructive to transplant Maui Creepers and Crested Honeycreepers to determine whether viable populations can exist.

Although species-area relationships are frequently explained as resulting from greater habitat diversity or larger population sizes (Whitehead and Jones 1969, Diamond 1975, Williamson 1981), in the Hawaiian rainforest habitat island series, the greatest numbers of species tend to occur in relatively undisturbed high-elevation areas. The relations in Figure 312 thus primarily reflect the functional association of intact communities with larger, higher, and hence more ecologically "buffered" areas.

Juvik and Austring (1979) applied biogeographic equilibrium theory to the endemic land birds of the Hawaiian Islands, using island area and all historically known species as data. Although they found a strong correspondence between island size and number of species, their results were brought into serious question by recent fossil finds of the extinct lowland avifauna

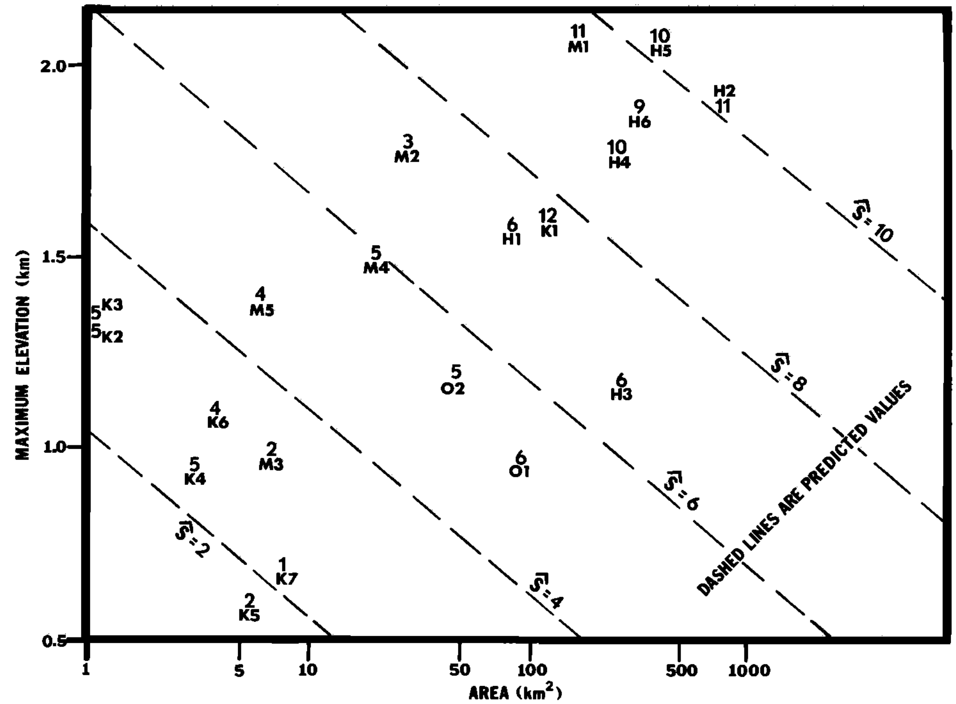

FIGURE 312. Scatterplot showing relationships between species richness, area, and elevation for 20 habitat islands of montane rainforest. (Horizontal axis is logarithmically scaled. Numbers in plot give the number of native forest bird species present in the habitat island. Code below species number identifies habitat island location as shown in Figure 311. Dashed lines give predicted species richness based on regression from elevation and area as described in the *Species-Area Relationships* section.)

(Olson and James 1982b). Even if the original avifauna did not follow the classical species-area equilibrium expectation, the analysis by Juvik and Austring may still rest on relevant ecological ground, however, because island size roughly indexes the accessibility of sites of Hawaiian cultural practices. Island size may therefore have been a good predictor in their study because it may effectively index the degree of human disturbance before Western contact.

RICHNESS AND DIVERSITY

Native species richness

The communities with the greatest number of native species are located in relatively undisturbed forests at higher elevations. Refugia having more species than other areas are found on Hawaii (upper Kau, upper Hamakua, North Hualalai, central Kona, the Puu Laau area of Mauna Kea), East Maui, Molokai, and Kauai (Alakai Swamp).

The habitat response graphs indicate that native species richness is greatest above 1500 m elevation in mesic and wet koa-ohia forests (Fig. 313). On Maui, richness is greatest at upper elevations in mesic ohia-koa and wet ohia forests. The strongest response to native species richness in the regression models (Table 67) is to elevation, which shows a bell-shaped curve (negative quadratic coefficient) in six models. The modes of elevational response are generally above 1700 m, except for the low-elevation Puna area. Molokai has a peculiar bimodal response that appears to reflect the devastation of mid-elevation forest on the east half of the study area by feral ungulates, particularly pigs and deer. Effects of ungulates may also explain the seemingly aberrant positive response on Molokai to matted ferns, which are characteristic of lower intensity disturbance.

Moisture is associated with higher native species richness in four regression models, which reflects the generally more intact nature of wet native forest compared with dry forest. The negative term in the Molokai model corrects for sparse dry forests at low elevations; the correlation between moisture and native species richness in that study area is weakly positive ($r = 0.08$).

Native species richness is highest in forested areas, indicated by positive tree biomass terms in the Kohala and Maui regression models, by

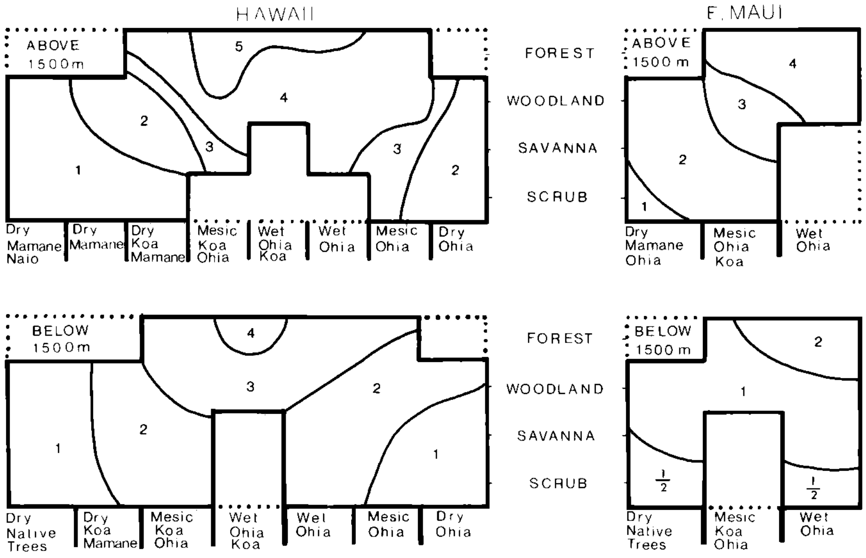

FIGURE 313. Habitat response graphs of native species richness (the number of native bird species occurring at a station).

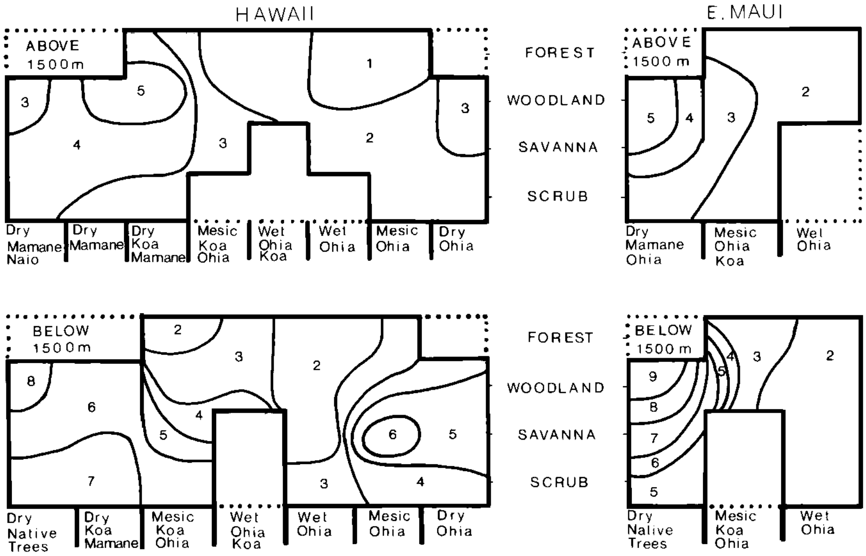

FIGURE 314. Habitat response graphs of introduced species richness (the number of introduced bird species occurring at a station).

upward-opening parabolas centered below mean tree biomass in the Kau, Hamakua, Kipukas, Kona, and Molokai models, and by positive terms for crown cover and canopy height in Puna. Crown cover has positive terms in the Kona and Puna models, but negative terms in Kau and Kipukas counterbalance tree biomass squared to yield a net effect of nearly linear response to tree biomass. Canopy height is of minor importance. Responses to individual tree species are minor, except for avoidance of introduced trees in three models.

Among understory elements, matted ferns are associated with lower native species richness. Passiflora is associated with lower species richness in Hamakua, and is a correction term for dry open forests on Maui, where it has a weak negative correlation with native species richness

TABLE 67
Regression Models for Habitat Response of Native Species Richness[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai	Kauai
Mean	3.44	3.03	1.97	2.56	2.32	1.19	2.04	1.82	0.82	5.96
SD	1.45	2.02	0.93	0.88	1.30	0.76	1.11	1.47	0.59	1.18
R^2	0.51*	0.67*	0.29*	0.36*	0.48*	0.27*	0.49*	0.59*	0.37*	0.04
Moisture	···	4.6*	···	2.1	12.2*	X	X	6.8*	−3.0	X
Elevation	6.5*	20.1*	6.5*	11.3*	6.7*	···	13.0*	6.2*	−5.1*	···
(Elevation)^2	−4.3*	−12.1*	−5.4*	−10.9*	−2.9	···	···	−5.1*	5.5*	···
Tree biomass	···	−4.5*	···	···	−10.8*	4.8*	2.5	8.7*	···	···
(Tree biomass)^2	7.9*	6.3*	···	4.4*	12.5*	···	···	···	6.0*	···
Crown cover	−4.3*	···	3.7*	−2.2	5.9*	···	···	···	···	···
Canopy height	···	···	2.9	−4.9*	2.5	2.1	···	···	···	···
Koa	5.4*	···	X	···	5.2*	X	X	···	X	X
Ohia	···	5.5*	···	···	···	X	···	4.3*	···	X
Naio	X	X	X	···	2.7	···	X	X	X	X
Mamane	X	···	···	4.8*	···	···	X	−4.3*	X	X
Intro. trees	X	−4.2*	···	X	−2.0	X	···	−2.1	···	X
Shrub cover	···	8.4*	···	···	···	−5.9*	···	···	···	···
Ground cover	···	−4.8*	···	···	···	···	···	2.4	···	···
Native shrubs	···	···	···	···	2.6	X	···	···	···	···
Intro. shrubs	X	8.4*	···	···	−2.3	X	···	···	···	···
Ground ferns	X	X	···	···	10.2*	X	···	···	3.9*	···
Matted ferns	···	−7.1*	−5.5*	···	···	X	−2.8	···	3.5*	···
Tree ferns	···	X	···	X	···	X	···	−4.3*	···	2.4
Ieie	X	X	···	X	−6.6*	X	X	2.3	X	···
Passiflora	X	−8.7*	X	X	···	X	···	2.5	X	X
Native herbs	X	X	···	···	−4.5*	X	···	···	···	···
Intro. herbs	X	X	−2.5	···	···	···	···	···	···	···
Native grasses	···	···	···	···	···	···	···	3.2	···	···
Intro. grasses	···	5.1*	−6.5*	···	···	−3.4	···	···	−3.4	···
Ohia flowers	···	4.9*	···	···	5.0*	X	2.7	···	4.8*	···
Olapa fruit	···	−3.5*	···	···	···	X	···	3.1	···	···
Mamane flowers	X	X	X	···	X	···	X	···	X	X
Mamane fruit	X	X	X	X	X	···	X	X	X	X
Naio fruit	X	X	X	X	X	···	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are *t* statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model. No model was fit for Lanai; mean value 0.35, SD 0.51.

TABLE 68
REGRESSION MODELS FOR HABITAT RESPONSE OF INTRODUCED SPECIES RICHNESS[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai	Lanai	Kauai
Mean	1.29	2.16	2.63	2.81	4.23	2.88	2.28	2.61	2.65	3.18	2.40
SD	0.83	1.12	1.32	2.09	2.31	1.63	1.15	1.95	1.37	1.28	1.22
R^2	0.26*	0.35*	0.58*	0.72*	0.46*	0.53*	0.20*	0.40*	0.41*	0.17*	0.39*
Moisture	···	···	−7.8*	−7.7*	−6.3*	X	X	−13.4*	−19.1*	···	X
Elevation	2.9	3.4*	−5.0*	2.9	7.2*	5.1*	···	7.3*	−2.6	···	−3.8*
(Elevation)^2	−4.7*	−4.4*	−11.5*	2.9	−9.8*	−5.5*	···	−8.0*	3.2	···	3.5*
Tree biomass	···	5.3*	6.6*	···	6.8*	−11.8*	···	8.6*	···	···	−2.5
(Tree biomass)^2	···	−4.0*	···	···	−6.3*	11.8*	···	···	···	···	···
Crown cover	−5.3*	···	−5.7*	···	−6.1*	···	−2.0	···	···	···	···
Canopy height	···	2.8	−4.7*	6.5*	···	12.5*	···	···	···	···	···
Koa	3.1	4.5*	X	···	···	X	X	···	X	X	X
Ohia	···	−13.8*	···	−7.7*	−4.4*	X	···	−5.0*	···	···	X
Naio	X	X	X	···	···	···	X	X	X	X	X
Mamane	X	···	3.9*	···	11.2*	···	X	2.3	X	X	X
Intro. trees	X	−3.0	···	X	6.1*	X	2.9	···	···	···	X
Shrub cover	−4.3*	−10.2*	4.2*	···	−2.1	−8.1*	···	···	···	···	···
Ground cover	···	3.6*	−2.9	···	2.1	···	···	···	···	···	···
Native shrubs	···	9.3*	···	···	···	X	···	···	···	···	···
Intro. shrubs	X	10.3*	···	···	···	X	···	2.1	···	···	···
Ground ferns	X	X	···	···	−3.6*	X	···	···	···	X	···
Matted ferns	···	−5.1*	···	···	−5.5*	X	···	···	···	−3.7*	···
Tree ferns	···	X	−6.9*	X	···	X	···	···	···	X	···
Ieie	X	X	···	X	···	X	X	···	X	X	···
Passiflora	X	6.2*	X	X	5.9*	X	···	8.0*	X	X	X
Native herbs	X	X	···	···	−3.4*	X	···	···	···	X	···
Intro. herbs	X	X	···	5.0*	5.0*	···	···	···	···	X	···
Native grasses	···	−6.2*	−4.4*	−5.4*	−5.4*	···	···	···	2.6	X	···
Intro. grasses	···	···	3.6*	···	2.8	−6.0*	4.8*	4.2*	···	···	···
Ohia flowers	3.0	6.8*	···	···	···	X	···	···	3.0	···	···
Olapa fruit	···	3.2	···	···	···	X	···	···	···	···	−2.5
Mamane flowers	X	X	X	···	X	···	X	−3.2	X	X	X
Mamane fruit	X	X	X	X	X	···	X	X	X	X	X
Naio fruit	X	X	X	X	X	···	X	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

TABLE 69
Regression Models for Habitat Response of Bird Species Diversity (Simpson's Index)[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai	Lanai
Mean	2.92	2.92	2.26	2.72	2.79	2.06	2.66	2.54	1.80	1.41
SD	1.04	1.46	0.72	0.86	1.03	0.69	1.05	1.29	0.59	0.37
R^2	0.23*	0.61*	0.39*	0.43*	0.30*	0.20*	0.32*	0.36*	0.33*	0.23*
Moisture	···	8.3*	−7.8*	···	2.4	X	X	···	−3.4*	···
Elevation	11.0*	16.6*	5.3*	9.3*	7.1*	···	9.7*	8.9*	−4.9*	···
(Elevation)^2	−10.1*	−9.1*	−4.8*	−9.6*	−7.5*	···	···	−7.6*	6.3*	···
Tree biomass	···	−2.0	···	···	−7.4*	···	−2.1	11.7*	7.5*	···
(Tree biomass)^2	4.7*	3.7*	3.5*	3.7*	8.6*	···	2.4	···	···	···
Crown cover	−3.2	···	···	···	···	···	···	···	···	···
Canopy height	···	···	···	···	5.2*	8.6*	···	···	···	3.0
Koa	···	···	X	···	6.0*	X	X	···	X	X
Ohia	···	···	···	−3.5*	−5.3*	X	···	···	···	···
Naio	X	X	X	−2.9	···	···	X	X	X	X
Mamane	X	−2.8	···	···	6.9*	−3.8*	X	−2.0	X	X
Intro. trees	X	−4.1*	···	X	2.3	X	···	···	···	···
Shrub cover	···	−3.0	···	···	−5.0*	3.4*	···	···	···	−3.7*
Ground cover	···	4.2*	···	···	2.6	3.1	···	3.4*	···	···
Native shrubs	···	5.2*	···	···	3.0	X	···	···	···	···
Intro. shrubs	X	10.5*	···	···	···	X	···	···	···	···
Ground ferns	X	X	···	···	4.1*	X	···	···	3.6*	X
Matted ferns	···	−7.9*	−9.6*	···	−5.8*	X	···	···	4.0*	···
Tree ferns	···	X	···	X	3.6*	X	···	−2.7	−2.3	X
Ieie	X	X	···	X	−7.4*	X	X	3.1	X	X
Passiflora	X	−2.7	X	X	2.0	X	···	3.8*	X	X
Native herbs	X	X	···	···	−2.1	X	···	···	···	X
Intro. herbs	X	X	−4.0*	2.6	···	···	···	···	···	X
Native grasses	···	−6.9*	···	−8.0*	···	···	···	···	2.7	X
Intro. grasses	···	···	−3.9*	2.4	···	···	···	···	···	···
Ohia flowers	−2.6	···	···	···	2.5	X	···	···	···	···
Olapa fruit	2.3	−4.8*	···	···	3.0	X	···	3.1*	···	···
Mamane flowers	X	X	X	···	X	···	X	···	X	X
Mamane fruit	X	X	X	X	X	···	X	X	X	X
Naio fruit	X	X	X	X	X	···	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model. No model was fit for Kauai; mean value 3.65, SD 0.72.

($r = -0.05$). Introduced grasses often indicate extensive disturbance and have a negative relation to native species richness in Puna, Mauna Kea, and Molokai. In Hamakua, introduced grasses have high cover in montane pastures with scattered koa trees where several native birds occur. Ohia flowers are important in four models and reflect the response of nectarivorous birds.

Introduced species richness

The number of introduced species reaches highest levels in our study areas on north Hualalai and on the dry south side of East Maui. The high number of introduced species in the Puu Waawaa area of Kona reflects the history of that area as a release site for introduced gamebirds (Lewin 1971) and passerines (van Riper 1978b). Introduced species richness peaks below 1500 m in dry woodlands, with unbroken forest and wet habitat supporting fewer introduced species (Fig. 314).

The regression models (Table 68) indicate that introduced species richness is greatest at lower elevations in dry partly open woodlands with an understory dominated by introduced plants. Five models show more introduced bird species in dry areas. In the Molokai model, the moisture relation overwhelms the other variables. Lower elevations are associated with a greater number of species in nine models. This reflects location of introduction sites and probably poor adaptation by many introduced species to the cold montane environment.

The responses to forest development are mixed, but frequently indicate a bell-shaped response to tree biomass. Crown cover is negative in four models and indicates that few gamebirds penetrate closed forests. This is further seen in the negative terms for ohia in four models and in the positive terms for mamane (characteristic of dry open woodlands) in three models. Introduced trees are associated with introduced birds in two models, but the negative term in Hamakua is a correction term ($r = 0.12$ between introduced species richness and introduced trees).

Introduced understory elements are associated with greater introduced species richness. Introduced bird species respond positively to introduced shrubs in two models, to passiflora in three, to introduced herbs in two, and to introduced grasses in four. Disturbed areas thus harbor greater numbers of introduced bird species than native communities and are potential avenues of dispersal. Response to native understory components is weak, except for four negative responses to native grasses (the positive response in Molokai was a correction term), and three negative responses to matted ferns.

Use of ohia flowers, and to a lesser extent olapa fruit, by the Red-billed Leiothrix, Japanese White-eye, and House Finch is seen in the positive terms for these variables.

Bird species diversity

The reciprocal of Simpson's index of diversity, $1/\Sigma\ p^2$, gives the number of equally common species that would produce the same heterogeneity as observed at a station (Peet 1974). This diversity index tends to be highest in well-developed forests at mid-elevations (Table 69). Although Kauai (Alakai Swamp) has the highest diversity of any study area, no model is fitted, indicating a homogeneous cluster. Bird species diversity peaks in well-developed forests with partly open shrub and closed ground cover, but is low in areas dominated by matted ferns.

Diversity increases in wetter habitat in the Hamakua and Kona models, but in Puna and Molokai the dominance of introduced birds, especially gamebirds, generates higher diversity in drier habitat.

Bell-shaped responses to elevation appear in six models. The modes occur between 1300 and 1700 m in most models, and at 800 m for the low-elevation Puna area. Hamakua has a mode of 2150 m, reflecting high diversity in disturbed montane koa-ohia pastures. Molokai has a bimodal response, reflecting two areas of high diversity, one of gamebirds in the lowlands, the other of passerines in montane forests.

Diversity responds positively to tree biomass in almost every forest, but crown cover and canopy height have little effect on diversity. Positive responses in Kona to mamane and koa reflect the extensive dry open forests. On Mauna Kea, the negative mamane term reflects the greater number of species associated with mixed mamane-naio areas, probably a result of the greater diversity of plant resources. Generally the responses to individual tree species are weak.

Bird diversity tends to increase with ground cover in four models. The negative relations to shrub cover in the Hamakua and Kona models are balanced by positive terms for native and introduced shrubs, suggesting higher diversity in partly open shrub cover. Matted ferns tend to lower diversity, as expected from their low cover and food value. In Hamakua and the Kipukas, the negative responses to native grasses reflect low diversity in high elevation scrublands. On Molokai the positive responses to native grasses, ground ferns, and matted ferns indicate higher densities in less disturbed areas. Other understory variables such as tree ferns, ieie, passiflora, introduced herbs, and introduced grasses have conflicting, usually weak, responses across the models; this pattern resists explanation and seems to reflect peculiarities within the individual species pools. Terborgh (1977) found a similar problem in analyzing bird diversity indices for study sites in the Peruvian Andes; fundamental differences in the natural history of the species in different guilds led to distinct patterns of response to elevation, making compound indices difficult to interpret.

Comparisons of habitat responses among community variables

The strong contrasts in habitat response between native and introduced species richness accent the retreat of native species to montane refugia, the lowland introduction sites of introduced passerines, and the abundance of gamebirds in dry open brush. Native species richness usually responds positively to elevation, whereas introduced species richness has negative responses. Diversity reflects the occurrence of native and introduced birds, and has a markedly bell-shaped response to elevation. Forests support a greater number and diversity of birds than deforested areas. This relationship is frequently noted among bird communities compared across landscapes (Johnston and Odum 1956, MacArthur and MacArthur 1961, Recher 1969, Karr and Roth 1971, Willson 1974, Sabo 1980, May 1982). Matted fern understories have few food resources and are often associated with reduced species richness. Increased food levels probably explain positive responses of introduced birds to introduced herbs (e.g., for gallinaceous birds) and passiflora, and of both native and introduced birds to ohia flowers.

General Patterns of Habitat Response

The Hawaiian Islands offer an ideal situation for studying avian habitat response. Striking variations in vegetation occur within distances of 10–30 km, encompassing montane rainforests, mixed mesophytic forests, fragments of rich dryland forest, dry subalpine woodlands, desert and subalpine scrublands, alpine grasslands, cinder deserts, grazed rangelands, and lush lowland rainforests composed entirely of introduced plant species. The land birds are generally rather conspicuous and offer an interesting contrast between coevolved endemic spepcies on the one hand and haphazardly introduced species on the other. Although local movements do occur, the land birds are year-round residents so that long-distance migration does not complicate the interpretation of habitat response.

An important approach in ecology is the search for repeated patterns to compare and contrast species responses to a spectrum of habitat features in order to gain insight into the factors determining habitat response (see MacArthur 1972:1). The 164 fitted models of species habitat response may be viewed as samples from the total population of habitat responses of Hawaiian forest birds. In this section we identify common patterns running through this set of case histories and relate these patterns of community structure to the patterns occurring in other bird communities. The major gradients structuring habitat response patterns among the Hawaiian forest birds in this study are (1) the "abiotic" landscape factors of elevation and moisture; (2) gross vegetation structure, especially the density and height distribution of foliage; (3) detailed physiognomic structure, floristic composition, and temporal phenological variation (essentially fine vegetation structure and correlated food resources); and (4) other factors inferred to be limiting, notably absence of water in arid areas, habitat heterogeneity, minimum forest size, and bioenergetic requirements. Before embarking on this discussion, however, let us first evaluate the relative importance of the habitat variables included in our analysis.

Relative importance of habitat variables

For a rough measure of the importance of each habitat variable in determining species response, we computed the percent of regression models into which a particular variable entered, out of all those models it could have entered. These percentages were tallied from the models analyzed earlier, according to three groups: introduced nonpasserines (gamebirds), introduced passerines, and native passerines (Table 70). In order to reduce the variation from minor variables and poorly-fit models, we based our calculations on those variables and regression models that had a significance level of 0.1% or lower; 155 fitted models met this criterion for analysis. Obviously this analysis provides an overview of the roles of different habitat variables; for a particular species, certain variables may be far more important than in the general pattern.

Elevation, moisture, and tree biomass (as an index of forest development) are important variables in all three groups of birds. Individual tree species and certain understory components, especially passiflora, are also major variables. Most understory components have little influence (<20% of the models) on any group.

Elevation has a dominant influence on habitat response and appears in 74% of all regression models. In 43% of all models the response to elevation is significantly curved (i.e., quadratic term present). In 28 models (18%) the response is truly bell-shaped (i.e., an inverted parabola with a symmetry axis located within one standard deviation of the mean elevation), indicating the importance of nonlinear effects. A similar role for nonlinear terms was found in a study of avian habitat response by Meents et al. (1983), where 41% of the models had polynomial terms.

Moisture is most important in gamebird regression models where it reflects numerous successful introductions in dry habitats. Although moisture enters fewer native passerine models, it is still important. The low percentage of native passerine models that incorporate moisture is a result of the tendency of those birds to inhabit wetter forests. Since wet habitats dominate most study areas, moisture would not enter a model if highest densities occur in moderately wet forests. Birds preferring either dry habitat or very wet rainforest, however, produce a moisture term in most models that indicates significant departure from the average moisture regime.

Forest development enters 52% of the regression models as tree biomass. Curved responses for this factor are less frequent than for elevation, with quadratic terms present in only 24% of all models. True bell-shaped responses are rare, occurring in only 2% of all models. Since tree biomass is entered into the regression models before crown cover and canopy height, these latter two variables index specific foliage configurations rather than general forest development (unlike in most other studies). Their occurrence in only 14% of all models indicates that, for many birds, the volume occupied by foliage is a sufficiently precise measure of the vegetation configuration. As identified in the species accounts, crown cover and canopy height tend to change the interpretation of models when tree biomass is also entered. When several of these related variables are included in a model, surrogate relations occur that sometimes indicate bell-shaped response, e.g., preference for partly open woodland. This phenomenon probably explains the low incidence of true bell-shaped curves for tree biomass. For a better indication of the frequency of bell-shaped response to forest development per se, canopy height, crown cover, and probably individual tree species should be deleted from the models. An alternative would be to remove the effect of tree biomass from these variables by a prior analysis of covariance, but this correction would differ for each study area, and the resulting models would be difficult to compare.

Individual tree species vary in their ability to shape habitat response patterns. Koa is important for native passerines, entering 51% of the regression models. Introduced passerines respond less strongly to koa, and in gamebird models, koa is a minor variable. Gamebirds have stronger responses than passerines to ohia and mamane, but usually these trees act as indicators of rainforest and dry open woodland, respectively. Mamane and naio sometimes indicate dry woodland in passerine models. Although the less frequent response of native birds to ohia (and ohia flowers) seems unexpected at first glance, most study areas have fairly high mean values for ohia, and no term is needed to indicate that response coincides with the mean value. The situation parallels that of moisture, and gamebirds have more frequent, but usually negative, responses to ohia. Introduced trees are relatively unimportant except to introduced passerines.

Most understory components generate feeble habitat response, with 13–29% of the models incorporating total shrub or ground cover. Taking 20% as a benchmark, we find that native shrubs, ground ferns, matted ferns, ieie, native herbs, introduced herbs, and introduced grasses generally fall below it, implying that, in general, birds

TABLE 70

RELATIVE IMPORTANCE OF HABITAT VARIABLES: PERCENTAGE OF MODELS IN WHICH VARIABLES ARE INCLUDED AT $P < 0.001$

Variable	Gamebirds	Introduced passerines	Native passerines
Number of species	12	13	14
Number of models	38	65	52
Moisture	62	56	43
Elevation[a]	79	71	73
Tree biomass[a]	63	42	56
Crown cover	16	18	12
Canopy height	16	23	10
Koa	15	33	51
Ohia	35	29	22
Naio	6	33	31
Mamane	35	30	32
Intro. trees	21	29	13
Shrub cover	21	25	15
Ground cover	29	26	13
Native shrubs	14	10	14
Intro. shrubs	12	20	20
Ground ferns	25	11	18
Matted ferns	6	13	18
Tree ferns	20	7	31
Ieie	5	15	32
Passiflora	45	19	50
Native herbs	4	11	18
Intro. herbs	16	23	19
Native grasses	32	21	31
Intro. grasses	13	18	23
Ohia flowers	...	14	29
Olapa fruit	...	12	10
Mamane flowers	...	12	7

[a] Percentage of models with linear term, quadratic term, or both.

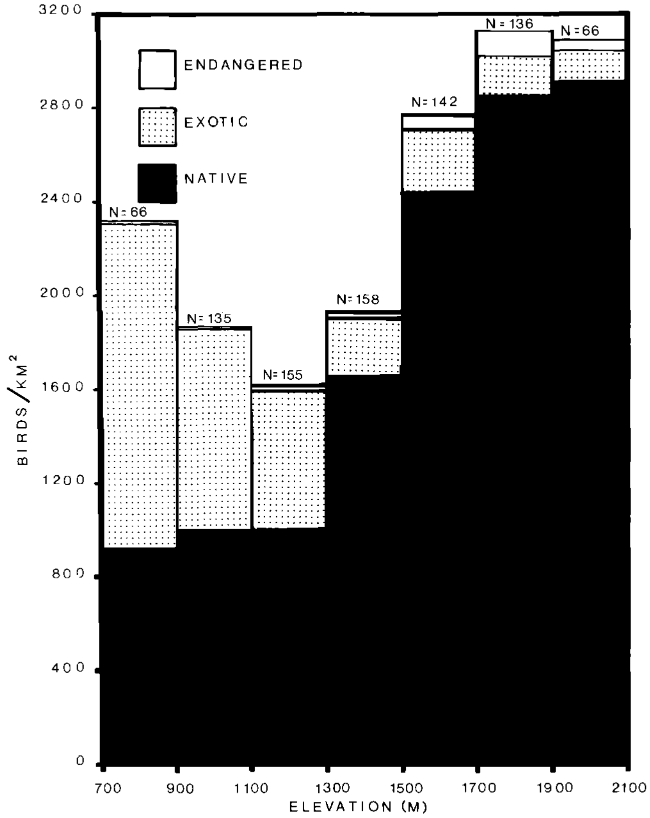

FIGURE 315. Relation of total native, introduced, and endangered bird density to elevation in the Kau study area. (N = number of stations sampled)

discriminate weakly among these habitat components. Birds tend to respond negatively to some of these elements, notably matted ferns and introduced grasses, because these plants lower habitat quality by displacing food source plants (e.g., fruiting shrubs). These minor understory variables often appear to act as indicators of disturbance. Introduced shrubs, native grasses, and tree ferns enter about 20% of the models. Native grasses often enter models as indicators of alpine grassland.

The understory variable with the greatest effect on habitat response is passiflora. Unlike other understory components, passiflora (in particular banana poka) offers abundant nectar and fruit and dominates sizable areas. It thus has mostly positive terms in the models, but some species (Omao, Elepaio, Akiapolaau) have lower densities in infested areas. Passiflora enters models with about the same frequency (37%) as individual tree species. Native passerines have the highest proportion of entries for this variable (51%). Its role in structuring habitat response is thus greater than would be predicted from its contribution to the configuration of the foliage column.

Abiotic factors

Elevation and moisture are geological and meteorological variables that are exogenous to the system. they interact with one another, affect many other habitat variables, and underlie landscape-wide patterning. Elevation enters three quarters of the fitted models and is closely related to temperature, introduction sites for introduced biota, the distribution of disease vectors, and disturbance from human activities. Moisture enters 53% of the models and is related to plant species richness in our study areas (Table 2), although dry lowland areas originally had more species than wet areas before Polynesian contact (Rock 1913).

The following are the main patterns of habitat response to these variables. Introduced passerine birds tend to be more common at lower elevations, reflecting the lowland introduction sites

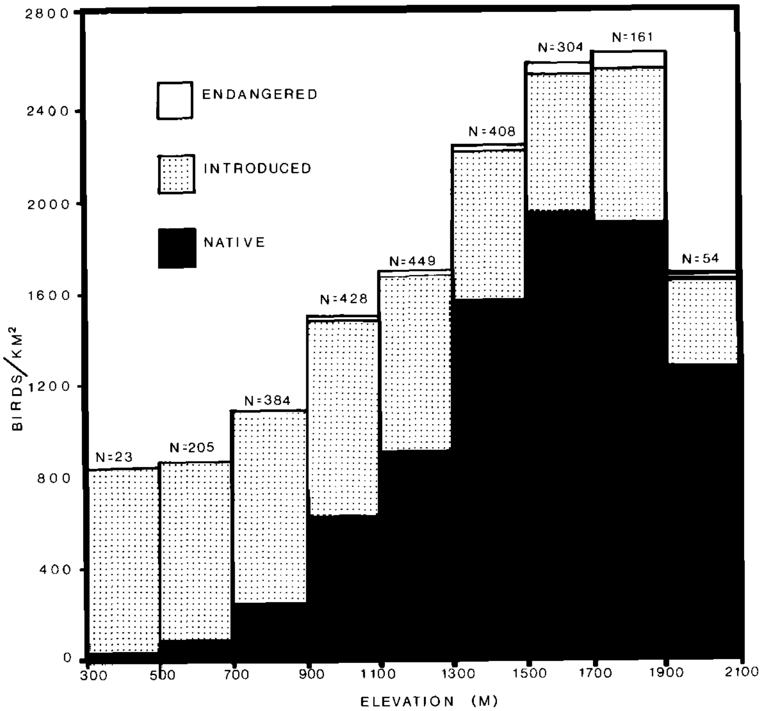

FIGURE 316. Relation of total native, introduced, and endangered bird density to elevation in the Hamakua study area. (N = number of stations sampled)

and probably lack of thermoregulatory adaptation of some species to the cold environments above 1500–2000 m. Introduced gamebirds tend to be more common in dry areas, probably because most species selected for introduction are natives of dry habitats. Native passerines tend to be more common at higher elevations below timberline in less disturbed native forests, probably because the habitat is relatively intact and the area relatively disease free. The responses of native, introduced, and endangered bird densities to elevation show similar patterns in the Kau (Fig. 315), Hamakua (Fig. 316), Kona (Fig. 317), and East Maui (Fig. 318) study areas. Endangered bird densities generally follow native bird densities, except for the sharp drop-off below 1300–1500 m. Native species tend to be more abundant in wet habitats than dry because of the greater number of woody plant species and the probable greater diversity of food resources. Bell-shaped responses to elevation are fairly frequent (18% of the species models), with the models for the Omao, Ring-necked Pheasant, Red-billed Leiothrix, House Finch, native species richness, and bird species diversity serving as typical examples. The habitat responses for many introduced birds seem very similar to their responses in their native lands, suggesting that habitat responses are closely related to innate physiological, morphological, and behavioral traits.

Terborgh (1977) found that the chronic environmental hardships associated with cool environments at high elevations generally result in depauperate avifaunas in the Peruvian Andes. This is most clearly reflected in the Hawaiian forest by the few introduced bird species that enter the montane rainforest. A similar reduction in the number of species at higher elevations also occurs in the subalpine zone of New England mountains (Able and Noon 1976, Sabo 1980, Sabo and Holmes 1983). Moisture has been less emphasized than elevation as a determinant of habitat response in most studies. Orians (1969) found that wet tropical sites have greater between-habitat species diversity than dry sites; wet tropical areas generally have greater productivity than dry areas (Lieth 1973). This pattern reappears in temperate grasslands, where low rainfall sites have fewer bird species and lower plant biomass than more mesic sites (Wiens 1973). Moisture is a primary gradient effecting bird species distribution in temperate deciduous forests (Bond 1957, Smith 1977, Kendeigh and Fawver 1981) and tropical lowlands (Karr and Freemark 1983),

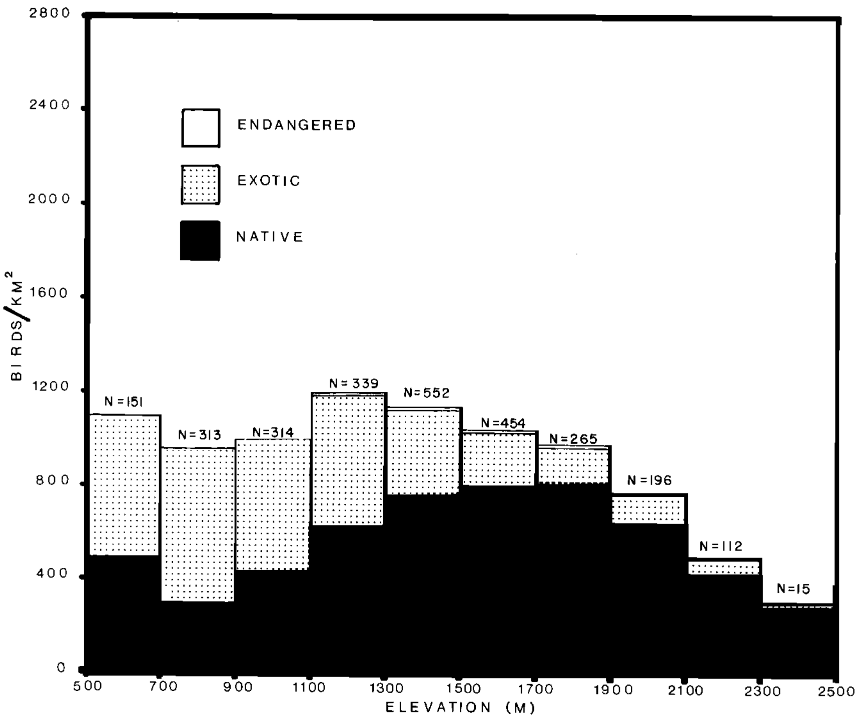

FIGURE 317. Relation of total native, introduced, and endangered bird density to elevation in the Kona study area. (N = number of stations sampled)

and guild structure in coniferous forests (Wiens and Nussbaum 1975).

Gross vegetation structure

Gross vegetation structure, the vertical layering of foliage, follows a gradient from grasslands to forests in structural development and overlies secondary patterns of ground and shrub cover. Although response to ohia dieback reflects response to gross structure, we defer our discussion of that topic to a separate section. The subtle habitat qualities of fine vegetation structure, discussed in a later section, were considered by several workers (MacArthur and MacArthur 1961, Recher 1969, DesGranges 1980) as unnecessary or irrelevant in explaining community patterns.

The most important variable describing gross vegetation structure in our study is tree biomass, which roughly indexes foliage volume, indicates position on the grassland-forest gradient, and integrates the effects of substrate, logging, grazing, and succession. Tree biomass enters 52% of all models. Less important, partly because of overlap with tree biomass and variables of floristic composition and detailed physiognomy, are canopy height, crown cover, shrub cover, and ground cover. As expected, the models show that forest birds need forests and gamebirds occur in open habitats. Native species richness and diversity are associated with more developed forests, but introduced species richness is strongly influenced by gamebirds and is highest in broken woodland. Several species are associated with specific shrub and ground cover configurations. The Ring-necked Pheasant, Common Peafowl, Wild Turkey, House Finch, and introduced species richness are associated with open shrubs and dense ground cover; Northern Cardinal, House Finch, and Iiwi with dense shrubs.

Willson (1974) showed the disproportionate influence on avian habitat response of the presence of trees, probably through adding new resources (Holmes, Bonney, and Pacala 1979). Owing to the great importance of trees, many multivariate studies of avian habitat response have shown that the most important variables are related to general habitat aspect, such as crown cover, canopy height, or shrub cover (James 1971; Anderson and Shugart 1974; Whitmore 1975, 1977; Sabo 1980; Rice et al. 1983). Studies on the effect of logging and thinning on bird response also indicate the importance of tree density and diameter (Hagar 1960, Kilgore 1971, Franzreb and Ohmart 1978, Szaro and Balda 1979), as have studies on bird distribution along plant succession gradients (Adams 1908; Odum

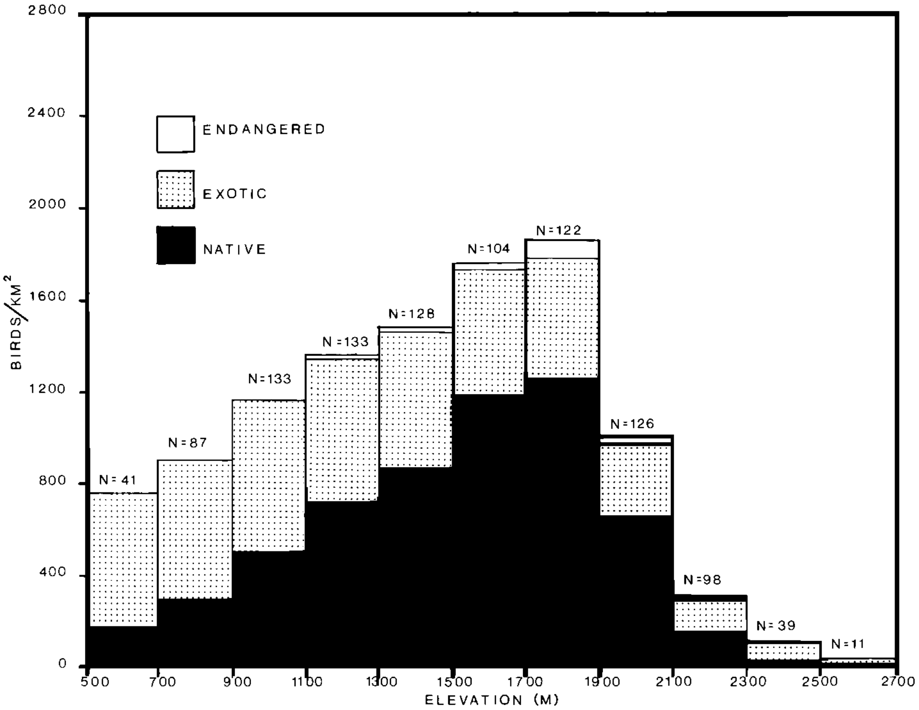

FIGURE 318. Relation of total native, introduced, and endangered bird density to elevation in the East Maui study area. (N = number of stations sampled)

1950; Johnston and Odum 1956; Salt 1957; Haapanen 1965, 1966; Shugart and James 1973; Głowacinski and Weiner 1977; Smith and MacMahon 1981; May 1982). The importance of the individual canopy, shrub, and ground layers was first studied in relation to information indices of bird species diversity and foliage height diversity (MacArthur and MacArthur 1961, MacArthur 1964, MacArthur et al. 1966, Recher 1969, Karr and Roth 1971). Gradually it was recognized that variation within individual layers is also important (Willson 1974, Folse 1982), and eventually many examples were reported where individual dominant plant species predict habitat responses better than height profiles (see references in *Fine vegetation structure* section, beyond).

Response to ohia dieback

Life history strategy of the dominant plant species also modifies bird distribution. Death and defoliation of canopy ohia trees occur in a few years over large areas of native montane rainforest in the dieback phenomenon (Mueller-Dombois and Krajina 1968, Petteys et al. 1975, Jacobi 1983, Mueller-Dombois 1983a). These areas are widespread at 600–1800 m elevation in the Kau, Hamakua, and East Maui study areas, and appear to be successional phenomena related to ohia's role as a pioneering species (Jacobi 1983, Mueller-Dombois 1983b). Often matted ferns dominate the understory after foliage loss of the canopy dominants. Obviously such changes in vegetation structure can have a major impact on avian communities. Comparing ohia dieback areas with adjacent tall closed ohia forests in Hamakua, dieback sites have 70% lower Apapane, 77% lower Iiwi, 47% lower Omao, and 93% lower Elepaio densities, but 30% higher Red-billed Leiothrix and 34% higher Japanese White-eye densities ($P < 0.05$ for all differences). The dieback areas are thus associated with much lower densities of native species and higher densities of some introduced species.

Fine vegetation structure

Variables describing detailed physiognomy, floristic composition, and phenological status form a loose group of fine habitat attributes. Often these attributes are directly related to food resources—specific flower or fruit resources, insect faunas associated with certain plant species, and understory components particularly low in food resources ("sterile"). Other times these variables act as indicators of specific configurations of environment and vegetation.

Ohia flowers are a key food resource. Ohia exhibits profuse flowering; most populations are obligate outcrossers and have a mutualistic relation with nectarivorous birds (Carpenter 1976). Ohia flowers are positively associated in our analysis with the Common Amakihi, Iiwi, Crested Honeycreeper, Apapane, Red-billed Leiothrix, Japanese White-eye, native species richness, and introduced species richness. Localized interference competition for nectar organizes native species into a dominance hierarchy (Baldwin 1953, Pimm and Pimm 1982), but does not modify large-scale habitat response (Mountainspring and Scott 1985). On Molokai and probably on Maui, a five-member dominance hierarchy based on ohia flowers originally occurred, with Bishop's Oo as the alpha member of the series, followed by Black Mamo, Crested Honeycreeper, Iiwi, and Apapane. These birds were primarily nectarivorous and usually drove away Common Amakihi and *Paroreomyza* creepers when they occasionally attempted to feed at flowers (Perkins 1903).

Olapa fruit, another important food resource in wet forests, generates positive response among several frugivores, notably the Omao, Puaiohi, Red-billed Leiothrix, and Japanese White-eye. Two nectarivores, Crested Honeycreeper and Apapane, also feed on olapa fruit when ohia flowers are scarce. Passiflora, particularly banana poka, attracts numerous species to its flowers and fruit. Common Amakihi and Iiwi feed on the nectar, and many introduced species feed on the fruit (Erckel's Francolin, Gray Francolin, Kalij Pheasant, Common Peafowl, Wild Turkey, Red-billed Leiothrix, Northern Mockingbird, Northern Cardinal, Yellow-fronted Canary) or on both (Japanese White-eye) (Warshauer et al. 1983). Not unexpectedly, passiflora is positively associated with introduced species richness. Mamane nectar is a dietary staple for Common Amakihi (van Riper 1984) and also attracts Iiwi and Apapane. Mamane flowers were quantified in only three study areas, however, so that their *prima facie* effect on habitat response is limited. Two variables, mamane fruit (pods) and naio fruit, were quantified only on Mauna Kea. Mamane pods attract the Palila, the honeycreeper adapted to feed on them, and the Northern Cardinal. Naio fruit sustains a number of frugivorous passerines and gamebirds, especially the Wild Turkey, Melodious Laughing-thrush, and Red-billed Leiothrix. The phenology of *Broussaisia, Clermontia, Coprosma, Freycinetia, Ilex, Myrsine,* and introduced *Eucalyptus* may also affect bird distribution, but we did not gather quantitative data for these species.

Many native passerines preferentially exploit certain plants. The habitat response pattern of Palila is closely correlated with the primary food source, mamane pods (van Riper 1980, Scott et al. 1984). Other native species are or were specialized to feed on particular plants and have habitat response patterns that probably reflect the distribution of food resources: Bishop's Oo, Hawaiian Akialoa, Iiwi, Black Mamo, and Hawaii Mamo on lobeliad flowers (Perkins 1903, Rock 1919, Spieth 1966); Kona Grosbeaks on naio seeds (Perkins 1893); Lesser and Greater Koa-Finches on koa seeds (Perkins 1893); Ou on ieie bracts (Perkins 1903); Hawaiian Crows on fleshy fruit (Giffin 1983); and Hawaiian Geese on succulent ground covers (Banko and Manuwal 1982). In this regard, the large number of potential food species in remnant mature dry forests (Table 2) offers a tantalizing suggestion of the complex ecological relationships that probably occurred between the recently discovered extinct honeycreepers (Olson and James 1982a, b) and the dryland flora.

The attraction of birds to flower and fruit resources is well-known. Lovejoy (1974) found that the more common bird species in the Amazon basin tend to use conspicuous flower, fruit, and army ant resources. In our study a similar pattern appears for species feeding on ohia flowers. Snow and Snow (1971) reported that the number of frugivorous and nectarivorous bird species increases with floristic diversity on Trinidad. Similar associations between the numbers of bird species and plant species have been found on subantarctic islands (Abbott 1974), the Galápagos Islands (Bowman 1961, Hamilton and Rubinoff 1964, Lack 1969, Harris 1973, Power 1975, Abbott et al. 1977), the California Channel Islands (Power 1972), and in South America (Terborgh 1977, Pearson and Ralph 1978). The role of food levels in determining distribution is illustrated by the dramatic response to conifer seeds in many continental species including Red Crossbill (*Loxia curvirostra*) (Griscom 1937), Pinyon Jay (*Gymnorhinus cyanocephalus*) (Ligon 1978), and Clark's Nutcracker (*Nucifraga columbiana*) (Vander Wall and Balda 1977), that may migrate hundreds of kilometers to areas with good seed crops. On a more subtle level, Sage Sparrows (*Amphispiza belli*) prefer to winter in mesquite habitat with abundant inkweed (*Suaeda torreyana*), because the seeds are a food resource (Meents et al. 1982).

Differential response to dominant plants by insectivorous bird species is related in some cases to insect resource levels. Swezey (1954) and Gagné (1979) found that many Hawaiian insect taxa are specific to certain plant hosts (usually at the generic level), and Gressitt and Samuelson (1981) noted substantial variation between host species in the abundance of wood-boring larvae. Resource levels seem to explain the extensive use of koa by Akiapolaau (C. J. Ralph, pers. comm.), of *Coprosma* and *Pelea* by Maui Parrotbill (S. Mountainspring, pers. observ.), and possibly of koa by Elepaio, Common Amakihi, and Hawaii Creeper (Conant 1981). The lower densities of Red-billed Leiothrix and Japanese White-eye in pure ohia forests may reflect the lower insect levels and lack of fleshy fruit compared with mixed stands. Several understory components bear neither fruit nor flowers and usually support low insect populations. For this reason matted ferns and tree ferns may be avoided by the Common Amakihi, Hawaii Creeper, Maui Creeper, Iiwi, Crested Honeycreeper, Kalij Pheasant, Elepaio, Red-billed Leiothrix, and Northern Cardinal. Matted ferns generate negative responses to the variables indexing community structure. Melodious Laughing-thrush, however, skulk in the underbrush and seem to find matted ferns with a few trees quite acceptable habitat. Although passiflora attracts many nectarivorous native species, the negative responses by the non-nectarivorous Omao and Elepaio suggest that passiflora lowers the resource base for these species.

Resource-based explanations were proposed to explain differential use of tree species by woodpeckers (Kilham 1964, 1970), of juniper and oak by foilage insectivores (Balda 1969), and of tree species by insectivorous passerines (Holmes, Bonney, and Pacala 1979, Sabo and Whittaker 1979, Holmes and Robinson 1981). The relative efficiency of foraging in different foliage configurations appears to influence avian use of tree species in these studies. Morse (1976) noted that some spruce (*Picea*) species are easier for warblers to forage in than others because of needle morphology and arrangement. Root (1967) emphasized the interaction between morphology and vegetation characters in determining foraging patterns. Some species are adapted to feed on a single taxon, such as the Point-tailed Palmcreeper (*Berlepschia rikeri*) on *Mauritia* palms (Vaurie 1980). Edington and Edington (1972) and Eckhardt (1979) emphasized the correlation of behavioral and morphological specializations with the preferred habitat. Innate and imprinted preferences for specific foliage types also affect habitat response (Klopfer 1963, Emlen 1981).

No functional coupling via food resources occurs when a floristic component acts as a surrogate or indicator species in the regression model to characterize a certain regime of temperature, moisture, forest development, etc. Mamane commonly acts as an indicator of dry, partly to very open woodland in models for the Elepaio, Chukar, California Quail, Eurasian Skylark, Northern Mockingbird, House Finch, Yellow-fronted Canary, and introduced species richness. The negative responses to ohia in Common Peafowl, California Quail, Zebra Dove, Eurasian Skylark, and Common Myna regression models reflect low numbers of these birds in wet closed ohia forests. Grazing activity is typically reflected in high cover values of introduced herbs, introduced grasses, and low covers of native grasses and ground ferns. By inference, grazing generates positive responses with the Common Amakihi, California Quail, Ring-necked Pheasant, and Japanese White-eye, and negative responses with Omao and Maui Creeper. Native grasses are typical of alpine grasslands and undisturbed forests, and indicate the restriction to forests of the Maui Creeper, Crested Honeycreeper, and Japanese Bush-Warbler, and low numbers of Elepaio, Wild Turkey, Spotted Dove, Common Myna, Japanese White-eye, Northern Cardinal, and House Finch in either or both habitats.

Other habitat features

A number of factors are indirectly inferred to determine the observed habitat responses. In semi-desert areas, drinking water is important for gamebirds, especially Chukar, California Quail, Spotted Dove, and Zebra Dove, and, to a lesser degree, Ring-necked Pheasant (Schwartz and Schwartz 1949). Introduced passerines (e.g., Saffron Finch, House Finch, Warbling Silverbill) are also attracted to drinking water in arid areas.

Habitat heterogeneity, or patchiness, may be a requirement of some species and permit more species to co-occupy an area (Levin 1974, Whittaker and Levin 1977). Obligate nectarivores and frugivores need a variety of flower and fruit species to provide year-round resources (Snow and Snow 1971, Pimm and Pimm 1982). Higher densities of Iiwi and Apapane tend to occur in areas where both mamane and ohia are in bloom, and areas with a greater density of understory components are preferred by Iiwi and Melodious Laughing-thrush. In intensive studies elsewhere in the tropics, tree falls increase local patchiness and are correlated with higher bird diversity (Willson and Moriarity 1976, Schemske and Brokaw 1981). Roth (1976) demonstrated a correlation between patchiness and bird diversity in subtropical scrub. On a larger scale, birds may use separate roosting and feeding areas, as demonstrated for Iiwi, Apapane (MacMillen and Carpenter 1980; C. B. Kepler and J. M. Scott, pers. observ.), and Spotted Dove (Schwartz and Schwartz 1949, 1951a).

The area of a general habitat-type needs to provide sufficient food resources and room for behavioral activities to support an adequate population size. Mosquito-free areas that may exist on West Maui or on the Olokui Plateau of Molokai are probably too small to support viable populations of many disease-susceptible species. The koa-ohia forests on north Hualalai have an area of only 16 km^2 and lack Akiapolaau. Assuming a density of 5 birds/km^2, the north Hualalai area would support 80 Akiapolaau; the small size of the area combined with the proximity of mosquito-infested areas at lower elevations might be insufficient to sustain a population indefinitely.

The interaction of thermoregulation and environmental adversity may underlie some habitat response patterns, particularly in determining upper and lower range boundaries. For example, Palila are heat-stressed at 31° C (Weathers and van Riper 1982); birds from the Mauna Kea population would not survive in many lowland areas. MacMillen (1974) found that Common Amakihi perish at 40° C, but both this species and Anianiau have thermoregulatory adaptations that result in energetic savings at the low ambient temperatures typical of montane forests at night. The relation of standard metabolic rate to body mass for Common Amakihi and Apapane deviates from the passerine allometric pattern; this adaptation conserves energy in cold, wet environments and is probably related to nectar exploitation (MacMillen 1981). Thermoregulatory adaptations to cold climates may slow dispersal into warmer lowland areas. On the other hand, roosting flights taken by Iiwi and Apapane appear to be energetically profitable because overnight energy savings result from thermal protection in mature forest and escape from nocturnal fog (MacMillen and Carpenter 1980). Our analysis suggests that Red-billed Leiothrix cannot sustain lowland populations, possibly because of thermal stress. Melodious Laughing-thrush and other introduced species may be absent from high montane rainforests because of poor adaptation to cold, wet environments. The critically high costs of overnight thermoregulation were first noted by Holmes, Black, and Sherry (1979) for passerines in a temperate montane forest. The preference of Spotted Owls (*Strix occidentalis*) for old growth coniferous forests reflects low tolerance to high diurnal temperatures (Barrows 1981). The temperature and moisture regimes of preferred breeding habitat are related to the thermoregulatory and metabolic differences among congeneric thrushes (Holmes and Sawyer 1975), finches (Salt 1952), and warblers (Sabo 1980). Variation of thermoregulatory parameters beyond normal allometric patterns is adaptive to warm environments for pigeons (Dawson and Bennett 1973), larks (Trost 1972), and the House Sparrow (Blem 1973). Kendeigh and Blem (1974) and Weathers (1979) more fully review the subject. Many native Hawaiian rainforest birds nest in cavities or protected sites (Scott et al. 1980, Kepler and Kepler 1983); this may be adaptive to frequent cold wet weather.

Conclusions on habitat response

The habitat response pattern of each species is unique. The many factors that are involved in determining habitat response recur and interplay in different patterns and at different levels of scale for each species. Although ecologists may have once attributed observed patterns to one "causal agent" (Cody 1974), studies of bird communities in tropical forests (Karr 1976a, 1980), shrubsteppes and grasslands (Rotenberry and Wiens 1980a), temperate montane forests (Sabo and Holmes 1983), and riparian vegetation (Rice et al. 1983) have shown that many underlying factors operate and interact over a wide range of spatial and temporal scales. The habitat responses we studied appear to reflect underlying factors of food, water, cover, and thermoregulatory adaptation to environmental adversity. In our study these factors appear as a tapestry pattern woven from the common threads that run through the habitat responses of individual species.

A critical objective of habitat response analysis is to characterize the major environmental gradients (or directions of variation) and to place the observed response patterns into this perspective. Adequate data are obviously necessary. Titus and Mosher (1981), for example, noted that variances for habitat variables in random samples stabilize after 50–60 sites, and several studies (James 1971, Whitmore 1975, Sabo 1980, Rice et al. 1983) utilized hundreds of sites to characterize landscape patterning in avian habitat response. It may be inappropriate to base broad-scale (continental) comparisons on as few as 20–30 point sites, as some workers have done. The regression models in our study are based on 77 to 2847 randomly sampled points (each with a minimum of two count periods). Those models based on low numbers of points (Lanai with 77, Kauai with 140, Kohala with 215) show few and weak relations, with probable major effects not always identifiable. In models based on 400–900 points (Kau, Kipukas, Molokai, and Puna), the major effects are usually identifiable, and many minor relations are also apparent. In the largest models (Hamakua with 2478 points, Kona with 2847), major relations achieve astronomical significance levels, minor relations are numerous, and in some cases variables with no presumed biological significance attain low statistical significance.

As the next higher level of abstraction from the individual community, the landscape is a useful construct for understanding variation within and between species (Whittaker 1967,

TABLE 71
Elevational and Lateral Distributional Anomalies[a]

	Elevational anomalies[b]								Lateral anomalies[c]				
	H1	H2	H3	H4	H5	M1	M2	K1	H6	H7	M3	M4	K2
Insectivores													
Elepaio	+	+	+	0	+	···	···	+	0	+	···	···	0
Kauai Oo	···	···	···	···	···	···	···	+	···	···	···	···	*
Maui Parrotbill	···	···	···	···	···	+	···	···	···	···	+	+	···
Common Amakihi	+	+	!	0	+	+	!	+	0	+	0	+	0
Anianiau	···	···	···	···	···	···	···	+	···	···	···	···	+
Nukupuu	···	···	···	···	···	r	···	r	···	···	r	r	*
Akiapolaau	+	+	x	+	x	···	···	···	+	+	···	···	···
Kauai Creeper	···	···	···	···	···	···	···	+	···	···	···	···	+
Hawaii Creeper	+	+	x	+	x	···	···	···	+	+	···	···	···
Maui Creeper	···	···	···	···	···	+	···	···	···	···	+	+	···
Akepa	+	+	x	+	x	+	···	+	+	+	r	+	+
Poo-uli	···	···	···	···	···	+	···	···	···	···	r	+	···
Nectarivores													
Iiwi	+	+	r	0	+	+	+	+	+	+	+	+	0
Crested Honeycreeper	···	···	···	···	···	+	···	···	···	···	+	+	···
Apapane	0	0	0	0	+	+	0	+	0	0	0	0	0
Frugivores													
Hawaiian Crow	x	x	x	+	···	···	···	···	···	x	···	···	···
Kamao	···	···	···	···	···	···	···	+	···	···	···	···	+
Olomao	···	···	···	···	···	x	+	···	···	···	x	x	···
Omao	0	+	+	r	x	···	···	···	0	0	···	···	···
Puaiohi	···	···	···	···	···	···	···	+	···	···	···	···	*
Ou	x	+	r	x	x	x	x	+	x	x	x	x	*

[a] Symbols indicate distributional patterns associated with the anomalies described in text: + = range truncated or species less common in anomaly area; 0 = no response to anomaly observed; ! = species more common in anomaly area; * = species confined to Alakai Swamp (non-anomaly area); r = species appears to respond to anomaly but too rare to quantify; x = species extinct in study area; ··· = species not present on island.

[b] Elevational anomalies by study areas: H1, Kau; H2, Hamakua; H3, Puna; H4, Kona; H5, Kohala; M1, East Maui; M2, Molokai; K1, Kauai, based on 1968–1973 data in Sincock et al. (1984).

[c] Lateral anomalies: H6, north Hamakua, Hawaii; H7, Kahuku tract (south Kona and Kau), Hawaii; M3, Waikamoi, Maui; M4, transect 11, Maui; K2, gradient into Alakai Swamp, Kauai.

Whittaker et al. 1973). The landscape is the set of permutations of habitat elements, although individual permutations are not equally common in nature. We found contour graphs of species response in habitat space to be effective for summarizing and displaying the major directions of variation, and regression models were found to be useful for examining the roles played by many different variables. When the landscape perspective is complemented by more detailed niche (within-community role) data, the underlying factors patterning species response could often be inferred and quantitatively modeled. The species accounts stress the importance of a knowledge of the ecological requirements and behavior of the species in understanding the factors determining habitat response. Although communities are sometimes conceptualized as *n*-dimensional hyperspaces (Hutchinson 1958, Whittaker 1977), species responses in these hyperspaces are individualistic. Each species uses community resources in a unique manner, so that underlying habitat factors are weighted differently by each species. The habitat response of a species is thus an idiosyncratic transformation, projection, or collapse, of the *n*-dimensional hyperspace. Essentially, then, the analysis must focus on many individual species in order to gain the "big picture," because no single species responds to all the factors determining habitat response and no superficial community approach can identify the actual factors determining the response patterns for the species present. Examining the variation between habitat responses thus offers a promising approach to identifying the factors that underlie community structure.

Distrubutional Anomalies

In a number of areas, densities of one or more bird species appear to be unexpectedly low. These "distributional anomalies" affected many native birds, and the geographic patterns could be characterized as related to (1) habitat structure, (2) elevation, (3) lateral anomalies that tend to lie perpendicular to the slope and not correspond with vegetation boundaries, (4) the Kona study area south of Hualalai, and (5) localized effects. We identified the distributional anomalies in the major HFBS study areas and classified each species as to the principal means of foraging (Table 71).

Distributional anomalies that correspond with major vegetation boundaries such as forest/nonforest and koa forest/ohia forest are fairly frequent and probably due to gross differences in habitat structure and food resources. This probably explains the absence or low densities of birds in places where non-forested areas adjoin forests: on Hawaii, in the Kapapala area between the Hamakua and Kau forests, in the Puu Lehua area between the Hualalai and central Kona forests, and in the Waimea Plains area between Kohala and Hamakua forests; on Maui, in the Kahikinui area and in the Haleakala Ranch area west of Waikamoi Preserve; on Molokai, in the eastern part of the study area that was devastated by feral ungulates; and on Lanai, in the areas surrounding the remnant forest. Distributional anomalies that are probably explained by less drastic vegetation boundaries include (1) the reduced densities of Elepaio and absence of Akiapolaau in the south half of the Kau study area, corresponding to the dropout of koa; (2) the great reduction or range termination of virtually all species at the boundary between mature forest and ohia dieback in Hamakua, with a less marked response occurring on East Maui where the dieback zone is smaller; and (3) the reduced densities of Common Amakihi, Akiapolaau, and Akepa along, and the range truncation of Ou at, the Saddle Road, probably reflecting the presence of several large lava flows and younger forests on more recent substrates.

Reduced densities and range truncations at lower elevations are very frequent, occurring in 81% of the cases tallied in Table 71. The three general foraging guilds show fairly consistent responses (88% of insectivore, 63% of nectarivore, and 89% of frugivore cases), suggesting that the phenomenon is not necessarily related to food resources. Elevational anomalies appear for every endangered passerine examined, and only the Apapane on Hawaii consistently shows no response, except in Kohala. In Puna and Molokai, the Common Amakihi shows the only reverse responses, greater densities at lower elevations, but this probably reflects their association with the drier habitats at lower elevations. The most striking elevational anomalies occur in the south corner of the Kau study area and in the Hamakua and East Maui areas, where virtually identical habitat at lower elevations is nearly devoid of birds that occur at higher elevations. The 1968–1973 survey of Kauai forest birds (Sincock et al. 1984) also showed virtual absence of most native species from low-elevation native forests.

A number of distributional anomalies occur along elevational contours. These distributional anomalies often occur within several kilometers of forest-edges. Examples of this include the Kahuku Tract between the Kona and Kau study areas, near Kukaiau Tract in north Hamakua, and on Waikamoi Preserve on East Maui, and equal 64% of the possible occurrences tallied in these three areas (Table 71). This does not appear to be an "edge effect" per se, however, because numerous species at other similar forest edge boundaries display no such effect. This pattern appears for every endangered passerine species in these three areas, with the possible exception of those too rare to sample. The pattern appears among 77% of the insectivores and 57% of the nectarivores. The Apapane and the only frugivore, the Omao, showed no response.

If mosquito-borne avian disease is indeed a major limiting factor of many species, as evidence presented in a later section suggests, then these lateral anomalies could be explained as areas of higher mosquito density due to prevailing wind regimes. Wind appears to be a dispersal agent for mosquitoes (Hopkins 1941, Russell et al. 1944, Wolfenbarger 1946), and trade wind patterns would be particularly effective in dispersing mosquitoes into unbroken forest from surrounding infested areas where the trade flow crosses over and around mountain shoulders. Strong winds during winter "Kona" storms may also contribute to the dispersal of mosquitoes into montane forests. Four such instances appear on Hawaii and East Maui: the northern ends of Mauna Kea and Haleakala, the southern end of Mauna Loa, and the southeastern end of Haleakala. The first three of these areas correspond sharply to the Kukaiau, Waikamoi, and Kahuku anomalies. We would expect a fourth anomaly to occur near the top of transect 11 on East Maui, west of Hana, and here, eight of the nine native passerines show a range truncation or a sharp reduction in densities. The disease factor may also explain many of the elevational anomalies discussed above, and an anomaly found in the Alakai Swamp. Several endangered species have declining densities along the gradient from the most remote part of the Alakai to the Kokee area, the natural access point with lower elevations. In addition several other species are confined altogether to the Alakai (Table 71). Mosquitoes occur in the Kokee area, but are either very rare or absent from the Alakai (J. L. Sincock, unpub. data), again presenting a striking coincidence.

In the Kona study area south of Hualalai, many species have strikingly lower densities than elsewhere on Hawaii (Akiapolaau, Hawaii Creeper, Akepa) or have become extirpated or extinct (Omao, Hawaii Oo, Ou, Palila, Lesser Koa-Finch, Greater Koa-Finch, Kona Grosbeak, Hawaiian Akialoa, Ula-ai-hawane, Hawaii Mamo). These

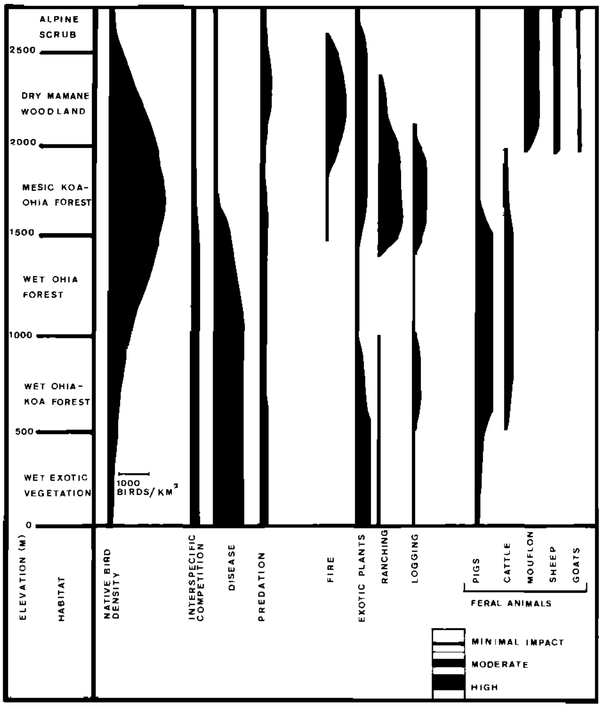

FIGURE 319. Generalized diagram of major limiting stresses on native bird populations, typical for area shown in Figure 320.

populations were apparently declining in the 1890s (Perkins 1903). The causes for the declines are unknown, but may include extensive habitat fragmentation due to coffee farming, logging, and grazing, as well as avian disease (discussed below).

Three localized anomalies were identified in our analysis. In the Mauna Kea study area, Elepaio, Palila, and Akiapolaau are nearly absent from the Pohakuloa Flats area, where the habitat is quite similar to that occupied elsewhere. Possible factors, including thermal stress, avian disease, site tenacity, past habitat disturbance, and military activity, were discussed by Scott et al. (1984). A second local anomaly occurs on the north slope of Hualalai, where Akiapolaau are absent from the koa-ohia forest that harbors Hawaiian Crow, Hawaii Creeper, Akepa, and other common native birds. Possibly the area and quality of that "habitat island" is inadequate to sustain indefinitely the Akiapolaau population. A third anomaly is the high density of Akepa near timberline in the middle of the Kau study area, contrasted with the almost complete absence of this species in the south part of that area.

Multidisciplinary approaches may be valuable in unraveling the factors causing some of these distributional patterns. Additional surveys to document seasonal and annual variation in the geographic distribution of the anomalies may also provide useful insight into their significance and on the role of sampling error in identifying their boundaries. Translocating radio-tagged birds into these areas and following them should provide valuable insight into why a species does not occur there naturally.

LIMITING FACTORS

Numerous factors stress endemic Hawaiian bird populations and propel many species towards extinction. A key principle in wildlife management is the identification and control of those factors that are particularly important in reducing the unimpeded rate of population increase inherent in a species (Leopold 1933, Giles 1978). The limiting factors of Hawaiian forest birds fall into these general categories: habitat modification, predation, disease, interspecific competition, and major environmental perturbations. Aside from these, pesticide contamination from agricultural practices is a potential problem for Hawaiian Hawks, Short-eared Owls, and possibly Hawaiian Crows and waterbirds.

The relative impact of different stresses varies among areas and species, and is conceptually de-