

An Ecological Model of the Effects of Exotic Factors on Limiting Hawaiian Honeycreeper Populations¹

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ABSTRACT. The object of this study was to construct a quantitative model to compare the effect of several exotic factors on limiting natural populations. The effect of habitat loss, range loss due to avian disease, feral ungulate activity, and interspecific competition for food resources from exotic birds on 33 populations of 16 Hawaiian honeycreeper species was examined. The impact of the four limiting factors was characterized in terms of the percent reduction in range or population density. Habitat loss resulted in a 74% average reduction in the original range; probable range loss due to disease averaged 46% of the available habitat; and feral ungulates and exotic birds lowered honeycreeper population densities by an average of 22% and 9%, respectively. The combined effect of the four limiting factors, which was modelled as their multiplicative product, represented an average loss of 89% in potential population size due to their operation, and accounted for 75% of the variation in present population sizes.

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INTRODUCTION

The relative importance of factors that limit the size of animal populations is a special concern in wildlife management (Leopold 1933). Attempts to quantify the relative roles of various factors have generally focused on detailed life history studies of individual species through techniques such as key factor analysis (Williamson 1971). In this paper I will develop a quantitative model to compare the relative effects of limiting factors of exotic origin on populations of the Hawaiian honeycreepers (Drepanidinae).

The Hawaiian honeycreepers have a spectacular range of morphological and behavioral adaptations to feed on foliage insects, timber-boring insects, nectar, fruits, seeds, molluscs, and seabird eggs (Amadon 1950, Berger 1981). Unfortunately, excessive perturbation from exotic elements to native Hawaiian ecosystems has created the highest concentration of endangered birds in the world (King 1978). Extant honeycreepers (Table 1) represent only 30% of the species present at Polynesian contact ca. 400 A.D. (Olson and James 1982); 14 of the 20 extant species are protected under the Endangered Species Act of the United States. Due to limited funding, identifying the relative roles that various exotic factors play in limiting honeycreeper populations is a crucial step in efficiently managing the recovery of endangered species.

Numerous exotic factors have been suggested as contributing to the decline of honeycreeper populations, including habitat loss due to human activity (Olson and James 1982, Berger 1981), gradual habitat degradation due to feral ungulate activity (Scott et al. 1986), avian disease (Warner 1968, van Riper et al. 1982), food competition from exotic birds (Mountainspring and Scott 1985), predation from rodents and carnivores (Perkins 1903, Atkinson 1977), invertebrate predators on the food base (Banko and Banko 1976), exotic plant invaders (Smith 1985, Scott et al. 1986), and wildfire in dry habitats (Tomich 1971). In this paper the effect on natu-

ral populations of habitat loss, avian disease, feral pig (*Sus scrofa*) activity, and food competition from the Japanese White-eye (*Zosterops japonicus*) will be modelled quantitatively for the honeycreepers inhabiting the islands of Hawaii, Maui, Molokai, Lanai, Oahu, and Kauai.

Inclusion of the last two factors in the model is well justified. In the wetter forests that most honeycreepers inhabit, the chief habitat modifier at present is the feral pig, whose rooting and wallowing activities drastically modify understory and eventually canopy composition (Tisdell 1982). The analysis of interspecific competition for food resources focuses on the Japanese White-eye because this abundant and omnivorous species appears to have the greatest impact of exotic birds on honeycreeper populations (Mountainspring and Scott 1985).

THE QUANTITATIVE MODEL

Shelford (1913) was the first to articulate the Law of Tolerance, stating that given a series of factors that operate independently to reduce a population from its potential, the combined effect of these factors can be characterized as their multiplicative product. A similar multidimensional conceptualization is found in the niche theory of Hutchinson (1958) and Whittaker et al. (1973). This concept provides the basis for the mathematical development below.

Let F_1 be the effect of factor 1 on reducing the population of a species. A value of 0.1 would signify that the population is reduced 10% due to the operation of factor 1. Let $F_{2..N}$ represent the effect of factors 2 through N, with each F_k constructed so as to account for the operation of F_1, \dots, F_{k-1} (i.e., the factors are orthogonal). The fraction of the population remaining after accounting for the operation of F_k is thus $1 - F_k$. The fraction of the potential population remaining after the combined effect of all factors is considered will be termed the Remaining Potential Population (RPP). This value is computed as the percent of the original population predicted to remain to permit comparison between species with different carrying capacities and is given by:

$$RPP = \prod_{i=1}^N (1 - F_i).$$

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TABLE 1
 Systematic arrangement (following Berger 1981) of the extant Hawaiian honeycreepers.

Species	Present habitat		Chief foods
	Forest type	Elevation (m)	
Laysan Finch*# (<i>Telespyza cantans</i>)	Dry scrub	0-15	Insects, seeds, bird eggs
Nihoa Finch*# (<i>Telespyza ultima</i>)	Dry scrub	0-270	Insects, seeds, bird eggs
Ou* (<i>Psittirostra psittacea</i>)	Wet	1000-1500	Fruit
Palila* (<i>Loxioides bailleui</i>)	Dry	2000-3000	Seed pods
Maui Parrotbill* (<i>Pseudonestor xanthophrys</i>)	Mesic to wet	1500-2000	Timber-boring insects
Common Amakihi (<i>Hemignathus virens</i>)	Dry to wet	0-3000	Foliage insects, nectar
Anianiau (<i>Hemignathus parvus</i>)	Mesic to wet	500-1500	Foliage insects
Kauai Akialoa*& (<i>Hemignathus procernus</i>)	Mesic to wet	1000-1500	Nectar, trunk insects
Nukupuu* (<i>Hemignathus lucidus</i>)	Mesic to wet	1000-2000	Trunk insects, nectar
Akiapolau* (<i>Hemignathus munroi</i>)	Dry to mesic	1000-2500	Trunk insects
Kauai Creeper (<i>Oreomystis bairdi</i>)	Mesic to wet	1000-1500	Trunk insects
Hawaii Creeper* (<i>Oreomystis mana</i>)	Mesic to wet	1000-2000	Trunk insects
Maui Creeper (<i>Paroreomyza montana</i>)	Mesic to wet	1000-2200	Foliage insects
Molokai Creeper*& (<i>Paroreomyza flammea</i>)	Wet	1000-1500	Foliage and trunk insects
Oahu Creeper* (<i>Paroreomyza maculata</i>)	Mesic to wet	1000-1300	Foliage insects
Akepa* (<i>Loxops coccineus</i>)	Mesic to wet	1000-2000	Foliage insects
Iiwi (<i>Vestiaria coccinea</i>)	Dry to wet	500-2500	Nectar, foliage insects
Crested Honeycreeper* (<i>Palmeria dolei</i>)	Wet	1500-2000	Nectar, foliage insects
Apapane (<i>Himatione sanguinea</i>)	Dry to wet	0-2500	Nectar, foliage insects
Poo-uli* (<i>Melamprosops phaeosoma</i>)	Wet	1500-2000	Molluscs, understory insects

* Endangered species.

Found only on Northwestern Hawaiian Islands.

& No sightings in past 20 years; may be extinct.

The variance (s^2) of this measure is given by:

$$s^2(\text{RPP}) = \prod_{i=1}^N s^2(F_i),$$

although in this study variances could be computed for only some of the factors.

Because population size has two components, area and density, the factors to be analyzed fall under two rubrics: those that are characterized as binary (all/none) in operation, and those that are continuous. The effects of habitat loss and disease are modelled as generating sharp geographic range boundaries; these are quantified in terms of the percent loss of range due to the operation of that factor. The effects of feral pigs and Japanese White-eyes are modelled as modifying the population density of affected species at the scale that the data were collected (see Wiens 1981); these are analyzed statistically to yield the percent difference in bird density due to their activities. To facilitate comparisons among the factors, it was as-

sumed that lost or unoccupied suitable habitat would support bird densities equivalent to those in occupied areas, if the limiting factors were not in operation. Thus, for both binary and continuous variables, this scaling represents the percent loss in potential population due to the operation of that limiting factor.

To validate the model (i.e., to make an assessment of its biological reasonableness) I examined the relationship between remaining potential populations as predicted by the model and actual present populations. This test assumes that present population sizes, which range from 30 to 1,100,000, will generally reflect the combined severity of the four exotic factors. Using the product-moment correlation test (Steel and Torrie 1980) to examine various transformations (linear, logarithmic, square root, arc sine), I found the best linear fit resulted from a logarithmic transformation applied to population size and a square-root transformation applied to relative remaining potential population. However, the choice of trans-

formation made little difference in the overall statistical patterns observed.

METHODS AND MATERIALS

Data used in the model resulted from extensive studies of bird populations, vegetation composition, mosquito distribution, and feral pig activity conducted by the U.S. Fish and Wildlife Service in native forests on the islands of Hawaii, Maui, Molokai, Lanai, and Kauai (Scott et al. 1986). A total of 10,667 stations were sampled during the 1968-85 period in the 14 study areas covering 4,663 km². Each was sampled twice in one breeding season, with selected stations being sampled for seasonal, annual, and long-term patterns in bird populations.

The present ranges of native birds on Hawaii, Maui, Molokai, Lanai, and Kauai were taken from Scott et al. (1986). Ranges of birds on Oahu were estimated from the data of Shallenberger and Vaughn (1978) and the Hawaii Audubon Society (R. L. Pyle, pers. comm.). Population densities of each bird species were computed for each station sampled according to the field and analytical methods of Reynolds et al. (1980) and Scott et al. (1986). These yielded population estimates with variances for each species (Scott et al. 1986).

Broad-scale, type-maps of the present vegetation cover were prepared for native forests on the main islands (See Scott et al. 1986). Similar maps of the original vegetation cover ca. 400 A.D. were constructed from a knowledge of present vegetation and climatic conditions, generally following the scheme of Ripperton and Hosaka (1942). Vegetation types were defined by combinations of moisture regime (dry, mesic, or wet), dominant tree species composition, and forest/non-forest status. This broad scale of classification accounted for over 70% of the observed variation in bird habitat response compared to a full suite of habitat variables, and was necessary in mapping the original vegetation patterns. To quantify the loss in range due to habitat destruction, the present area of those habitat-types that a species inhabits (including portions presently unoccupied because of other factors such as disease) was divided by the original area of those habitat types. This value was then subtracted from unity.

The probable loss in range due to the presence of disease was modelled with mosquitoes as a surrogate indicator. This reflected a growing body of evidence that extensive range losses of many species resulted from their susceptibility to avian malaria and avian pox spread by mosquitoes (Warner 1968, van Riper et al. 1982, Scott et al. 1986). To compute the approximate loss in range due to avian disease, the area of unoccupied available habitat that corresponded with the presence of mosquitoes was divided by the area of present available habitat; this value was then subtracted from unity. Regional distributions of adult mosquitoes on Hawaii and Maui were given in Scott et al. (1986). Systematic campsite records and incidental observations were used to construct comparable maps for Molokai, Lanai, Oahu, and Kauai.

The sampling unit for the data used in analyzing the effect of feral pigs and Japanese White-eyes was the individual station. The variables used were: (1) the densities of honeycreeper populations; (2) feral pig activity, as indexed by a visual estimate of the percent of ground cover that was disturbed by recent rooting and wallowing activity; (3) the population density of Japanese White-eyes; and (4) habitat variables of elevation, crown cover, canopy height, tree species composition, understory cover and composition, and flowering and fruiting phenology of certain dominant species.

An analysis of covariance was used to remove the confounding effects of habitat factors. For pig activity, the habitat factors removed were elevation, moisture regime, canopy cover, canopy height, tree species composition, understory type classes, and geographic area (study area on an island). With exotic birds, the effects of 29 habitat variables were removed in a partial correlation analysis of each study area (Mountainspring and Scott 1985). Fewer covariant habitat variables were used with pig activity than with exotic birds because pig activity affected the finer details of habitat structure. Thus, an analysis of covariance with a larger number of habitat variables obscured some of the response. The use of a greater number of covariant habitat variables with exotic birds in part reflected an attempt to account for modifications of habitat structure by pig activity.

The effects of feral pigs and Japanese White-eyes were quantified as percent change in density that resulted from their activity to permit comparisons of species and of factors. Applying regression analysis to all stations with data, honeycreeper response was computed as the percent difference in densities between stations where the factor had a value of zero, and stations where the factor had its mean value. Thus,

the percent difference provided a statistical quantification accounting for variation in density of the bird and in values of the limiting factor.

From standard regression analysis (Draper and Smith 1981), the predicted density at no effect (B_0) was calculated by:

$$B_0 = B - r \times E \times s(B)/s(E),$$

where B is the mean bird density in a study area, r is the partial correlation between bird density and an exotic factor, E is the mean value of the factor, $s(B)$ is the standard deviation of bird density, and $s(E)$ is the standard deviation of the factor. Owing to the large sample sizes involved, the variance of B_0 was approximated closely by:

$$s^2(B_0) = (1 - r^2) \times s^2(B).$$

The percent reduction (PD) in bird density due to the difference between no effect and the mean effect was then quantified as:

$$PD = 100 \times (B_0 - B)/B,$$

with its variance approximated by:

$$s^2(PD) = s^2(B_0)/B_0^2.$$

When these values were computed for individual study areas, I observed that local and seasonal effects and large variances obscured the overall statistically significant patterns that were present. To overcome this limitation, I pooled data across study areas, weighting observations by population size. Species lacking data for these variables had values entered as zeroes (i.e., no effect), because, based on the known natural history in most cases, this seemed to be a reasonable representation of their biological relations.

RESULTS AND DISCUSSION

The values for habitat loss (Table 2) reflect the loss of available habitat for each species since Polynesian contact. The losses for extant species range from 42% for the Apapane on Hawaii to 92% for the Palila on Hawaii. Among extant populations, those on Hawaii, Molokai, and Kauai retain the greatest proportion of their original habitat, with losses averaging 66%, 67%, and 68%, respectively. On Maui, the losses average 79%, and on the heavily disturbed islands of Lanai and Oahu the average loss of suitable habitat reaches 89%. Habitat loss has generally been greatest in dry forests; thus, dry forest species such as the Palila and some of the extinct honeycreepers tended to suffer greater losses in range through habitat loss than did wet forest species such as the Iiwi and Apapane. At least 15 honeycreeper species that inhabited only dry lowland forests and woodlands became extinct long before Western contact due to burning and clearing by Polynesians (Olson and James 1982).

The probable loss of range due to the presence of mosquitoes varies from 0% for the Apapane on Lanai to 94% for the Oo on Kauai (Table 3). This variation probably reflects differences between populations and species in susceptibility to avian disease, such as has been found with malaria (van Riper et al. 1982). Range losses due to disease commonly reach values of 61-74% on Hawaii, 58-80% on Maui, 82-83% on Molokai and Oahu, and 65-71% on Kauai, with higher values in the case of some species with extensive portions of mosquito-infested available habitat. The Apapane appears to be the most resistant species, with only 0-11% of the available habitat unoccupied. Many honeycreepers that became extinct after Western contact on Molokai, Lanai, and Oahu were very likely victims of avian disease, because mosquito-free refugia on these islands are small or non-existent (Scott et al. 1986).

Feral pig activities have a strong influence on species associated with understory vegetation (Table 4), notably the Poo-uli and Maui Parrotbill whose densities were reduced 57% and 46%, respectively, by the mean pig

TABLE 2

Habitat loss, as percent of the original range that has been converted to exotic vegetation for 16 Hawaiian honeycreeper species. An x indicates that population became extinct in recent time; .. indicates species did not occur historically on that island.

Species	Hawaii	Maui	Molokai	Lanai	Oahu	Kauai
Ou	83	x	x	x	x	69
Palila	92
Maui Parrotbill	..	86	x
Common Amakihi	61	82	84	x	91	71
Anianiau	69
Nukupuu	..	86	x	71
Akiapolau	75
Kauai Creeper	71
Hawaii Creeper	62
Maui Creeper	..	86	..	x
Oahu Creeper	91	..
Akepa	62	75	x	62
Iiwi	52	77	59	x	85	62
Crested Honeycreeper	..	75	x
Apapane	42	70	59	89	90	62
Poo-uli	..	75

activity in the study area. These species are probably impacted by a loss in foraging sites, since they use diverse understories (Mountainspring, in press). In the upper Waimea Canyon study area on Kauai, Nukupuu densities are reduced by 91% due to pig activity; the data to determine whether this pattern is typical in other areas on Kauai and Maui are lacking. On Maui, the Nukupuu does tend to occur in areas near where the Poo-uli occurs, suggesting some similarity in the response of these two species to this variable. Pig activity also affects other trunk foragers, reducing densities by 36% for the Akiapolau, 28% for the Kauai Creeper, and 25% for the Hawaii Creeper. Although pigs do not usually damage mature boles, many insect species move along the trunk between nocturnal feeding sites in the foliage column and diurnal hiding sites in the ground layer (F. G. Howarth, pers. comm., Moeed and Meads 1983). The negative relationship between pig activity and trunk foragers sug-

gests that disruption of the ground layer by pig activity depresses insect populations having diel movements and as well as probably other invertebrates that depend on the ground layer at some life stage. Very little response was noted for the Common Amakihi, Anianiau, Maui Creeper, and Akepa, which feed primarily on foliage insects; for the Iiwi, Crested Honeycreeper, and Apapane, which feed primarily on flower nectar; or for the Palila, because few pigs occur in its range. Probably the nomadic Ou is not locally affected much by pigs, but an effect might appear at a larger scale of resolution.

Japanese White-eyes significantly depress densities of some species. Two endangered species on Hawaii island, the Hawaii Creeper and Akiapolau, register average depressions in density of 25% and 24% respectively (Table 4). The related Kauai Creeper shows a significant loss of 19%. The 15% loss in Iiwi densities probably reflects the strong dependence on nectar at all seasons

TABLE 3

Range loss, as percent of available habitat that is apparently unoccupied due to the presence of disease vectors (i.e., mosquitoes), for 16 Hawaiian honeycreeper species. An x indicates the population has become extinct in recent time; .. indicates species did not historically occur on that island; parenthetic values are rough approximations.

Species	Hawaii	Maui	Molokai	Lanai	Oahu	Kauai
Ou	58	x	x	x	x	94
Palila	37
Maui Parrotbill	..	80	x
Common Amakihi	19	11	72	..	(2)	53
Anianiau	46
Nukupuu	..	80	x	93
Akiapolau	70
Kauai Creeper	71
Hawaii Creeper	61
Maui Creeper	..	58	..	x
Oahu Creeper	(93)	..
Akepa	74	80	x	65
Iiwi	26	22	83	x	(82)	63
Crested Honeycreeper	..	77	x
Apapane	11	4	10	0	(2)	3
Poo-uli	..	80

TABLE 4

Percent reduction in population densities for 15 Hawaiian honeycreepers due to feral pig activity and competition for food resources from the Japanese White-eye. Values represent data pooled for all populations. No data are available for the Oahu Creeper. Negative values indicate greater population due to the factor; .. indicates insufficient data for calculations due to small sample size.

No. Species	Feral pig activity		Interspecific competition	
	Mean Effect	SE	Mean Effect	SE
1 Ou
2 Palila	0	0
3 Maui Parrotbill	46	10
4 Common Amakihi	5	1	3	2
5 Anianiau	-1	4	2	5
6 Nukupuu	91	5
7 Akiapolaaui	36	5	24	6
8 Kauai Creeper	28	8	19	10
9 Hawaii Creeper	25	7	25	7
10 Maui Creeper	8	6	1	9
11 Akepa	4	8	6	5
12 Iiwi	0	4	15	3
13 Crested Honeycreeper	5	10	-4	9
14 Apapane	-3	3	-2	3
15 Poo-uli	57	39

(Mountainspring and Scott 1985). Based on its ecological similarity to the Akiapolaaui, the rare Nukupuu is probably also affected significantly by white-eyes (Mountainspring and Scott 1985). The other species for which responses could be quantified show statistically insignificant responses to white-eyes. Because of their feeding specializations, the Ou, Palila, and Maui Parrotbill are probably relatively unaffected by white-eyes.

The combined effect of the four limiting factors, as modelled by their multiplicative product, has reduced

honeycreeper populations on the average by 89% of their potential. The combined effect is highly correlated with present population sizes (Fig. 1; $r = 0.867, P < 10^{-6}$) and indicates that the four factors account for 75% of the variance in population size. This trend is apparent for the populations on Hawaii, Maui, and Kauai, and for the Common Amakihi, Iiwi, and Apapane on different islands. Of course, given the correlational nature of this analysis, some caution should be exercised in extrapolating from these results.

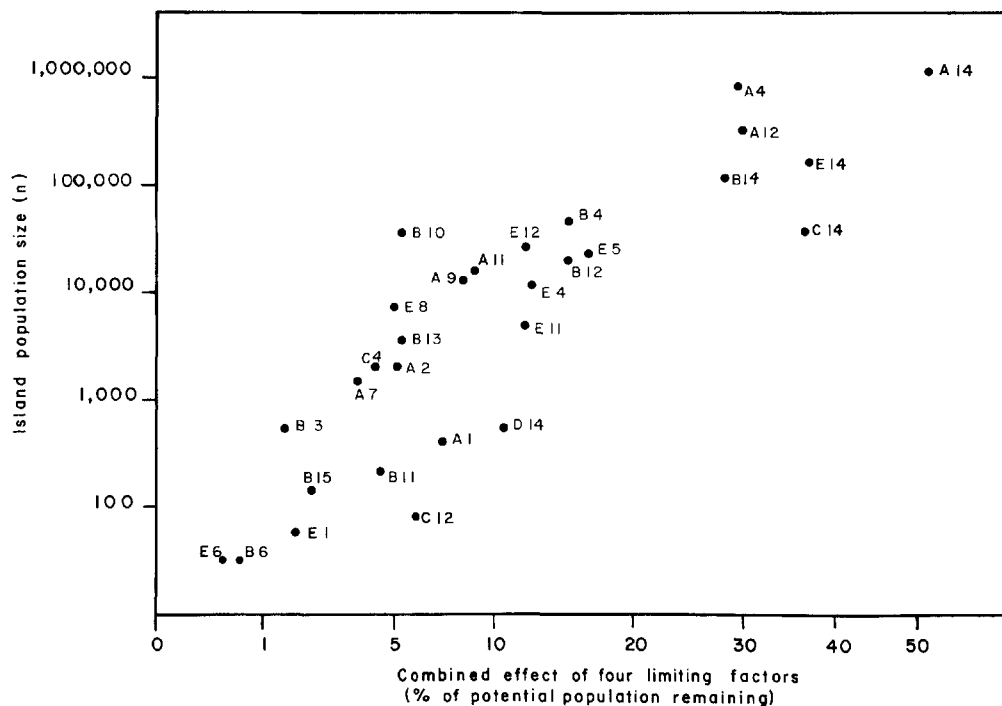


FIGURE 1. Relationship of combined effect of four limiting factors on the sizes of 29 Hawaiian honeycreeper populations. The vertical axis has logarithmic scaling; the horizontal axis has square root scaling and is expressed as the percent of the potential population calculated to remain after accounting for the operation of the four exotic factors. Codes for species are given in Table 4; island codes are A = Hawaii island, B = Maui, C = Molokai, D = Lanai, E = Kauai.

The relative importance of the four limiting factors analyzed is indicated by the mean depression each makes on bird range or density. The mean value among all populations for loss of available habitat is 74%, for range loss due to avian disease 46%, for lower densities due to feral pig activity 22%, and for lower densities due to Japanese White-eyes 9%. For some species, however, a particular factor is far more important than these averages indicate.

FUTURE RESEARCH NEEDS

In general, the model developed here characterizes a transient perspective and does not account for the integrating effect of factors operating through time. Thus, the model does not adequately address the effect on honeycreeper populations of gradual habitat degradation due to human activity, development of disease resistance, long-term damage by feral pigs to ecosystem structure, gradual competitive displacements by exotic birds, or synergistic relationships among exotic factors. Far more extensive research on malaria, pox, other diseases, and their vectors is required for total understanding of the role disease plays in limiting honeycreeper populations. Inclusion of data on seasonal and annual trends would also strengthen the model, although data on such species as the Palila (Scott et al. 1984) or Maui Parrotbill (Mountainspring, in press) suggest that distribution and habitat association patterns are relatively constant over time compared to temperate continental bird populations. The model does offer good evidence that preserving key parcels of remaining native habitat at elevations above the mosquito distribution is important in recovery efforts for endangered species. The strong negative association between feral pig activity and certain species likewise points to the need for control programs in some remote montane rainforest areas.

Another improvement in the model would be inclusion of variance estimators for the areally-oriented variables of species range, habitat-type maps, and distribution of disease vectors. This might be possible through verification measures made at numerous sampling points. A statistically rigorous framework with provisions for independent verification, as sometimes used in discriminant function analysis, would be a logical step in the development of models to quantify the effect of limiting factors on natural populations.

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