



## International Association for Ecology

---

Niche Specialization and Species Diversity along a California Transect

Author(s): Andrew R. Moldenke

Source: *Oecologia*, Vol. 21, No. 3 (1975), pp. 219-242

Published by: [Springer](#) in cooperation with [International Association for Ecology](#)

Stable URL: <http://www.jstor.org/stable/4215184>

Accessed: 19/06/2014 16:03

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at  
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Springer and International Association for Ecology are collaborating with JSTOR to digitize, preserve and extend access to *Oecologia*.

<http://www.jstor.org>

## Niche Specialization and Species Diversity along a California Transect

Andrew R. Moldenke

Board of Studies in Biology, University of California, Santa Cruz, California 95060

Received June 4, 1975

*Summary.* The structure of the food-web at the flower-herbivore interface was examined along a transect of fourteen communities across central California. All results are commensurate with the hypothesis that in most environments there is selective pressure towards specialization. However, it is only in the most predictable or stable environments that the resultant diminishment of behavioral and genetic flexibility is in a sense “permitted” by subsequent natural selection. In the most extreme environments, behavioral specialization may be a necessary prerequisite permitting briefly thriving ephemeral populations which must recolonize frequently. The data results indicate: 1) Total species number increases with stability and predictability of the climate; 2) As the climate ameliorates, niche-specialization is a progressively more successful strategy; 3) The percentage of niche-specialized species of both plants and flower-feeding herbivores increases in the most severe environments at the expense of the more moderately specialized species; 4) Energetic flow chart redundancy increases in extreme environments; 5) Especially important to an understanding of pollination interactions is the fact that similar physiognomic communities at very different altitudes are in all cases much more similar than different community types within a research site.

### Introduction

Analysis of the variation in magnitude of the flora and fauna present in different localities is a problem in species packing. On a large scale, regions of higher net production or greater diversity of habitat would be expected to support a larger number of species. Within a fixed amount of community niche space, the total number of species can be increased in two ways: the specialization of the fundamental niche may increase, or the niche space in which a species can compete optimally may be decreased without concomitantly decreasing the fundamental niche (increased niche overlap). Niche specialization should be more frequent as a strategy in predictable climatic regimes; in such environments the persistence of close-tracking specialists should be less subject to population extinction.

It is not possible to compare two areas solely on the basis of climatic and geologic data and to predict therefrom an expected increase in total species diversity based on increased community niche space. Any conclusion derived from this indirect approach as to the relative emphasis on niche specialization will not and cannot distinguish between increased specialization and increased overlap. In order to distinguish between these two alternatives, they must be monitored directly.

Several factors make the interface between the flowers of plants and their pollinators an advantageous system for this type of analysis. Relative to such plant components as roots and leaves, floral resources are materially and temporally finite. At the same time, such resources form an integral part of every

terrestrial ecosystem. Furthermore, the herbivores utilizing these resources represent a diversity of taxonomic groups within the insects. Thus, the resource and consumer segments are so broadly defined that the analysis attains predictive potential which need not be limited in its applications to narrowly defined taxonomic groupings.

In this study, a quantified measure of the ecological distinctness of the taxa present within a community is utilized in the analysis of species diversity. In any geographical site there may be a number of organisms recognized taxonomically as distinct species, but this number indicates nothing about the extent to which these species are morphologically, behaviorally or bioenergetically distinct. The index proposed by Hendrickson and Ehrlich (1971) will be used to answer quantitatively such questions as the following:

Given an assemblage of kinds present, how similar or divergent are their patterns of interaction in the food web of the community? Are they ecologically equivalent or different? For instance, are ten sibling species of bees, all of which feed on the same family of plants, any more or less "diverse" than ten totally unrelated species of bees feeding on the same plant family? What then is the situation with ten unrelated species of bees feeding on ten unrelated species of plants?

## Methods

### *Site Selection*

This methodology was designed in coordination with Peter Raven of the Missouri Botanical Garden to allow the comparison of equivalent community segments on a hemispheric scale. The research scheme as it now stands consists of six altitudinal transects: 1) temperate, personal, in central California; 2) subtropical, with J. Neff at San Diego, California (Moldenke and Neff, in prep.); 3) subtropical, with Haroldo Toro in central Chile (Moldenke and Neff, in prep.; Moldenke and Toro, in prep.); 4) tropical, Ray Heithaus of Northwestern University in Costa Rica (Heithaus, 1973, 1974); 5) convergent evolution in deserts, with Jack Neff in Arizona and Catamarca, Argentina (Neff and Moldenke, in prep.).

Within each transect, sites 1–2 km<sup>2</sup> in extent were selected as representative of the diversity of major community types. The studies presented here were conducted at the Farallon Islands, the Coastal Sage at Point Reyes, the Stanford University Campus Experimental Area (Jasper Ridge), the weedy ecosystem of the San Francisco Bay Area, montane Camp Mather, the timberline Hall Experimental Station at Tioga Pass, and the Arctic-Alpine at Dore Crest. The characteristics of each site are summarized below:

Farallon Islands: SE Farallon Island; sea level; 37 hectares in extent; located 34 km offshore San Francisco and Point Reyes; residence of ca. 25000 seabirds; dominant plants *Lasthenia* and *Spergularia*; weather characterized by abundant fog and strong winds; flora (Coulter, 1971); years of study 1969–1970.

Point Reyes (Marin Co.)/Pescadero (San Mateo Co.); sea level to 100 m; Coastal Sage and Dunes community; two separate communities each ca. 0.5 km<sup>2</sup> in extent necessary, due to the lack of relatively undisturbed coastal communities in central California; dominant plants *Baccharis*, *Lupinus arboreus*, *Mesembryanthemum*; flora (Thomas, 1961; Ferris, 1970); Point Reyes source of Farallon flora and fauna, connected 15000–20000 years ago by now submerged ridge; *Apis mellifera* rare; years of study 1971–1972.

Stanford University, Jasper Ridge Biological Preserve (San Mateo Co.); altitude 33–150 m; diverse region with Oak-Woodland (*Quercus douglasii*), Oak-Madrone Forest (*Q. kelloggii*, *Arbutus menziesii*, *Sequoia sempervirens*), Serpentine Grassland (*Lasthenia*, *Linanthus*, *Festuca*, *Stipa*, *Bromus*, *Orthocarpus*) and Chaparral (*Ceanothus*, *Arctostaphylos*, *Diplacus*, *Adenostoma*) Communities; each ca. 0.5 km<sup>2</sup> in extent; flora (Porter, 1962); years of study 1969–1970; *Apis mellifera* extremely abundant; regions protected from grazing for 8 years.

Palo Alto and Stanford University (Santa Clara Co.); altitude sea level; introduced weedy community in areas of disturbance; flora (Thomas, 1961); years of study 1969–1970.

Camp Mather (Tuolumne and Mariposa Cos. border); altitude 1500–1825 m; diverse region with Pine Woodland (*Pinus ponderosa*, *Libocedrus decurrens*, *Chamaebatia foliolosa*); Chaparral (*Adenostoma*, *Ceanothus*, *Arctostaphylos*) and Grassland (*Stipa*, *Festuca*, *Bromus*, *Perideridia*, *Microseris*) Communities; years of study 1971–1972; *Apis mellifera* common; Grassland community heavily grazed each year after peak blooming period, other communities undisturbed.

Tioga Pass, Hall Experimental Station of the Carnegie Institution (Mono Co.); timeline, 3333–3500 m; diverse region with very little disturbance in Forest (*Pinus flexilis*, *P. albicaulis*), Talus Fell-Field (*Castilleja*, *Penstemon*, *Senecio*, *Arnica*, *Erigeron*, *Poa*) and Alpine Marsh Meadow (*Carex*, *Eleocharis*, *Phleum*, *Oryzopsis*, *Potentilla*, *Gentiana*) Communities; flora (Clausen, 1969); years of study 1969–1970; no *Apis* present.

Dore Pass (Mono Co.); Alpine Tundra at 4000–4200 m; undisturbed high ridge on backbone of Sierra Nevada; years of study 1969–1970.

For each site, the area was mapped and the distribution of both the distinctive community types and the broad ecotonal areas were plotted. Plant censuses were carried out only within distinct communities; herbivore analyses were carried out including ecotones as well. Each community was studied throughout the entire blooming season for two successive years.

### Plant Censusing

Once a community had been defined on a map, coordinates were applied. Successive numbers drawn from a random numbers table designated point sites within the community. The point was designated as the corner of a sample square plot ten meters on a side. Overlapping sample plots or plots which included some aberrant feature of the landscape (such as a road or lake) were excluded. Ten sample plots in each community type were censused. Extremely abundant or densely clustered annuals and perennial grasses were estimated as closely as possible within each of nine equal subplots within each plot. A cumulative census was compiled from the ten data groups to represent the community in the final analysis. A complete listing was also kept of the species encountered in the community but not represented in the census data. With infrequent exceptions, the censuses contain all the nonrare species represented in each community. Species/area curves were utilized to check for adequacy of replicates sampled.

For each species, a floral biomass figure was determined representing as nearly as possible the species' contribution to the flower biomass resource of the community. This statistic is calculated by multiplying the two larger linear dimensions of the flower (inflorescence) by the number of flowers (inflorescences) per plant and the number of individuals of that particular species represented in the census. Noncompact inflorescences were squeezed by hand before the measurement was made, in such a way as to eliminate air space from the measurements. The number of flowers per plant was usually estimated from several representative plants; if a given species was usually characterized by numerous few-flowered individuals and few many-flowered ones, the smaller and fewer-flowered group would be sampled. Thus, the floral biomass figure actually comprises an approximate floral size index rather than any caloric measure.

### Herbivore Censuses

To assess the nature and extent of plant/herbivore-interactions, insects were collected as they fed on flowers throughout the study sites. Every vector observed on any plant was collected and killed in a vial containing cyanide; a separate vial was kept for collections on each plant species. A set path through the experimental site was chosen anew on each visit and each day. The paths crisscrossed the entire area (when possible) in a relatively nonoverlapping design. All portions of the site were sampled in an equivalent manner. Insofar as was possible, all species of flower-herbivores at each host plant were collected in the relative abundance that each herbivore visited each plant species (but see below). Each community was sampled intensively on approximately two days every week and a half throughout the entire season of anthesis. Sampling was without replacement, and the removal of individuals conceivably could alter the flower-visiting frequency of competitors. A significant alteration

in the behavior of specialist species is highly improbable (Linsley, 1958); however, the removal of a large percentage of the efficient specialists from a food source may well permit exploitation by generalists. Though I clearly did not remove a majority of any population in question, in no case did I mark individuals in an attempt to determine actual population size and the possible effects of nonreplacement sampling. Authoritative determinations of the collected material was made by taxonomic specialists whenever possible.

The number of insects actually collected at each plant species and then processed and identified is not always representative of the natural relative abundance of insect species. There are two principal sources of experimental bias:

1) Not all of the flower-visiting herbivores possess the same facilities of locomotion. The most wary species and the ones that fly the fastest and are most elusive are underrepresented in the collected sample (e.g. *Emphoropsis*, *Anthophora* spp.). Data from the first year of study as to percent success of capture of these very exceptional taxa (less than 0.01% of the total individuals) was used to correct partially for this bias.

2) The most abundant insect species are underrepresented because the collection choice always prefers the less abundant "search image" (Hartly, 1953). Collection is also least representative on the most abundant plant species because of the same search image predispositions (e.g. *Andrena baeriae* on *Lasthenia chrysostoma*, *Callimoxys sanguinicollis* on *Ceanothus* spp.). This more serious bias cannot be corrected without a more intensive study, for even with reference to field notes, there remains a subjective factor unaccounted for. Corrections were applied to the data (available in Moldenke, 1971, thesis data appendix; Moldenke and Neff, 1974a, b) whenever possible to render them a more accurate reflection of actual field conditions.

Since the size of the vectors may be important in that it is probably correlated with their differential energetic and physiological requirements, a semiquantitative biomass statistic was calculated for each species. Biomass represents the product of the width and breadth of the thorax multiplied by the length of the insect (wings always excluded).

Honeybees, though present at two of the four sites (Stanford and Mather), were not included in this study. It is important to remember that all the niche structure examined in this paper is primarily the result of thousands of years of coevolutionary history of the California flora and fauna, although it has been modified to a significant degree by 250 years of selective competition with honeybees.

### Breeding Systems

Since it is the breeding system of any given population that ultimately permits or facilitates its competitive existence in a given area, every effort was made to determine the basic strategies of as many species concerned as possible. Compatibility data was determined for most species either by bagging flowers in the field or transplanting them to insect-free conditions in greenhouses. Nylon curtain material (mesh width 0.4 mm) was found to be sufficiently efficient in excluding insects and least traumatic to the plant. As a consequence of the very large number of species, only a few inflorescences of each could be bagged or only a few individuals transplanted to greenhouse conditions. Individual variability may therefore have occasionally resulted in incorrect compatibility judgments for a species as a whole.

Obviously, "compatible" and "incompatible" are but end points of what is in fact a continuous spectrum. Nevertheless, nearly all the species examined in this investigation segregated into two distinct fertility classes under insect-free conditions—below 15% and above 85% seed set—and these two extremes of the compatibility spectrum are defined operationally as incompatible and compatible, respectively. No effort was made to assess post-zygotic germination success of the seeds involved; but in any case, it would be among the relatively few seeds of the species already scored as self-incompatible that germination failures would be anticipated.

### Weather Data

Official U. S. Weather Bureau Stations exist on the Farallon Islands, Point Reyes and adjacent to Jasper Ridge (Redwood City). The Carnegie Institution has had long-established weather stations at its Mather and Timberline Research Laboratories. A useful summary of California weather patterns is that of Felton (1965).

Table 1. Species diversity measured in transect sites

	Jasper Ridge <sup>a</sup>	Mather <sup>a</sup>	Timber- line <sup>a</sup>	Point Reyes	Dore Crest	Weeds	Farallon Islands
Increasing severity and unpredictability of climate							
Flowering plants							
# Species	537	321	360	191	81	156	32
H	2.62	2.82	3.19	2.77	3.26	1.67	1.05
M	0.16	0.14	0.10	0.13	0.05	0.38	0.58
Flower-visiting herbivores							
# Species	737	630	350	103	78	50	17
H	3.19	3.79	2.65	1.99	3.29	2.51	1.20
M	0.10	0.05	0.08	0.37	0.07	0.16	0.73

<sup>a</sup> Climatic references in Felton, 1965; average values obtained by summing resident community types in Table 2.  $H = -\sum (p_i) \log(p_i)$ .  $M = \frac{\sum (n_i^2 - N)}{N^2 - N}$ .

Climatic severity is least at Jasper Ridge, increasing as one approaches the Farallon Islands to the west and as one climbs in altitude to Dore Pass to the east. In California, as the season progresses and air temperature increases, the plants inhabiting open grassland communities face severer water stress, whereas flower-visiting insects need to expend less energy in thermoregulation.

## Results

### *Total Number of Species*

As expected, the total number of species of both plants and insects decreased with increasing altitude and severity of the climate along this transect (Table 1). The low number of resident species on the Farallon Islands is due partially to its isolation from the continental resource of possible colonists. Although the islands periodically have been connected to Point Reyes on the mainland by a now submerged ridge, intervening distance is now 34 km (Milliman and Ernery, 1968). Point Reyes is noted for its rich flora and fauna, characteristic of maritime northern California, and it is safe to assume that the Farallon Islands supported a much more diverse assemblage of organisms when they were connected to the mainland. Their present isolation has led to colonization by vast numbers of sea birds which thrive in the marine upwelling caused by the formation. The shortage of materials for nest building is so severe that once the breeding season has begun, not a scrap of photosynthetic matter remains on the islands in regions not constantly disturbed by Coast Guard personnel. The growing season for the plants and the flower resource available for exploitation is thus absolutely limited to very early spring, a time of constant strong offshore winds and omnipresent fog. The climate at Point Reyes is similarly severe for poikilothermous insects, as strong moist winds characterize the region during the entire year.



*Diversity Indices*

If the commonly used indices provide meaningful representations of species diversity, values of  $H$  should decrease and values of  $M$  should increase in regions of lesser climatic stability or greater disturbance (Simpson, 1949; Margalef, 1957; Lloyd and Gelardi, 1969). As shown in Table 1, the values for both plants and herbivores on the offshore island and the weedy communities as well as the herbivores at Point Reyes are overwhelmingly in the anticipated direction. The plant diversity values at Point Reyes are not low since, as previously noted, the coastal environment is seriously detrimental only to the cold-blooded flying insects. A most remarkable result of the diversity studies is the unexpectedly high levels of both plant and herbivore diversity at the Timberline site. Species count values in particular are much higher than results obtained in the alpine Rocky Mountains (Moldenke and Lincoln, in prep.). A very large element in both the alpine flora (Chabot and Billings, 1972) and pollinator fauna in the alpine Sierra Nevada is comprised of taxa evolutionarily associated with the North American deserts. These taxa have become established in the Sierra by colonizing the abrupt eastern desert slopes and competing with the much more tenuous biogeographic southern extensions of the boreal biota in California than exist at a similar latitude in Colorado (Moldenke and Lincoln, in prep.).

$H$  and  $M$  diversity values are not always correlated. Since they measure total count and equality of relative abundance in different ways, this is to be expected with such large data sets. It emphasizes the fact that differences that would be judged of great significance under one index are not necessarily significantly different in a parallel manner under the other diversity assay.

However, along the transect from sea level to 4000+ meters for both plants and pollinators, the trend in both  $H$  and  $M$  diversity appears to be inversely correlated to total species number. As can be seen from Tables 1 and 2, this discrepancy arises from the pooling of data from separate communities within each site to obtain a value for the overall site. Thus, while interspecific competition results in the partitioning (*i.e.* between habitat diversity or  $\beta$ -diversity) of the region into three quasi-distinct and noninteractive units at Timberline, the corresponding number of communities are five at Jasper Ridge, three at Mather and only one at Dore Crest. When values for individual plant communities are examined, a second order effect is strikingly apparent in that similar communities under different climatic regimes (from Jasper Ridge, Mather and Timberline) are more similar than the distinct communities at the same climatic site (Table 2). Herbivore diversity values do not reflect this trend in community distinctness since a large percentage of the fauna travels freely between communities as defined primarily in terms of resident flora (Table 3). The major factor involved in the relative ordination of these values is the distribution of abundances and not total number of kinds (as exemplified in Fig. 1).

The frequent inverse correlation of herbivore species count and species diversity indices is complex and will be considered below. The values of the plant indices are clearly correlated with the presence of annual plants. Annual plants characteristically appear in the census data as either rare scattered individuals or huge assemblages of thousands of individuals. Communities with a heavy emphasis on

Table 2. Community diversity measures ranked by data from plant censuses. Diversity values are primarily determined by community type and heavily influenced by the equitability component of diversity

H	M	Community type	Total species
3.90	0.03	Mather Forest	182
3.74	0.04	Subalpine Forest	126
3.58	0.04	Oak Madrone Forest	104
3.30	0.05	Dore Crest Arctic/Alpine	79
3.07	0.09	J. R. Chaparral Scrub	90
3.02	0.09	Subalpine Talus Scrub	181
2.77	0.13	Coastal Sage Scrub	191
2.70	0.13	Mather Grassland	103
2.70	0.15	Subalpine Marsh-Meadow	137
2.20	0.17	Serpentine Grassland	150
1.88	0.32	Oak Woodland	134
1.81	0.25	Mather Chaparral Scrub	62
1.67	0.38	Weeds	254
1.05	0.58	Farallon Island	32

Table 3. Community diversity measures ranked by data from flower-herbivore censuses. Diversity values are lowest for climatically the severest and most unpredictable communities. Diversity values are strongly influenced by the equitability component of diversity and little correlation exists with community type

H	M	Community type	Total species
3.85	0.05	Mather Forest	334
3.77	0.05	Mather Grassland	426
3.75	0.05	Mather Chaparral Scrub	324
3.53	0.08	Serpentine Grassland	388
3.43	0.08	J. R. Chaparral Scrub	484
3.31	0.09	Subalpine Forest	202
3.29	0.07	Dore Crest Arctic/Alpine	77
3.03	0.12	Oak Woodland	260
2.86	0.13	Subalpine Marsh-Meadow	158
2.57	0.13	Oak Madrone Forest	63
2.50	0.16	Weeds	50
2.00	0.37	Coastal Sage Scrub	191
1.78	0.40	Subalpine Talus Scrub	337
1.20	0.48	Farallon Island	17

annual plants have the lowest diversity indices, and the apparent increase in plant diversity indices with altitude is correlated with a decreased emphasis on annual plants. Annuals comprise 34% (by species) of the flora at Jasper Ridge, 15% Mather, 6% at Timberline and less than 1% at Dore Crest. With a similar resultant increase in diversity indices, the incidence of clustered annuals decreases progressively from Grassland to Scrub to Forest Communities.



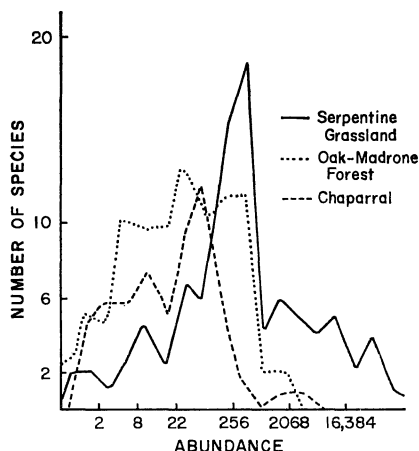


Fig. 1. Relative abundance of flowering plants in three Jasper Ridge communities. Comparison of diversity values with total species count emphasized equitability component of diversity measures. Serpentine Grassland ( $S = 150$ ;  $H = 2.20$ ;  $M = 0.17$ ); Oak-Madrone Forest ( $S = 104$ ;  $H = 3.58$ ,  $M = 0.04$ ); Chaparral Scrub ( $S = 90$ ;  $H = 3.07$ ,  $M = 0.09$ )

#### *Breeding Systems as Indicators of Niche Dimensions*

As the climate becomes increasingly severe and unpredictable, our hypothesis would predict a decreasing degree of success for poikilothermous pollen vectors and a consequent increase in genetic self-compatibility and wind pollination. Insect flower-herbivores are indeed significantly less abundant as the climatic severity increases. My collection data demonstrates that ten days of spring or early summer collecting at Jasper Ridge produce as many vectoring individuals as an entire season (16 weeks) at Timberline. Two years of collecting at Dore Crest yielded only 1 100 vectors, a total easily collected in several hours at Jasper Ridge or a day at Mather.

Since the occurrence of pollinating agents in sufficient numbers is therefore far from a predictable certainty under the climatic regimes of extremely high altitudes, one would expect that plants which depend on the wind as the sole vector would have had particular success. The percentage of the flora (by species) that is wind-pollinated at Jasper Ridge is 17%, whereas at Timberline it rises to 40%. This strategy fails at even higher elevations where the wind is so strong as to militate against effective wind pollination. In these locations nearly all the apparently anemophilous plants reproduce by apomixis, by vegetative reproduction, or by obligate selfing (*e.g.* *Poa*, *Bromus*, *Carex*, *Calamagrostis*).

The evolution of self-compatibility from the usual ancestral self-incompatibility does not necessarily imply that low levels of cross-pollination are characteristic of any given population. Nevertheless, the opportunity is present for progressive diminution of the genetic repertoire through selfing under conditions in which vectors are not available. At least 61% of the species at Timberline are known to be self-compatible with more than 50% habitually setting predominantly selfed seed. The corresponding figures for Jasper Ridge are 40% self-compatibility

Table 4. Importance of inbreeding along transect. All figures are rounded off to the nearest 5%, since an average of 10% of the taxa have not been successfully assayed for compatibility in each community. Presented data represent the percentage of taxa that have been investigated

	% of flora self compatible	% of flora habitually selfed	% obligate selfers or apomicts
Farallon Island	100	70	40
Weeds	95	50	15
Dore Crest	60	45	35 <sup>a</sup>
Timberline	80	45	25
Mather	45	25	5
Jasper Ridge	60	30	15

<sup>a</sup> Flora 10% apomictic by species, all other sites the apomixis level is less than 1%.

and 22% habitual selfing (discounting the annual species inhabiting serpentine grasslands, which are considered separately below).

It has been shown for habitually inbred taxa that continued selection for inbreeding is a result of the competitive superiority of inbred populations, which are comparatively more niche-specialized than outbred systems (Baker and Stebbins, 1965). It is the very specialization of such adaptive strategies that enables inbreeders to coexist in competition with the greater genetic repertoire of outbreeders. As the environment changes through geologic time, particular species characterized by narrow niche dimensions are rapidly destroyed; but as representatives of an adaptive strategy they are rapidly replaced in a constantly changing array. Their generally shorter life cycle and *r*-reproductive strategy lead to the rapid fixation of new types in the most rapidly altered environments. With their greater genetic repertoire, outcrossing species are able to adapt to changing conditions and hence often remain as a stable *K*-reproduction element in a constantly evolving community. In contradistinction to our original hypothesis, this line of argument would indicate that there may be considerable emphasis on niche specialization in terms of breeding systems in the areas with the most disturbance (Table 4).

The Farallons and the weedy community clearly are characterized by the greatest disturbance. They correspondingly show the most pronounced degrees of self-compatibility and habitual selfing, regardless of the available pollinators. The weedy community throughout the Mediterranean climates of the world characteristically has by far the largest available vector resource—*Apis*, *Musca*, *Lasioglossum* (s. lato), *Eristalis*—of any community. Likewise, the grassland and chaparral communities, which are periodically ravaged by fire, are characterized by both the largest number of pollinating insects (species, individuals and biomass) (Table 5) and the greatest emphasis on potentially selfing successional species (Table 4).

Within the Jasper Ridge, Mather and Timberline communities the number of self-incompatible broad-niched plants is directly correlated with diversity index values. Self-compatibility as an adaptive strategy also shows a much greater correspondence between similar communities under different climatic regimes

Table 5. Available potential vector diversity and abundance

	Total Vector species	Total vector indivs.	Total vector biomass
Mather Chaparral Scrub	324	170 375	6864100
J. R. Chaparral Scrub	484	115 396	2526500
Mather Grassland	426	100 822	3477601
J. R. Grassland	388	98452	2922040
Mather Forest <sup>a</sup>	334	68640	3095022
J. R. Oak Woodland	260	30732	1694023
Point Reyes Coastal Scrub	191	31936	2531785
Subalpine Talus Scrub	337	13681	1858722
Subalpine Forest	202	10263	820249
Oak-Madrone Forest	63	6368	293847
Subalpine Marsh-Meadow	158	5101	268407
Dore Crest Arctic/Alpine	77	1182	511843
Farallon Island	17	1551	45155

<sup>a</sup> More than 95% of the vectors in the Mather Forest frequently only the open sunny glades, inhabited often by plant species normally more frequent in the grasslands or chaparral (45.4% overlap of flora; 69.0% overlap of fauna).

Table 6. Measures of genetic self-compatibility in different community types. Compatibility is especially important in grasslands by all measures, but least so in terms of biomass. In forest communities all the large or common plants are heavily outcrossed and incompatible; pollinators are very infrequent, but nearly all species are perennial. The lack of potential pollen vectors at the high altitudes is reflected by a noticeable increase of compatible plants in all community types

	% species	% individuals	% biomass
Timberline Meadow	74	97	55
Mather Grassland	87	97	90
J. R. Grassland	79	85	70
Timberline Forest	61	90	>0.01
Mather Forest	49	75	>0.01
J. R. Forest	44	48	>0.01
Timberline Scrub	65	85	49
Mather Scrub	31	81	>1
J. R. Scrub	46	60	>1

than between distinct communities at the same site (Table 6). In direct opposition to the original hypothesis, when separate communities are considered cumulatively for each site, there is a significant decrease in the genetically incompatible broad-niched species with increasing severity and unpredictability of climate. Self-incompatible species that are not additionally apomictic comprise 40% of the flora at Jasper Ridge, about 30% at Mather, 20% at Timberline and less than 5% at Dore Crest.

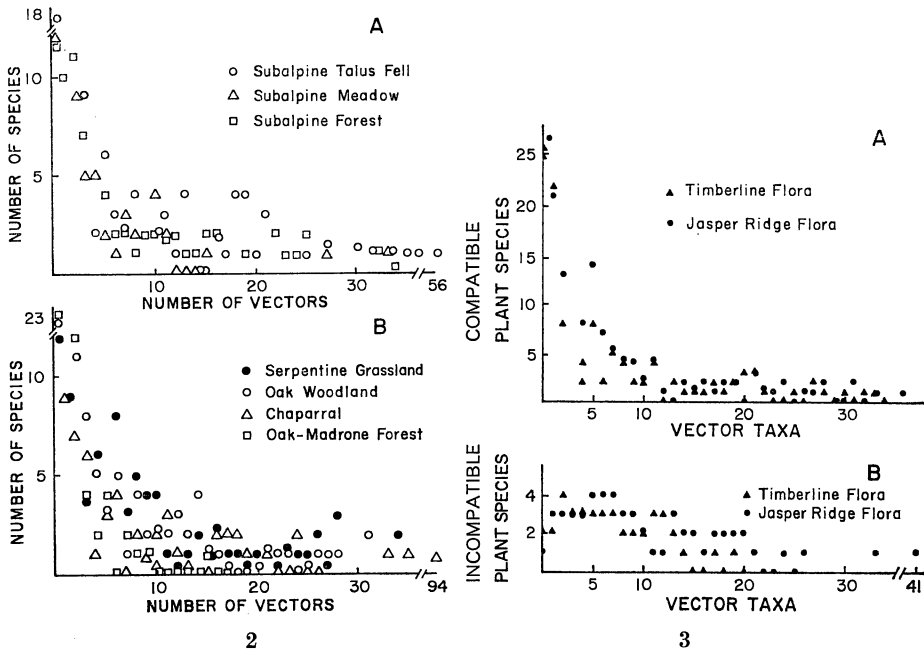


Fig. 2A and B. Spectrum of vectors utilized by plants along transect. Shape of the curve is very similar in all communities studied. The majority of plant species utilize less than three vectors each; a few are characteristically visited by many taxa. There is a dip in the curve for each community studied in the region of 6–8 vectors per plant

Fig. 3A and B. Spectra of vectors supported by incompatible (B) and compatible (A) plants. In every community studied distinct curves characterize the compatibility systems. A much larger percentage of incompatible plants supports large numbers of vectors

#### *Niche-Specialization of Plant/Pollinator Interactions*

Our hypothesis assumes that in regions of climatic stability, populations are less likely to experience crash/outbreak cycles and hence plants should be able to compete successfully through the coevolution of breeding systems dependent on only one or two species of vectors. Such a system would clearly be maladaptive under circumstances of wide fluctuations in the numbers of either the plant or the potential vector.

Such 1:1 or 1:2 systems are exceptional in all of the sites studied. In most cases, plants with such specialized pollination syndromes have lost their obligate dependence upon pollen vectors through the evolution of self-compatibility. Nearly all genetically incompatible plants that are clearly successful as competitors within a community (and do not represent occasional individuals outside the breeding range of the species) are visited by many species of flower-herbivores. The pattern in which the flowering plants divide up the pollen vector resource is very similar in all communities studied (Fig. 2), although too few vector species are present at Dore Crest, the Farallons or the weedy communities to draw valid comparisons. There are a very large number of species visited by one species or

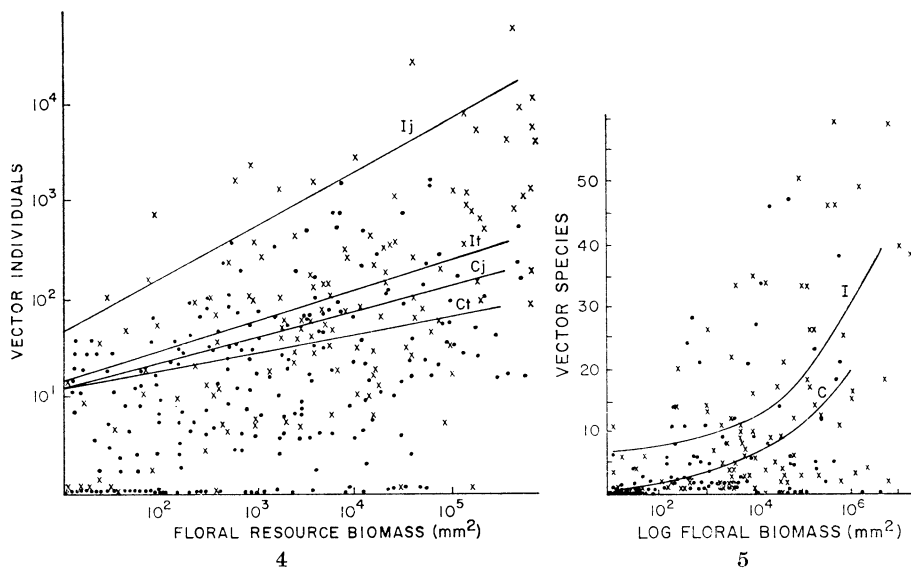


Fig. 4. Correlation of biomass of resource base with number of herbivore individuals. Flower resources with biomass less than 10 excluded from graph because points are too dense to represent graphically. Taxa from Timberline (*t*) and Jasper Ridge (*j*) included. Incompatible plants (*I*) support a larger number of herbivores than compatible species (*C*) in both communities

Fig. 5. Correlation of biomass of resource base with diversity of herbivores supported. Taxa from Timberline and Jasper Ridge plotted. Data plotted near origin only representative. In both sites incompatible plants (X) support characteristically higher levels of diversity than compatible plants (●)

no pollinators at all, and a small number of plant species visited by very large numbers of pollinator taxa in all communities.

A consistent distinction between the spectra of vectors of compatible and incompatible species is apparent in every community (Fig. 3). The number of individuals of vectors of both compatible and incompatible plants is directly correlated with local floral biomass (Fig. 4). Many more vector individuals generally are associated with incompatible plants. This distinct difference in pollinators supported is reflected also when total species supported is examined (Fig. 5). Many species (both compatible and especially incompatible ones) produce sufficient energy and larval food supplies to support far more vector species and individuals than is justifiable by any additional seed set. These species might be considered pollinator saturated. Many obligately specialized monophagous species frequently encountered on incompatible plants are in competition with each other and with generalists for an apparently finite resource. In view of the efficiency of certain well documented 1:1 systems (Faegri and van der Pijl, 1966), why have such apparently "energetically inefficient" systems been evolved and maintained in temperate California? [The work of Moldenke and Neff (MS in prep.) shows the same situation in semiarid California and Chile.] As a long-term investment, perhaps it provides the flexibility necessary to attract the requisite pollinators when the plant species is in extremely low densities.

Table 7. The correlation of diploidy and high diversity values along transect

Research site	Species diversity (H)	Diploid	Ploidy high polyploids <sup>a</sup>
Timberline	3.19	27%	42%
Dore Crest	3.26	35%	30%
Point Reyes	2.77	56%	12%
Jasper Ridge	2.62	58%	9%
Mather	2.82	68%	5%

<sup>a</sup> Defined as hexaploidy or higher levels.

#### *Plant Ploidy Levels as Indicators of Specialization*

The evolution of plants is often characterized by a close correlation between polyploidy, outcrossing and apomixis and the resultant patterns of ecological and genetic diversity evidenced (Stebbins and Babcock, 1939). Available data on the ploidy levels of the plant taxa relevant to this study was assembled from the published literature (Moldenke, 1974). Counts had been made for about 70% of the low altitude flora, diminishing to less than 50% of the high altitude species. Nevertheless, enough taxa had been counted to demonstrate very distinct differences between the communities studied (Table 7).

Diploidy is the characteristic mode at most sites and within most communities. Tetraploidy is highly characteristic of the weedy and serpentine grassland communities. Communities characterized by polyploidy (hexaploidy and higher levels) are limited to the highest altitudes of Timberline and Dore Crest. In the regions characterized by diploid breeding patterns, species with increased ploidy levels are almost without exception limited to habitually inbred and/or rare annual taxa. At the higher elevations polyploid species are some of the most common and important community elements.

The significance of these patterns will be considered in the discussion.

#### *Niche-Specialization of Floral-Herbivores*

The number of food-plants per species of herbivore is remarkably similar in most communities studied (Fig. 6). The vast majority of floral herbivores are observed to utilize only 1–4 food plants; however, each community contains species that derive nourishment from many species of plants. The two exceptions to this rule are the weedy and Dore Crest communities, in which the relative proportion of polylectic species is far greater than the proportion of oligolectic ones. This is especially notable in the weedy community in which there is only one facultatively specialist bee (*Megachile rotundata* on *Lotus corniculatus*).

In the weedy community and the arctic-alpine community, since a large proportion of the "entomophilous" floral types is never visited at all, there is ample potential for the invasion and establishment of numerous monophagous flower-herbivores. The results of this investigation, however, indicate that there must have been stringent selection against the establishment of specialist species in these environments. Generalist species are intuitively better able to survive catastrophic declines in the population of a given food plant than are specialists,



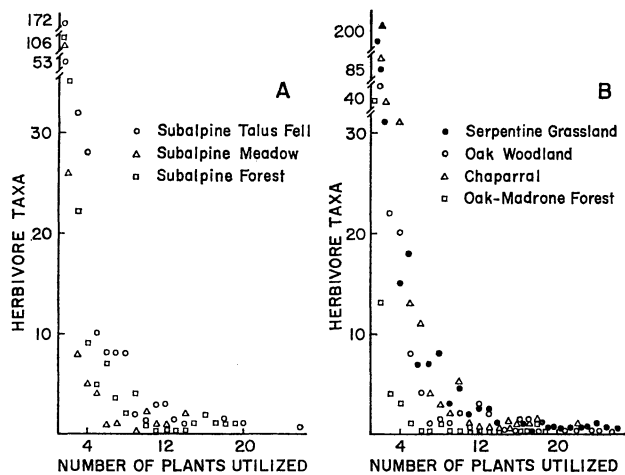


Fig. 6 A and B. Spectrum of herbivore feeding patterns. In all communities (except Weeds, Dore Crest and Farallon Island) a similar relationship exists. Nearly all herbivore species consume only a very few host taxa; few consume many taxa

Table 8. Diversity of specialized feeding bees

Research site	≠ monophagous species present	% monophagous species present <sup>a</sup>
Jasper Ridge	50	19 %
Mather	43	39 %
Timberline	25	41 %

<sup>a</sup> Species with abundance less than 5 excluded from table, since distinction between rare generalist and rare specialist difficult to establish at any particular site.

since they retain the plasticity to switch to an alternate food source when their favorite is depleted. Thus, selection on a community basis would favor generalist flower-herbivores in the least predictable and most stringent communities.

Polylectic bee pollinators are of vastly different importance at the various sites. More than 98% of the Point Reyes pollinator biomass and approximately 80% of the biomass of vectors at Timberline are encompassed in seven and three species of polylectic bumblebees, respectively. At Jasper Ridge, on the other hand, polylectic species comprise a nearly negligible fraction of the total bee biomass. The highest number of specialist taxa occurs at Jasper Ridge, diminishing as the altitude increases and reaching the lowest levels in the severe climates of Point Reyes and Dore Crest (Table 8). Though total specialist species count and biomass of generalists follow the pattern predicted, it should be noted that the percentage of specialist with respect to total bees is inversely correlated with increasing altitude (see "Discussion").

*Patterns of Food Web Interactions as Measures of Community Specialization*

Hendrickson and Ehrlich (1971) originally introduced a critical conceptual advance into the study of species diversity. By modifying the Simpson diversity index of statistical predictability content into matrix form, it is possible to incorporate into the index the degree of similarity between different resident species. By utilizing both the Simpson and Hendrickson indices, it is possible to isolate the component of total diversity which is function of the "degree of similarity" of the organisms present.

$$\text{Simpson rewritten: } 1 - M = \frac{\sum_{i=1}^s (n_i) \sum_{j=1+i}^s (n_j)}{N^2 - N}.$$

$$\text{Hendrickson and Ehrlich: } 1 - M' = \frac{\sum_{i=1}^s (n_i) \sum_{j=1+i}^s (d_{ij})(n_j)}{N^2 - N}$$

where:  $(d_{ij})$  is defined as a scaled estimator of the difference between any two species ( $i$ ) and ( $j$ ) in a square matrix.

The similarity variable  $(d_{ij})$  can be defined in any sense the investigator wishes.

One example of a triangular matrix where  $(d_{ij}) = (d_{ji})$  is a numerical taxonomy in which the "taxonomic" contributant to the diversity of a community could be assayed. At higher altitudes many fewer major groups are represented, and those that are present contain a very large number of sympatric species. The total number of plant families represented with more than two species at Jasper Ridge is 46, whereas the number at Timberline is 24. The percentage of monotypic genera of plants at Timberline is 63%, while at Jasper Ridge it climbs to a value of 85%; the corresponding statistics for bees are 26% and 40%.

Values of this diversity index were calculated with respect to both the degree of niche overlap of the food sources of the flower-herbivores and the niche-specialization of the flowering plants with respect to the vectors they utilize to accomplish pollination.

If  $(d_{ij})$  is defined as:

$$(d_{ij}) = \frac{\text{number of food sources utilized by } i \text{ not also by } j}{\text{total number of food sources of } i}$$

a value of  $M'$  (total diversity) can be calculated with a square matrix on the basis of the distinctness of herbivore diversity relative to the feeding habits of herbivores as they competitively interact within the framework of a certain community (Table 9). The richer diversity of species under more moderate climates is attained by a great deal more distinctness in ecological function of the individual taxa than in high altitude communities. In other words, although a community type may contain more species of herbivores at lower altitudes, these additional species are "added" by additional niche specialization and not by increasing niche overlap. The correlation of herbivore niche-specialization with climatic stability is apparent within each separate community as well. The niche size of pollen-vectoring systems is most noticeably broadened only in the most severe environments and disturbed communities.

Table 9. Niche overlap as measured by Hendrickson and Ehrlich index. Under each heading the left-hand figure represents the Hendrickson value; the right-hand figure in parentheses is the difference between the Hendrickson and Simpson values attributable to the similarity of competing taxa. The greater the difference, the greater the overlap in resource utilization patterns of herbivores and the more generalized are the vectors utilized by plants. High values of the Hendrickson index as well as large difference values indicate high degrees of overlap in the climatically severe and unpredictable communities.  $[(d_{ij})$  as defined in text for herbivores;  $(d_{ij})$  for plants represents the number of vectors utilized by plant ( $i$ ) not utilized by plant ( $j$ ) divided by the total number of vectors utilized by plant ( $i$ )]

	Animal abundance	Animal biomass	Plant abundance	Plant biomass
Farallones	0.87 (0.13)	0.58 (0.57)	0.86 (0.28)	0.98 (0.85)
Weeds	0.66 (0.50)	0.79 (0.36)	0.69 (0.31)	0.69 (0.57)
Point Reyes	0.65 (0.28)	0.48 (0.33)	0.33 (0.20)	0.41 (0.25)
Dore Crest	0.62 (0.55)	0.61 (0.33)	0.19 (0.14)	0.27 (0.12)
Timberline	0.42 (0.34)	0.45 (0.29)	0.20 (0.10)	0.24 (0.10)
Mather	0.35 (0.30)	0.29 (0.25)	0.20 (0.06)	0.49 (0.14)
Jasper Ridge	0.39 (0.29)	0.24 (0.10)	0.29 (0.13)	0.47 (0.33)

Discussion

*The Relation between Total Species Number and Breeding Systems*

It is well known that inbreeding groups and consistent sib-maters demonstrate a pattern of geographic distribution consistent with the assumption of rapid divergent evolution. Inbred species, though often very abundant locally, tend to be narrowly defined both geographically and ecologically. The patterns of local variation that they manifest are a delight to taxonomists, and they are consistently recognized as large numbers of distinct taxa. On the other hand, outcrossing species as a rule are widespread geographically and composed of populations within which a great deal of variability is maintained, enabling the species to live under a variety of circumstances. Since within-population variability is often so large in comparison to between-population variability, taxonomists lump a large spectrum of variability within the component species of outcrossers. Estimations of total species number do not distinguish between these taxonomic artefacts and can be extremely misleading as to the amount of “diversity” (which is ultimately equivalent to genetic diversity or component niche size) that a region can support.

This distinction is particularly important in studies of pollination coevolution because those regions of the world most notable for their large number of bee species (California, Chile, South Africa, Australia, Morocco) and complex patterns of pollination interactions are characterized by the largest percentage of small, aggregate nesting, inefficiently flying, distributionally restricted bees (Linsley, 1958). These species are presumably highly inbred and concomitantly genetically specialized as well; species counts in these regions may actually bias the conclusions in the direction of greater diversity than is warranted.

In each of these areas of Mediterranean climate, the flora is correspondingly enriched by the addition of generally inbred annual species. California is noted

for the total number of native plant species; this exceptional diversity is correlated with the exceptional diversity of geological relief in the state, but selection has most notably affected the pattern of divergent speciation in the annual element of the flora. About 50% of the California flora are annuals, approximately three times the world average (P.H. Raven, pers. comm.).

### *Ploidy Levels as Indicators of Niche-Specialization*

Investigations over the past 20 years by many workers (review, Stebbins, 1971) have shown that polyploids most often originate as a result of the crossing of gametes derived from very different genetic stocks of the same species or from interspecific or intergeneric hybridization. When duplication of the chromosomes occurs under these conditions, it facilitates the segregation of balanced chromosomal complements and consequently increases fertility in the next generation. About half of the world's flowering plants are of polyploid derivation (Grant, 1963). If the polyploid is capable of assuming an ecological role different from that of its parents, it may be especially favored under conditions in which new habitats are developing. Hence, tetraploidy has been demonstrated to have selective value at the dynamic boundaries between different communities (Baker and Stebbins, 1965), in the evolution of weedy taxa from the native flora (Zohary, 1965), and during the advance and retreat of glaciers (Stebbins, 1971). The basis of this selective value lies in the merging of two differing fundamental niches into one larger more generalized niche. Regions characterized by a higher proportion of tetraploids may be assumed to be regions in which there has been strong initial selection for the generalized-niche strategy.

Though polyploidy may have the effect of niche-broadening at its inception, it ceases to do so once it has become established or progressively elaborated. Mutations which increase a plant's adaptability spread rapidly throughout populations of outcrossing diploids; such widespread taxa remain morphologically rather similar throughout their range, even though each population may be fine-tuned to a particular environment. On the other hand, polyploidy, because of the conservative and buffering effect it has on the spread of mutant alleles, is a mechanism by which occasional fortuitous mixings of diverse genetic stocks can be replicated through repeated generations without change due to meiotic segregation. Such highly specialized taxa, however, are characterized by narrow ecological tolerances. Polyploidy, once achieved, facilitates continued fertile miscegenation with the parent taxa. When such further backcrossing produces adaptive offspring, new polyploid races originate, which are suited to slightly different environments. An array of highly specialized autogamous polyploid races can contain as much "diversity" within its "collective gene pool" as a similarly distributed single outcrossing diploid species (Stebbins and Babcock, 1939).

It is not surprising then to find that the constituents of the floras associated with disturbance are polyploid. The polyploidization enabled them to move into new environments, and once established, the buffering aspects of polyploidy permitted efficient niche-specialization, which was competitively advantageous in the utilization of highly unpredictable resources. Emphasis on tetraploidy in the weedy community is predicted on the basis that this era is mankind's first

global disturbance, whereas floras subject to the effects of intermittent glaciation have had to survive several catastrophic climatic fluxes. More than 70% of the high altitude flora at our study sites is polyploid with the majority highly polyploid; 45% of the weedy flora is polyploid with the majority only tetraploid. The percentage of diploids in the flora is directly correlated to the value of the diversity indices (Table 7). Areas characterized by high diversity indices are generally further characterized by generalized niche features of increased outcrossing and genetic self-incompatibility, and the lowest proportion of obligate selfers and polyploids.

The serpentine grassland community differs significantly from neighboring sea level communities in extraordinarily high levels of genetic self-compatibility (80%) and polyploidy (55% tetraploid). Kruckeberg (1954) has shown that species characteristic of serpentine substrates grow much better on substrates with a normal  $\text{Ca}^{++}/\text{Mg}^{++}$  content. They are limited to the serpentine areas, however, by competition with species unable to grow in this severe edaphic environment. The clearest explanation of the occurrence of serpentine endemics postulates the occasional miscegenation of species on normal soils with the fortuitous result of serpentine tolerance, followed by population expansion and niche-specialization in the poisonous environs.

Areas characterized by polyploidy are therefore regions of niche-specialization in the long-run. That they are correlated to regions of high habitual inbreeding and disturbed, poisonous or extreme climatic environmental conditions is contrary to the hypothesis that niche specialization is a viable strategy only in areas of stability.

#### *Semantics*

The usual and convenient separation of herbivores into "specialist" and "generalist" has proved to be misleading in the preliminary analysis. Listings of specialist bee species encountered in these studies indeed show that the largest number inhabited Jasper Ridge (Table 8). Since Jasper Ridge is at a lower altitude and possesses a less rigorous climate than Mather or Timberline, selection would be expected to have brought about the narrower partitioning of niches through interspecific competition for limited resources. When the proportion of these specialist species in the total bee fauna is calculated, however, very different implications arise. At Jasper Ridge 20% of the total bee fauna are specialists, but at Timberline 40% of the species qualify. This finding is contrary not only to the competition/stability hypothesis, but to most others that might be advanced. A possible explanation for its occurrence requires a redefinition of "specialist". One would expect that a polyphagous insect species would visit the available plant species in direct proportion to its abundance; that is, rare insects would visit few plant species, commoner species would visit more, and the most abundant insects would visit nearly all the entomophilous plant species present. However, the data indicate that a very large percentage of insect flower-herbivores visit two to five different plant species (*i.e.* are oligophagic) in every community regardless of climatic stability or the total number of herbivore species (Fig. 6).

If this behavior is taken as typical or representative, significant deviations from this norm can be set aside as "superspecialists" (absolute monophags) and

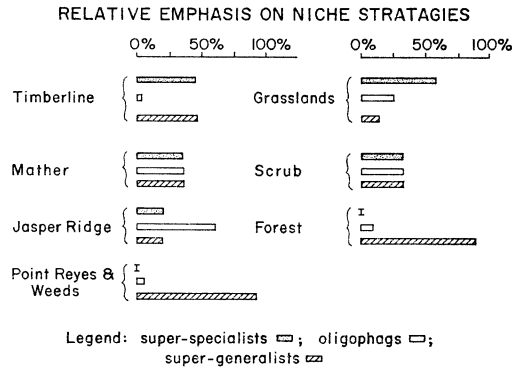


Fig. 7. Relative emphasis on herbivore utilization strategies. All communities at a site were averaged for site values; all sites were averaged for community values. Each statistic represents averaged total species, individuals and biomass supported; since these quantities are not strictly additive statistics are rounded to nearest 5%

“supergeneralists” (extreme polyphags). If all aspects (*e.g.* numerical abundance, biomass, and total species count) of bee occurrence are summed and averaged, a very distinct pattern of resource utilization emerges for the different research sites (Fig. 7). At Mather monophags, oligophags and polyphags are equally represented. At Jasper Ridge oligophags are emphasized at the expense of either extreme category; the reverse pertains under the Timberline climatic regime.

Thus, the supergeneralists in the high-altitude environment may be successful on a long-term basis because their broad feeding habits may enable them to survive periodic climatic catastrophies better than more narrowly restricted insects. The occurrence of a high proportion of monophagic bees in high-elevation communities may be interpreted as an alternative strategy of highly efficient herbivore species that successfully exploit incompletely utilized resources. In this sense it is the very specialization of the monophags that permits them to compete successfully against the extreme generalists. Oligophags have neither the efficiency of the true specialists in dealing with any one food source nor the flexibility of the true generalists in utilizing any available resource. Hence, they are unable to compete effectively against either the monophags or the super-generalists.

#### *Niche-Specialization of Flower-Herbivores*

Herbivore specialization is much more in evidence at the more clement lower altitudes. This tendency toward specialization is evidenced by a larger total number of specialist species, a nearly insignificant percentage of supergeneralists, high species diversity indices and a much smaller redundancy value in the Hendrickson/Simpson index comparison. Monophagic specialists comprised 46% of the individuals collected at Jasper Ridge, but only 20% of the individuals at Timberline, 6% at Point Reyes and 2% at Dore Crest. Essentially no specialists live on the environmentally rigorous Fallon Islands and the continually disturbed weedy campus.



Table 10. Importance and behaviour of bumblebees. Bumblebees increase in abundance correlated with increasing severity of environment. In the more extreme environments their flower visiting habits become significantly more generalized. All figures rounded to nearest 5%; significant bias in studying such extremely abundant taxa requires a  $\pm 5\%$  confidence about these statistics

Research site	% of bee fauna present	Increasing severity of environment	% of insect-pollinated flowers visited
Jasper Ridge	5%	↓	15%
Mather	75%		15%
Timberline	50%		90%
Point Reyes	80%		95%

Specialization of flower-herbivores with increasing stability and concomitant increasing number of flowering plant species may be seen within an important subset of these herbivores (Table 10). Bumblebees (*Bombus* spp.) comprise a conspicuous element of the bee biomass at every site except the Farallon Islands, where they do not occur. Since any individual flowering species is limited in both its floral food content and the time of the year it is available, all bumblebees are forced into the strategy of polyphagy in order to support large colonies and year-round activity. However, the degree of polyphagy of bumblebees varies quantitatively at the different sites. This difference is not correlated to the total number of bumblebees in the region; hence, it must be the result of selection on the quantitative nature of their feeding habits (Table 10). The environmental conditions of the Coastal Sage community at Point Reyes are especially severe for poikilothermous insects, and hence, bumblebees clearly demonstrate the tendency for niche-narrowing under favorable climatic regimes. The Hendrickson indices show that on a community basis not only are flower-herbivores more specialized but that less overlap occurs as well (Table 9).

*Energetic Inefficiency and the Significance of Pollen Vectors*

The degree of cross-pollination and the relative efficiency of seed-set per flower produced are crucial parameters within each population of every species. Theoretically, the amount of pollination that occurs by obligate specialists is directly dependent on the amount of food provided by the flowering plant. However, if an excess of energy is produced at each flower, the potential vector may derive all its nourishment from a few flowers and very little cross-pollination will occur (Heinrich and Raven, 1972). All plants, therefore, must strike an effective balance between providing enough nourishment to feed potential vectors and insuring that each vector must visit many flowers.

Once specialized pollination systems have been established, it is to the advantage of the plant to limit the numbers of nonspecific vectors which consume nectar and are not responsible for much of the pollination. However, this evidently does not usually occur except in cases involving hummingbird pollination, and plants that are visited by an apparently very efficient vector usually support several different monophagic vectors and many polyphagous ones as well (*e.g.*

*Lasthenia*, *Ceanothus*, *Ranunculus*). The number of individual insects supported in this manner is very large, and consequently the nectar produced by each plant requires a very large energetic expenditure. So much nectar and pollen is produced in some cases that the major flower-herbivores visit plants only within a very limited area and hence account for gene flow only between individuals in close proximity.

The efficient pollination of individuals within a population is clearly necessary for the maintenance of that species in that locality. However, from a long-term view, the most important feature is the spread of beneficial genotypes to other populations. Plants may accomplish this by either efficient seed or efficient pollen dispersal. More than 95% of the insect flower-herbivores occurring along this transect can be observed to conduct all of their pollinating activity within a single plant population. As Heinrich and Raven point out, the maintenance of long-distance vectors having a high metabolic rate requires large predictable supplies of nectar. Successful plants that expend much more energy than their competitors to support a large spectrum of vectors, while being pollinated only to an equivalent degree, presumably are compensated for their energetic output by the advantages of long-distance interpopulation outcrossing. In the long view, infrequent visitation by hummingbirds, large anthophorid bees, butterflies, sphynxids, bumblebees and large bombyliid flies probably has evolutionary significance qualitatively different from that of the more commonly observed vector species. Although the common, short-range insect vectors may maintain large plant populations, the infrequent interpopulation vectors may play an equally important role in maintenance and expansion of the species as a whole.

#### *Niche Specialization and the Nature of Communities*

Large numbers of plant associations are definable as highly correlated statistical units; the correlation can never be complete since the boundary between such communities is never clear-cut and many plant species exist in varying degrees of success in several plant communities. The selective forces envisioned as responsible for between-habitat  $\beta$ -diversity (MacArthur, 1965; Whittaker, 1960) involve the assumption that it is generally beneficial for any species to be in direct competition with as few other species as possible. The greater the predictability of one's biotic environment (*e.g.* where other cohabiting species are competitors for a limited resource), the more efficiently the species as a whole is able to compete. The spectra of compatibility, diversity index, ploidy, life-form, pollination specialization and other parameters are notably characteristic of a community type and frequently show much greater correspondence between similar communities in different areas than obvious correlation to divergent community types in the same region.

Animal species also tend to become associated in units roughly coincident with the plant communities. Animals, however, being capable of individual movement, are not so constrained by physical community limits as are plants. Indeed,  $\beta$ -diversity of insect flower-herbivores is much less than that of plants at any site. The pattern of interactions exhibited by one species in two different environments may or may not be similar. Specialist flower-herbivores at Timber-

line visit related plants in neighboring communities, whereas the specialist flower-herbivores at Jasper Ridge visit unrelated plants in neighboring community types. Hence, an insect species described as monophagous in a Jasper Ridge community often qualifies as oligophagous when all its behavior at the site is taken into account. Therefore, within any one community at Jasper Ridge specialist life-styles are even more important than comparisons at a site scale indicate. It is difficult to evaluate the import of these basic differences in  $\beta$ -diversity since it wasn't practical to determine the home ranges of individuals.

### Conclusions

The varied aspects of diversity have very often been confused in the past. To examine the common assumption that increased climatic stability and predictability facilitate niche specialization and the possible consequence of a greater number of cohabiting species, a multifaceted approach is essential. The results of a conceptually very similar study (Colwell, 1969) indicated that this assumption might be true for the temperate and tropical rotting-fruit eaters.

The most striking results of the present studies demonstrate the necessity for analyzing this question on a community scale. Two community types differing both in structure and location should not be directly compared. Similar communities or associations may be compared profitably from many different perspectives often with seeming discrepancies in trends towards niche specialization.

Significance certainly must be attached to the emphasis on generalized niche parameters if this transect is indeed representative of altitudinal and climatic variation in the Temperate Zone. [Additional transects reported in Moldenke and Neff (in prep.) substantiate these observations.] In terms of biomass contribution to the community, plant species are overwhelmingly characterized by outcrossing, genetic self-incompatibility, diploidy, perennial habit and noticeable lack of exclusive pollen vector systems. Flower-herbivores are likewise noticeable for the emphasis on between-community or intracommunity oligophagy. Similar investigation in the tropics (Heithaus, 1974), the arctic (Mosquin, unpub.; Kevan, 1970), the deserts (Moldenke and Neff, in prep.) and the Mediterranean region of Chile (Moldenke and Neff, in prep.) will aid in a generalized answer to this question on a world scale.

Within this study transect assumed to be representative of variations within the temperate zone, divergent emphases on niche specialization occur. In the majority of cases plant niche size appears to become narrowed in response to disturbance and severe environmental conditions. Under disturbed conditions this life-style appears to complement what is often the major outcrossing, diploid community component, surviving competition from the more generalized and successful species only in these marginal or disturbed conditions. Under very severe environmental conditions specialization is the rule as evidenced by a totally annual, self-compatible, habitually inbred flora of the offshore island and a highly self-compatible and apomictic alpine flora characterized further by extensive vegetative reproduction and many environmentally delimited, highly polyploid, coenospecific complexes.

Flower-herbivores display two types of niche-specialization phenomena. In the high alpine environment, the oligophagic component of the community is reduced and the proportion of total monophagic specialists is the highest observed in any community. This emphasis on monophagy is similar to the abundance of specialized annuals in the disturbed flora. However, in terms of quantitative community dynamics, generalized feeding behavior is heavily emphasized in both severe and disturbed environments. Supporting this hypothesis of increased niche-specialization under less severe environmental fluctuations are: a heavy emphasis on the number of individuals of monophagic herbivores; the less significant degree of niche-overlap (Hendrickson and Ehrlich index); and the more pronounced between-habitat element in diversity at the lower altitudes.

*Acknowledgments.* I wish to express my sincerest thanks to Val Chase, Larry Gilbert, Al Johnson, Hal Mooney, Jack Neff, Dave Parsons, Margaret Sharp Parks, Mike Singer, Robbin Thorp, Ward Watt and especially Peter Raven for their continued interest, ideas and assistance in the research reported herein. I am also indebted to the staff of the Inyo National Forest at Lee Vining, the Stanislaus National Forest at Groveland, William Heisey and Malcolm Nobbs of the Carnegie Institution at Stanford, F. Sibley of the Point Reyes Bird Observatory, the United States Coast Guard and Malcolm Coulter for their assistance on the Farallon Islands. A very large number of scientists assisted in the determination of the more than 333,000 insects involved in this study; especially Paul Arnaud, Ned Bohart, Richard Bohart, Howell Daley, Norm Downie, George Eickwort, Al Grigarick, Jack Hall, Hugh Hockett, Paul Hurd, Wally LaBerge, Rich Rust, Ev Schlinger, Jerry Rozen, Roy Snelling, Bill Stephen, Robbin Thorp, P.H. Timberlake and J. Richard Vockeroth who donated many hours of expert assistance. I appreciate the suggestions of Peter Raven, Kathleen Feerick, Daniel Janzen and Monte Lloyd in reviewing versions of this manuscript. I am most grateful though to Alison Feerick Moldenke for her assistance in the field, her valuable ideas on the progression of the research and her invaluable assistance in the preparation of the final manuscript.

This paper is derived from a thesis submitted to Stanford University in partial fulfillment of the requirements for the doctoral degree. The research was supported in large part by a NIH Training Grant in Population Biology to Stanford University.

### References

- Baker, H.G., Stebbins, G.L.: The genetics of colonizing species. Symposium on general biology, vol. I, 588 pp., Int. Union Biol. Sci. New York Academic Press 1965
- Chabot, B.F., Billings, W.D.: Origin and ecology of the Sierran alpine vegetation. *Ecol. Monogr.* **42**, 164–199 (1972)
- Clausen, J.: The Harvey Monroe Hall Natural Area. Carnegie Inst. Washington Publ. No. 459, 48 pp. (1969)
- Colwell, R.K.: Ecological specialization and species diversity of tropical and temperate arthropods. University of Michigan, Ph. D. Thesis (1970)
- Coulter, M.: Flora of the Farallon Islands, California. *Madrono* **21**, 131–137 (1971)
- Faegri, K., van der Pijl, L.: Principles of pollination ecology, 248 pp. Toronto: Pergamon Press 1966
- Felton, E.L.: California's many climates, 169 pp. Palo Alto: Pacific Books 1965
- Ferris, R.S.: Flowers of Point Reyes National Seashore, 119 pp. Berkeley: University of California Press 1970
- Grant, V.: Origin of adaptations, 606 pp. New York: Columbia University Press 1963
- Hartley, P.H.T.: An ecological study of the feeding habits of English titmice. *J. anim. Ecol.* **22**, 261–288 (1953)
- Heinrich, B., Raven, P.H.: Energetics and pollination ecology. *Science* **176**, 597 (1972)

- Heithaus, E. R.: Species diversity and resource partitioning in four neotropical plant-pollinator communities. Ph. D. Thesis, 148 pp., University of Michigan, Microfilm Services of Stanford University (1973)
- Heithaus, E. R.: The role of plant pollinator interactions in determining community structure. *Ann. Mo. Bot. Gdn.* **61**, 675–691 (1974)
- Hendrickson, J., Ehrlich, P. R.: An expanded concept of “species diversity”. *Notulae Naturae* **439**, 1–6 (1971)
- Kevan, P. G.: High arctic insect-flower relations: The inter-relationships of arthropods and flowers at Lake Hazen, Ellesmere Island, N.W.T., Canada. Ph. D. Thesis, 399 pp., University of Alberta (1970)
- Kruckeberg, A. R.: The biology of serpentine soils. *Ecology* **35**, 267–274 (1954)
- Linsley, E. G.: The ecology of solitary bees. *Hilgardia* **27**, 543–599 (1958)
- Lloyd, M., Gelardi, R. J.: A table for calculating the equitability component of species diversity. *J. Anim. Ecol.* **33**, 217–226 (1964)
- MacArthur, R. H.: Patterns of species diversity. *Biol. Rev.* **40**, 510–533 (1965)
- Margalef, R.: La teoria de la informacion en ecologia. *Memorias de la real Academia de Ciencias y Artes*, vol. 33, p. 373–449 (1957)
- Milliman, J. D., Ernerly, K. O.: Sea levels during the past 35 000 years. *Science* **162**, 1121–1123 (1968)
- Moldenke, A. R.: Studies on the species diversity of California plant communities. Ph. D. Thesis, University of Michigan, Microfilm Services of Stanford University (1971)
- Moldenke, A. R.: A contribution towards a chromosome atlas of the California flora. *Int. Biol. Prog. Origin and Structure of Ecosystems. Tech. Rept. No. 74–10*, 74–22, 74–23 (1974)
- Moldenke, A. R., Neff, J. L.: Studies on the species diversity of California plant communities. Part II. *Int. Biol. Prog. Origin and Structure of Ecosystems. Tech. Rep. No. 74–13*, 233 pp. (1974)
- Moldenke, A. R., Neff, J. L.: Studies on the species diversity of California plant communities. Part III. *Int. Biol. Prog. Origin and Structure of Ecosystems. Tech. Rep. No. 74–14*, 179 pp. (1974)
- Moldenke, A. R., Neff, J. L.: Pollination ecology as a tool for studying ecosystemic organization: Convergent evolution in Chile and California. In preparation
- Porter, D.: The vascular plants of the Jasper Ridge Biological Experimental Area of Stanford University, Mimeographed, 28 pp. (1962)
- Simpson, E. H.: Measurement of diversity. *Nature (Lond.)* **161**, 688 (1949)
- Stebbins, G. L.: Chromosomal evolution in higher plants, 216 pp. Menlo Park: Addison-Wesley Publ. 1971
- Stebbins, E. H., Babcock, E. B.: The effect of polyploidy and apomixis on the evolution of species in *Crepis*. *J. Hered.* **30**, 519–530 (1939)
- Thomas, J. H.: Flora of the Santa Cruz Mountains of California, 434 pp. Stanford: Stanford University Press 1961
- Whittaker, R. H.: Vegetation of the Siskyou Mountains of Oregon and California. *Ecol. Monogr.* **30**, 279–338 (1960)
- Zohary, D.: Colonizer species in the wheat group, p. 403–423. In: H. G. Baker, G. L. Stebbins (1965), op. cit.

Dr. Andrew R. Moldenke  
Board of Studies in Biology  
University of California  
Santa Cruz, California 95060, USA