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THE FLORA OF GREAT BASIN MOUNTAIN RANGES: DIVERSITY, SOURCES, AND DISPERSAL ECOLOGY

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Abstract.—The high elevation floras of 9 mountainous "mainlands" (3 in the Sierra-Cascade system and 6 in the High Plateau-Wasatch-Teton system) and 15 isolated mountain "islands" in the Intermountain Region have been analyzed. Mainland floras support more species per unit area and show a smaller increase in diversity as area is increased than islands. In this respect, the isolated mountains behave as true islands. The number of en demics is low on the islands (never exceeding 5 percent of any flora), however; and the island floras are over whelmingly dominated by species with no apparent modifications for long-range dispersal. Furthermore, the east ern mainland has exerted a far greater influence on the flora and the vegetation of the islands than has the western mainland, despite the fact that the former is downwind of the islands. Thus, evidence from endemics, dispersal ecology, and sources of the floras suggests that the isolated mountains have not acquired their full floras by long-range dispersal. We conclude that although the floras of the islands have many insular characteristics, they were less isolated in the relatively recent past than at the present. The island floras do not appear to be in equilibrium in the sense that immigrations equal extinctions.

The biogeography of disjunct segments of similar habitat has intrigued biologists since the days of Charles Darwin (1859) and A. R. Wallace (1880). Their pioneering obser vations were based primarily on oceanic is lands, but others have analyzed the biology of such habitats as caves (Culver, Holsinger, and Baroody 1973), woodlots (Curtis 1956), fresh water lakes (Barbour and Brown 1974), and isolated patches of herb land in high-elevation forests (Vuilleumier 1970).

The appeal of islandlike environments to biologists is partially explained by the fact that complete inventories of selected taxa can be prepared for several disjunct points in a reasonably short time. Furthermore, is land systems are ideally suited for the anal ysis of such dynamic processes as dispersal, competition, and evolution. Basic principles of community structure and trophic dynam ics also appear to have been better demon strated and more easily studied in island systems than in larger, more heterogeneous environments (Lindeman 1942, Simberloff and Wilson 1970, Brown 1971a, Heatwole and Levins 1972, and MacArthur, Diamond, and Karr 1972).

In this paper we consider the vascular plant floras of islandlike enclaves of mesic environment on high mountains in the deserts of the Great Basin. In the strictest sense, these high mountains are less isolated than oceanic islands, since dispersing prop agules or their carriers may rest in the desert and survive to move on again. Also, species of the mountain islands could evolve (and apparently often have) from the floras of the unfavorable environments that sepa rate the islands (Billings 1977). Furthermore, evidence suggests that at varying times in the Pleistocene many of the islands were connected by vegetation similar to that now confined to the slopes of the mountains (Wells and Jorgensen 1964 and Wells and Berger 1967). Nevertheless, the tops of the high mountains of the arid West provide disjunct patches of habitat that may have much in common with real islands.

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METHODS

This paper is based entirely on published floras or checklists of workers who have collected extensively on specific mountain ranges. We utilize 9 floras from the more-or-less continuous mountain systems that flank the Great Basin on the west and east and floras or checklists for 15 mountain ranges in or near the Great Basin (Fig. 1, Table 1). We have assumed that the floras of the relatively continuous flanking mountain systems (the Cascade-Sierra system in California and the Teton-Wasatch-High Plateau system in Wyoming, Idaho, and Utah) have long had relatively free access to large floras adapted for life at high elevations and thus qualify as mainland floras in the parlance of island biogeographers.

The mountain islands have been assigned discrete boundaries which are defined by the 7500 foot contour line. The size and elevation of these islands and their distance from the mainlands were taken from topographic maps. Island-to-mainland distances were computed by summing the distances
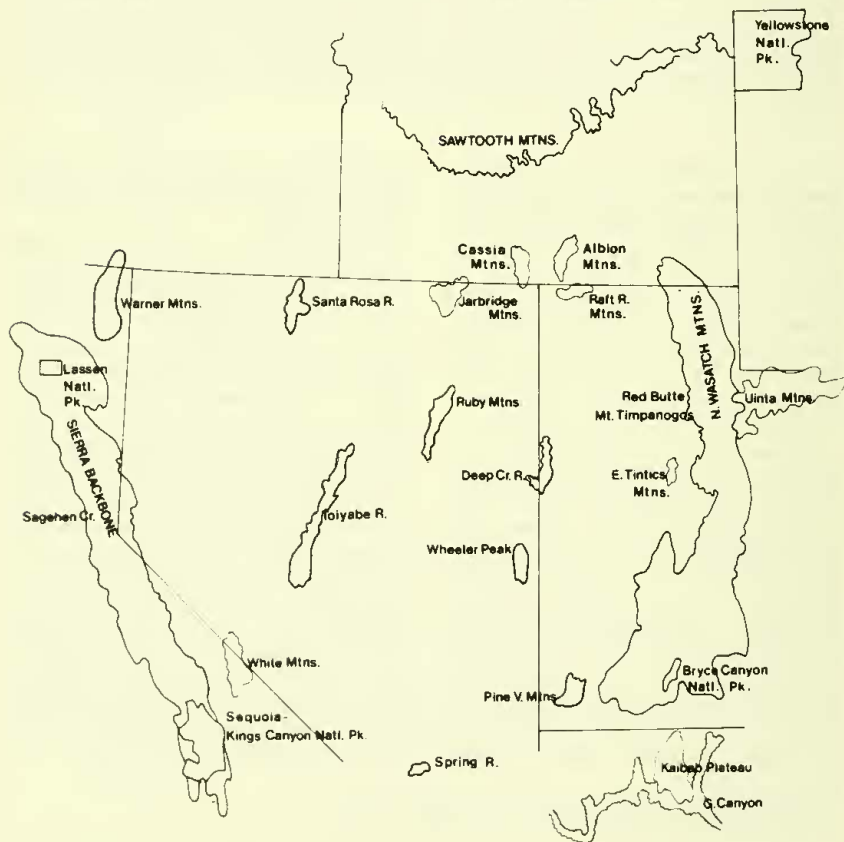

Fig. 1. Location of the floras considered.

TABLE 1. Species diversity and physical characteristics of the study areas.

Mountain Islands	No. of Vascular Plant Species	Area above 7500 Feet (sq. miles)	Maximum Elevation (ft.)	Width of Barrier Island-Mainland (Miles)		Source of Floristic Information	
				Western	Eastern		
1. Albion Mountains	220	43	10,335	153	74	Buchanan	1976
2. Cassia Mountains	107	10	8,060	145	78	Buchanan	1976
3. Deep Creek Mountains	349	131	12,101	148	106	McMillan	1948
4. East Tintic Mountains	127	5	8,218	248	14	Nebeker	1975
5. Jarbidge Mountains	422	205	10,789	126	116	Lewis	1975
6. Kaibab Plateau	400	522	9,045	285	44	MacDougall	1947
7. Pine Valley Mountains	231	79	10,325	245	9	Atwood and Higgins	1976
8. Raft River Mountains	315	64	9,892	151	57	Preece	1950
9. Ruby Mountains	471	364	11,387	92	132	Lewis	1971
10. Santa Rosa Mountains	176	48	9,779	191	200	Lewis	1976
11. Spring Range	284	125	11,918	140	114	Clokey	1951
12. Toiyabe Mountains	351	448	11,788	59	195	Linsdale et al.	1952
13. Warner Mountains	236	116	9,892	69	300	Milligan	1969
14. Wheeler Peak	305	175	13,063	142	86	Lewis	1973
15. White Mountains	486	381	14,246	8	228	Lloyd and Mitchell	1973
Mainland Areas							
16. Bryce Canyon Natl. Park	218	40	9,105	—	—	Buchanan and Nebeker	1971
17. Lassen Volcanic Natl. Park	441	27	10,497	—	—	Gillett et al.	1961
18. Mount Timpanogos	490	28	11,750	—	—	Allred	1975
19. Northern Wasatch Mountains	609	1,050	9,980	—	—	Holmgren	1972
20. Red Butte Canyon	350	1	8,235	—	—	Arnow	1971
21. Sagehen Creek Drainage	366	4	8,844	—	—	Savage	1973
22. Sequoia-Kings Canyon Natl. Park	1,082	1,014	14,495	—	—	Rockwell and Stocking	1969
23. Uinta Mountains	579	3,630	13,498	—	—	Graham	1937
24. Yellowstone Natl. Park	791	3,000	11,358	—	—	Despain	1975

across inter-island barriers of desert (areas below 7500 feet) along the shortest route possible from a particular island to the nearest edge of each mainland.

It should be noted that our island areas and distances to mainlands do not always agree with those reported by Brown (1971a), Johnson (1975), and Behle (1977), who have used some of the same islands that we have. Those discrepancies arise from the manner in which the mainland and island borders are defined by the several authors. Brown (1971a), for example, combined the White and Inyo ranges, but the flora used in our work (Lloyd and Mitchell 1973) covers only the White Mountains. Johnson (1975) let the lower edge of forest or woodland serve as the edge of his islands, while we have followed Brown (1971a) and used the 7500 foot contour as the island edge. In Johnson's (1975) work, the Pine Valley Mountains were considered to be part of the mainland, but our criteria dictate that those mountains be considered an island.

As noted elsewhere in this symposium (West et al. 1977), distance to the nearest mainland is a weak ecological variable in the Great Basin, since each mountain range has probably received migrant species from both mainlands. We measured the width of valley barrier between each mountain system and both mainlands in an effort to obtain a better understanding of the biogeographic consequences of distance.

Johnson (1975) and Harner and Harper (1976) demonstrated that habitat diversity exerts a strong influence on diversity of birds and vascular plants, respectively. Johnson (1975) used plant criteria to quantify habitat diversity for birds on Great Basin mountains, but his criteria for habitat diversity would lead to circular logic if they were used to help explain plant diversity. Conceivably, one could devise a habitat diversity measure based on physical characteristics of the sample areas, but a useful measure would probably require more information about individual mountain ranges than is now available. Accordingly, we have used only area, elevation, and location in our analysis of factors controlling plant diversity.

The component species of each checklist have been individually considered for inclusion in our study. We have eliminated species from the checklists which are not known to occur above 7500 feet. Species that are potentially able to survive and reproduce in desert environments have also been excluded. This latter criterion was used to improve the likelihood that the islands considered are at least currently functioning as islands. We experienced difficulty in rigidly applying this last criterion, since some species which occur above 7500 feet along the eastern edge of the Great Basin do not extend above that elevation in the Sierras. We have included all species which occur above 7500 feet on the eastern edge of the Great Basin (that do not tolerate deserts) but normally occur below that elevation on the western mainland.

For each species included in the study, we have noted lifeform, likely means of dispersal, and geographic range. The lifeform categories recognized are: 1) annual, 2) perennial forb, 3) perennial graminoid, 4) shrub, or 5) tree. Categories of dispersal include: 1) megawind, 2) miniwind, 3) sticktight, 4) fleshy fruit, or 5) no apparent modification. Species were placed in the following groups with respect to geographic range: 1) occurring on both mainlands, 2) confined to the western mainlands and a few isolated mountains, 3) confined to the eastern mainlands and a few isolated mountains, or 4) known only from one or a few mountains in this study. Because the authors of the several checklists were uneven in their treatment of taxa of subspecific rank, we have ignored such taxa.

It will be recognized that many arbitrary decisions are required to classify all of the species in respect to the foregoing characteristics. We have followed the lifeform classification given in the index of Holmgren and Reveal (1966), except that we

have separated annual plants from perennial herbs. We consider megawind propagules to be dust-like seeds (as in orchids) and seeds with large plumose appendages (as in milk-weeds) that can be expected to be regularly transported over a mile by wind. Miniwind propagules are considered to include such fruits as winged utricles of some chenopods, samaras of maples, grass caryopses that have large surface-to-volume ratios, and winged seeds of conifers. Normal dispersal distance of miniwind propagules is probably no more than a few yards. The sticktight category includes "hitchhiker" fruits such as those of *Xanthium*, *Arctium*, *Circaea*, and *Bidens* which are presumably adapted for dispersal on the fur or feathers of vertebrates. Under the heading of fleshy fruits, we include drupes, pomes, berries, and fleshy cones such as those borne by *Juniperus*. We as-sume that such propagules appeal to and are often dispersed by birds. Propagules des-ignated as having no modifications for dis-persal are produced by a great variety of dry-fruited species in which seeds are rela-tively large, have a small surface-to-volume ratio, and are without wings or plumose ap-pendages.

The categorization of individual species according to geographic range also present-ed difficult problems. Once the floras were recorded on computer cards, the species were separated into the four floristic groups previously mentioned. Examination of the lists thus compiled demonstrated that some of the species that supposedly occurred only on western mainlands did in fact also occur infrequently on the eastern mainlands, even though they were not encountered on any of the checklists. In like manner, some spe-cies on the list of taxa found only on check-lists from the eastern mainlands are known to occur (usually sparingly) on the western mainland. Finally, species that occur on is-land checklists but not on mainland lists are rarely local endemics, but are instead north-ern or southern species or uncommon main-land species that have reached some of the isolated mountains. Despite these defi-

ciencies of the geographic range lists, we have used them for certain analyses that would have been otherwise impossible to make.

We have used Holmgren and Reveal (1966) as our nomenclatural authority for all species occurring in the Great Basin. No-menclature of species that occur in Califor-nia but do not occur in the Great Basin fol-lows Munz and Keck (1959). Species mentioned that occur to the south of the study area but not in California are named according to Kearney and Peebles (1951) or Clokey (1951). Problems of synonymy were largely resolved with the Holmgren and Re-veal (1966) checklist.

Results

The Study Areas

Our floristic samples are drawn from 6 states and from areas ranging in size from 1 to 3,630 square miles. The mainland floras are distributed across a north-south gradient of about 450 miles in the west (3 floras) and 600 miles in the east (6 floras). The 15 is-lands are geographically centered on the Great Basin and are spread across more than 400 miles of distance in both north-south and east-west directions (Fig. 1). Max-imum elevation varies from 14,495 to 9105 ft above sea level among mainland areas and from 14,246 to 8235 ft among islands (Table 1).

Unfortunately, few climatological stations are maintained at high elevations in the re-gion. The few data that are available sug-gest that the climates of eastern and west-ern mainlands are somewhat similar in respect to annual precipitation and poten-tial evaporation at comparable elevations, while the island areas tend to receive less precipitation and to experience greater po-tential evaporation than either mainland. Conditions conducive to aridity appear to be maximal on the more southerly of the mountain islands considered (United States Department of Interior 1970).

The Flora

A total of 2,225 different species occur above 7500 ft elevation in the 24 floras considered in this paper. Approximately 27 percent of those species occur on both mainlands and on occasional mountain ranges between the mainlands. Some 29 percent of the species appear on the western but not the eastern mainland, and roughly 30 percent of the species are repre sented on the eastern but not the western mainland. The remaining species (about 14 percent) were recorded only on island checklists (Table 2).

Species representative of those occurring on both mainlands include the following:

Aconitum columbianum Nutt.
Balsamorhiza sagittata (Pursh) Nutt.
Carex aurea Nutt.
Carex lanuginosa Michx.
Elymus glaucus Buckl.
Epilobium angustifolium L.
Equisetum arvense L.
Fritillaria atropurpurea Nutt.
Geum macrophyllum Willd.
Glyceria elata(Nash) A. S. Hitchc.
Hackelia floribunda (Lehm.) I. M. Johnst.
Lonicera involucrata (Rich.) Bank
Osmorhiza chilensis Hook. & Arn.
Populus tremuloides Michx.
Pinus ponderosa Laws.
Purshia tridentata (Pursh) DC.
Ribes cereum Dougl.
Sitanion hystrix (Nutt.) J. G. Smith
Thalictrum fendleri Engelm.
Viola adunca J. G. Smith

TABLE 2. General distributional character istics of the flora considered.

Total species	2,225
Species occurring on checklists from both mainlands	613
Species confined to western mainland or occurring on western mainland and some islands but not on eastern mainland	646
Species confined to eastern mainland or occurring on eastern mainland and some islands but not on western mainland	678
Species recorded only on islands	288

Species confined to the western mainland or that occur on the mainland and a few iso lated mountains include the following:

Agropyron pringlei (Scribn. & Sm.) Hitchc.
Allium obtusum Lemmon
Artemisia douglasiana Bess.
Bromus breviaristatus Buckl.
Carex amplifolia Boott
Carex tahoensis Smiley
Cheilanthes gracillima D.C. Eaton
Cryptantha mohavensis (Greene) Greene
Hulsea brevifolia Gray
Libocedrus decurrens Torr.
Mimulus torreyi A. Gray
Oryzopsis kingii (Bol.) Beal
Pinus jefferyi Grev. & Balf.
Populus trichocarpa Torr. & Gray
Prunus emarginata (Dougl.) Walp.
Sequoiadendron giganteum (Lindl.)
Stipa californica Merr & Davy
Taxus brevifolia Nutt.
Trifolium andersonii A. Gray
Tsuga mertensiana (Bong.) Carr.

Species confined to the eastern mainland or to that mainland and a few islands are rep resented by the species listed below.

Abies lasiocarpa (Hook.) Nutt.
Acer grandidentatum Nutt.
Balsamorhiza macrophyllum Nutt.
Besseya wyomingensis (A. Nels.) Rydb.
Calamagrostis scopulorum M. E. Jones
Ceanothus martini M. E. Jones
Chlorocrambe hastata (S. Wats.) Rydb.
Clematis columbiana (Nutt.) Torr. & Gray
Erigeron ursinus D.C. Eaton
Geum rossii (R. Br.) Ser.
Hierochloë odorata (L.) Beauv.
Mertensia arizonica Greene
Moldavica parviflora (Nutt.) Britton
Orthocarpus tolmiei Hook. & Arn.
Pinus edulis Engelm.
Picea pungens Engelm.
Primula parryi A. Gray
Quercus gambelii Nutt.
Ribes wolfii Rothrock
Thermopsis montana Nutt.

Species occurring on the checklists of some of the isolated mountains but on neither mainland include local endemics as well as more widespread species that penetrate our area from primarily northern or southern floras. Representatives of each of these groups are listed below.

Endemics Listed by Location

Ruby Mountain Area
Castilleja linoides Gray
Eriogonum kingii Torr. & Gray
Primula capillaris Holmgren & Holmgren
Spring Range
Angelica scabrida Clokey & Mathias
Antennaria soliceps Blake
Castilleja clokeyi Pennell
Cirsium clokeyi Blake
Opuntia charlestonensis Clokey
Penstemon keckii Clokey
Potentilla beanii Clokey
Silene clokeyi C. L. Hitchc. & Maguire
Synthyris ranunculina Pennell
Tanacetum compactum Hall
Toiyabe Mountains
Draba arida C. L. Hitchc.
Mertensia toyabensis Macbr.
Wheeler Peak
Eriogenum Holmgrenii Reveal
Species Entering from North
Castilleja viscidula A. Gray
Cymopterus nivalis S. Wats
Erigeron watsoni (A. Gray) Cronq.
Selaginella selaginoides (L.) Link
Species Entering from South
Agastache pallidiflora (Heller) Rydb.
Antennaria marginata Greene
Aquilegia triternata Payson
Arenaria confusa Rydb.
Eleocharis montana (H.B.K.) Roem. & Schult.
Festuca arizonica Vasey
Muhlenbergia wrightii Vasey

In respect to lifeform characteristics, the floras of the mainlands and islands (both close to and well removed from the mainlands) do not differ significantly (Table 3). We had anticipated that since perennial forbs show a preference for more mesic sites (Harner and Harper 1973) and the island habitats appear to be more xeric than the mainlands, such species might be under-represented on the isolated mountains. The data lend no support to that idea. Woody species and graminoides are also uniformly distributed among the floristic groups reported in Table 3.

The number of annual species is considerably higher on the western as opposed to the eastern mainland (Table 3). In fact, if only herbaceous species are considered, Chi-square analysis demonstrates that the number of annual species on the two mainlands departs significantly from random expectations. Also, significantly fewer annual species occur in the combined flora of the islands than on the western mainland, but the island flora does not differ from that of the eastern mainland in this respect. Chabot and Billings (1972) have noted that annual species are more common in the alpine flora of the Sierras than in other alpine floras of North America.

Floristic Diversity Considerations

Species-area relationships for the total flora and various lifeform subsamples there-

TABLE 3. Lifeform relationships of the floras considered. The criterion for separation of near and far islands was a barrier width of less than or greater than 100 miles. The following four islands constitute the "far islands" category: Deep Creek, Jarbidge, Santa Rosa, and Spring. Expected numbers of species in each category (assuming random distribution of lifeform classes among floras) is enclosed by parentheses.

Floristic Group	Lifeform Class Perennial Herbs					
	Trees	Shrubs	Forbs	Graminoides	Annuals	Total
W. mainlands	27	111	696	226	181	1,241
	(28.1)	(114.4)	(734.9)	(214.7)	(148.9)	
E. mainlands	27	119	754	213	139	1,252
	(28.4)	(115.4)	(741.4)	(216.6)	(150.2)	
Near islands	30	108	776	204	147	1,265
	(28.7)	(116.6)	(749.1)	(218.9)	(151.7)	
Far islands	18	77	440	136	73	744
	(16.9)	(68.6)	(440.6)	(128.7)	(59.2)	

Summation Chi-Square = 18.285

(Not a significant departure from random expectations at 12 degrees of freedom and the 0.95 probability level.)

of are shown for both mainlands and islands in Figure 2. Three generalizations can be drawn from that figure: 1) there are consistently more species per unit area on the mainlands than on the islands, 2) floristic diversity increases faster on islands than mainlands as area increases, and 3) area usually accounts for more of the variation in species diversity on islands than on mainlands (i.e., correlation coefficients for species-area relationships are usually larger for islands than for mainlands). Observations 1 and 2 have been duplicated in numerous island biogeographic studies (MacArthur and Wilson 1967) and are commented on here only to emphasize that the isolated mountains

under study do exhibit strong similarities with true islands.

The third observation may be partially attributable to the classification of a single flora. We have treated the Bryce Canyon flora as mainland, but Figure 2 demonstrates that its flora and lifeform subsamples consistently fall on the species-area trend line for islands and well below the trend line for mainlands. Correlation coefficients for both mainlands and islands would have been improved had we classified Bryce Canyon as an island. The area lies at the southern extremity of the more-or-less continuous system of highlands extending south from northern Utah and along the western
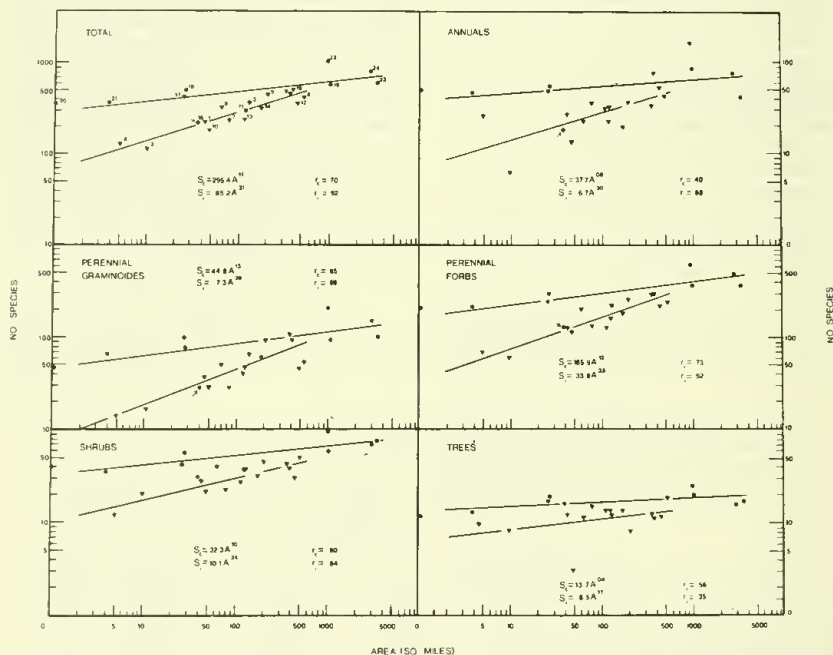

Fig. 2. Species-area relationships for mainland and island floras. Relationships for the total flora and various lifeform subsets thereof are shown. Mainland data are represented by dots; insular floras are shown with triangles. The individual floras are identified in the diagram for total species combined: numbers correspond to specific floras identified in Table 1. Subscript c indicates mainland correlation coefficients or regression equations; subscript i indicates island coefficients and equations. S represents number of species and A represents area.

edge of the Colorado Plateau. We initially considered the habitat breaks along the highland corridor to be short and in consequential as migration barriers and thus settled on the mainland classification for the area. In retrospect, it seems likely that the narrowness of the corridor has combined with general climatic differences and unusual soils to effectively filter out numerous northern taxa that would otherwise be ex pected in the area.

Slopes (Z-values) for the species-area regression lines of Figure 2 are shown as the exponents of area (A) in the equations associated with the figure. The Z-value of 0.11 for total flora on the mainlands is slightly smaller than values commonly re ported (e.g., 0.12–0.17 by MacArthur and Wilson 1967). The average Z-value of .19 reported for nested quadrats in pinyon- juniper ecosystems of Utah and New Mexico (Harner and Harper 1976) should prob ably not be compared to the Z-values ob tained for mainlands in this study, since it seems likely that Z-values for nested quad rats where the largest sample area is only a few acres will always be larger than values for regional floras from areas ranging in size from a few to several hundred square miles.

The Z-value of 0.31 for the total flora of islands (Fig. 2) is well within the range of values (0.20–0.35) reported for a variety of kinds of biota on true islands and close to the theoretically expected value of 0.26–0.27 (MacArthur and Wilson 1967). We call attention in passing to the fact that woody plants have flatter species-area re gression lines than perennial herbs on both mainlands and islands.

The flatness of species-area regression lines for mainlands has been attributed to the fact that small sample areas there carry individuals of many species that are poorly adapted to the sample area but nevertheless occur there because vigorous populations of each such taxon exist in nearby, suitable habitats (MacArthur and Wilson 1967). The steepness of species-area trend lines for is lands is related to at least two factors: 1)

decreasing likelihood of an island being col onized by dispersing taxa as size decreases and 2) increased likelihood of local extinc tion of small populations on little islands.

Brown (1977) reports Z-values of 0.165 for boreal birds and 0.326 for boreal mam mals on sites of isolated Great Basin moun tains. He has previously reported a Z-value of 0.428 for boreal mammals, using a more restricted group of species and a different set of mountains (Brown 1971a). Our Z- value for vascular plants on isolated moun tains thus lies between those for boreal birds, which seem definitely to be in equi librium on the mountains (i.e., neither in creasing or decreasing in respect to number of species per unit area over long time peri ods), and small boreal mammals, which are believed to be losing species by local ex tinction faster than new taxa can colonize. Plants in general appear to behave more like mammals than like birds on the moun tains considered, and perennial herbs yield Z-values that are especially steep and ap proach the values reported for mammals.

Both area and maximum elevation of the mountain ranges were strongly positively correlated with total vascular species on those ranges in this study (Table 4). There was a weak negative correlation between number of species and distance to the near est mainland. In multiple correlation analy sis, only area makes a large contribution to the coefficient of multiple determination (R^2). Elevation appears to be so closely cor related with area ($r = 0.66$) that it brings little new information into the multiple cor relation analysis. Distance also enters the multivariate equation; but it, like elevation, contributes only slightly over 0.01 to the R^2-value (Table 4).

The overwhelming dominance of area in the multiple correlation analysis is, in all probability, an illusion. Wyckoff (1973) and Harner and Harper (1976) have demon strated that both environmental favorability (annual precipitation and/or soil texture) and environmental heterogeneity (variation in soil characteristics, elevation, and/or ex-

posure) exert a strong influence on the number of vascular plant species per unit area. However, since area subsumes all of these variables, it alone consistently accounts for a highly significant amount of the variation in floral diversity in almost any suite of samples. Unfortunately, data on environmental favorability and heterogeneity are not available for the sample of mountains considered here. We have thus resorted to the use of the less definitive but nevertheless useful variables of area, elevation, and distance.

We commented earlier on the complicating effect of two close mainlands in island biogeography studies. In order to better evaluate the influence of distance between island and mainland on floristic diversity of the islands, we have measured the width of unfavorable habitat separating every island from each mainland. Then, by using only species that appear to be confined to one mainland or to one mainland and a few islands (i.e., species common to both mainlands or unique to islands were excluded), we used simple and multiple correlation to analyze the relative influence of area, elevation, and distance from mainland on the number of species from either eastern or western mainlands on the 15 islands. The results (Table 5) show that distance now becomes the major factor influencing the number of western mainland species on the islands. For eastern mainland species, distance is not significantly correlated with

number of species in simple correlation analyses, but it makes a sizeable contribution in the multiple correlation analysis. The dissimilar results for species number-distance relationships for species of western or eastern mainland origin may be related to the fact that the islands considered are on the average more distant from the western mainland (149 miles) than from the eastern (117 miles). In any event, the results in Table 5 seem to suggest that use of a single distance (distance to nearest mainland) as in Table 4 may obscure the importance of distance in studies of island floras.

We recognize also that a decrease in species of any given checklist is to be expected as one moves away from the center of the geographical area sampled for the checklist. Such a decrease with distance would be expected even in large continental areas of relatively uniform climate, topography, geological substratum, and geological history and may have nothing to do with dispersal habits of the species. The decrease may reflect nothing more than the difficulty experienced by locally evolved taxa as they attempt to expand their range through established vegetations.

Sources of the Flora

In this section we consider the question of source of the floras of the isolated mountains. How important a contribution do local endemics make to the floras of the isolated ranges? Are the island floras derived

TABLE 4. Factors influencing the number of vascular plant species on the 15 mountain islands. Distance is measured to the nearest mainland area having an elevation over 7500 ft.

Factor	Simple Correlation Coefficient (r) with Number of Species	Contribution to Coefficient of Multiple Determination (R^2)
Area of island	.879	.777
Elevation of highest peak	.668	.014
Distance to mainland	−.091	.013
		Total.799
	$R =$	.894

equally from eastern and western mainlands, or is one source more important than the other?

In respect to endemics, the data suggest that their contribution to the floras of the isolated mountains is comparatively minor. The number of endemics of moderate-to-high elevations appears to be considerably larger on the Spring Range (the Charleston Mountains which Clokey [1951] studied are part of this range) than on any other range considered here. Yet even on the Spring Range, which Clokey (1951) considered to be about five million years old, endemics account for only about 5 percent of the flora above 7500 ft. Endemics account for less than 2 percent of the White Mountain flora (Lloyd and Mitchell 1973). In contrast, plant endemics on many remote oceanic islands account for over 50 percent of the flora (Carlquist 1974). Such data force one to conclude that the mountain ranges considered are far less isolated than remote oceanic islands such as St. Helena, the Hawaiian Islands, or New Caledonia, where the majority of the flora is endemic.

In order to evaluate the relative contribution of western and eastern mainland floras to individual islands, we have separated out species unique to western as opposed to eastern mainlands (see Table 2). The relative contribution of uniquely western or eastern species on individual islands is plotted against distance to the respective mainlands in Figure 3. The data demonstrate that the eastern source area consistently contributes many more species to the islands than does the western source area. On only one island (the White Mountains) does the western mainland contribute a larger percentage of the total flora than the eastern. As will be shown later (Fig. 4), the preeminence of the eastern source area in island floras can be demonstrated for all dispersal types.

To further illustrate the relative contribution of the respective mainlands to the island floras, we have compiled a similarity matrix for all possible combinations among the 24 floras (Table 6). Various inter-relationships among floras are summarized in Table 7. At first glance, the low sim-

TABLE 5. Factors influencing the number of vascular plant species on the islands when species occurring on both mainlands and on islands only are excluded. Width of barrier (distance) separating an island from each mainland has been determined for all islands.

	Western Mainland Species		
Factor	Simple Correlation Coefficient (r) with Number of Species		Contribution to Coefficient of Multiple Determination (R^2)
Area of island	.502		—
Elevation of highest peak	.644		.092
Distance to W. mainland	−.646		.417
		Total	.509
		R =	.714
	Eastern Mainland Species		
Factor	Simple Correlation Coefficient (r) with Number of Species		Contribution to Coefficient of Multiple Determination (R^2)
Area of island	.590		.348
Elevation of highest peak	.306		—
Distance to E. mainland	−.137		.156
		Total	.504
		R =	.710

ilarity values seem to indicate little com-
monality among floras, but those values
must be evaluated in light of the way in
which they are computed: for example, the
37 percent similarity value between the
Ruby and Deep Creek Mountains represents
223 species common to those ranges. Read-
ers are referred to the similarity equation
given in the legend for Table 7 for details
of computation.

Several relationships reported in Table 7
merit attention: 1) internal similarity of the
floras from the western mainland is almost
identical to the comparable figure for east-
ern mainland floras, 2) the island floras are
less similar to each other than are floras
from either mainland, 3) island floras are,
on the average, more similar to eastern
mainland floras than to western mainland
floras, and 4) even islands closest to the
western mainland have slightly closer floris-
tic affinities with the eastern, rather than

the western, mainland. The second of the
foregoing items indicates, as one might ex-
pect, that the flora of individual mountain
islands tends to be a more random assem-
blage of species than is found in individual
floras on either mainland. Items 3 and 4 in-
dicate that the island floras have been more
influenced by the eastern than the western
mainland, despite the fact that they lie
"downwind" (in this case, the prevailing
westerly winds) from the western mainland.
This last fact is visually conspicuous in the
field since many of the dominant plants of
most of the isolated mountain ranges have
eastern affinities. Examples of such domi-
nant, or at least abundant, plants include
the following:

Agropyron spicatum (Pursh) Scribn. & Smith
Amelanchier alnifolia (Nutt.) Nutt.
Amelanchier utahensis Koehne
Artemisia arbuscula Nutt.
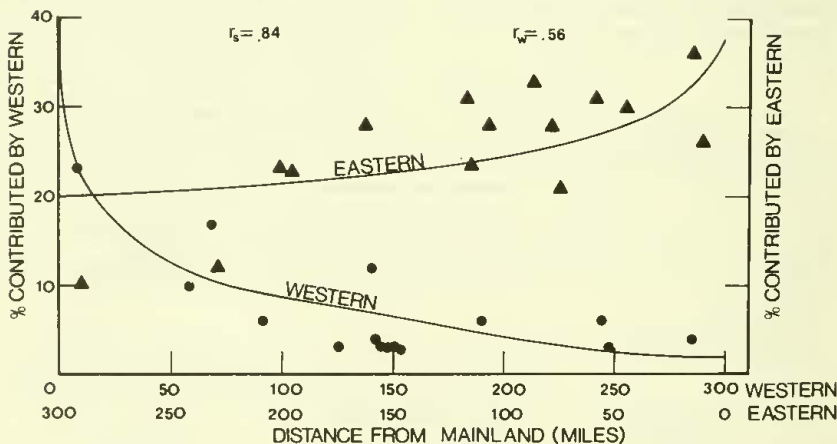*Artemisia tridentata* Nutt.

Fig. 3. Percent of the flora contributed by species that appear to have immigrated from the western as
opposed to the eastern mainland. The western contribution is shown by dots, the eastern by triangles. The
r_s-value represents the correlation coefficient for the curvilinear correlation between percent of species
contributed by the western mainland and distance from that mainland. The r_w-value is the correlation
coefficient for the curvilinear relationship between contribution of eastern species and distance (length of
low elevation barrier between the islands and the eastern mainland). Individual islands can be identified
in the figure by referring to island-mainland distances in Table 1.

Bromus anomalus Rupr.
Caltha leptosepala DC.
Ceanothus martini M. E. Jones
Delphinium occidentale (S. Wats.) S. Wats.
Geranium fremontii Torr.
Holodiscus dumosus (Hook.) Heller
Juniperus osteosperma (Torr.) Little
Lathyrus pauciflorus Fern.
Lewisia rediviva Pursh
Oenothera caespitosa Nutt.
Pachistima myrsinites(Pursh) Raf.
Phlox longifolia Nutt.
Primula parryi A. Gray
Ranunculus jovis A. Nels.
Valeriana occidentalis Heller

Since others (McMillan 1948 and Major and Bamberg 1967) have speculated about the relative effectiveness of northern and southern migration lanes from the western outliers of the Rocky Mountains in providing species for interior Great Basin mountains, we have investigated that problem using the similarity matrix of Table 6. Below we have summarized the relations of four interior ranges in the Basin (Deep Creek, Ruby, Toiyabe, and Wheeler Peak) with three northern sources (northern Wasatch, Mount Timpanogos, and Red Butte Canyon) and two southern sources (Bryce Canyon National Park and Pine Valley Mountains).

Mountain Range	Average Percent Similarity with Three Northern Sources	Two Southern Sources
Deep Creek	31.7	21.0
Ruby	29.7	15.0
Toiyabe	25.0	18.5
Wheeler Peak	24.3	21.5

The data demonstrate that although both northern and southern routes have fed species onto the isolated mountains, the northern route seems consistently to have been more effective than the southern. The low similarity of the four interior mountain ranges with the East Tintic Mountains and their higher similarity with mountain ranges such as the Jarbidge to the north suggests that migration from the western outliers of the Rockies has been primarily along the northern rim of the Great Basin and south-

ward along the north-south-oriented mountain ranges rather than westward across the dry basins that separate the ranges of central Utah and Nevada. That hypothesis is strengthened by the low similarity shown by the East Tintic Mountains with the three northern sources (average similarity of 18 percent).

Certain species seem clearly to have reached the interior mountain islands of the Great Basin via the northern route, while others have apparently reached those islands via the southern route. Species representative of each route are noted below.

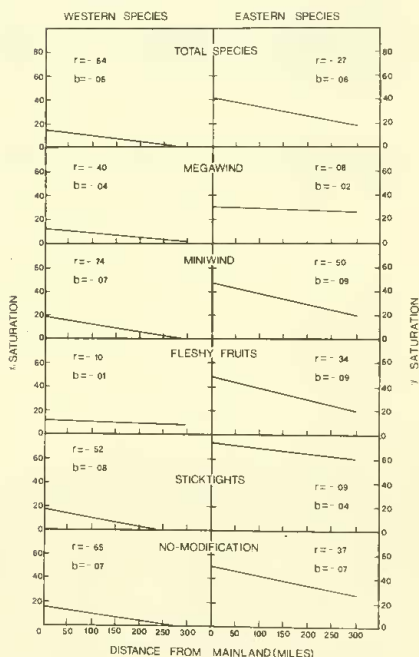Northern Route

Ceanothus velutinus Dougl.

Fig. 4. Regression lines relating percent saturation of eastern or western floristic elements on the 15 islands to distance to mainland. Distance is defined as in Fig. 3. Regression coefficients (r-values) larger than .514 are significant at the 0.05 probability level. The b-values are slopes for the regression lines.

Kalmia polifolia Wang.
Ledum glandulosum Nutt.
Pinus albicaulis Engelm.
Rubus parviflorus Nutt.
Southern Route
    Arctostaphylos patula Greene
    Nicotiana attenuata Torr.
    Peraphyllum ramosissimum (Nutt.) Rydb.
    Pinus aristata Engelm.
    Pinus ponderosa Laws.

Dispersal Ecology

Plant dispersal habits in both mainland and island floras are dominated by types which have no apparent modifications for dispersal and types with weak modifications for dispersal by wind (Table 8). For convenience, we refer to the latter category as the "miniwind" modification. Species whose propagules have no apparent modifications for dispersal account for from 50.4 to 53.7 percent of the species in the floras consid-

ered in Table 8. Species having miniwind propagules contribute between 28.8 and 33.5 percent of the species. Together, these two dispersal types account for almost 85 percent of the species considered. On the average, species having propagules modified for long-range dispersal by wind (megawind dispersal type) contribute almost 7.5 percent of all species in our floras. Fleshy fruited species contribute slightly fewer species (average 6.1 percent of all species), and species dispersed by sticktights contribute the few remaining species (about 2.5 percent).

Our data indicate that dispersal types modified for long-range movement (i.e., fleshy fruit and megawind categories) show no tendency to be overrepresented on the remote islands (Table 8). In contrast, Carlquist (1967) has shown that as many as 58 percent of the plant species that reach

TABLE 6. Similarity among the 24 floras as determined with the Jaccard (1912) similarity index. Values report-ed are percent similarity for all possible pairs of floras. Checklist numbers correspond to those assigned to each area in Table 1.

											Checklist No.													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1																								Albion
2	21																							Cassia
3	27	15																						Deep Cr.
4	17	11	18																					Tintic
5	28	16	32	15																				Jarbidge
6	17	11	23	13	19																			Kaibab
7	16	12	22	17	18	19																		Pine V.
8	34	22	41	18	33	20	21																	Raft R.
9	25	14	37	13	40	19	15	29																Ruby
10	26	19	21	17	30	12	14	27	23															Santa Rosa
11	14	8	23	15	16	25	22	19	17	13														Spring R.
12	20	12	29	17	28	20	20	29	27	25	25													Toiyabe
13	19	16	18	11	23	14	14	21	19	22	11	19												Warner
14	27	15	39	19	31	21	20	33	36	25	22	29	18											Wheeler
15	16	9	25	12	21	19	18	22	24	17	27	31	18	25										White
16	19	12	20	18	17	27	19	21	15	16	25	17	12	23	15									Bryce
17	14	9	17	7	23	11	13	16	21	17	12	17	23	14	17	9								Lassen
18	25	14	32	18	33	21	21	31	32	18	18	23	18	25	21	19	18							Timpanogos
19	24	14	35	15	34	24	21	32	32	18	19	28	19	25	22	18	22	47						N. Wasatch
20	26	17	28	21	32	19	22	32	25	20	17	24	21	23	16	17	17	44	40					Red Butte
21	15	12	18	8	23	11	12	16	19	15	10	19	25	15	18	9	38	18	21	17				Sagehen Cr.
22	11	6	16	6	20	12	11	14	21	10	13	18	15	14	28	9	29	17	24	15	24			Sequoia
23	21	11	31	11	31	24	17	28	30	15	18	22	17	26	20	19	17	37	39	28	16	20		Uinta
24	17	9	24	9	31	17	14	23	29	14	12	20	16	20	19	12	21	32	38	26	19	23	35	Yel

remote oceanic islands are dispersed inter- nally by birds (mostly fleshy fruits). Prop- agules borne externally on birds by virtue of being held in place by barbs or prickles (sticktights) also account for many (fre- quently over 20 percent) of the in- troductions. He found windborne seeds to be poorly represented (usually less than 10 percent of the flora) on all save the closest

of the remote islands. He considered ecolog- ical conditions on the island to be strong determinants of the dispersal types that suc- ceeded.

In contrast to Carlquist's findings, Hed- berg (1970) found wind-dispersed plants to represent almost 30 percent of the flora above about 7900 ft on the mountains of east Africa. In Hedberg's study, plants dis-

TABLE 7. Floristic similarity relations among the floras considered. The index of similarity used is that of Jaccard (1912). Jaccard's index is computed as follows:

$$ SI = \frac{C}{A + B - C} \times 100. $$

In the equation, C represents the number of species common to the two floras, A is the number of species in flora A, and B is the number in flora B.

Areas Considered	No. of Floras Involved	No. of Comparisons Averaged	Average Percent Similarity
Western mainland (internal similarity)	3	3	30.3
Eastern mainland (internal similarity)	6	15	30.1
Mountain islands (internal similarity)	15	105	21.0
W. mainland compared with islands	18	45	15.0
E. mainland compared with islands	21	90	21.4
W. mainland compared with E. mainland	9	18	17.3
Four closest islands to W. mainland compared to W. mainland	7	12	18.1
Four closest islands to W. mainland compared to E. mainland	10	24	18.8
Four closest islands to E. mainland compared to W. mainland	7	12	11.4
Four closest islands to E. mainland compared to E. mainland	10	24	21.0

TABLE 8. Plant dispersal habits of the floras considered. Expected number of species in each category (assuming random distribution of lifeform classes among floras) is enclosed by parentheses. Island groups are defined as in Table 3.

Floristic Group	Mega- wind	Mini- wind	Fleshy Fruits	Stick- tights	No Modification	Total
W. mainland	93	358	88	36	666	1,241
	(92.3)	(395.8)	(75.3)	(30.9)	(646.7)	
E. mainland	104	414	77	26	631	1,252
	(93.2)	(399.3)	(75.9)	(31.1)	(652.4)	
Near islands	83	415	65	30	672	1,265
	(94.1)	(403.5)	(76.7)	(31.5)	(659.2)	
Far islands	55	249	43	20	377	744
	(55.4)	(237.3)	(45.1)	(18.5)	(387.7)	

Summation Chi-Square = 15.501

(Not a significant departure from random expectations at 12 degrees of freedom and the 0.95 probability level.)

persed internally by birds accounted for only 1 to 2 percent of the alpine flora of east Africa.

The relationship between various dis persal types and island-to-mainland distance is presented in Figure 4. There, we regress percent saturation of species of various dis persal habits (i.e., the number of species of a given dispersal habit on each island is ex pressed as a percentage of the number of species of that dispersal habit that would be expected in an area of comparable size on the appropriate mainland) against distance. As expected, the regression lines all have negative slopes, and there is a slight (but statistically nonsignificant) tendency for dis persal types that are easily dispersed over long distances (megawind and fleshy fruit types) to have regression lines with gentler slopes than are obtained for species that are less likely to be dispersed far from the par ent plant. Average slope values for western and eastern mainlands and each dispersal type are shown below.

Dispersal Type	Average Slope Value
Megawind	.03
Fleshy Fruits	.05
Miniwind	.08
Sticktight	.06
No Modification	.07

The data in Figure 4 also support our earlier conclusion that the eastern mainland has exerted a greater influence on the mountain islands than has the western mainland. Every dispersal type shows greater saturation for eastern species than for spe cies from the western mainland. Since the number of species originating from each of the two mainlands is roughly equal (see Table 2), the results in Figure 4 suggest that species from the eastern mainlands have been about four times as effective in reaching and surviving on the islands as those from the west. On the average island, west ern species have a saturation value of 8 per cent, but the comparable value for species from the eastern mainland is 36 percent.

The great disparity between correlation coefficients for saturation-distance analyses for eastern and western species in Figure 4 is noteworthy. In five of the six analyses the r-values are much larger for western spe cies. It seems possible that those values re flect a differential in age of the two floristic elements on most of the islands. If the Rocky Mountains are much older than the Sierras, as Billings (1977) reports, it is pos sible that the eastern floristic element has dispersed essentially to its limit and is now poorly related to distance, while the west ern element is still actively dispersing.

Finally, we call attention to a con spicuous relationship between range limits of species and plant lifeform. Our data demonstrate that woody plants and per ennial graminoid species are over represented in the broad-range category (i.e., occurring on both mainlands) and un derrepresented in the category of species unique to islands (Table 9). Perennial forbs, on the other hand, display a significant ten dency toward underrepresentation in the broad-range category and over representation in the island-only class. An nual species show no significant trends in this respect. It seems possible that the pat terns observed reflect evolutionary rather than dispersal processes. In general, woody plants and graminoides appear to be ecolog ically broad niched and to have the ability to become community dominants. In con trast, many perennial forb genera seem to be narrow niched and to rarely achieve a dominant place in their community.

Discussion

Mountains as Islands

One might expect an island flora to be distinguished from that of the nearest main land in a variety of ways. As we began this study, it seemed to us that insular floras should display 1) an overrepresentation of species modified in one way or another for

long-distance dispersal, 2) fewer species per unit area than observed on the mainland, 3) steeper species-area curves than for mainland floras, 4) uneven stocking of species ecologically preadapted for existence on available islands, and 5) higher rates of endemism than the mainland.

Our results demonstrate that the isolated mountains of the Intermountain West satisfy some of our preconceived notions and thus qualify as islands, but they fail to qualify on other counts. The islands do indeed have fewer species per unit area than adjacent mainlands, and species-area trend lines for islands are steeper than those for mainlands (Fig. 2). Although the amount of endemism is low on the islands (always less than 5 percent), the amount still appears to be higher than on areas of comparable elevation and size on the mainlands. Too, there is uneven stocking of species on the islands. The Pine Forest Mountains of extreme northwestern Nevada, for example, are stocked by *Pinus albicaulis* Engelm., the Santa Rosas by *Pinus flexilis* James, while the Jarbidge and Ruby Mountains to the east and the Sierras to the west have both. The observed distribution pattern for these and many other species [e.g., *Abies concolor* (Gord. & Glend.) Lindl. and *Picea engelmannii* Parry ex Engelm.] seems explainable only in terms of randomness of colonization and/or extinction (See Critchfield and Allenbaugh 1969 for range details for these and other conifers in the Great Basin.)

Our expectations relative to an overrepresentation of species modified for long-range dispersal on the islands in large part failed. The isolated mountains are overwhelmingly dominated by species with no obvious means for being dispersed great distances. Furthermore, there is no tendency for species with modifications for long-distance dispersal to be overrepresented on even the most distant islands (Table 8). Our data do, however, show a weak tendency for percent saturation of poorly dispersed species (i.e., no-modification, miniwind, and sticktight categories) to decline faster and more reliably (larger r-values) with distance than for megawind and fleshy-fruited species, which are probably more easily dispersed (Figure 4).

Recent literature references demonstrate that at least some of the species that we have classified as unmodified for dispersal are, in fact, highly adapted for dispersal by vertebrate animals. Although we placed all conifers with unwinged seeds in the unmodified-for-dispersal category, a recent paper by Vander Wall and Balda (1977) shows that the Clark's Nutcracker regularly disperses the seeds of several pines (*P. edulis, P. albicaulis,* and *P. flexilis*) in a sublingual

TABLE 9. Plant lifeform relative to the range limits of the species considered. Expected number of species appears in parentheses in each category.

Range Category	Lifeform Class				Total Species
	Woody Plants	Perennial Herbs		Annuals	
		Forbs	Graminoides		
Occurring on both mainlands	94	333	114	72	613
	(70.0)	(368.6)	(98.9)	(75.5)	
Occurring on one mainland only	140	795	215	174	1,324
	(151.1)	(796.2)	(213.6)	(163.0)	
Occurring on islands only	20	210	30	28	288
	(32.9)	(173.2)	(46.5)	(35.5)	

Summation Chi-Square = 36.020**

(A significant departure from random expectations at 6 degrees of freedom and the 0.99 probability level.)

pouch and caches them in soil suitable for their germination and growth. In addition, the Nutcracker is known to occasionally feed on the winged seeds of *Pinus aristata* and *Pinus ponderosa* in northern Arizona. Vander Wall and Balda (1977) have evi dence for the dispersal of seeds over 13 miles in a single flight by the Nutcracker. In California, the Nutcracker regularly feeds on and caches the seeds of *Pinus monophylla* Torr. & Frem. and *Pinus jefferyi* as well as *Pinus albicaulis* and *Pinus flexilis* (D. Tomback, personal communication). Johnson (1975) suggests that the Piñon Jay and the Band-tailed Pigeon may also be in volved in long-distance transport of con iferous tree seed. J. Pederson (personal com munication) reports that the Band-tailed Pigeon has been taken several miles from the nearest *Quercus gambelii* in south eastern Utah with a crop full of unbroken acorns. Staniforth and Cavers (1977) demon strate that some seeds of two *Polygonum* species (*P. lapathifolium* L. and *P. pensylvanicum* L.) retain viability after passing through the digestive tract of the cottontail rabbit in eastern Canada. The foregoing data lead us to suspect that large seeds from the dry fruits of many species will eventu ally be shown to be dispersed by vertebrate animals.

The foregoing discussion is an acknowl edgement that we have underestimated the number of plant species that are modified for long-range transport on our islands. Nevertheless, the number of species in the no-modification and miniwind categories is so great on the islands that we are still forced to conclude that the vast majority of the species there did not reach those sites by long-range dispersal. Although the high elevation community types may never have been able to survive on the valley floors at any time during the Pleistocene, as Wells and Berger (1967) argue, many of the com munity components may have been able to migrate directly across valley floors during that period. Also, as Billings (1977) empha sizes, climatic cooling would have signifi-

cantly narrowed the barriers between is lands.

Our discussion of mountains as islands would not be complete without some com ment on the question of equilibrium of spe cies number on the islands. Brown (1977) contends that birds are and small mammals are not in equilibrium on isolated mountains in our study area. Are the plants in equilib rium? It will be recognized that the equilib rium argument is based on two assumptions: 1) local extinctions do occur, and 2) new in troductions occur as often as extinctions on each island. Both assumptions are difficult, if not tactically impossible, to test con clusively. A definitive test would require that we know of every population of every species on every island, and that we mon itor each island regularly enough (preferably annually) in order to know when a species became extinct or immigrated and became established there. Obviously, such data are not available for any island in our study. As a consequence, any statement about the status of our islands relative to the equilib rium question must be based on inferences, not facts.

With respect to extinctions, there is con clusive evidence that *Pinus aristata* and *Pinus flexilis* coexisted with *Abies concolor* and *Juniperus osteosperma* on Clark Moun tain in southeastern California about 25,000 years ago (Mehringer and Ferguson 1969). Today neither of these pines occurs there. Similarly, *Pinus monophylla* and *Juniperus osteosperma* existed on the Turtle Range 14,000 years ago (Wells and Berger 1967), but do not occur there now. The relatively steep species-area curves for herbs (Fig. 2) may indicate extinctions, but we can offer no evidence in support of that possibility.

Concerning new immigrations onto the isolated mountains, there are abundant re cords of exotic species invading at lower elevations (Young, Evans, and Major 1972). Nevertheless, we know of no documented cases of unaided immigrations onto the mountains of species that cannot survive in at least some microsites on the valley floors.

There is strong evidence that species modified for long-range dispersal are not overrepresented on the islands relative to the mainlands (Table 8). If extinctions and immigrations had been in equilibrium, even since the close of the Pleistocene, one might have expected long-range dispersal types to be at least somewhat overrepresented on is lands; but even that tendency is not ob served (Table 8). As noted above, there is a weak tendency for percent saturation of long-distance dispersal types to decline less rapidly against distance from the mainland than for supposedly less well-dispersed taxa. These two bits of evidence lead us to ten tatively conclude that the flora of the iso lated mountains is not in equilibrium, even though some species do appear to be moving about in the area.

If the islands are not in equilibrium, the extinction rate must be low for all plant groups and especially so for the woody taxa. We draw this inference from the relative flatness of the species-area curve for most plant groups (Fig. 2) in contrast to mammals (Brown 1977). Intuitively, this infer ence seems valid since herbaceous plants as primary producers should be able to maintain larger populations than their vertebrate consumers. Woody plants (especially trees) would be expected to maintain smaller populations than their vertebrate consumers, but would have far greater longevity. Trophic position and longevity likely have much to do with the relative extinction rate of vertebrates and plants. Plant groups of differing trophic habit (e.g., vascular saprophytes and nongreen parasites such as *Corallorhiza* and *Orobanche*, respectively, ver sus photosynthetic forms) and longevity should show different extinction rates.

We had not expected to find the eastern mainland (Rocky Mountains) floristic ele ment to be so much more successful than the western mainland (Sierra) element on the Great Basin mountains. As others have noted in this symposium, the Rocky Mountain element also dominates the avian fauna (Behle 1977 and Johnson 1977) and the al-

pine flora (Billings 1977) of the isolated mountains. The evidence seems to imply that three basic factors have combined to give the Rocky Mountain element an ad vantage over that from the Sierra. Those factors are: 1) time, 2) geological parent material, and 3) climate.

As Billings (1977) has noted, most of the Great Basin mountains are younger than the Rockies and older than the present Sierra Nevada and Cascade ranges. Thus, species from the east have had longer to colonize the isolated mountains than high-elevation taxa from the Sierra, since that flora must have arisen much later than the first. In ad dition, propagules of species unique to the western mainlands would have had great difficulty establishing themselves on the mountain islands even after reaching them, since most habitats would have already been occupied by eastern taxa.

Plants originating at higher elevations on the western mainland could generally be ex pected to be adapted to acidic soils, since the Sierra Nevada is primarily composed of acidic, igneous rock (Major and Bamberg 1967). Soils on the isolated Mountains, how ever, have prevailingly basic to circumneutral soils. Again, taxa from the eastern mainland would have an advantage in colonizing the islands, since the western outliers of the Rockies are prevailing formed from calcareous rocks. In this connection, it is significant that Billings (1950) found as semblages of Sierra plants in the western Great Basin to be confined to acidic habitats on hydrothermally altered rocks.

Finally, western plants have evolved in an environment that is less continental (i.e., more moist and thermally less variable) than that associated with the isolated mountains of concern or the western outliers of the Rockies. Johnson (1977) considers the cli matic variable to be highly influential in confining western bird species to the Sierras. We believe that continentality may similarly increase the difficulty of estab lishment of western plant species that are dispersed to the mountain islands. As in the

preceding cases, species from the east would be better preadapted for life on the islands.

Niche Expansion

Brown (1971b) has shown that the altitudinal range of a normally low-elevation chipmunk (*Eutamias dorsalis*) expands upward on Great Basin mountains which lack a high elevation congener (*E. umbrinus*). In the course of our work on isolated mountains in the Region, we have observed several cases in which plant species also display a niche expansion in the absence of normal competitors. Although quantitative data are lacking, we take this opportunity to put such anecdotal evidence as is available on record.

An apparent case of niche expansion is presented by *Abies lasiocarpa* in the Jarbidge Mountains. There, in the absence of its common coniferous competitors (e.g., *Abies concolor, Picea engelmannii, Picea pungens,* and *Pseudotsuga menziesii* (Mirb.) Franco), *Abies lasiocarpa* plays a major role in forest vegetation from the sagebrush-grass and streambank communities at low elevations to timberline. We know of no other place where this species succeeds in such a variety of habitats.

A double zone of *Artemisia tridentata* occurs on mountainsides of Nevada and western Utah. There the species commonly dominates a wide belt both below and above the juniper-pinyon zone. It appears likely that *Artemisia* has simply moved into a zone that is elsewhere dominated by larger mesophytes such as *Quercus gambelii, Pinus ponderosa,* or a rich mixture of mountain brush species.

In the northern Wasatch Mountains, the range of *Acer grandidentatum* extends many miles farther north than that of its common associate in the south, *Quercus gambelii.* In mixed stands of *Acer* and *Quercus, Acer* is normally conspicuous only on slope bases and ravine edges. North of the limits of *Quercus,* however, *Acer* dominates both slopes and depressions. The phenomenon

can be seen with particular clarity in the southwest corner of Cache Valley, Utah.

Although *Chamaebatiaria millefolium* (Torr.) Maxim, occurs on both of the mainlands recognized in this study, it is rarely a conspicuous component of the vegetation on either. On the remote islands, however, *Chamaebatiaria* is often common and a conspicuous part of the vegetation.

Finally, West et al. (1977) review evidence suggesting that the anomalously high upper elevation of the juniper-pinyon zone on many of the isolated mountains of the Great Basin may be attributable to the low diversity of the high-elevation flora and the paucity of well-adapted competitors. They note also that the niche of both juniper and pinyon appears to be severely compressed on the west flank of the southern and middle Wasatch Range where *Quercus gambelii* and *Acer grandidentata* combine to form a dense woodland. Both juniper and pinyon occur in the flora there, but neither is an important part of the vegetation.

Adequacy of Checklists

In the inception of this study, we were concerned that the checklists on which our work would be based would be too incomplete to give meaningful results. In retrospect, we acknowledge that all of the lists are probably incomplete. Undoubtedly, additional effort will add a few species to some lists and many to others. Nevertheless, the lists have yielded results that seem reasonable and defensible. Furthermore, the sample on hand is already sufficiently large to minimize the possibility that new collections will seriously alter species-area relationships or lifeform and dispersal-type spectra for the floras.

Management Implications

Species-area curves reveal much that should be useful to natural resource managers. The curve for trees on islands in Figure 2, for example, suggests that the Santa Rosa Mountains are drastically understocked with trees. Could trees be successfully in-

troduced there to provide shelter for ani-
mals or construction materials for man?
Since other islands in the study support so
many more tree species than that range, we
suspect that introduction of one or a few
carefully selected tree species into favorable
sites would have a high probability of suc-
cess there.

Species-area curves also have many useful
implications for conservation programs for
unusual and rare plant and animal species.
Managers will find the basic theory relative
to rare species and size of reserves nicely
capsulized in the following short, non-
technical papers: Terborgh (1974 and 1976),
Diamond 1976, Whitcomb et al. (1976), and
Simberloff and Abele (1976).

Johnson (1975) developed a habitat diver-
sity index that accounted for a major por-
tion of the observed variation in number of
bird species on isolated mountains in the
Great Basin. Behle (1977) has verified that
the index is a useful indicator of bird diver-
sity throughout the Basin. Since that index
is based on various plant parameters and
the presence or absence of free flowing wa-
ter, it has relevance to our discussion here.
Many of our small, arid mountain ranges in
the Intermountain West have only a few
acres of complex forest habitat (a prime
variable in Johnson's index) in a single loca-
tion and but a few score feet of flowing
water. Since the index shows that bird di-
versity is highly dependent upon such habi-
tat, it would seem prudent for developers
interested in preserving the natural biotic
diversity of the environment to insure that
roads, campgrounds, or buildings not in-
fringe upon such habitats. Yet, unfortu-
nately, our developments often are centered
directly on such microenvironmental rari-
ties. By so locating developments, we al-
most insure that we will lose some and per-
haps many plant and animal species from
the entire range. The campground at Blue
Lake on the Pine Forest Range in north-
western Nevada is a prime example of such
faulty planning. With foresight, the devel-
opment could have been placed well away

from the lake but still in the open pine
groves. Water could have been piped to the
campground with minimal disturbance to
the natural system around the lake. Instead,
the current plan places every visitor in a
position to disturb the several unusual plant
and animal species that perhaps occur at
only that spot on the entire range.

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