

To the Graduate Council:

I am submitting herewith a dissertation written by Raymond A. McCord entitled "Biogeography of the Vascular Flora on Islands in the Bering Sea Region." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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BIOGEOGRAPHY OF THE VASCULAR FLORA
ON ISLANDS IN THE BERING
SEA REGION

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ABSTRACT

The theory of island biogeography developed by MacArthur and Wilson was used to examine biogeographic patterns in the vascular flora on islands in the Bering Sea Region. The basic relationships between the number of species and the size, indices of environmental heterogeneity, and isolation of the islands were studied. Those relationships were also examined for families, groups of species defined by type of dispersal, and subsets of the flora that were related to the mainland source areas.

The floristic data for 29 islands and six source areas in the Bering Sea Region were compiled primarily from the published works of Hult  n. Information from recent collections in the Aleutian Islands was also added to the floristic data set.

Geographic variables included area, maximum elevation, distance to source areas and other islands, and latitude. Measures of topographic complexity were calculated from samples of the number of contour lines per unit area on topographic maps. Indices of the size and complexity of island shape were developed from radial measurements of the islands. The size and shape of an island were also represented by the number of bays and total length of mapped streams. The depth and width of interisland passes, percentage of near shore area, distance along current paths and distance to the limit of pack ice were used to represent the local isolation of the Aleutian Islands.

The relationships between the floristic and geographic variables were analyzed with correlation and multiple regression. Patterns in

the floral similarity of the islands were examined with cluster analysis.

The biogeographic patterns of the vascular flora of the islands in the Bering Sea Region are similar to the ones predicted by the theory of island biogeography that was developed by MacArthur and Wilson. The number of species is positively correlated with the area. The log-log model is the best form of this relationship. The number of species is also positively correlated with maximum elevation and other indices of environmental heterogeneity. Correlations between the total number of species and the distance to source areas are not significant. Significant negative correlations are observed between the proportion of species related to a source area and the distance from the source area. Similar to the prediction of the theory of island biogeography, "near" islands are observed to have a significantly steeper species-area curve than "far" islands.

The results of multiple regression analyses indicate the following order of the importance of the types of geographic variables in the prediction of the number of species: area, complexity of island shape, distance to source areas, and maximum elevation or topographic diversity. The width of the interisland pass is the most important variable representing the local isolation of an island in the multiple regression models.

The results of cluster analyses show that neighboring areas tend to have greater floristic similarities than more distant areas. These results suggest the existence of a pattern of isolation across the region. Differences in the isolation of groups of species with different dispersal abilities are observed from the results of cluster

analyses. The results of cluster analyses also indicate that the flora of the Aleutian Islands tends to be more similar to the North American source areas than the Asian source areas.

Significant positive correlations between the number of species in families and the total number of species are observed. The significance of correlations among the numbers of species in families is not known or previously reported.

Geographic variables related to the size, environmental heterogeneity, and isolation of an island can be used to predict the number of species on islands in the Bering Sea Region. The relationships between the floristic and geographic variables are also similar to the ones used by MacArthur and Wilson in the development of the theory of island biogeography.

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INTRODUCTION

The theory of island biogeography proposed by MacArthur and Wilson (1963, 1967) has been used to interpret the biogeography of many taxa in many regions (Simberloff 1974). A majority of these studies have been conducted in tropical and subtropical areas. The purpose of this study was to examine the usefulness of the theory for empirically predicting biogeographic patterns on islands in a high latitude location. The vascular flora of the Aleutian and other Bering Sea islands was selected for this analysis. The islands for which the flora is fairly well known have the range of size and isolation that is needed to adequately observe the patterns predicted by the theory of island biogeography.

Several other aspects of the geography of the Aleutian Islands were useful for developing and analyzing secondary ideas. The Aleutian Islands are located between two continental areas (Figure 1) that may both serve as potential source areas for the flora of the islands. The theory of island biogeography of MacArthur and Wilson has not been interpreted in the context of multiple source areas. The linearity and length of the island chain also provide opportunities to search for evidence of the "stepping stone" effect.

The inclusion of islands in the northern part of the Bering Sea (St. Paul, St. George, Nunivak, St. Matthew, and St. Lawrence) also permitted the study of changes in the biogeography across the latitude range of this high latitude region. The islands of the northern Bering Sea have also been the subject of previous studies of biogeography

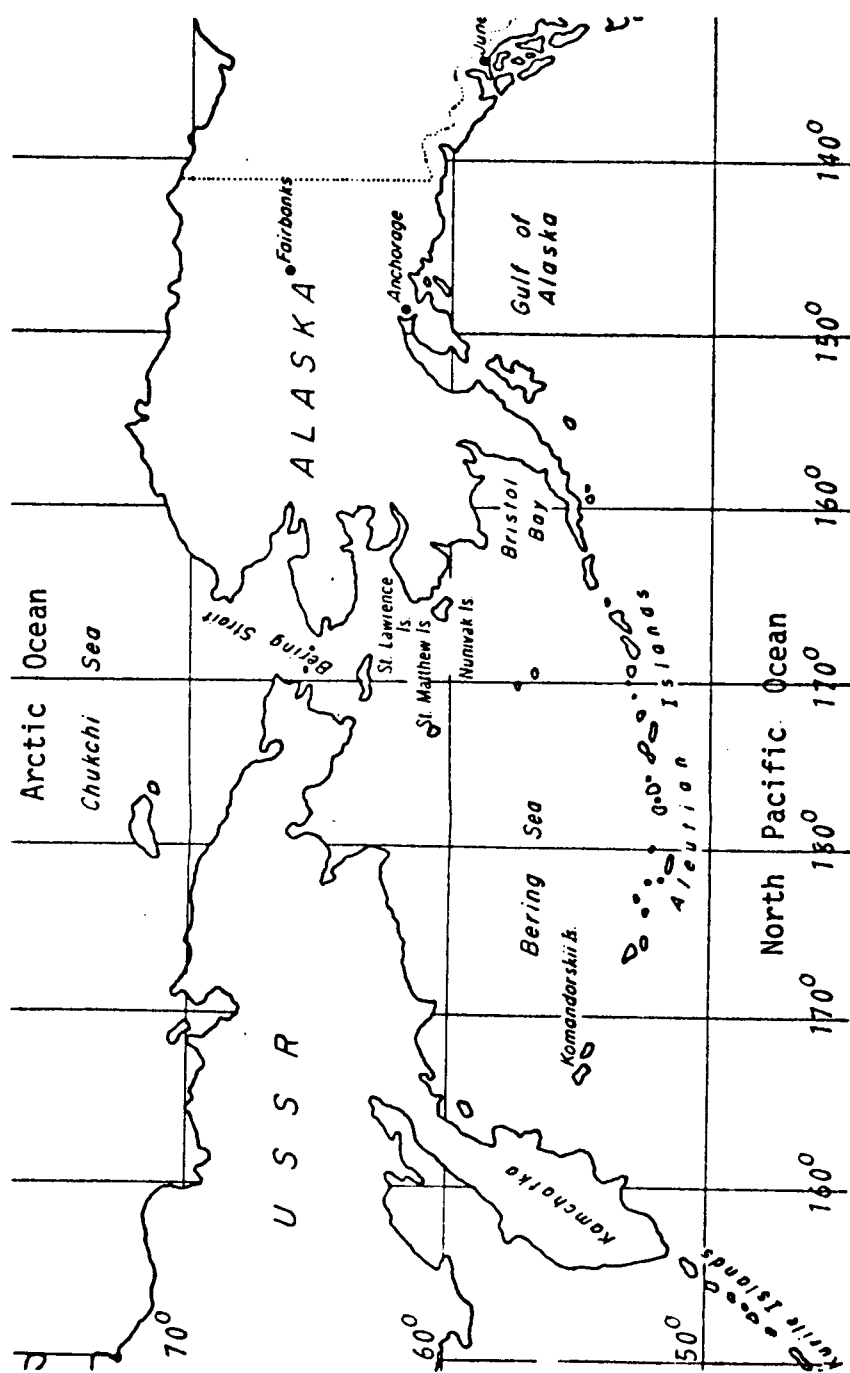


Figure 1. Map of the Bering Sea Region. (Adapted from Hood and Kelley 1974.)

because of the possible existence of the Bering Land Bridge in this region (Hopkins 1967). The previous studies of the biogeography of the region can be compared to the results of this study of theoretical island biogeography. The depauperate nature of the flora of this region and the relatively simple structure of the plant communities also permit the development of other indices and methods of analysis that are useful for interpreting biogeographic patterns.

CHAPTER 1

THE THEORY OF ISLAND BIOGEOGRAPHY AS STATED BY MACARTHUR AND WILSON

During the development of their theory of island biogeography, MacArthur and Wilson (1963, 1967) noted two major trends that were often described by biogeographers. The first trend was a relationship between the logarithm of the number of species of an area and the logarithm of the size of the area. Preston (1962) was cited for describing this species-area relationship as a canonical result of the lognormal abundance distribution of species. MacArthur and Wilson also noted that area by itself did not have any direct effect on the number of species. The size of an area was considered to be correlated with the heterogeneity of the environment of the area.

Fewer species on islands which are more distant or isolated from source areas than "near" islands was the second major trend considered by MacArthur and Wilson in the development of their theory. Distance by itself was not thought to affect directly the number of species on an island. Instead, it was thought to affect other determinants of the number of species on an island.

MacArthur and Wilson (1967) proposed the following equilibrium model for the number of species found on an island as an attempt to link the observed patterns of species-area and isolation with biogeographical and ecological processes. The main principle of the equilibrium model was that the number of species on an island was the net result of the immigrations and extinctions of species which had

occurred during the development of the biota of the island. Figure 2 shows the proposed changes of the immigration and extinction rates during the process of colonization and the resulting increase in the number of species in the biota of the island. MacArthur and Wilson (1967) hypothesized that during the early part of the colonization process the immigration rate would be high due to the high probability of an immigrant being a new species. The extinction rate was hypothesized to be low during this time due to the relative abundance of resources and the lack of interference between species.

As the number of species increased during colonization, the rate of immigration of new species would be reduced due to the decreased likelihood of the immigrants being a new species. The increased number of species was also hypothesized to result in an increase in the extinction rate because the average population size would be reduced. The smaller populations were described as having a greater extinction rate because of the increased likelihood of extinction when the death of all of the individuals of a species occurred in a short period of time (less than one year). The increased extinction rate during the later stages of colonization was also attributed to an increased amount of interference between the species present on an island.

When the number of species for an island reached equilibrium, the biota of an island was hypothesized to have equal, but nonzero, immigration and extinction rates (Figure 2, point A). Because of the balance between the immigration and extinction rates, the number of species was described to be the result of an equilibrium phenomenon.

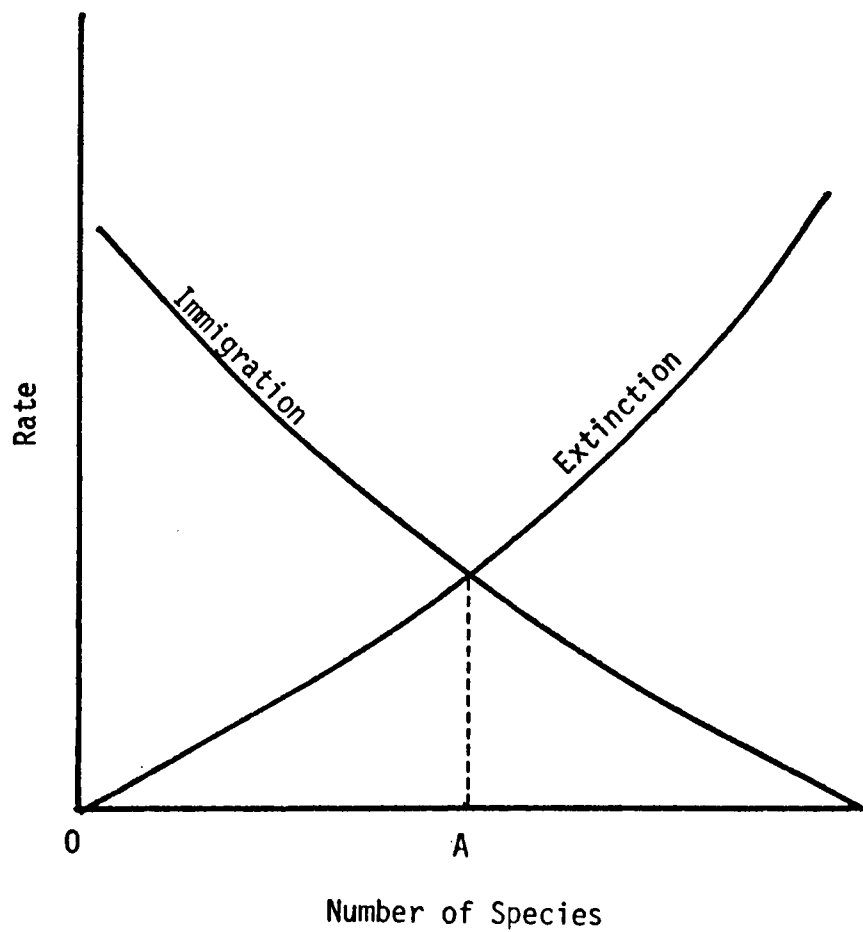


Figure 2. Equilibrium model for the number of species.
(After MacArthur and Wilson 1967.)

The equilibrium model also provided a means of representing the effect of changing the area and isolation of an island on the total number of species of the island. Figure 3 shows the hypothesized effects of these geographic variables on the equilibrium model. The area of an island was hypothesized to affect primarily the extinction rate of the model. Smaller areas were hypothesized to have smaller populations which have a greater probability of random extinction of the species for that island. The isolation of an island or its distance from a source of propagules of colonizing species was hypothesized to affect primarily the immigration rate. Islands with greater isolation were hypothesized to have lower immigration rates due to the lower number of propagules passing by the island. When the islands are very close to a source area, the size of the island was said to affect the immigration rate because of changes in its "target size." However, the change in the "target size" of islands of different sizes is trivial at greater distances.

By noticing the changes in the equilibrium value of the number of species on different types of islands, it was possible to observe two major biogeographic trends from the results of the equilibrium model. The first trend was that if isolation is held constant across a series of islands while area changes, the equilibrium number of species will increase or decrease as the corresponding extinction rate decreases or increases (Note points B, C, and E on the horizontal axis in Figure 3). Therefore, the equilibrium model of island biogeography was proposed as a possible mechanism that could explain the observed species-area relationships on islands.

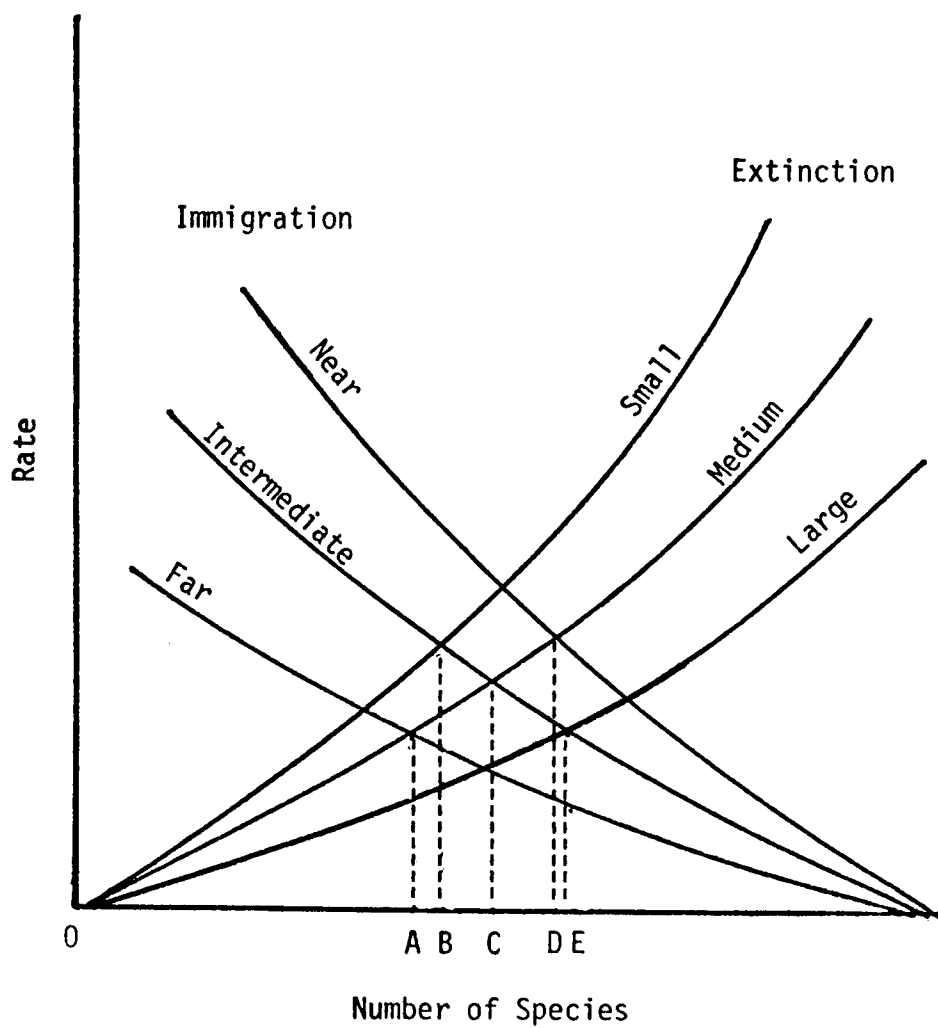


Figure 3. Equilibrium model for the number of species showing the effects of the isolation and size of an island. (After MacArthur and Wilson 1967.)

A decrease in the number of species on an island as the isolation of the island increases was the second major biogeographic trend that resulted from changing the relationships in the equilibrium model. If the area of a series of islands was constant while the degree of isolation changed, the immigration rate would decrease or increase inversely with changes in isolation. The change in the immigration rate would result in a corresponding shift in the number of species for islands of a constant size (Note the points A, C, and D on the horizontal axis in Figure 3).

The results of the equilibrium model also indicated that the slope of the species-area curve would be greater for "far" islands than for "near" islands. That can be observed graphically in Figure 3 by noting that the immigration curve for "far" islands intersects the extinction curves for islands of varying size over a greater range of numbers of species than the steeper immigration curves for "near" islands. The absence of true isolation barriers between habitat islands on mainland areas was also said to reduce the slope of the species-area curve for those areas (Preston 1962). The reduction in the slope of the species-area curve was attributed to smaller samples having a greater frequency of "rare" species that were actually transient or marginally associated with the area.

MacArthur and Wilson (1967) also considered the effect of other attributes of an island's geography on the equilibrium model. In the previous description, the isolation of an island was stated as the distance of an island from one source area. However, it is more realistic to expect the isolation of an island to depend on the

distance of an island from all possible source areas. Such source areas are not necessarily limited to mainland areas, but may also include neighboring islands. The complex biogeographic interaction of an island with many other islands has been described in the "stepping stone" hypothesis. The hypothesis stated that species may colonize an island by way of a series of colonization events on other islands. While the colonization of the farthest island in a chain is dependent upon the compound probability of all other intermediate colonization events, colonization by the "stepping stone" principle may be more likely than colonization of the island by a single dispersal event over a long distance.

Another attribute of the island which was considered by MacArthur and Wilson (1967) to have an effect on the interpretation of the equilibrium model was the heterogeneity of the environment. If the environment of an island was very heterogeneous, then multiple immigration-extinction equilibria could be functioning simultaneously. Therefore, changes in the environmental heterogeneity should be considered when the validity of the equilibrium model is assessed for a group of islands. MacArthur and Wilson (1967) suggested that indices of environmental heterogeneity be used with area in multiple regression models to predict the number of species. That approach was said to permit the empirical determination of the importance of the factors that were related to area.

CHAPTER 2

SURVEY OF RESEARCH ON THE THEORY OF ISLAND BIOGEOGRAPHY

Research which has attempted to verify the reality of the theory of island biogeography proposed by MacArthur and Wilson (1967) can be divided into two general kinds. One kind has performed experimental manipulations with biotas on artificial or natural substrates. Information on the species-area curves, immigration and extinction rates, and interisland isolation has been obtained from those experimental studies. Experimental studies, if properly designed, can test the validity of the mechanisms of the equilibrium model (Simberloff 1974).

A second and more common type of research has empirically searched for the predicted biogeographic patterns in naturally occurring biotas of islands or habitat islands. Information on the immigration and extinction history has also been occasionally included in the studies on the naturally occurring biotas (Diamond 1969). However, those data are difficult to obtain and their accuracy is debatable (Lynch and Johnson 1974).

Several researchers (Simberloff 1974, 1976b, 1978; Connor and Simberloff 1978; Connor and McCoy 1979) have recently pointed out that the observation of patterns similar to those predicted by the theory cannot be used as proof for or against the theory of island biogeography. The currently accepted approach to the theory and its use as a framework for testing additional ideas will be discussed later.

The section below gives a brief review of the general types of island biogeographic studies that have been attempted. More thorough reviews of the subject can be found in Simberloff (1974), Diamond and May (1976) and Connor and McCoy (1979).

I. EXPERIMENTAL STUDIES

Experimental studies using both artificial and natural substrates have been designed to test the equilibrium model of island biogeography. Those studies were designed with frequent sampling periods so that the colonization curves and the immigration and extinction rates could be approximated. Examination of those curves provides a direct test of the relationships proposed by MacArthur and Wilson (1963, 1967) in their equilibrium model.

Cairns et al. (1969) used plastic sponges in a freshwater environment to observe the colonization of the sponges by protozoans. They sampled the sponges periodically and observed an exponential colonization curve similar to the form predicted by the equilibrium model. Nonzero immigration and extinction rates were observed. Evidence for the presence of a continuous turnover of species, as the total number of species approached equilibrium, was also obtained. A significant negative immigration rate curve was observed during the study. However, the slope of the extinction curve was not significantly different from zero.

Schoener (1974a) analyzed data from studies on the biological fouling of flat surfaces under water (wooden panels, floats, etc.). She found that the colonization curves were similar to the form

predicted by the equilibrium model 67 percent of the time. In an experimental study, Schoener (1974b) followed the colonization of plastic sponges in a marine environment. The sponges were of different sizes and different distances from source areas. Those experiments revealed the existence of an equilibrium value for the number of species. The results also showed a larger number of species on larger sponges. The population sizes on the larger sponges were also greater. However, the turnover rates on larger sponges were greater than those on smaller sponges. That result was opposite from the one predicted by the equilibrium model of MacArthur and Wilson. The distance effect was not demonstrated by this experiment. The absence of a distance effect may be due to the absence of true isolation from the source area in the marine environment.

Schoener et al. (1978) used artificial substrates of a constant size in the marine environment for an experiment designed to determine if the effect of a latitudinal trend in the size of the species pool (decreasing number of species with increasing latitude) would be reflected in the colonization curve and the equilibrium value for the number of species. The final numbers of species across a wide range of latitude were not significantly different. The only difference observed across latitude was that the colonization curves were initially steeper in the tropical areas. Inadequate knowledge of the size of the species pool, differences in the types of species interactions in tropical and temperate areas, and insufficient substrate area to clearly demonstrate the effect of the size of the species pool were offered as explanations for the nonsignificance of results.

Simberloff and Wilson (1969, 1970) conducted biogeographic experiments on natural mangrove islands in the Florida Keys. They experimentally defaunated a set of mangrove islands and monitored their recolonization. The results of those experiments also provided evidence for an equilibrium model similar to the one proposed by MacArthur and Wilson. Simberloff and Wilson observed colonization curves similar to those predicted by the theory of island biogeography. The number of species after recolonization was similar to the number of species before defaunation. That result was also given as evidence for the existence of an equilibrium value for the number of species on an island. Nonzero turnover rates were also observed throughout the study on a control island and on the experimental islands after the number of species at equilibrium was approached. Those results further support the existence of the processes of an immigration-extinction equilibrium. An island farther from the source of colonizing propagules was observed to reach an equilibrium value for the number of species after a long period of time. That result was given as evidence for the reduced immigration rate of a far island. A similar relationship was proposed in the theory of MacArthur and Wilson.

Heatwole and Levins (1972) also analyzed the results of the experiments by Simberloff and Wilson and stated that some inherent trophic structure might be a part of the equilibrium theory of island biogeography. That interpretation was based on a similarity of the trophic structure before and after defaunation. Simberloff (1976c) dismissed the analysis of Heatwole and Levins as invalid because the

data from several islands were pooled together. Simberloff attributed the trophic similarities as being related to differential dispersal characteristics of the colonizing species and the similarity of the available resources throughout the study.

Simberloff (1976a) conducted an experiment on mangrove islands which was designed to study the effect of altering the size of an island. The results of that study showed that when the size of an island was experimentally decreased, the number of species also decreased. However, the change in the turnover rate, which was proposed by the theory of island biogeography to be greater for smaller islands, was not consistently increased or decreased with the reduction of the size of the island.

The experimental studies on island biogeography tended to support some form of an immigration-extinction equilibrium model similar to the one proposed by MacArthur and Wilson. However, the details of the components of the model were not always strictly similar to the proposed model. A fair interpretation of the experimental results is that some form of the equilibrium model exists but the proposed model probably does not yet include all of the factors that affect colonization and the number of species on islands.

The results of the experimental studies must also be interpreted within the limitation of the sampling success. It is likely that not all of the immigration and extinction events were recorded in the sampling. The proportion of the events that were missed was also unknown and debatable (Simberloff 1969, Gilroy 1975).

II. ANALYSES OF BIOGEOGRAPHIC PATTERNS OF BIOTAS ON ISLANDS

The theory of island biogeography has prompted numerous studies on biogeographic data from islands and "habitat" islands. The logic used in most of these studies was that if the theory of island biogeography was realistic, then the observed patterns of species distributions should be similar to the patterns predicted by the theory.

The general approach used in studies of natural patterns is to attempt to explain the variation of the total number of species in an area from the geographic characteristics of the area. The size of the area is a geographic attribute that has been commonly related to the number of species. Linear, semi-log and log-log species-area relationships have been examined. While MacArthur and Wilson (1967) accepted the log-log form proposed by Preston (1962), Connor and McCoy (1979) have shown that none of the forms of the species-area relationship is the best form for a majority of the studies. The species-area relationship was often stated to be dependent upon a relationship between increasing area and increasing environmental heterogeneity (Simberloff 1974). To further explain the variation in the number of species, geographic characteristics such as maximum elevation were often included in analyses as a representation of environmental heterogeneity. The effects of the geographic isolation of an island on the number of species have also been included in the analyses of studies of patterns of island biogeography. The simultaneous effects of the various geographic factors were usually

analyzed with multiple regression techniques (see review by Simberloff 1974).

An example of an exception to the general pattern of island biogeography studies described above is a study of birds on the Channel Islands (Diamond 1969). That study attempted to include an analysis of turnover rates similar to those included in the experimental studies. The results and interpretations by Diamond were criticized by Lynch and Johnson (1974) because of possible inadequacies and inconsistencies in the data compiled for Diamond's analysis.

Connor and McCoy (1979) and Simberloff (1974, 1976b) have presented fairly complete surveys of research that has related the naturally occurring patterns of species to the theory of island biogeography. Therefore, the review of studies of island biogeography presented here is not comprehensive, but is intended to present the range of taxa, regions, geographic and biotic variables, and relationships that have been previously studied.

The theory of island biogeography was developed partially from the distributional patterns of birds on oceanic islands. Birds are by far the most common taxon that has been used for studies of island biogeography (for examples see Abbott 1974, 1978; Diamond and Mayr 1976; Lack 1969). Studies of island biogeography have also been conducted on snails (Heller 1976), insects (Abbott 1974, Goldstein 1975), reptiles (Case 1975), and plants (Amerson 1975, Power 1975, McNeil and Cody 1978, Johnson and Raven 1973) on true islands.

Most of the studies of island biogeography tended to support the species-area relationship expected from the theory of island

biogeography. An example of an exception was found by Diamond and Mayr (1976) who reported the absence of a species-area relationship for birds with good dispersal ability. Heller (1976) also explained the absence of a species-area relationship in the distribution of snails on the Aegean Islands because of a previous absence of isolation during the Pleistocene when continental connections existed.

MacArthur and Wilson (1967) also envisioned the application of the theory of island biogeography in the interpretation of biogeographic patterns on habitat islands in continental areas. Studies in that type of area have since included arthropods in caves (Vuilleumier 1973), fish and snails in lakes (Barbour and Brown 1974, Aho 1978a, 1978b), mussels in rivers (Sepkoski and Rex 1974), birds and mammals on mountain tops (Vuilleumier 1970, Brown 1971, Smith 1974, Johnson 1975, Picton 1979), mammals in nature preserves (Miller and Harris 1977, Helliwell 1976, Usher 1979), weeds in vacant lots in urban areas (Crowe 1979, Davis and Glick 1978), and parasites on patches of host plants (Strong 1974, Strong and Levin 1979).

The results of searching for a species-area relationship for these habitat islands were generally consistent with the relationship predicted by MacArthur and Wilson. Similar to the pattern hypothesized by MacArthur and Wilson, the habitat islands tended to have a smaller value for the slope of the species-area curve than the true islands. However, the species-area relationship and relationships with distance may be obscured by the absence of true isolation between habitat islands on continental areas (Brown 1971, Helliwell 1976, Miller and Harris 1977).

At the time this study was initiated, most of the studies of island biogeography had been performed with data from the temperate and tropical regions of the world. One stated purpose for studying the biogeography of the flora of the Aleutian Islands was to extend the latitudinal range of the regions considered in investigations of island biogeography. Nilsson and Nilsson (1978a, 1978b) have since reported on the island biogeography of plants on islands in a lake in Sweden and on birds from the same region. Their studies were located slightly farther north than the Aleutian Islands, but in a more temperate climatic region.

Numerous additions and modifications have been made to the variables used to represent the area and environmental heterogeneity of an area in the later studies of island biogeography. Simpson (1974) and Juvik and Austring (1979) used the size of islands from previous time periods when sea level was lowered during Pleistocene glaciations. The percentage of an island covered with vegetation and the number of species of plants have often proved to be important predictors of the number of animal species on islands (Power 1972, 1975; Amerson 1975). The structural complexity of host plants was also successfully included in the analyses of the biogeography of plant parasites (Lawton and Schroder 1977, Strong and Levin 1979). The number of soil types was used by Johnson and Simberloff (1974). Maximum elevation is commonly included in the analysis as an index of environmental heterogeneity (Diamond 1972, Hamilton et al. 1964, Case 1975, Power 1975).

The concept of the isolation of an island or habitat island has been represented in a number of ways. A simple representation of

isolation was the distance from the island to the mainland source area (for examples see Case 1975, Diamond 1972). However, that has often proved to be unsatisfactory (for examples see Abbott 1974, Johnson and Raven 1973, Diamond 1969, Juvik and Austring 1979). MacArthur and Wilson (1967) clearly stated that isolation was not likely to be that simple to represent. In their "stepping stone" hypothesis, they attempted to take into account the effect of the presence of other islands on the overall isolation of an island. In response to ideas that are similar to the "stepping stone" hypothesis, researchers have also represented isolation with measures such as distance to the nearest neighboring island (Hamilton et al. 1964, Amerson 1975, Power 1975, Johnson 1975, Simpson 1974), distance to the center of the archipelago (Johnson and Raven 1973), and average interisland distance (Cook 1974).

The distance variables were usually less important than the area and environmental heterogeneity variables in the prediction of the number of species on an island. The predictive importance of different types of geographic variables was usually analyzed with stepwise multiple regression techniques. The geographic variables were used as independent variables and the number of species as the dependent variable (for examples see Johnson et al. 1968, Johnson and Raven 1973, Power 1972, 1975). That analysis technique provided information on the relative portion of the variance in the number of species that was explained by the geographic variables. Relationships between the number of species and the distance variables were often not significant. The general absence of clear and significant distance

relationships may be due to an inadequate representation or understanding of an island's isolation (Connor and Simberloff 1978). Carlquist (1967) commented that the environmental limitations of an island may also obscure the effects of isolation. Data on long distance dispersal and the effectiveness of dispersal mechanisms are also difficult to measure directly.

In addition to the total number of species, several other variables have been used to represent different attributes of a biota. Terborgh (1973) analyzed and interpreted the biogeographic patterns of the number of species in bird families. Hamilton and Rubinoff (1964, 1967) and Johnson and Raven (1973) analyzed the number of endemic species on the Galapagos Islands. Nilsson and Nilsson (1978b) studied the number of species of plants with different dispersal types. In an analysis of isolation effects, Diamond et al. (1976) grouped bird species in the Solomon Islands by dispersal ability. Hunt and Hunt (1974) examined biogeographic relationships for birds in different trophic groups. Power (1975) related indices of species diversity to the structural diversity of the vegetation of the island. Terborgh (1973), Power (1975), Abbott (1977), and Connor and Simberloff (1978) analyzed relationships between the indices of the similarity of species composition and interisland distance.

In general, the usage of most of the variables reviewed above has been successful in the sense of statistical significance. However, relationships representing the effects of isolation have not always been reported as successful. Since nonsignificant results are often dismissed as meaningless (Connor and Simberloff 1978, Connor and

McCoy 1979), they are not usually reported. Therefore, it is difficult to know exactly what range of hypothesized relationships and variables has been considered. The results of this study will report at least briefly all nonsignificant relationships that were analyzed.

Recent papers (Simberloff 1978, Connor and Simberloff 1978, Connor and McCoy 1979) have criticized the logic of using biogeographic patterns similar to those predicted by the theory of island biogeography as evidence for the equilibrium model proposed by MacArthur and Wilson (1967). Simberloff (1978) showed by simulation that stochastic and deterministic colonization events were both likely to produce results not significantly different from those commonly observed for the similarity of species compositions between islands. Since the predicted pattern of species similarity was not the result of only one type of process, evidence of the predicted pattern does not strictly imply the existence of the equilibrium model of island biogeography. Connor and Simberloff (1978) stated similar arguments for the expected amount of species similarity among islands. They also presented a general critique of the methods used for collecting and analyzing biogeographic data. Diamond and Mayr (1976) suggested that the species-area curve may be only an artifact of the lognormal distribution of species abundance. Connor and McCoy (1979) presented several logical dilemmas that affect the interpretation of the species-area curve. Those dilemmas were also centered around the possibility that more than one mechanism could produce the same species-area pattern. Connor and McCoy (1979) also presented

evidence that a consistent form (log-log, semi-log, etc.) of the species-area curve could not be declared. Until those dilemmas are eliminated, empirical proof of the theory of island biogeography is not possible.

Because of the questions raised in the logic of using analyses of natural biogeographic patterns as evidence to support the theory of island biogeography proposed by MacArthur and Wilson (1967), especially their equilibrium model, this study cannot be considered a rigorous test of the theory. In this study, the theory of island biogeography was used as a framework upon which to structure the analyses of biogeographic data and the development of secondary ideas.

CHAPTER 3

THE ENVIRONMENT OF THE ISLANDS OF THE BERING SEA REGION

I. GEOGRAPHY

Most of the islands in the Bering Sea Region are located along the southern boundary of the Bering Sea in the Aleutian Islands. The Aleutian Islands are an arc-shaped chain of islands extending for about 1760 kilometers southwesterly from the end of the Alaska Peninsula toward the Kamchatka Peninsula of Asia (Figure 1, page 2). The Aleutian Island Chain contains over 200 islands (Sekora 1973). The Commander Islands (Bering and Copper) are located between the west end of the Aleutian Island Chain and the Kamchatka Peninsula. Other islands that are located in the northern and eastern regions of the Bering Sea are the Pribilofs (St. Paul and St. George), Nunivak, St. Matthew, and St. Lawrence (Figure 4).

The Aleutian Islands are of volcanic origin. The subduction of the Pacific Plate under the North American Plate is presently given as the explanation of the pattern of volcanism which forms the island chain along the Aleutian Ridge (Coats 1962, Anderson 1970). Evidence for the tectonic activity includes the presence of the Aleutian Trench south of the island chain, and the occurrence of seismic activity and volcanism in the island chain.

Most of the present islands in the Aleutians have remained isolated from continental regions and other islands throughout the last 10,000 years. Hopkins (1972) has presented evidence for the

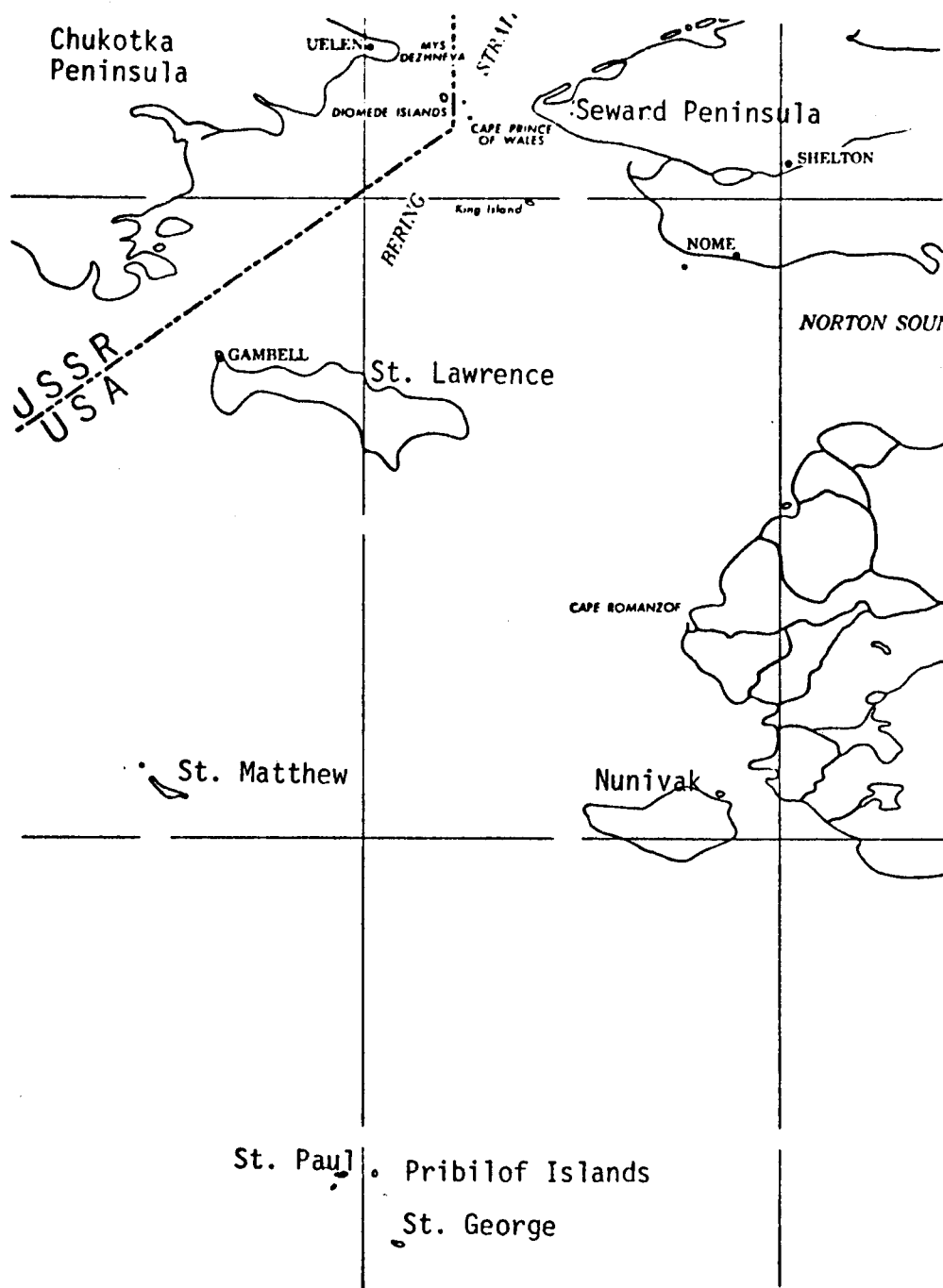


Figure 4. Islands in the northern and eastern Bering Sea.
 (Map adapted from 1:10,000,000 scale World Outline Maps, sheet 29,
 Army Map Services, Corps of Engineers.)

lowering of sea level during the Wisconsin glacial maximum (prior to 10,000 years before present) by about 100 meters. The dashed line in Figure 5 shows the boundary of the islands at that lower level. The regions from Adlia to Tanaga and Amchitka to Kiska would have been joined into continuous areas when the water was at this level. All of the islands in the chain as far west as Umnak were probably connected to the western end of the Alaska Peninsula.

The continental shelf of the eastern and northern Bering Sea is of significance to biogeographers and anthropologists because it was exposed during the Pleistocene glacial maximum and formed a terrestrial connection between Asia and North America. That connection is known as the Bering Land Bridge (for a general review, see Hopkins 1967). All of the islands in the northern part of the Bering Sea are on this land bridge and were connected to both Asia and North America. Hopkins (1973) has reviewed a longer history of the sea level changes in the Bering Sea Region.

II. GEOLOGY

The islands of the Bering Sea Region are almost all volcanic in origin. Agattu Island (Figure 5) is an exception to the general pattern of volcanic rock types present in the Aleutians. It is composed of sedimentary rocks which were later uplifted (Gates et al. 1971). The volcanic rock types in the region range from Mesozoic basalts to Tertiary and Recent andesites (Coats 1956). The only geographic pattern in the rock types is that the more recent rocks tend to be toward the northern side of the Aleutian Islands (Coats 1962).

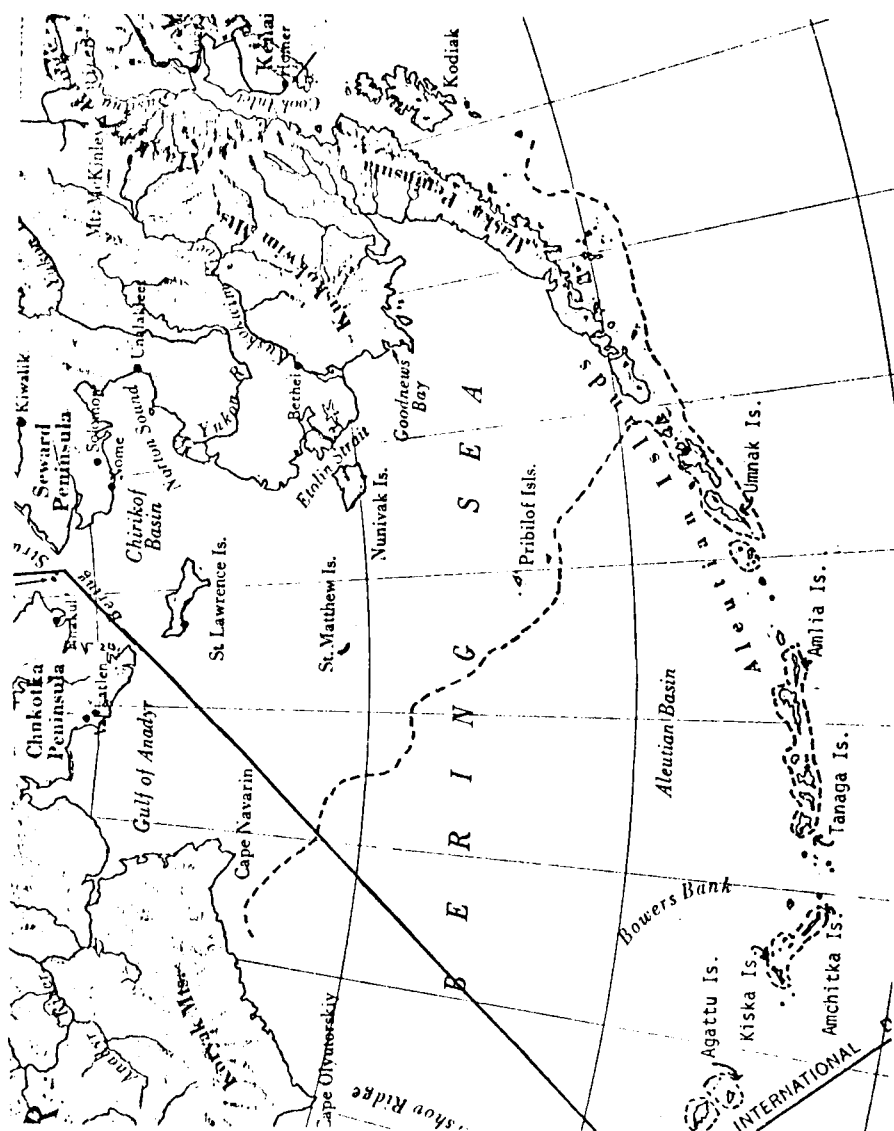


Figure 5. Map of the Bering Sea Region showing the shoreline during the Wisconsin Glacial Maximum. The dashed line is the current 100 meter depth contour. (Map adapted from Hultén 1968, depth information from NOAA 1976 and Defense Mapping Hydrographic Center 1943.)

Volcanic activity is still present in the Aleutian Islands. Black (1974, 1976) reported four to six major or minor ash layers on Umnak and Adak in the last 10,000 years. Stewart (1975) and Coats (1950) have reviewed the incidence of volcanism in the Aleutian Islands in the last 200 years. The long term effects of volcanic ash falls on the vegetation and topography of the islands are generally unknown. Wilcox (1959) reported that ash falls in Alaska of less than one foot were not observed to have a significant effect on the vegetation after a few years. The vegetation on areas of new lava flows must go through the process of primary succession. In contrast to ash falls, lava flows have long term effects on the vegetation and topography.

The southern and western parts of Alaska were described as having been under a continuous continental ice sheet during the Wisconsin glacial maximum (Hopkins 1972). Black (1974) presented evidence that the ice sheet may have extended out the Alaska Peninsula and the Aleutian Island Chain to Umnak. However, Black (1974, 1976) and Everett (1971, 1977) did not observe any evidence of a continental ice sheet during the Wisconsin on the central and western part of the island chain. The current interpretation of glaciation in the central and western Aleutian Islands is that mountain glaciers, unusually heavy snowfields, and ice sheets were probably formed locally on islands throughout the chain. The local glaciers remained until about 10,000 to 12,000 years ago (Black 1976). It is not known if they occupied all of the land surface and eliminated all of the vegetation of the region. The Bering Land Bridge and the west central part of Alaska were not glaciated during Wisconsin time (Hopkins 1972).

III. SOILS

The soils of the islands of the Bering Sea Region range from unweathered lava flows to sand at dune sites to peat that is several meters thick. Everett (1971, 1977) has presented an explanation of the soil formation processes on Amchitka Island in this region. The primary factors affecting the soil formation process in this region are climate and vegetation. Most of the types of volcanic bedrock weather readily and specific differences in the rock types do not significantly affect the soil formation processes (Everett 1977).

Soils with a thick peat horizon usually form in the bottoms and on the lower slopes of valleys. The peat layer thins to expose the mineral soil and rocks on the upper slopes and ridge crests. The formation of this peat soil is attributed to the very slow rate of decomposition of organic matter. Decomposition is slow because of low soil temperatures throughout the year and the general saturation of the soil. Another pattern in the thickness of the peat layer corresponds with changes in elevation. Ulrich (1946) noticed an increase in the patchiness of the vegetation and a reduction in the size of the plants at higher elevation. Corresponding with the changes in the vegetation, a thinner peat layer is observed at higher elevations. The peat on Amchitka Island is younger than 10,000 years in age (Everett 1977). The age of the peat indicates that most of it has formed since the melting of the last local ice sheet.

IV. OCEANOGRAPHY

The primary aspects of oceanography which have significant effects on the biogeography of the flora of the region are the pattern of the currents and the temperatures. The pattern of the currents is important in the potential transport of propagules throughout the region. The pattern of the water temperatures of the Bering Sea and the North Pacific Ocean is the major determinant of the climate of the region (Armstrong 1977).

The general scheme of the major currents is shown in Figure 6. The currents close to the islands and between the islands are complex and not well known (Reed 1971, Favorite 1974). Significant tidal currents in the interisland passes have been reported by Favorite (1974). Anticyclonic gyres within sections of the Aleutian Island Chain have also been hypothesized (Hughes et al. 1974). It is interesting to note that the Aleutian Island chain is generally isolated from the coastal region of the Kamchatka Peninsula by the pattern of the currents. The currents of the northern part of the Bering Sea result in a net flow north through the Bering Strait into the Arctic Ocean (Coachman et al. 1975).

Hypotheses for the patterns of the currents in the Bering Sea Region during the presence of the Bering Land Bridge have not been reported. Due to the blockage of the net northward flow through the Bering Strait, it is possible that the flows into and out of the Bering Sea through the region of Aleutian Islands were different when the Bering Land Bridge was present. However, the major currents were

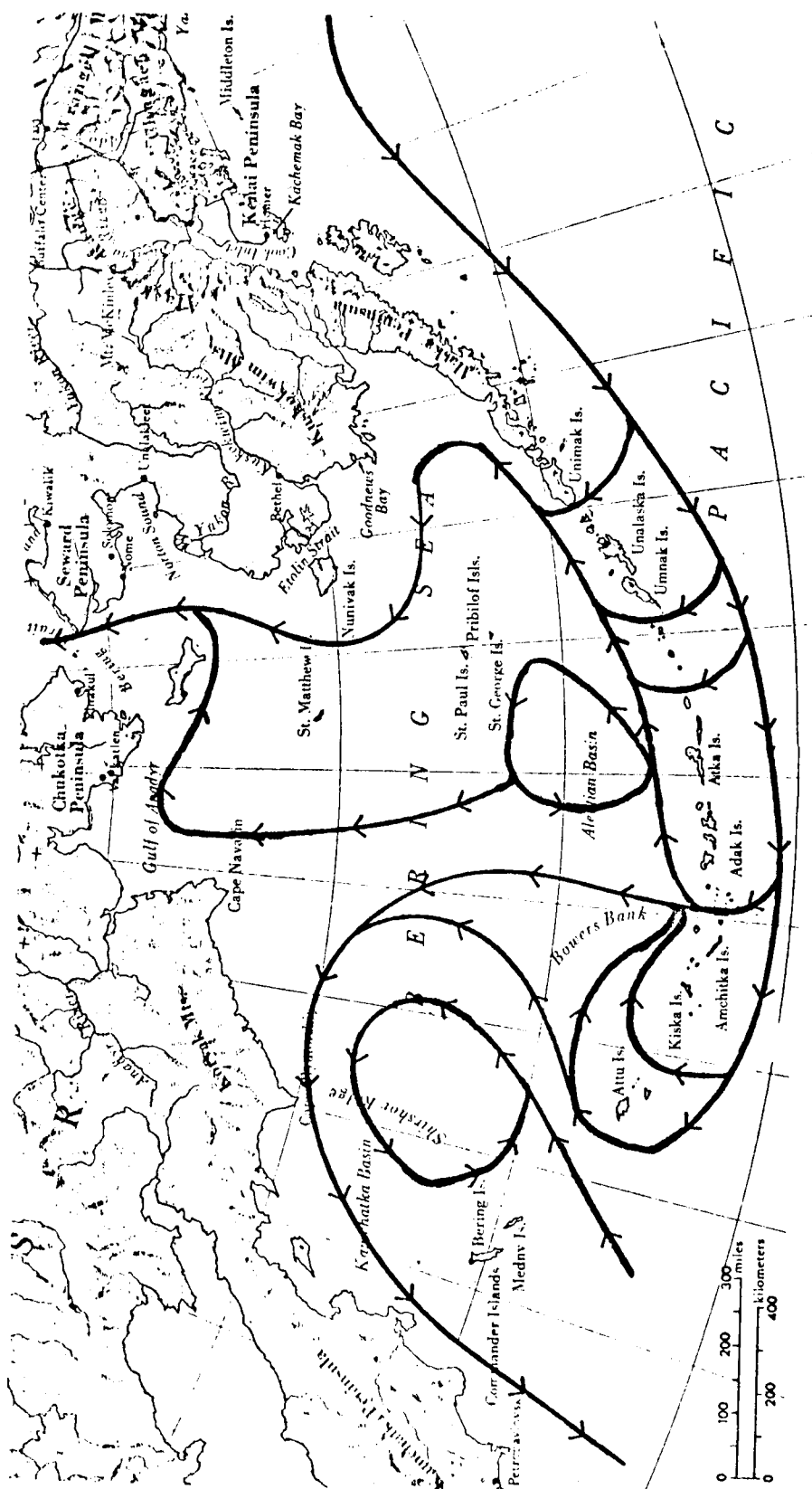


Figure 6. Schematic representation of major currents in the Bering Sea Region. (Map adapted from Hultén 1968; current information from Hughes et al. 1974.)

probably similar to the ones presently found in the southern and western Bering Sea.

V. CLIMATE

The climate of the islands in the Bering Sea Region is determined mainly by the pattern of the temperature of the water bodies of the region (Armstrong 1977). Major air pressure systems form as a result of the heating and cooling of the air as it passes over the colder Bering Sea and the warmer Pacific Ocean waters. The north Pacific is warmed by waters moving north in the Japanese Current. Those air pressure systems result in a maritime climate with frequent cloud cover and fog over the islands. The maritime climate is characteristically cooler in the summer and warmer in the winter than continental regions at similar latitudes (Watson 1968). Since cloud cover is very common, the overall insolation at ground level is significantly lower than the expected insolation for regions of this latitude (Armstrong 1977). The reduced insolation and the thermal stabilization by the surrounding water bodies result in a daily air temperature range of about 4° C. (Armstrong 1977).

Permafrost is not known in the Aleutian Islands. It may be under only part of St. Lawrence Island (Wahrhaftig 1965). However, soil temperatures remain generally below 8° to 10° C (Everett 1977).

The islands in the northern part of the Bering Sea are generally cooler in the winter and receive less precipitation than the Aleutian Islands (U. S. Weather Bureau 1965). The mean temperature for Adak in January is approximately 1° C while on St. Lawrence it is about

-12° C. However, in July the means are 9° C on Adak and 8° C on St. Lawrence. The eastern Aleutian Islands are slightly warmer in the summer with a mean temperature of 10° C (Watson 1968). The Aleutian Islands receive about 1500 mm. of total precipitation per year. In contrast, St. Lawrence Island, which is in the northern part of the Bering Sea, receives only about 300 mm. of total precipitation per year (U. S. Weather Bureau 1965). All of the precipitation measurements for the region are relative due to problems that are associated with measuring precipitation in conventional rain gauges during periods of high winds. Moisture from blowing fog that is removed by the vegetation is also not measured.

The climatic history of the Aleutian Islands and the Bering Land Bridge has been interpreted from palynological evidence. Hopkins (1972) stated that the Bering Land Bridge probably had a continental climate which is drier than the one that is presently observed over the Bering Sea. The climate during the Hypsithermal was slightly warmer and drier than the present climate or the climate immediately after the Wisconsin glacial maximum (Heusser 1973). However, a study of pollen profiles from Adak Island did not show the effect of the Hypsithermal on the vegetation (Heusser 1978). Black (1974) stated that a slightly higher sea level appears to have existed during the warmer Hypsithermal interval.

VI. VEGETATION

The vegetation of the islands of the Bering Sea Region has been classified as maritime tundra (Amundsen 1977). With the exception of

a few trees which were planted in the Aleutians during World War II and forests on part of Kodiak Islands, the islands are treeless. Portions of the eastern part of the Aleutian Islands have plant communities with erect shrubs such as Salix Barclayi and Alnus crispa (Hultén 1960), but communities with erect shrubs as dominants are not found on the rest of the islands. The overall height of the vegetation is less than 50 to 75 cm. In protected valley bottoms, it may reach 100 to 150 cm. in height. Most of the community types in this region are some form of a crowberry-sedge-grass-lichen meadow (Amundsen 1977, Shacklette et al. 1969, Hultén 1960). Some of the higher elevation areas also have plant communities with a significant heath component (Heusser 1978).

It is unusual for a region of the latitude of the Aleutian Islands to be treeless. The vegetation of the adjacent continental areas is typically a coniferous forest (Good 1974). Current explanations for the absence of trees in the vegetation include the reduced level of insolation due to the high frequency of cloud cover, generally low soil temperatures, severe winds and isolation of the islands (Amundsen 1977). The lower insolation reduces productivity. The low soil temperatures retard respiration. Severe winds cause transpiration stress in the shoots during the winter when the soil moisture is frozen and unavailable. Winds also cause physical abrasion with ice particles to the exposed shoot parts. Tree seedlings planted on Adak in 1976 were observed in 1979 to be undamaged in protected sites. On exposed sites or when the shoot extended above the surrounding vegetation, dead trees and shoot tips were frequently observed. The successful production of viable seeds has not been observed in Sitka spruce (Picea sitchensis)

trees planted on Adak Island. Viable seeds were found in cones collected from spruce trees on Sand Point in the Shumagin Islands.

The structure of the vegetation is usually a thick rhizomatous mat. Effective sexual reproduction is not common in the species of this flora. The fragmentation of rhizomes is probably the most effective mode of reproduction. The rhizomes of different species are complexly interlaced. Because of the complex rhizome pattern and the frequency of vegetative reproduction, it is usually very difficult to determine the extent of an individual plant.

Colinvaux (1964, 1967a, 1976b), Heusser (1973, 1978) and Nybakken (1966) have conducted palynological studies on islands in the Bering Sea Region. They all concluded that the vegetation of the islands has not changed significantly in the last 10,000 years. Nybakken (1966) reported no change in the vegetation on Umnak for the last 5,000 years. Heusser (1973) noted an increase in willow pollen on Umnak Island during the last 10,000 years. The increase in willow pollen was said to correspond to warming during the Hypsithermal. A similar change in the pollen profiles was not observed by Heusser (1978) on Adak Island in the central Aleutians. Colinvaux (1967b) reported an increase in spruce pollen about 10,000 years ago on the Pribilof Islands. He hypothesized that the warming at the end of the glacial period may have permitted the establishment of spruce along the southern edge of the Bering Land Bridge. However, it is not clear if the forests of Asia and North America ever merged.

Colinvaux (1967a) noticed the deposition of birch pollen possibly from a birch tundra which may have occurred on St. Lawrence

Island immediately after the last glacial period. Increases in spruce and alder in the pollen profile were interpreted as a possible response to the climatic warming during the Hypsithermal (Colinvaux 1967a, 1967b). The pollen grains of those genera were thought to have originated not from plants on the island, but from advancing shrub and forest areas on the mainland.

CHAPTER 4

MATERIALS AND METHODS

I. SELECTION OF ISLANDS AND SOURCE AREAS

Floristic and geographic data were compiled for 29 islands in the Bering Sea Region. The flora of six mainland areas that were considered potential source areas for the flora of the islands was also tabulated. The availability and adequacy of floristic information for vascular plant species were the criteria used to determine which islands were included in the floristic data set. With the exception of Amchitka and Adak Islands, collections of the flora of most of the islands included in this data set are probably incomplete.

Table 1 lists the islands included in the floristic data set. Figure 7 shows the location of these islands. Nineteen of the 29 islands included in this biogeographic study are part of the Aleutian Island Chain. Five of the remaining islands are in the northern part of the Bering Sea. They are St. Paul, St. George, Nunivak, St. Matthew and St. Lawrence. Bering and Copper Islands were also included from the Commander Islands which are west of the Aleutian Island Chain. Peninsula and Big Konuiji Islands are a part of the Shumagin Islands which are south of the Alaska Peninsula. Kodiak Island is located south of the eastern part of the Alaska Peninsula.

The boundaries of the mainland source areas (Figure 8) were determined from the geographic and physiographic boundaries of the regions. The Alaska, Kamchatka, Seward, and Chukotka Peninsulas are

Table 1. Islands from the Bering Sea Region included in the floristic data set.

Island Name	Island Group
Sanak	Aleutian
Unimak	Aleutian
Akun	Aleutian
Akutan	Aleutian
Unalaska	Aleutian
Umnak	Aleutian
Carlisle	Aleutian
Amlia	Aleutian
Atka	Aleutian
Adak	Aleutian
Kavalga	Aleutian
Gareloi	Aleutian
Semisopochnoi	Aleutian
Amchitka	Aleutian
Kiska	Aleutian
Buldir	Aleutian
Alaid	Aleutian
Agattu	Aleutian
Attu	Aleutian
Copper	Commander
Bering	Commander
Big Konuiji	Shumagin
Peninsula	Shumagin
Kodiak	----
St. Paul	Pribilof
St. George	Pribilof
Nunivak	Northern Bering Sea
St. Matthew	Northern Bering Sea
St. Lawrence	Northern Bering Sea

Figure 7. Location of islands included in the floristic data set. (Map adapted from Hultén 1968.)

Sanak (1), Unimak (2), Akun (3), Akutan (4), Unalaska (5), Umnak (6), Carlisle (7), Amlia (8), Atka (9), Adak (10), Kavalga (11), Gareloi (12), Semisopochnoi (13), Amchitka (14), Kiska (15), Buldir (16), Alaid (17), Agattu (18), Attu (19), Copper (20), Bering (21), Big Konuiji (22), Peninsula (23), Kodiak (24), St. Paul (25), St. George (26), Nunivak (27), St. Matthew (28), St. Lawrence (29).

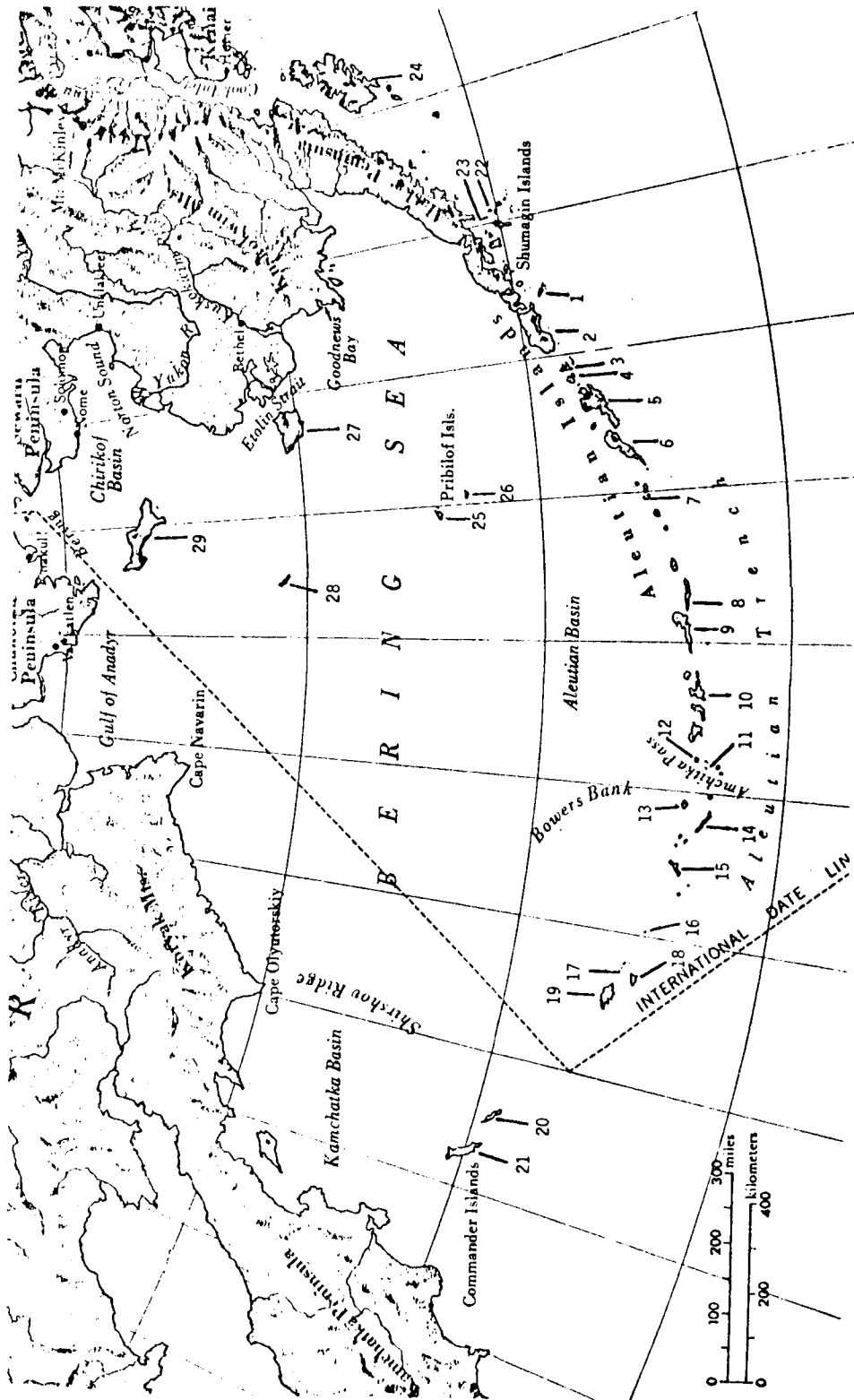


Figure 7.

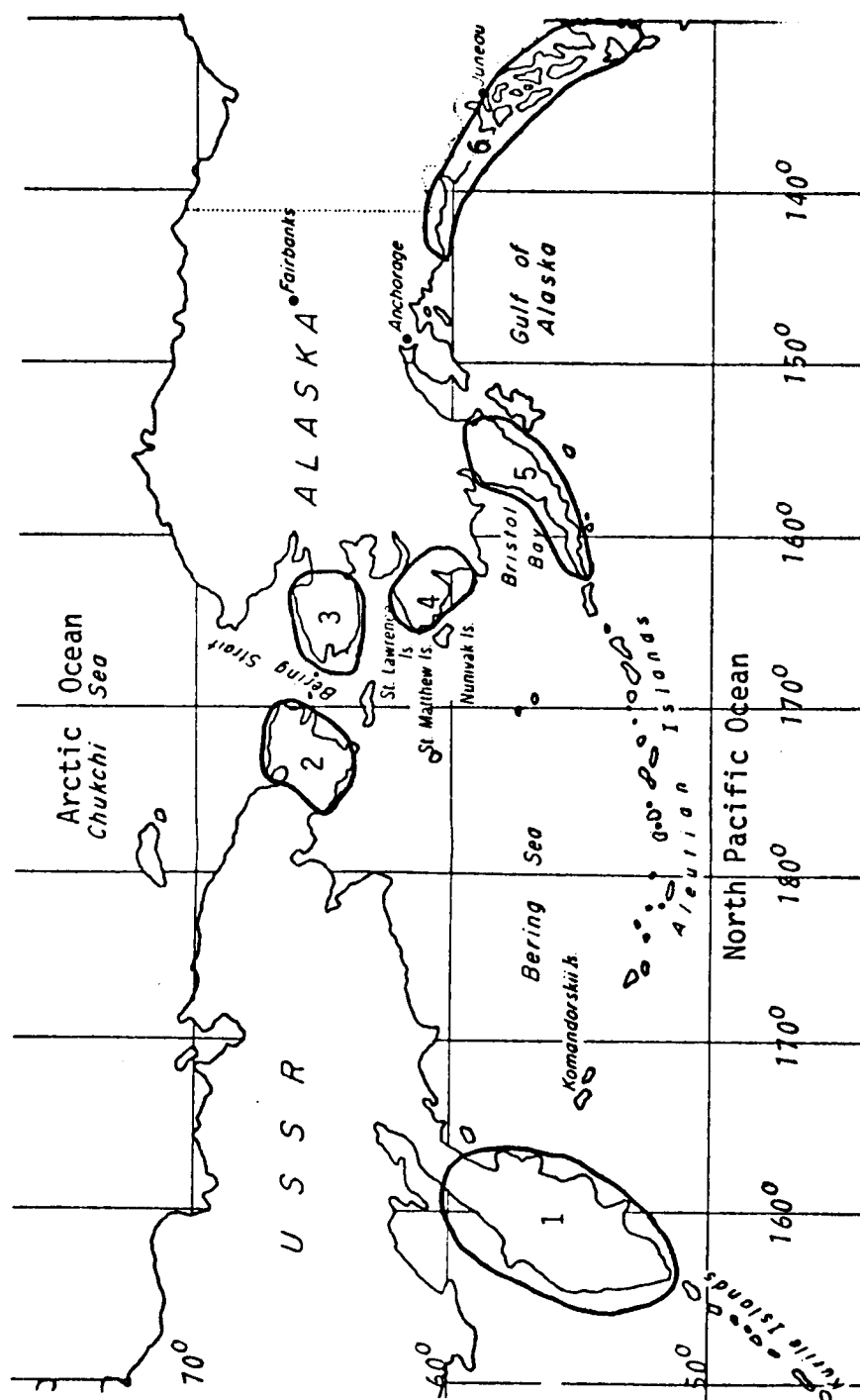


Figure 8. Location of source areas included in the floristic data set. (Map adapted from Hood and Kelley 1974.) Kamchatka Peninsula (1), Chukotka Peninsula (2), Seward Peninsula (3), Yukon Plain (4), Alaska Peninsula (5), Southeastern Coast (6).

all geographically distinct areas. The Alaska and Kamchatka Peninsulas appeared to be the most logical source areas for the Aleutian and Commander Islands. Seward and Chukotka Peninsulas were added to the floristic data set when the islands in the northern Bering Sea were added to the study. The regions are also biogeographically interesting since they are in the region of the Bering Land Bridge. The Yukon Plain source area corresponds roughly to the Yukon-Kuskokwin Coastal Lowland Physiographic Division of Wahrhaftig (1965). The Yukon Plain was included as a source area because this area was not glaciated during the Wisconsin glaciation and may have been a refugium for plants during that time (Hopkins 1972). The southeastern coastal area of Alaska was added as a source area in the data set because the pattern of the currents (Figure 6, page 31) indicated that it might be a potential source area for water dispersed propagules.

II. FLORISTIC DATA

The floristic data for vascular plants for the islands were compiled primarily from the published works of Hultén (1928-1930, 1960, 1968, 1973). Hultén has been fairly thorough in compiling floristic records and reviewing specimens from both American and Asian collections. I searched for reports of plant collections made since the last published work of Hultén. Most of these collections have been made by either workers from The University of Tennessee, Knoxville (Amundsen 1977, Clebsch et al. 1975) or the U. S. Fish and Wildlife Service (Byrd 1976, Day and Early 1977, and Moe and Day 1977). I also reviewed the specimens in the herbarium of the Aleutian Island National

Wildlife Refuge on Adak Island. Information of the flora of the Yakutat Peninsula in the southeastern coastal source area was obtained from an unpublished report by Alaback (1975). The presence/absence data set of the flora for all of the islands and source areas used in this study is in the Appendix (Table A-1). Bibliographic information for these data is included in that table.

The nomenclature and taxonomy of Hultén (1968) were used for the compilation of the floristic data. Synonymous records due to nomenclatural changes were identified and combined. The information in Hultén (1960, 1968) was adequate for discerning the history of the nomenclatural changes. Species which were known to be introduced to the region were not included in the floristic data set. The inclusion of introduced species would result in a bias in the data that would not reflect the natural biogeographic patterns. The floristic information for all subspecies of a species were combined. Most of Hultén's (1968) subspecies designations were used for geographically distinct sections of the distribution of species. Because the subspecies rarely have overlapping distributions, little ambiguity was added to the data when the subspecies were combined.

Numerous variables for the islands were synthesized from the presence/absence data in the floristic data set. The fundamental variable synthesized from the floristic data was the total number of species per island, the main biogeographic variable predicted by the theory of island biogeography developed by MacArthur and Wilson (1967). Tabulations of the number of species for diverse families (Table 2) were also compiled, and used in analyses in which it was attempted to

Table 2. Families for which the number of species were separately analyzed (nomenclature after Hultén 1968).

Family Name	Common Name
Gramineae	Grasses
Cyperaceae	Sedges
Orchidaceae	Orchids
Caryophyllaceae	Pinks
Cruciferae	Mustards
Saxifragaceae	Saxifrages
Rosaceae	Roses
Ericaceae	Heaths
Scrophulariaceae	Figworts
Compositae	Composites

determine if differences existed between the biogeographic patterns of plant families. The number of families per island was also determined. The data for these floristic variables of the islands are reported in the Appendix (Table A-2).

Plant species were assigned to groups based on their type of dispersal. Table 3 shows the groups of dispersal types designated. While these dispersal types are similar to the ones used by Nilsson and Nilsson (1978b), the development of the groups and the assignment of species to the groups was done independently of their work. Information on the dispersal types of species in published references such as Ridley (1930) was used when possible. If information was not available in this source, the descriptions and drawings in Hultén (1968) were used to assign species to dispersal groups. Personal observations of part of the flora were also used to assign species to dispersal groups. The dispersal code for each species is a part of

Table 3. Description of dispersal types used to form groups of species.

Description of Dispersal Type	Mode of Dispersal
Spores	wind, water
Very small seeds (e.g., orchids)	wind, water
Seeds with plumes	wind
Seeds in fleshy fruits	water, birds
Caespitose, graminoid plants without extensive rhizomes ^a	severe winds, over ice
Seeds with wings	wind
Plants found in wet or aquatic habitats	water
Seeds in capsules	wind
Graminoid plants with extensive rhizomes ^a	water, wind (?)

^aFragments of vegetative parts of the plants were the structures considered as the dispersal units of these types.

the presence/absence data set (Appendix, Table A-1). Appendix Tables A-3 through A-11 also provide species lists for each dispersal type and specific reference information. The number of species in each dispersal group for the islands are reported in the Appendix, Table A-12.

Other criteria by which the numbers of species for the islands were tabulated were related to the reported presence of species in source areas. The number of species on an island was counted for two different relationships to the flora of each source area. The first count was the number of species on an island which were also reported from the flora of a given source area. This count variable will be called the number of species on an island which are in common with a source area. A second count was made for the species on an island which were also reported from the flora of a given source area and not reported from any other source area. This count will be referred to as the number of species on an island which are restricted to a given source area.

The count of the number of species for each island which were also reported from all six source areas is another grouping of the species which is related to the flora of the source areas. This count was used as an indication of the number of universally distributed species on each island. The numbers of species for each island that were related to the source areas are in the Appendix, Table A-13.

Random subsets of species were also used for the purpose of counting the number of species per island. The random subsets were

generated by using a random number function in a Fortran-10 program which periodically permitted the inclusion of species from the presence/absence data set after skipping over a random number of other species. The random subsets were used as controls for interpreting the randomness in the patterns of other subsets of the flora (families, etc.).

For all of the subsets described above (families, dispersal types, source area affinities, and random subsets), presence/absence data sets were also generated. These presence/absence data sets were used for the calculation of Jaccard's qualitative species similarity index (Muller-Dombois and Ellenberg 1974) between all pairs of islands and source areas. The formula used for this similarity index (S) is $S = C/(A+B+C)$. C is the number of species found in both areas. A is the number of species found only in the first area and B is the number of species found only in the second area. This similarity coefficient was selected because it is related to the conditional probability of a species occurring in two areas when the number of species absent from both areas is excluded (Anderberg 1973). The similarity values were used in the cluster analysis procedure described later.

The observed and expected number of species in common between two islands were other measures used to represent interisland similarity. Methods given by Simberloff (1978) were used to calculate the expected number of species in common for a pair of islands. The expected number of species is equal to the product of the number of species on the two areas divided by the total number of species in the species pool which could be potential members of the flora of the islands.

III. GEOGRAPHIC DATA

Size and Shape Variables

The geographic variables and their units that were used in this analysis of island biogeography are shown in Table 4. The primary geographic attribute of an island used by MacArthur and Wilson (1967) in their theory of island biogeography is the area of an island. The area of the islands in this study was obtained either from Sekora (1973) or by weighing known areas of map copies and calculating the area of an island from the weight of a cutout of the island. Maps used for this process are a part of the U.S.G.S. 1:250,000 scale topographic map series for Alaska. Area data and other geographic information for the Commander Islands were determined from the 1:1,000,000 scale topographic map of the region that was prepared by the Army Map Service of the Corps of Engineers.

Maximum elevation for each island was used as an index of environmental heterogeneity of an island. The maximum elevation values were obtained from the topographic maps of the area. In another attempt to represent the elevational characteristics of an island, the area for each 305 meter (1000 feet) elevation interval was determined. The cutout and proportional weight method was also used for these area determinations of the elevation intervals.

Several measures were used to represent the topographic complexity of each island. The procedure developed for the representation of the complexity of an island's topography is as follows. An eight square per inch grid (made from a transparency copy of graph

Table 4. Geographic variables measured for the islands.

Geographic Variable	Units
Area	hectares
Area per 1000 ft. elevation interval	hectares
Maximum elevation	meters
Mean of topographic contour lines	# contour lines/sample square
Variance of topographic contour lines	# contour lines/sample square
Topographic diversity	# contour lines/sample square
Mean of the radii	0.25 kilometers
Variance of the radii	0.25 kilometers
Mean of the radial deviations	0.25 kilometers
Variance of the radial deviations	0.25 kilometers
Number of bays	----
Length of mapped streams	kilometers
Percentage of near shore area	percent
Recent volcanic activity	presence/absence
Number of geologic periods of rocks	----
Latitude	degrees
Distance to source areas	kilometers
Distance to other islands	kilometers
Distance along current paths	kilometers
Width of interisland pass	kilometers
Depth of interisland pass	meters
Distance to pack ice limit	kilometers

paper) was laid over the 1:250,000 maps of this region. At that scale, each square is a 63 hectare area on the island. For every eighth row and column of squares on the island, the number of 61 meter (200 foot) contour lines in each square was recorded. From the sample squares, the mean and variance of the number of contour lines per square were calculated for each island. The Shannon index of general diversity (Odum 1971) was also calculated for these data. The proportion of the sample squares in each number of contour lines group was used as the proportion of "individuals" per group for the calculations of this diversity index. The diversity index was another attempt to represent the complexity of the topography of an island.

The objective of all of the variables synthesized in the process of sampling the number of contour lines per square was to develop some univariate representation of the ruggedness and complexity of the surface of the islands. The topography has been noted as one of the factors influencing the pattern of the vegetation of this region (Amundsen 1977). Flat islands would have a low mean, variance, and diversity in the number of contour lines per square. Mountainous islands would have greater values for these variables. These variables were generally intended to be independent of the size of an island and representative of the environmental heterogeneity.

Measurements of the length of several radii of an island were used in another attempt to represent the shape of an island. The length of the radii of an island was used to represent both the size and the degree of circularity of the island. Because the islands of the Bering Sea Region are predominately of volcanic origin, deviations

from a circular shape are an indication of the complexity of the shape of an island due to more than one volcano or geologic event. Differences in the complexity of the shape of the islands also affect the regional climate and microclimate and soils of an island.

The technique used for these measurements began with laying a transparent piece of polar graph paper over a map of an island. A uniform position for the graph paper on the islands was determined by centering the graph paper at the center of the longest diameter of the island. After the polar graph paper was in place, the lengths of 36 radii were measured in units of 250 meters (millimeters on the 1:250,000 scale topographic maps). The radii were located in 10 degree rotational increments around the circle.

From the radial measurements several summary statistics were calculated. The mean and variance of the radii were calculated to represent the size and gross deviation from circularity of the island shape. Relative values of the radii were also calculated by dividing the radii by the longest radius. The division was used to remove the effect of the size of an island from these measurements. The relative values were then used to obtain representations of the complexity of an island's shape which were independent of its size. The mean and variance of the relative values were also calculated.

The radial measurements of an island were also used to represent the regularity of the shape of sections of the island. This regularity was represented by calculating the absolute value of the difference between the length of one radius and the length of an adjacent radius. The difference values will be referred to as radial deviations.

An island with a circular and uniform shape, such as the one that occurs for a single volcanic cone (Figure 9A), would have small values for the deviation between adjacent radii. An island with a noncircular and complex shape would have large deviations between the adjacent radii (Figure 9B). The mean and variance of these radial deviations were calculated to provide univariate representations of the shape of an island. Because the deviations in the radial measurements are also related to the size of an island, relative values for the deviation measurements were also calculated from radii that were divided by the value of the longest radius. The mean and variance of the relative radial deviations were also calculated.

Observations on Adak Island indicated that the number of bays or inlets and the total length of the streams on an island may be important to the biogeographic characteristics of an island. These ideas were based specifically on the observation that each bay or inlet has its own characteristics of exposure to incoming propagules of plants from the surrounding water. Many of the rare species, especially some of the orchids, also appear to be found mostly along streams. Some of these rare plants also appear to be restricted to one drainage area. Cypripedium guttatum on Adak is an example of this pattern of distribution.

The number of bays and inlets greater than one kilometer by one kilometer in width and indentation into the island was counted for each island. The number of bays on an island is not strictly independent of the size of the island because it is partially related to the length of the shoreline. Because of the range of shapes of the

islands, the determination of the number of bays also involved some subjectivity.

The total length of streams per island was measured by laying a thread along the streams shown on the 1:250,000 scale topographic maps. The accuracy of the total length of streams shown on maps is probably biased by a varying quantity of information with which these maps have been made.

The percentage of the area of an island which was within one kilometer of the shore was used to represent the differences in the exposure of the islands to the surrounding waters and the plant propagules they might contain. The near shore areas were calculated by the cutout and proportional weight method described earlier.

A final series of surface complexity values was determined from the geologic attributes of the Aleutian Islands. The presence or absence of recently active volcanoes was noted for each island from information reported by Coats (1950). The number and kind of geologic periods of rock types of an island were also noted from maps produced by the U. S. Geological Survey (U.S.G.S. Bulletin Series 1028A-U) and the Geologic Map of Alaska (Dutro and Payne 1954). These variables were used only as categorical variables in one-way analysis of variance of the number of species per area. They are admittedly unrefined in their level of resolution, but this was the maximum level of uniform resolution which could be obtained for most of the islands in the data set. The Aleutian Islands were also assigned into three general topographic shape categories. The shape categories were 1) volcanic cone (for example, Carlisle), 2) terrace or bench shape (for example,

Amchitka), and 3) volcanic cone plus bench shape (for example, Unimak).

The latitude of the island was also included in the geographic data set. The latitude values were obtained from the map of the region produced by NOAA (1976).

The values of the size and shape variables of the islands are reported in the Appendix, Tables A-14 and A-15.

Distance Variables

The distances between all of the islands and source areas were calculated as representations of the isolation of the islands. Because the mercator projections used for the maps of this region have nonlinear and complex changes in scale between latitudes, consistent distance measurements were difficult to obtain directly from the available maps. Therefore, great-circle distances were calculated between the islands and the source areas using the longitude and latitude coordinates from locations on the islands. The nearest pair of points for each island pair was used for the interisland distance measurements.

The calculations of the great-circle distances from the coordinates were performed with the following equation from Bowditch (1958):

$$\text{hav}(D) = \text{hav}(D_{lo}) \times \text{Cosine}(L1) \times \text{Cosine}(L2) \times \text{hav}(La).$$

$$\text{hav}(z) = \text{haversine}(z) = (1 - \text{Cosine}(z))/2.$$

D_{lo} = the difference between the longitudes of the two points.

$L1$ = latitude of one point.

$L2$ = latitude of the other point.

La = the difference between the latitudes of the two points.

D = distance in degrees (one second equals one nautical mile or 1.85 kilometers).

The longitude values used in these calculations were reduced by a constant to remove the effect of going past the 180 degrees longitude. The longitudes from the eastern hemisphere were treated as if they continued to increase farther away from the western hemisphere.

Because the effective distance between the islands and from the islands to the source areas may actually be along the path of the major water currents, great-circle distances along the current paths were also calculated. The distance along the path of the westward and eastward currents were calculated by summing the shortest length of segments along the current paths shown in Figure 10 to each of the Aleutian Islands in the data set.

To additionally represent the degree of isolation of an island from the water current, the depth and width of the largest interisland pass adjacent to the islands in the Aleutian Chain were recorded from bathymetric measurements on maps of the area (NOAA 1976 and Defense Mapping Agency Hydrographic Center 1943). The volume of water flowing through an interisland pass has been shown to be related to the depth and width of the interisland pass (Favorite 1974).

A final measure of the degree of isolation of an island in the Aleutian Chain was the distance from the island to the nearest point on the southern limit of winter pack ice. The limit of pack ice (Figure 11) approximately follows the edge of the continental shelf (McRoy and Goering 1974). The great-circle distance from the islands to the limit of the pack ice was also calculated by the computational formula given above.

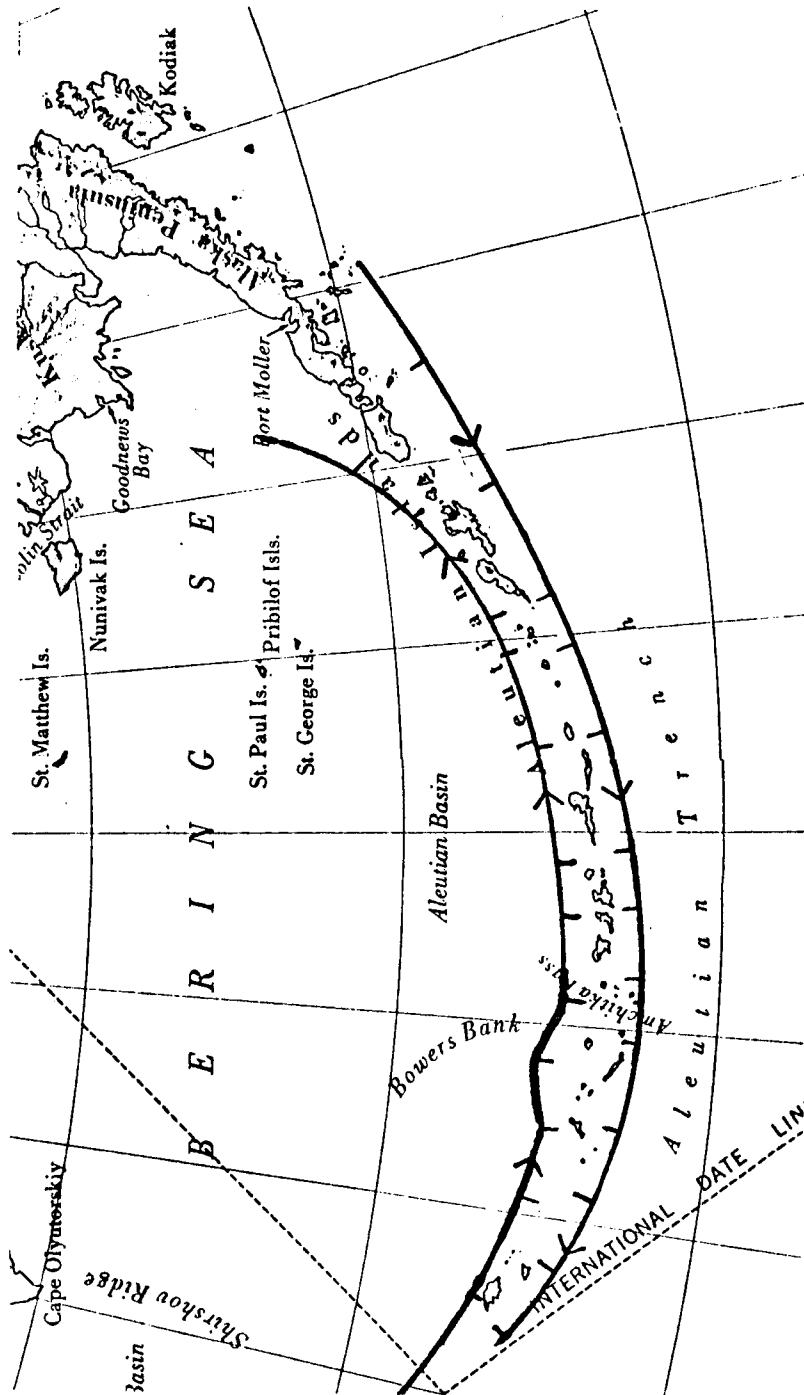


Figure 10. Segments along the major current paths used to calculate distances to the Aleutian Islands from the source area regions. (Map adapted from Hulten 1968; current pattern adapted from Hughes et al. 1974.)

The distance and isolation variables discussed in this section are reported in the Appendix, Tables A-16 and A-17.

IV. STATISTICAL ANALYSIS TECHNIQUES

A significance level of 0.05 for type I error was used for all analyses in this study.

Correlation

Pearson's product-moment correlation coefficient was used to analyze bivariate relationships between the geographic and floristic variables of the islands. The correlation coefficients and their probability of significance were all computed with PROC CORR of SAS (Barr et al. 1976). The probability of significance of the correlation coefficient is the chance of the value of the coefficient or a value greater arising from a truly uncorrelated relationship.

Several assumptions and limitations need to be stated for the meaningful interpretation of correlation coefficients. The first assumption was that the variables have a bivariate normal distribution (Sokal and Rohlf 1969). It was also assumed that the relationship between the two variables was linear and not curved (Zar 1974). When interpreting correlation coefficients, it must also be remembered that cause and effect are not implied by a significant relationship between two variables. Correlation coefficients merely represent the degree of association between the values of two variables. The square of the correlation coefficient is equal to the proportion of the variance that is explained by the variation in the other variable (Sokal and Rohlf 1969). Correlation coefficients were used in this study to

assess the degree of nonrandomness in the bivariate relationships between floristic and geographic variables.

When logarithmic transformations are applied to variables, caution must be used in simultaneously interpreting the significance of the correlation coefficients for untransformed and transformed values (Zar 1974). In other words, after the values are logarithmically transformed for the purpose of removing curvilinearity in the relationship, the data must still meet the assumptions of correlation (normality, etc.). Zar (1974) pointed out that it is not possible for both the untransformed and transformed values to simultaneously meet these assumptions. In this study, simultaneous interpretations of transformed and untransformed values will be considered in the perspective of these limitations. The transformations were used only in this study for the purpose of developing linear relationships.

Multiple Regression

Multiple regression techniques have been used in several studies of island biogeography (Simberloff 1974). Multiple regression has the same assumptions of normality and linearity as correlation (Sokal and Rohlf 1969). In addition to those assumptions, dependence and independence relationships were assumed between the variables used in the analysis. Independence between the independent variables was an additional assumption for data that were used in multiple regression.

The objective of multiple regression is to determine an equation that best predicts a single dependent variable from a linear combination of independent variables (Zar 1974). The general form of a multiple regression equation is:

$$Y_i^* = a + b_1 X_{1i} + b_2 X_{2i} + b_3 X_{3i} \dots$$

Y_i^* is an estimate of the dependent variable being predicted by the independent variables X_{1i} , X_{2i} , X_{3i} The b's are the partial regression coefficients used to weight the independent variables in a linear combination for estimates of the value of Y. The intercept value of Y_i^* , when all of the X's are zero, is "a." The criterion used to specify which set of b's result in the best prediction model is the ratio of the variance component of Y explained by the estimated Y^* and the total variance of Y (Sokal and Rohlf 1969). The F-test may be applied to the ratio of variances to test the significance of the relationship specified by the multiple regression.

The multiple regressions used in the analyses for this study were performed with the MAXR option of PROC STEPWISE of SAS (Barr et al. 1976). This technique is a stepwise multiple regression procedure which enters the variables one at a time into the regression model. After the best variable is found, the procedure adds other variables to the multiple regression model by selecting the variable which will cause the maximum improvement in the coefficient of determination (R^2) of the model.

The results obtained from a stepwise multiple regression procedure provided a relative indication of the importance of each variable to the overall predictive success of the multiple regression model. Therefore, it was possible to observe the relative importance of the geographic variables, such as area and distance from a source area, in the prediction of the number of species per island.

Simberloff (1974) pointed out some of the logical limitations that may result during the interpretation of multiple regression analyses for the study of island biogeography. Most of the problems are related to the implied independence and dependence relationships assumed between the variables. A corresponding mechanism of cause and effect for these relationships is often difficult to describe and document. This type of limitation will be considered in the interpretation of the results of multiple regression analyses.

Analysis of Variance

One-way analysis of variance tests for this study were performed with PROC GLM of SAS (Barr et al. 1976). The assumptions required for analysis of variance were similar to the ones for correlation and regression. The null hypothesis of analysis of variance was that the group means of a variable are not significantly different. The alternate hypothesis was that the group means are significantly different (Sokal and Rohlf 1969). This statistical analysis technique was used to test for differences in the number of species per area in groups of islands defined by the categorical variables that were determined from the geological and geographical attributes of the islands.

Cluster Analysis

A cluster analysis technique was used to search for geographic patterns in the similarity of the flora of the islands of the Bering Sea Region. The cluster analysis procedure used for this study was programmed by Sepkoski (1974) and was used by Sepkoski and Rex (1974)

in a biogeographic study of the faunas of rivers. This cluster analysis procedure was an unweighted pair-group technique that used an average value of the association between the observations and clusters which were merged. This technique was an agglomerative procedure which functions by grouping together the pairs of samples or clusters which have the highest average value of association between the members of the groups (Anderberg 1973). The unweighted procedure was used because it retains equal importance of the individual observations during the calculation of the average association values used to determine similarities between clusters. The unweighted pair-group method that is based on averages is a very commonly used clustering procedure (Sneath and Sokal 1973). This program was modified for the use of the qualitative Jaccard similarity index discussed earlier as the measure of association of the samples (islands).

Cluster analysis is not a statistical technique that can be used to test hypotheses. Significance levels cannot be determined for rejecting or accepting hypotheses of the expected structure of the cluster analysis results. Differences between the results of cluster analyses also cannot be tested. However, cluster analysis can be considered a statistical technique in the sense that it can summarize attributes of a data set.

In this analysis of the biogeography of the flora of the islands of the Bering Sea Region, the simplest interpretation of cluster analysis results was the comparison of the number of nearest neighbors that were clustered together by the analysis. The relationships

between the source areas and island groups shown by the cluster analysis were another aspect of the results that could be biogeographically meaningful. The interpretation of groups of islands defined by the cluster analysis was also based on common size and shape characteristics.

CHAPTER 5

OVERVIEW OF HYPOTHESES AND ANALYSES OF THIS STUDY AND COMPARISON WITH PREVIOUS STUDIES

I. HYPOTHESES AND ANALYSES OF THIS STUDY

The original design of the hypotheses tested in this study was based on the general predictions made by the theory of island biogeography of MacArthur and Wilson (1967). Two types of relationships were analyzed from that theory. The first was between the number of species per island and the size of the island. Several geographic variables associated with the environmental complexity of an island, such as the size and shape of an island, were examined during the analyses of this type of relationship.

The second type of relationship included in this study was between the number of species per island and the isolation of the island. The isolation of the islands in the region is more complex than the distance from an island to a single source area. Because of that complexity, the isolation of an island was represented by the distance to several source areas. Those distances were related to several different components of the flora.

The two general relationships described above were initially analyzed as bivariate relationships. The primary methods of analysis of these relationships were inspection of bivariate plots and calculation of correlation coefficients. With this approach, the relationships between the floristic and geographic variables were

examined one pair at a time. Such an approach to biogeographic relationships was simple to portray graphically. It was also simple to explain. However, such an approach contradicts the holistic philosophy of ecology. The success of demonstrating such a bivariate relationship may be limited by these contradictions with the holistic philosophy.

A more holistic approach to the hypothesized relationships was attained with multiple regression techniques. Multiple regression permits the simultaneous consideration of size and isolation attributes of islands in a relationship with the number of species per island. With this technique of analysis, it was possible to observe the total level of prediction of the number of species that can be made from all of the kinds of geographic variables. The relative importance of each geographic variable to the total prediction by the multiple regression was also obtained with that technique.

The analytical approach of cluster analysis is complementary to the bivariate and multivariate approach of correlation and regression. In correlation and regression, an a priori relationship of interest is first specified and then it is either accepted or rejected by a statistical test. The relationships portrayed in the results of cluster analysis are controlled entirely by patterns in the floristic data. The usefulness of these relationships is a posteriori because the cluster analysis is meaningful only when the resulting pattern can be interpreted or explained with an a posteriori classification of the cluster groups. That classification is ideally based on some common attribute of the members of the group. In this study, the results of

the cluster analyses of floristic data were interpreted primarily with classification by either the size or location of the islands.

All of the types of analyses discussed above were performed with several subsets of the flora. Biogeographic patterns for the family, dispersal, and source area groups of species were examined to see if those subsets of the flora had different biogeographic patterns. When different biogeographic patterns were found for the subsets, specific differences that are common among the species of the subset were examined to determine if an explanation could be given for the biogeographic differences.

Relationships between the number of species in the subsets of the flora (families, etc.) were also examined as a secondary product of the process used to analyze the major biogeographic relationships.

II. OTHER BIOGEOGRAPHIC STUDIES ON THE FLORA OF THE ISLANDS OF THE BERING SEA REGION

Previous studies of the biogeography of the flora of the islands of the Bering Sea Region are few. The availability of floristic data for the region was a limitation to this type of study (Hultén 1960).

Hultén (1960) concluded that the flora of the Aleutian Islands was related primarily to the Asian flora on Kamchatka. His argument for that conclusion was based on two observations concerning the types of plant communities in the area. The first observation was that most of the communities in the Aleutian Islands were the same as the plant communities found on Kamchatka. The only difference between the plant communities on the Aleutian Islands and Kamchatka was that some of the

Asian species were replaced by American species in the plant communities on the Aleutian Islands. Hultén (1960) also observed that the American species in the Aleutian Islands did not appear to form their own stable plant community. Therefore, Hultén argued that the American species were a recent addition to the flora of the Aleutian Islands. Hultén (1960) also discounted the suggestion of Tatewaki and Kobayashi (1934) that the Aleutian Islands were in a floristic region that was separate from Kamchatka.

The primary objective of the other studies of the plant geography of the Bering Sea Region (Hultén 1963; Tatewaki 1963a, 1963b; Lindroth 1963) was to describe the general patterns of the distribution of the flora of the area. The number of species of different floristic elements across the region were mapped or counted (Hultén 1963, Tatewaki 1963a). The floristic elements were defined by criteria that were based on the geographic extent of the distributions of species. For example, Hultén (1963) mapped the ranges of the number of species also found in continental North America and not Asia, those found in continental North America and the eastern part of Asia, the number of circumpolar species. etc. Tatewaki (1963b) used a similar approach and presented specific tabulations of the occurrence of each species in different regions of the Bering Sea. Those tabulations were also compiled for several other taxonomic levels.

Hultén (1963), Tatewaki (1963a), and Lindroth (1963) have shown that the influences of the floras from Asia and North America appear to decrease with increasing distance from these areas. The pattern of the distribution of the North American species across the islands

appears to involve a larger number of species over a greater distance than the species from Asia (Tatewaki 1963a). The most common pattern of distribution for the species of the area was one across only part of the islands of the Bering Sea Region.

Tatewaki (1963b) proposed Hultén's line as a phytogeographic division between the Commander Islands and the Aleutian Islands because he observed a strong break in the distributional patterns of several species at this location. Hultén (1963) also showed that the islands in the Northern Bering Sea contain a larger continental floristic element than the Aleutian Islands. Hultén (1963) believed that that pattern was due to the continental connection which occurred between the islands and continents during the existence of the Bering Land Bridge. The coastal plants in the northern islands also show a pattern which indicated that they dispersed there after the islands were isolated by water.

III. COMPARISON WITH OTHER STUDIES

A major difference between the methods used in the previous studies of plant geography and this study is that the previous studies did not statistically or graphically analyze the values from individual islands. Groups of islands were the smallest unit of observation in these earlier studies. No attempt was made in them to determine if the differences observed between the groups of islands were statistically significant.

Another difference in the approach of the earlier studies and this one is that the earlier studies did not include any interpretation

of differences in the flora which could be due to differences in the environmental complexity of the islands. Attributes of islands such as size, topographic complexity, and isolation from nearby islands were not considered in earlier studies of plant geography. The differences due to changes in location were the only patterns interpreted in these earlier studies.

In general, the ideas used from MacArthur and Wilson's theory of island biogeography have encouraged a quantitative approach to the testing of hypotheses related to the biogeographic patterns. The more comprehensive perspective resulting from the greater number of types of environmental factors included in the analyses is also another benefit from the theory.

CHAPTER 6

RESULTS AND DISCUSSION

Analyses of bivariate relationships between floristic and geographic variables are the first kind of result discussed in this chapter. Geographic variables related to size, shape and habitat diversity of the island are considered first. The discussion of these variables is followed by one of variables which are related to the geology of the islands. Relationships between isolation, represented by distance from source areas, and several subsets of the flora are then presented and discussed. Other variables which are representative of local isolation of the islands are also discussed. Changes in the pattern of regional similarity of floristic subsets are interpreted with cluster analyses. The combined effects of all of the geographic variables are analyzed simultaneously with multiple regression techniques.

I. BIVARIATE RELATIONSHIPS BETWEEN FLORISTIC AND GEOGRAPHIC VARIABLES

Number of Species and Area

The species-area relationship is the primary one presented and discussed in other studies of island biogeography. Recently the form and meaning of the relationship has been criticized by Conner and McCoy (1979). In response to the criticism that the log-log relationship is not always the best form, the linear, semi-log and log-log

species-area relationships are presented in this study. The linear model of the species-area relationship has a significant correlation coefficient of 0.719. Figure 12 shows that the curve representing the relationship is nonlinear. The correlation coefficient of this relationship is not meaningful because the relationship is nonlinear. Figure 13 shows the semi-log form of the species-area relationship. The significant correlation coefficient of 0.768 for this relationship is also not meaningful since the relationship is nonlinear. The log-log species-area relationship (Figure 14) has a significant correlation coefficient of 0.791. This curve is more linear than the semi-log model and is considered to be the best of the three models presented. The log-log species-area relationship from this study is similar to the patterns shown by MacArthur and Wilson (1967) in their theory of island biogeography.

The log-log species-area model is also linear and significantly correlated for several families and other subsets of the flora (Table 5). Correlations between the number of species in families may indicate that significant collection bias is not present in the data. Figure 15 shows the relationship ($r = 0.827$) between the number of species of sedges, which are often inconspicuous and difficult to collect thoroughly, and the number of species of composites, which are conspicuous and easy to collect. Other interpretations of this kind of relationship will be discussed later.

The generality of the species-area results suggests that some universal mechanism or pattern may exist between the number of species on an island and the size of the island. May (1975) and Preston (1962)

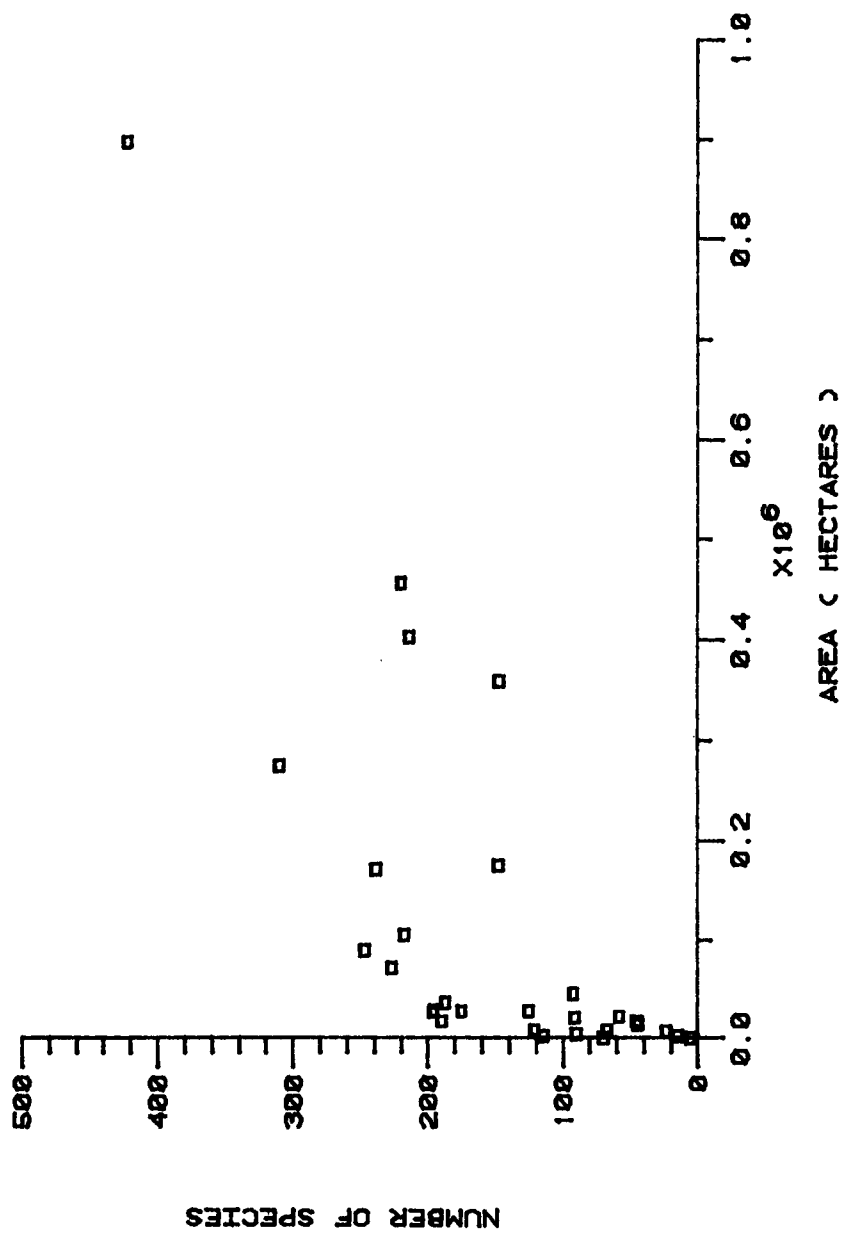


Figure 12. Relationship between the number of species and area on a linear scale
($r = 0.719$).

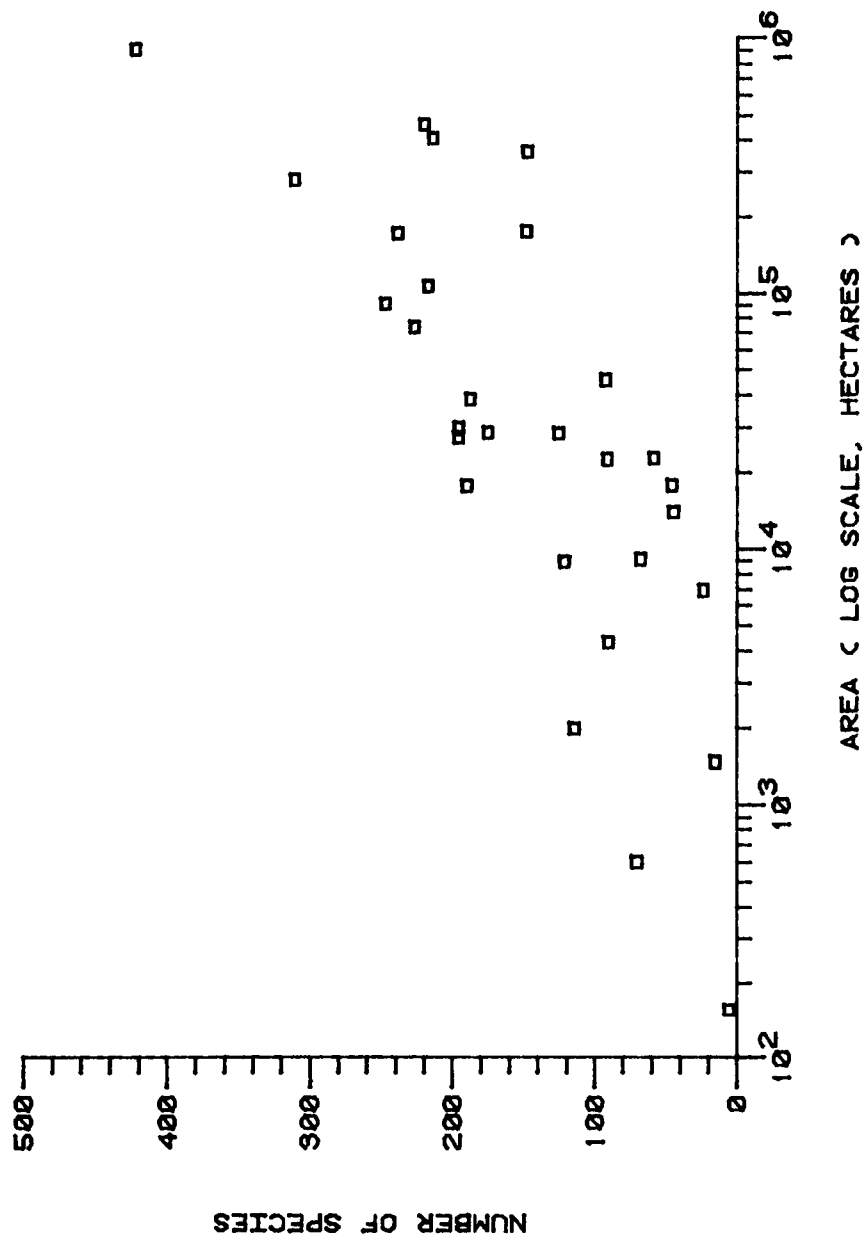


Figure 13. Relationship between the number of species and area ($r = 0.768$, semi-log scale).

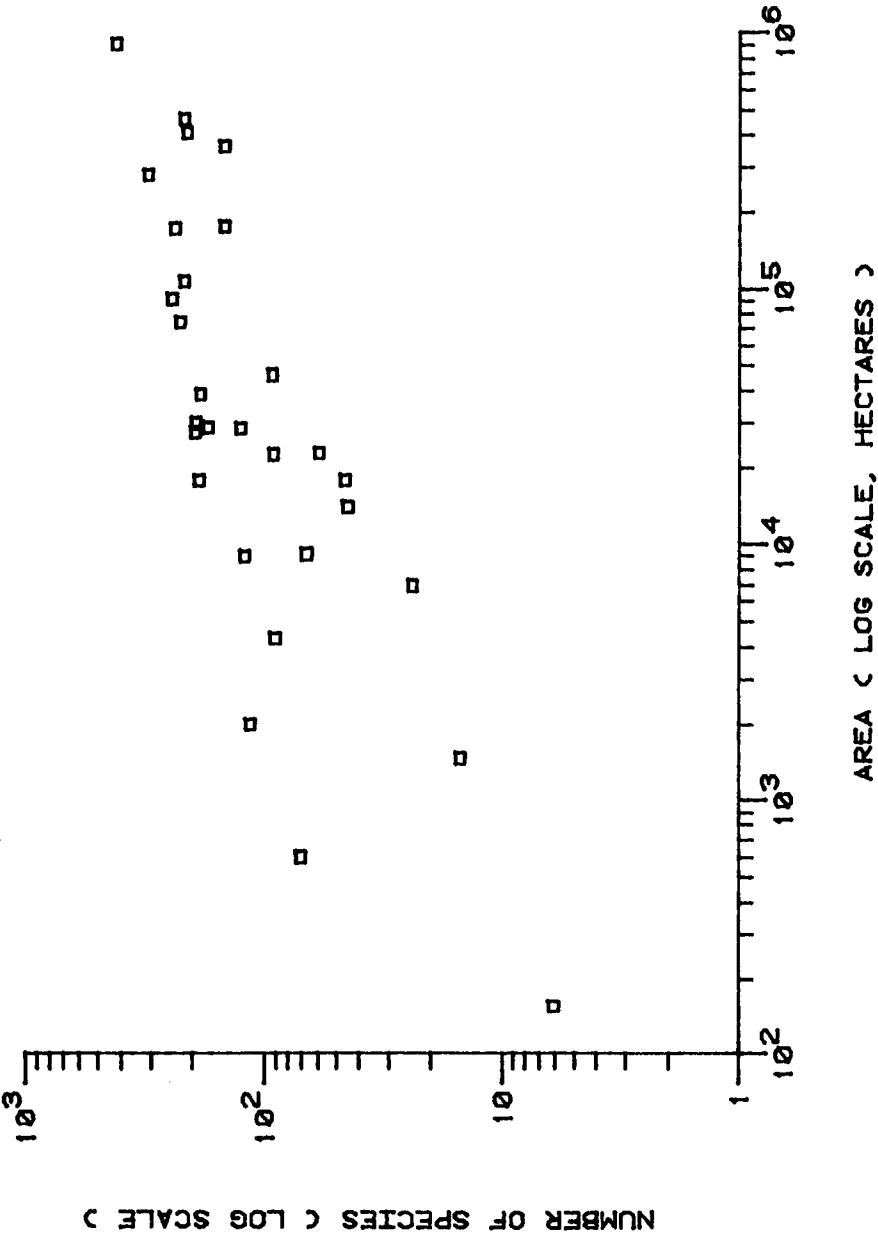


Figure 14. Relationship between the number of species and area ($r = 0.791$, log-log scale).

Table 5. Correlation coefficients between selected floristic variables and geographic variables related to island size and topographic complexity.

Floristic Variables ^a	Geographic Variables ^b				
	LAREA	LA01	TODI	LNBY	LSTRKM
LSPNO	0.791	0.709	0.382	0.629	0.662
LSPF25	0.684	0.633	0.188 ^c	0.521	0.596
LSPF32	0.496	0.486	0.614	0.521	0.596
LSPF89	0.750	0.658	0.447	0.552	0.707
LSPAP	0.791	0.711	0.397	0.639	0.663
LRSAP	0.542	0.597	0.256 ^c	0.429	0.408
LALSSP	0.784	0.689	0.364 ^c	0.596	0.646
LNFM	0.752	0.685	0.455	0.596	0.624

^aAbbreviations of floristic variables:

LSPNO = Logarithm of the number of species

LSPF25 = Logarithm of the number of grass species

LSPF32 = Logarithm of the number of orchid species

LSPF89 = Logarithm of the number of composite species

LSPAP = Logarithm of the number of species in common with the Alaska Peninsula

LRSAP = Logarithm of the number of species restricted to the Alaska Peninsula

LALSSP = Logarithm of the number of species from all source areas.

LNFM = Logarithm of the number of families.

^bAbbreviations of geographic variables:

LAREA = Logarithm of the area of the island

LA01 = Logarithm of island area between 0 and 1000 ft. elevation

TODI = Diversity of the number of contour lines per sample square

LNBY = Logarithm of the number of bays

LSTRKM = Logarithm of the length of mapped streams.

^cNot significant, $\alpha = 0.05$.

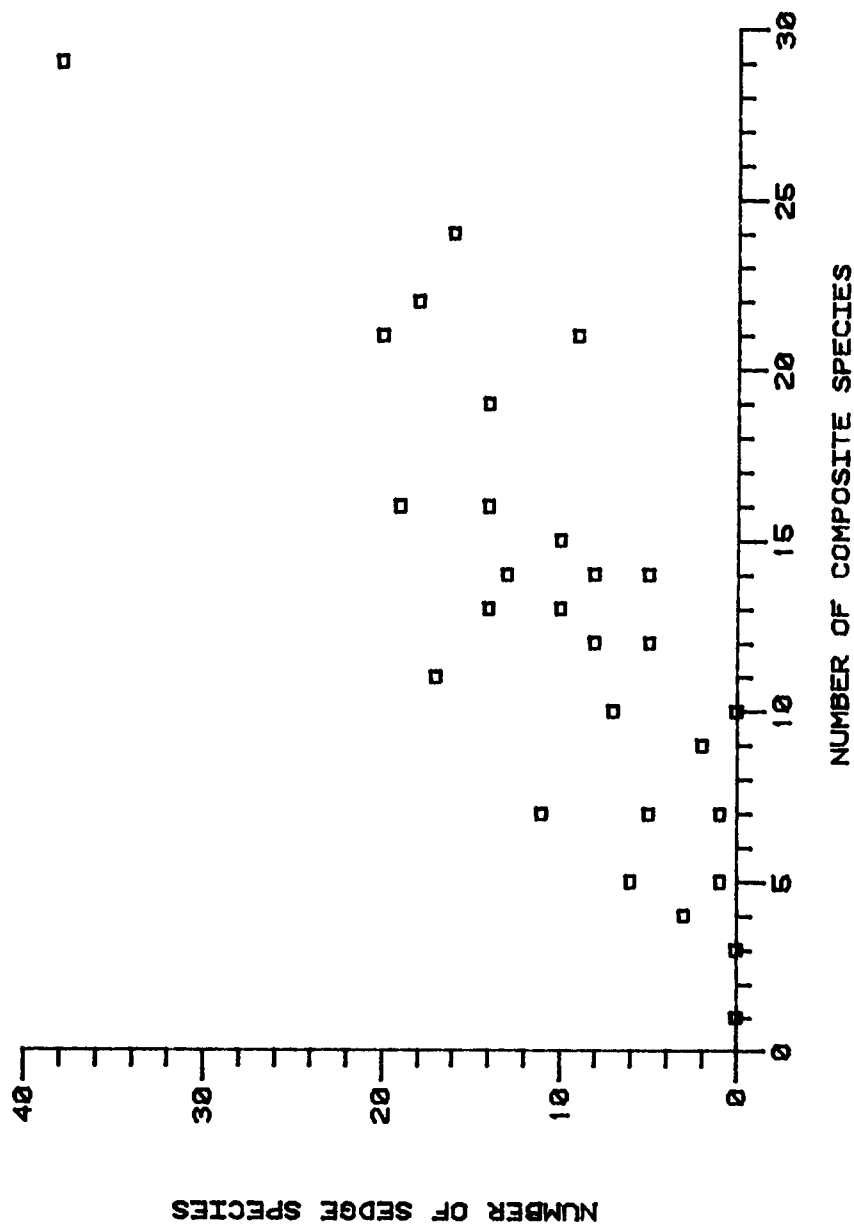


Figure 15. Relationship between the number of species of sedges and the number of species of composites ($r = 0.827$).

have stated that the universality of the species-area relationship is connected to the lognormal abundance distribution of most taxonomic groups. When the abundance of individuals per species, species per genera, and genera per family are "canonically" distributed, then the "species-area" relationship will be significant for several taxonomic levels (Preston 1962). Evidence of a "canonical" distribution in this flora is given by the significant correlation ($r = 0.932$) of the relationship between the number of families per island and the number of species per island (Figure 16).

MacArthur and Wilson (1967) explained the species-area pattern with the immigration-extinction equilibrium model. The analyses of this study do not indicate what mechanism, if any, is responsible for the observed species-area relationship. Under the extreme climatic conditions and isolation resulting from the relatively long distances across the Bering Sea Region, it is interesting that it is still possible to observe the species-area pattern. It seems reasonable to state that the species-area pattern is fundamental since it appears not to be sensitive to the extreme and unusual geographic setting of these islands.

The slope of the log-log species-area curve, z , is about 0.36, and is slightly above the range (0.20-0.35) expected by MacArthur and Wilson (1967). However, Connor and McCoy (1979) have also suggested that the value of the slope may not be meaningful and that it is only an artifact of the log-log transformation on lognormal distributions that are correlated.

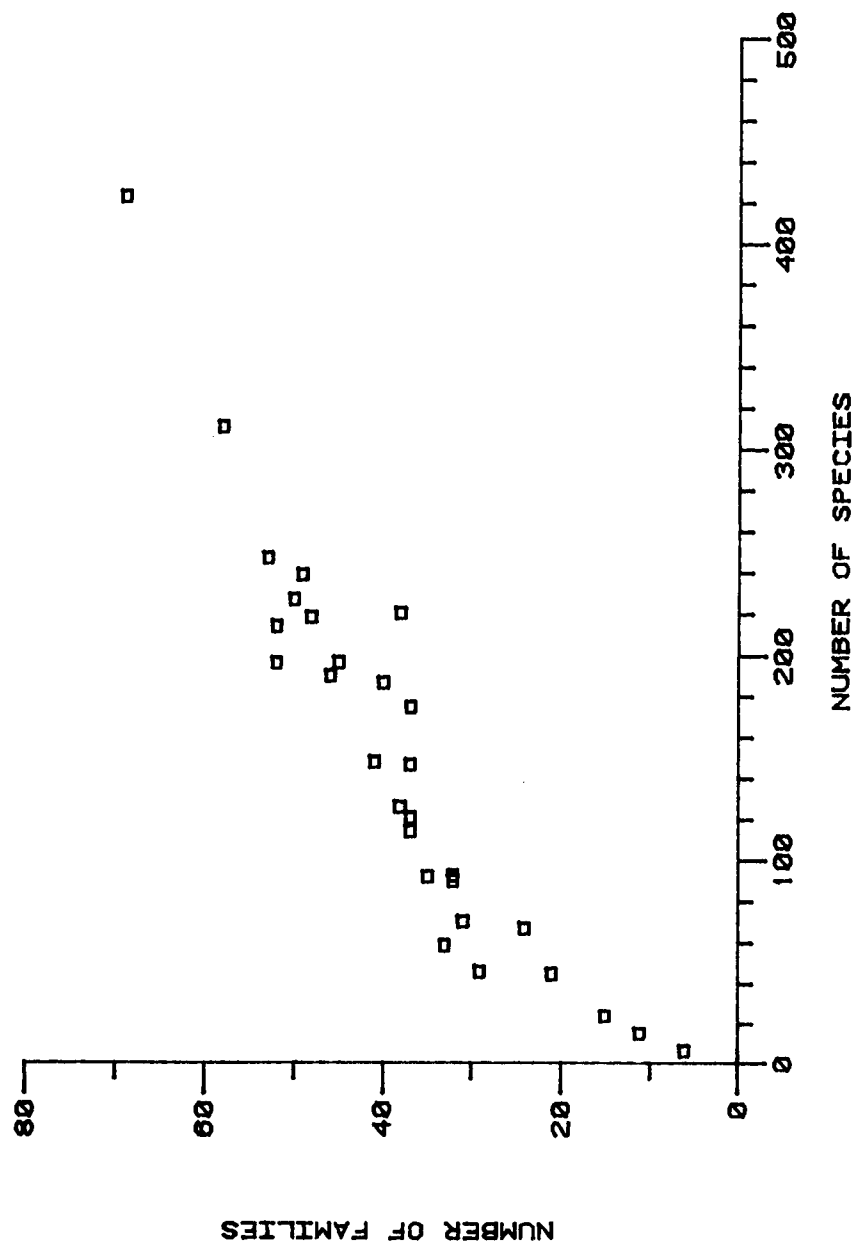


Figure 16. Relationship between the number of families and the number of species ($r = 0.932$).

When the area of the islands was partitioned into 1,000 foot intervals of elevation, correlations between the number of species and the area values are similar to those with the total area of the island. The higher elevation intervals, such as 3,000 to 4,000 feet and greater than 4,000 feet, are not useful in correlation analyses since the values for many of the islands are zero. The results from the lower elevation intervals were similar to each other and the total area of the island. Examples of correlations with the area between 0 and 1,000 feet are shown in Table 5. The similarity in these results may be due to the absence of a gradient of plant communities across changing elevations.

Number of Species and Maximum Elevation

Maximum elevation is usually positively related to the number of species because it represents changes in the habitat diversity of an island (Diamond 1972). The relationship between the number of species and maximum elevation (Figure 17) is not significantly correlated ($r = 0.337$). The weakness of this correlation is not surprising since it assumes that other factors which may affect the number of species, such as area and isolation, may be ignored. When the relationship between the number of species and maximum elevation was examined for only the Aleutian Islands (Figure 18), it is found to be significantly correlated ($r = 0.471$). The change in the significance of this relationship may be due to the reduced latitudinal range of the Aleutian Islands. It is possible that some interaction between maximum elevation and latitude was removed from the analysis

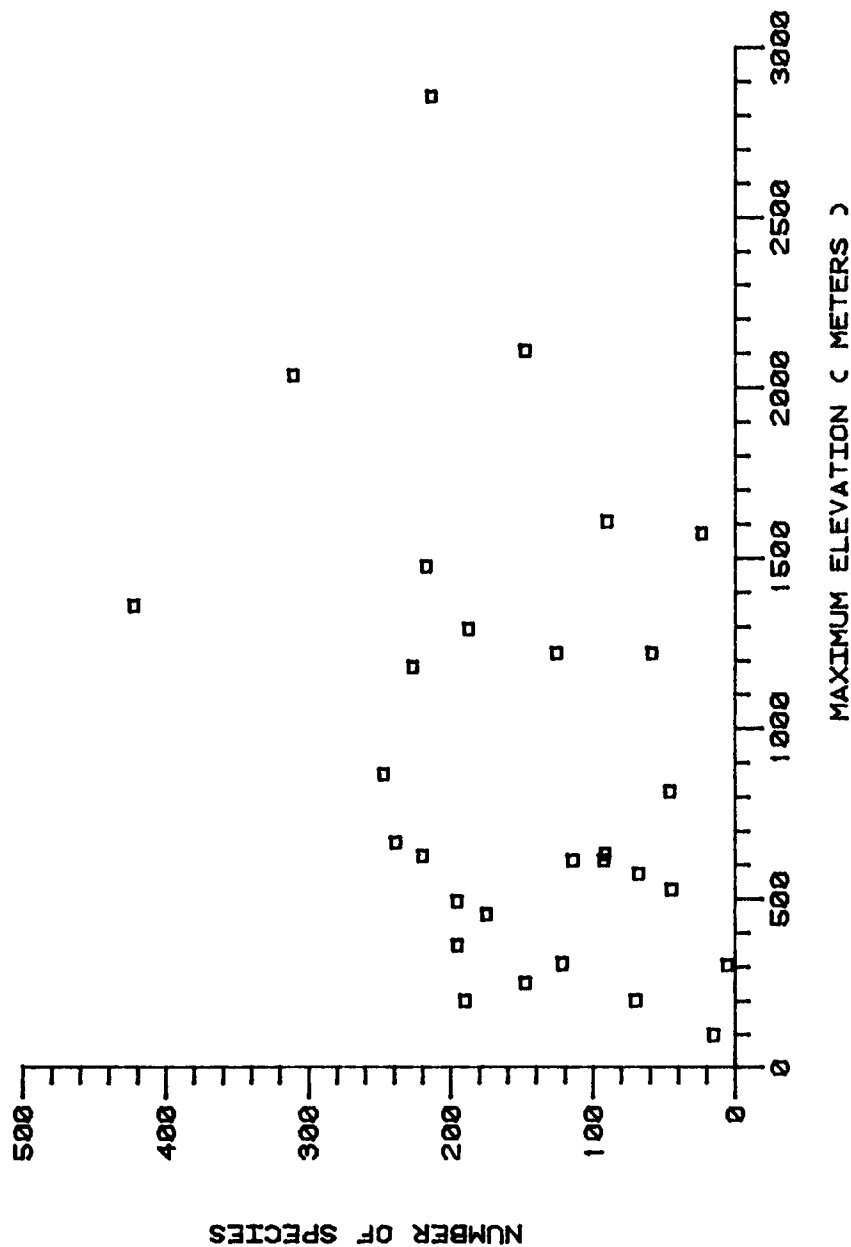


Figure 17. Relationship between the number of species and maximum elevation. The correlation coefficient is not significant.

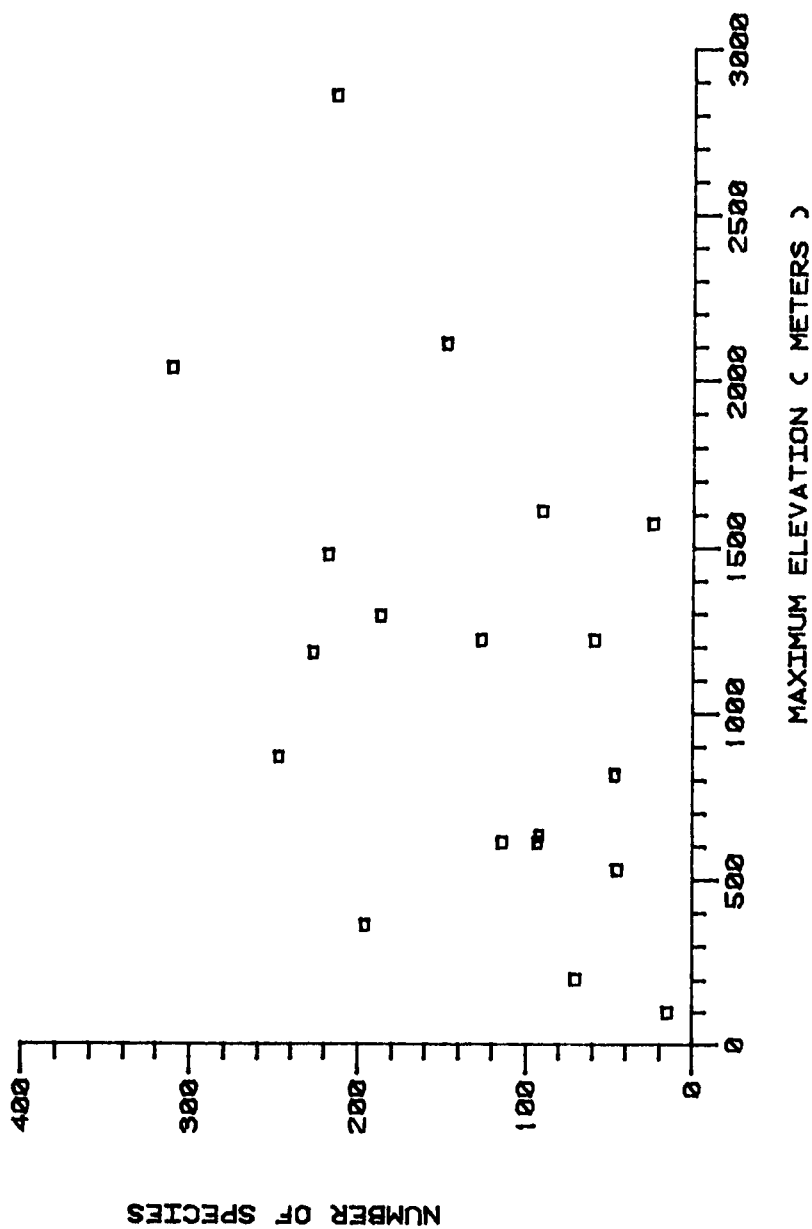


Figure 18. Relationship between the number of species and maximum elevation for only the Aleutian Islands ($r = 0.471$).

when the northern islands were removed. The relationship between the number of species and maximum elevation is positive and is consistent with the results of other studies of island biogeography (Simpson 1974, Case 1975).

Elevation is not significantly correlated with the number of species in several families and other subsets of the flora (Table 6). A positive correlation ($r = 0.437$) between the number of orchid species per island and the maximum elevation is one exception to the pattern of nonsignificant correlations. This result is surprising because the orchids of this area are not alpine species. The number of orchid species appears to be greater in areas which are topographically more complex. It is possible this relationship between the orchids and the maximum elevation is an artifact of this topographic effect.

Another exception to the absence of the relationship with maximum elevation is the significant correlation ($r = 0.410$) between maximum elevation and the number of species which are restricted to the southeastern coastal source area (Figure 19). This is the only number of species related to a source area which is correlated with maximum elevation. A possible explanation for this relationship is that the southeastern coastal region has more high elevation area and may contain a larger number of alpine species which are also found in the high elevation areas of the islands.

Number of Species and Topographic Diversity

Several variables were synthesized to represent differences of the topographic complexity of the islands. Topographic complexity is

Table 6. Correlation coefficients between selected floristic variables and geographic variables (elevation, radial measurements, latitude, near shore area).

Floristic Variables ^a	Geographic Variables ^b								
	ELIS	RAM	RADM	RRAM	RRAV	RRADM	RRADV	LAT	PNSA
SPNO	0.337 ^c	0.766	0.838	-0.080 ^c	0.347 ^c	0.475	0.218 ^c	0.304 ^c	-0.536
SPF25	0.342 ^c	0.620	0.753	-0.186 ^c	0.434	0.481	0.266 ^c	0.183 ^c	-0.481
SPF32	0.437	0.413	0.573	0.216 ^c	0.071 ^c	0.295 ^c	0.011 ^c	-0.288 ^c	-0.342 ^c
SPF89	0.276 ^c	0.791	0.834	0.087 ^c	0.282 ^c	0.426	0.209 ^c	0.359 ^c	-0.544
SPAP	0.408	0.773	0.822	-0.073 ^c	0.325 ^c	0.447	0.183 ^c	0.261 ^c	-0.541
RSAP	0.406	0.727	0.762	0.023 ^c	0.205 ^c	0.365 ^c	0.090 ^c	0.331 ^c	-0.534
ALSSP	0.282 ^c	0.742	0.785	0.087 ^c	0.421	0.482	0.298 ^c	0.384	-0.531
NFAM	0.380	0.650	0.715	-0.037 ^c	0.326 ^c	0.461	0.176 ^c	0.125 ^c	-0.484

^aAbbreviations of floristic variables:

- SPNO = Number of species
- SPF25 = Number of grass species
- SPF32 = Number of orchid species
- SPF89 = Number of composite species
- SPAP = Number of species in common with the Alaska Peninsula
- RSAP = Number of species restricted to the Alaska Peninsula
- ALSSP = Number of species from all source areas
- NFAM = Number of families.

Table 6 (Continued)

^bAbbreviations of geographic variables:

ELIS = Maximum elevation

RAM = Mean of the radii

RADM = Mean of the radial deviations

RRAM = Mean of the relative radii

RRAV = Variance of the relative radii

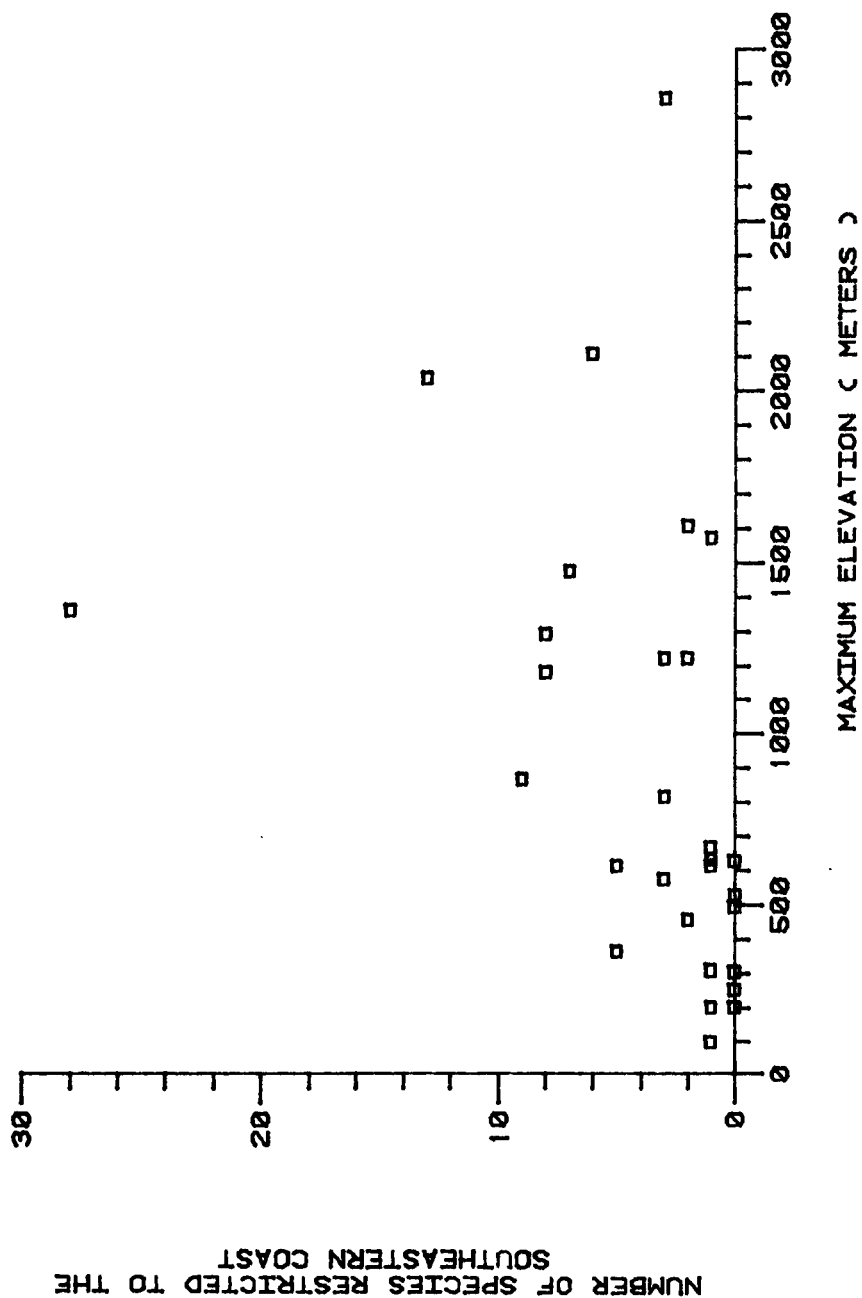
RRADM = Mean of the relative radial deviations

RRADV = Variance of the relative radial deviations

LAT = Latitude

PNSA = Percentage of area near the shore.

^cNot significant, Alpha = 0.05.



related to the number of habitats on an island. Topography has been observed to have a significant role in soil formation (Everett 1977) and the distribution of plant communities (Amundsen 1977).

As was described in the methods section, three variables were used to represent topographic complexity from the number of contour lines per sample square on a map. These variables are the mean (TOMN), variance (TOVA), and diversity (TODI) of the number of contour lines per sample square, all of which are correlated with one another (Appendix, Table A-18). TODI is most highly correlated in the significant relationships with the number of species (Table 5, page 76). The most linear model of these relationships is with the logarithm of the number of species. However, as was observed in the relationships with maximum elevation, not all of the relationships with TODI are significant (Table 5). The numbers of species of orchids, heaths, and species in common with the flora of the southeastern coastal source area are positively correlated with increasing topographic diversity (Figures 20, 21, and 22). These correlations are all weak, but this is expected since other factors which may affect the number of species in the groups, such as area and isolation, are not constant.

Number of Species and Radial Measurements

A series of variables related to island size and shape were derived from measurements of radii of the islands. The mean of the radii is related exponentially to the area of the island since the islands are of volcanic origin and are often circular in shape. The mean of the radii and the number of species are positively correlated ($r = 0.766$) and the relationship is nearly linear (Figure 23).

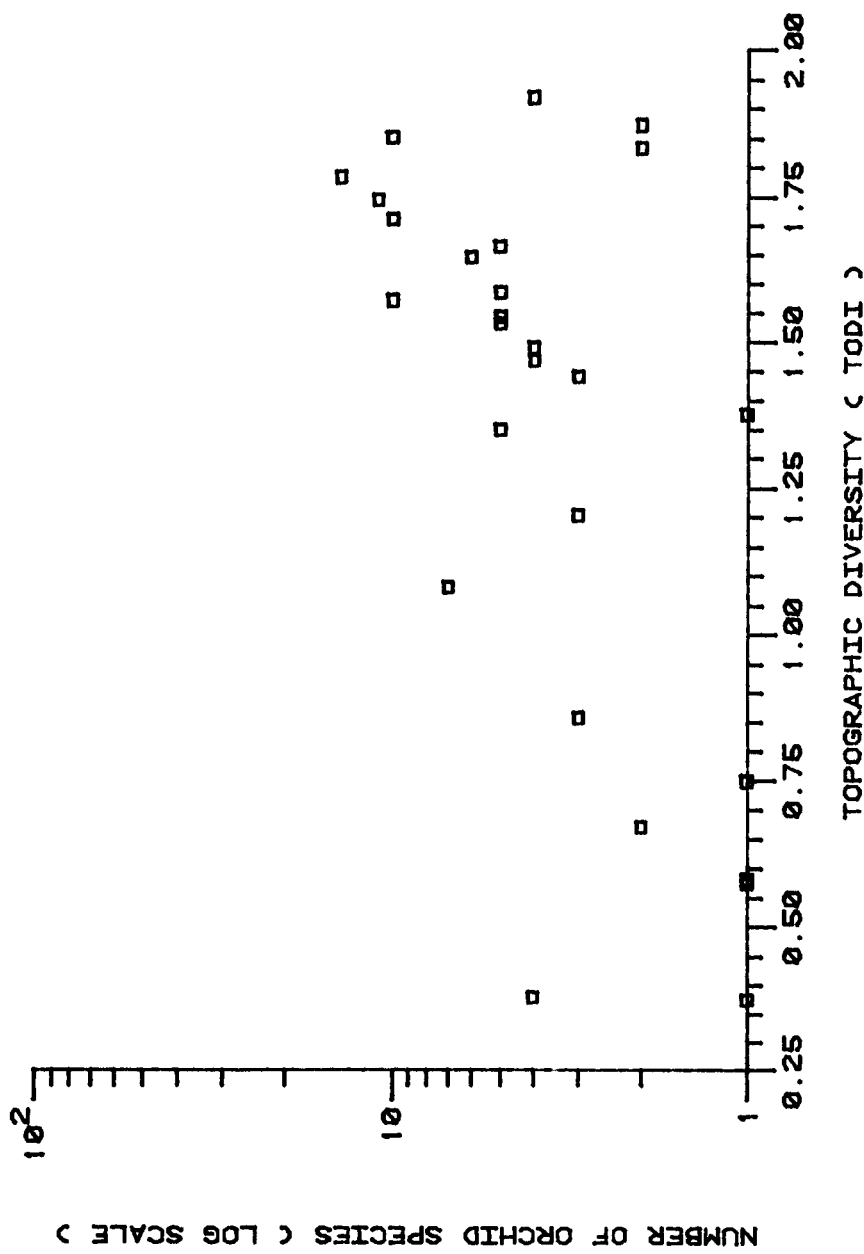


Figure 20. Relationship between the number of species of orchids (log scale) and topographic diversity ($r = 0.614$).

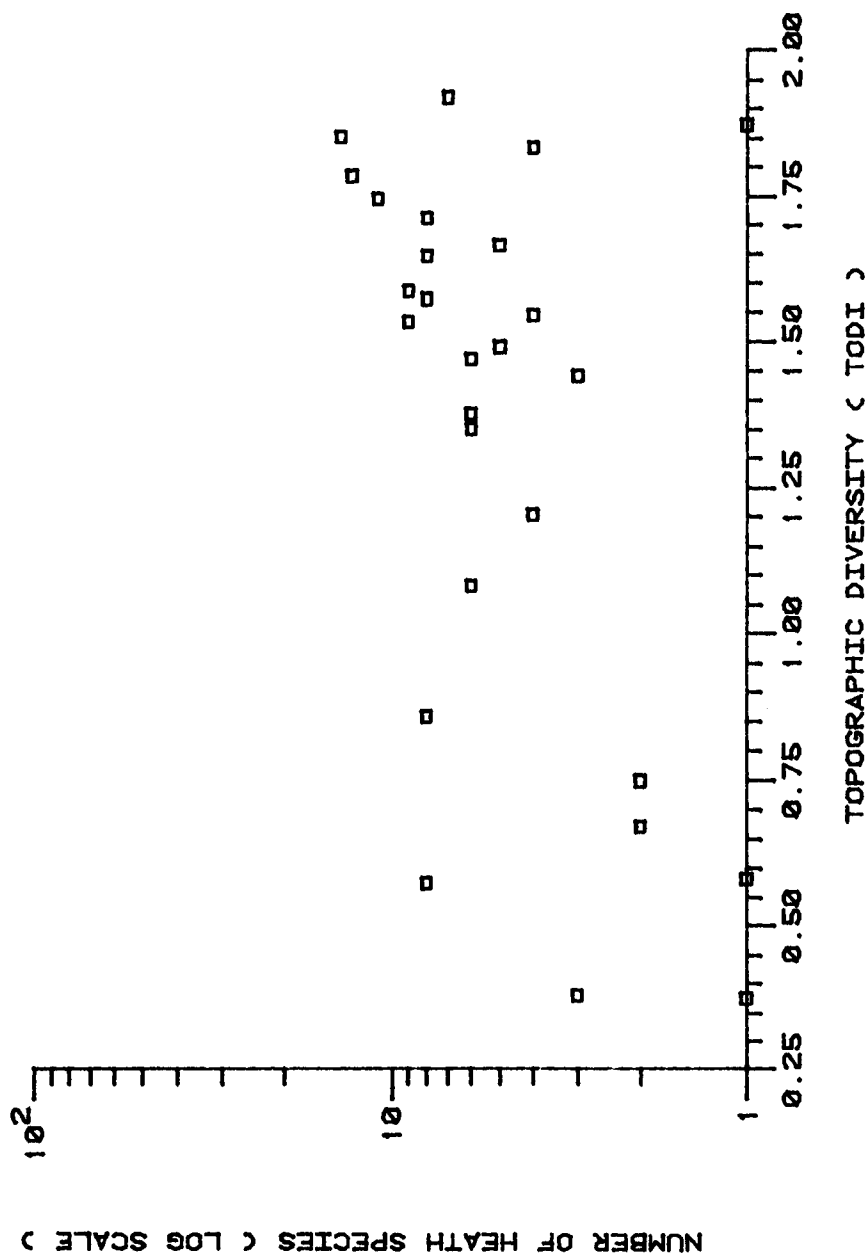


Figure 21. Relationship between the number of species of heaths (log scale) and topographic diversity ($r = 0.515$).

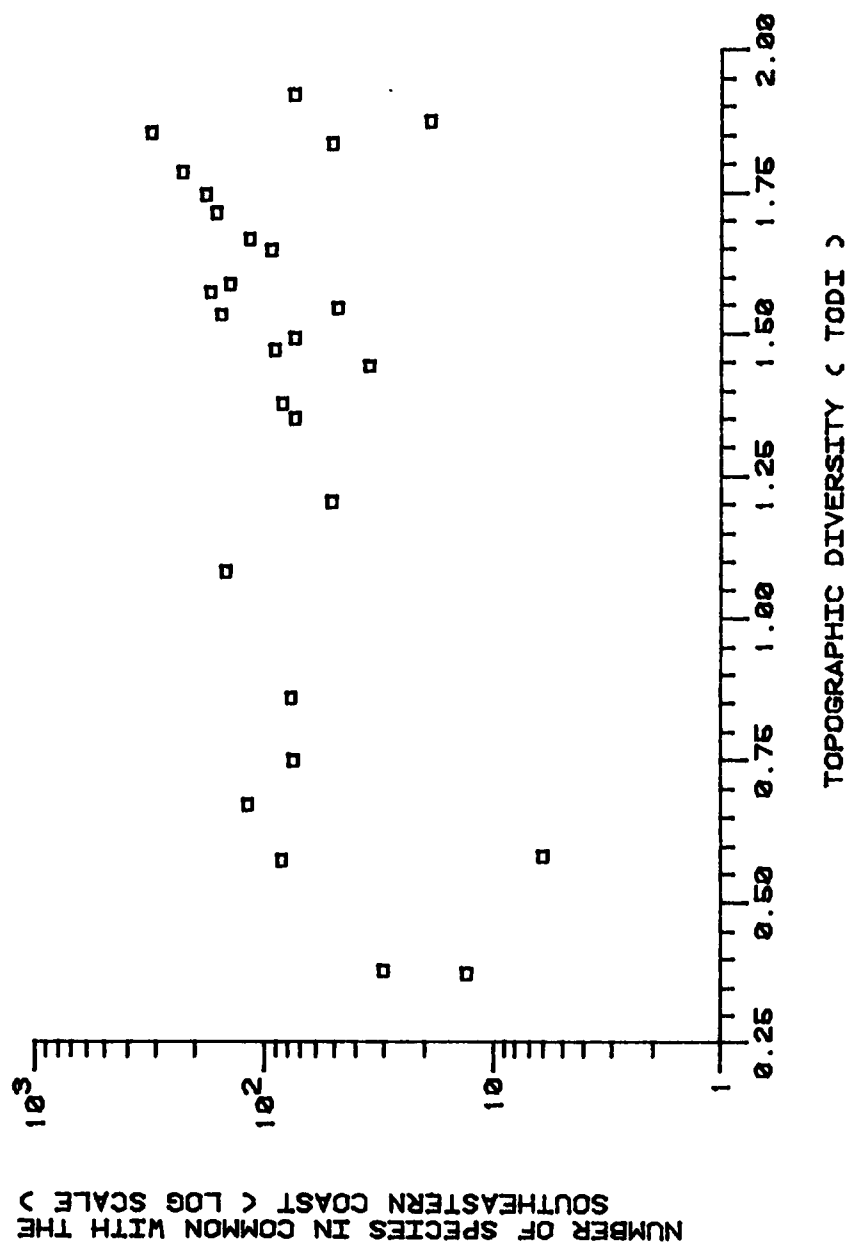


Figure 22. Relationship between the number of species in common with the Southeastern Coastal source area (log scale) and topographic diversity ($r = 0.485$).

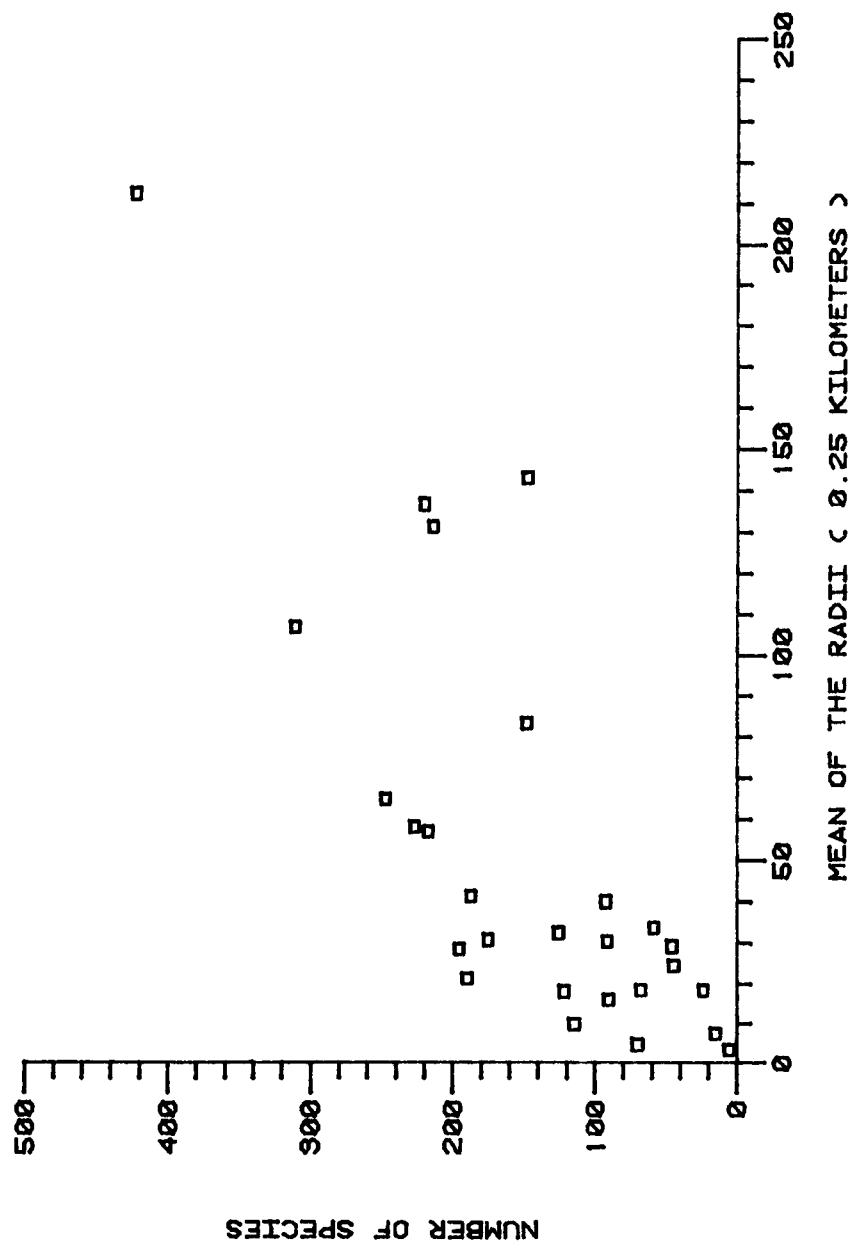


Figure 23. Relationship between the number of species and the mean of the radii
($r = 0.766$).

This correlation is probably due to the relationship between area and the mean of the radii (Appendix, Table A-18).

Another variable synthesized from the radial measurements of the islands was the variance of the radii. The variance of the radii was intended to represent three aspects of the geography of the islands. First, it is related to size by way of the magnitude of the measurements. Second, it will increase with the deviation from circularity of the shape of the island. Deviation from circularity of the island indicates that the island arose from more than one volcano or geologic event. The variance of the radii also responds, to a lesser degree, to changes in the island shape from a uniform to a more complex shoreline. A complex shoreline is usually related to a more complex topography on the island. The relationship between the total number of species and the logarithm of the variance of the radii is positive and significantly correlated ($r = 0.734$) (Figure 24).

A more specific representation of the deviation of the radii was determined by calculating the absolute value of the difference between one radius and the radius adjacent to it. This measurement, which will be called radial deviation, is dependent on changes in the shape of adjacent sectors of the island and is not simply the average of the squared deviations from the mean which variance calculations are based on. The magnitude of the deviation will also respond to the size and shape of an island as was described for the variance of the radii. The relationship between the number of species and the mean of the radial deviations is shown in Figure 25. The mean of the radial deviations is the only geographic variable which has a greater

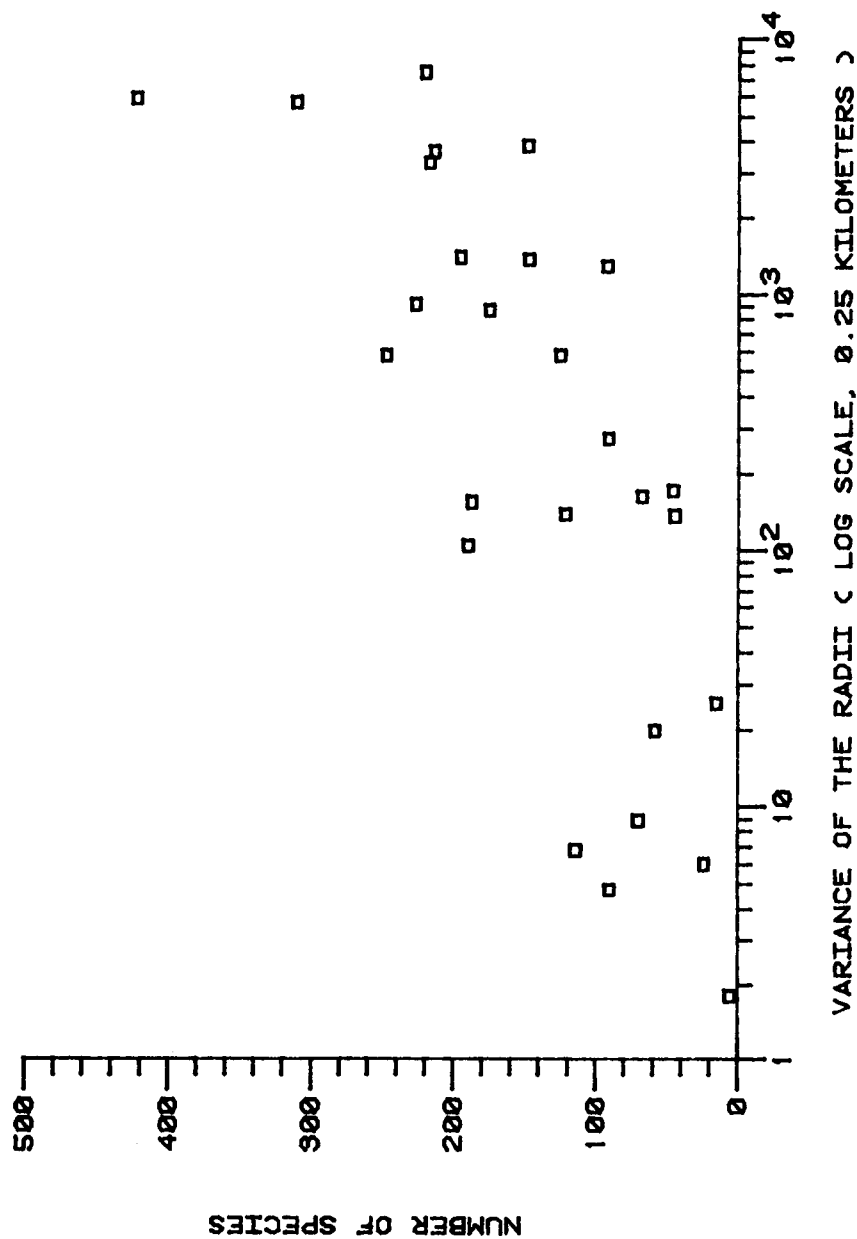


Figure 24. Relationship between the number of species and the variance of the radii
($r = 0.734$, log scale).

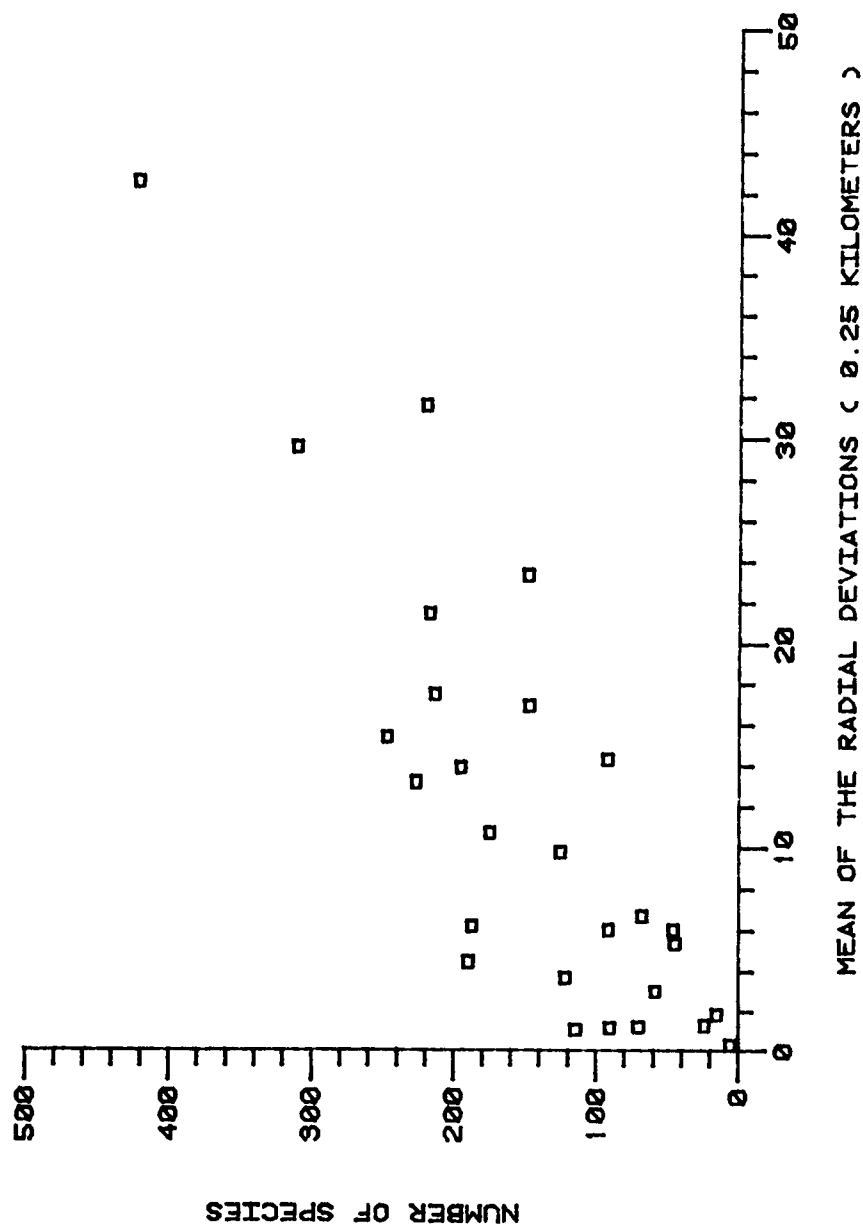


Figure 25. Relationship between the number of species and the mean of the radial deviations ($r = 0.836$).

correlation coefficient ($r = 0.836$) with the number of species than the log-log species-area relationship. The increase in the correlation coefficient is attributed to the mean of the radial deviations representing not only the size of an island, but also the complexity of its shape. The complexity of an island's shape is thought to affect environmental factors on the island such as the number of soil types, and the regional climate and microclimate. The mean of the radial deviations is also highly correlated with the number of species in families (Table 6). Figure 26 shows a linear relationship between the number of species of composites and the mean of the radial deviations.

The relative values of the radial measurements, calculated by division by the longest radius, are not significantly correlated with the number of species (Table 6). The absence of significant relationships for these variables is not surprising since the relative values represent the differences between the islands after most of the differences due to size of the island were factored out. These variables were intended primarily to represent the effect of shape in multiple regressions that included area and other geographic variables. These relative values of the radial measurements are discussed later in the multiple regression section.

Number of Species and Other Geographic Attributes

Several other geographic attributes of islands were also analyzed for relationships with the number of species. They included the number of bays, total length of mapped streams and latitude. The number of bays and stream kilometers are both correlated with area and each other (Appendix, Table A-18). However, the relationships observed between

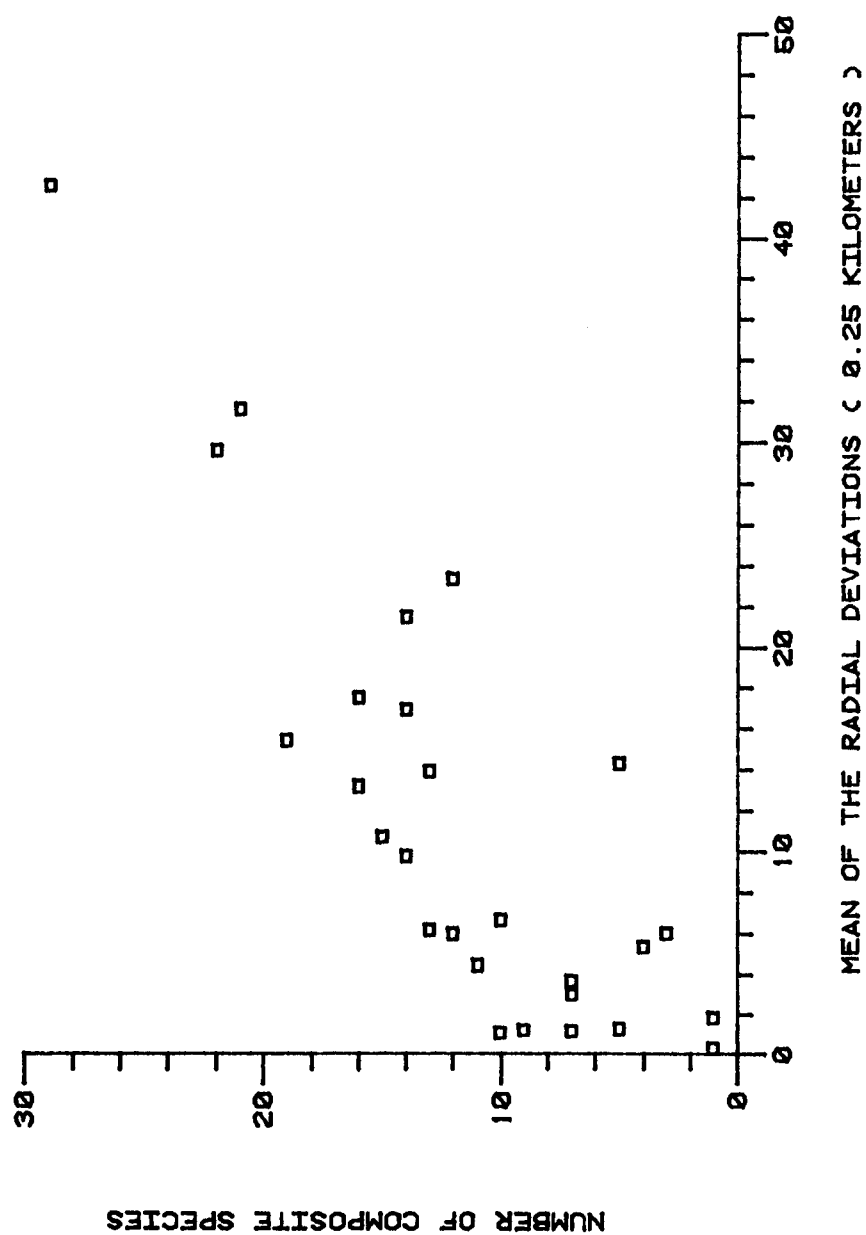
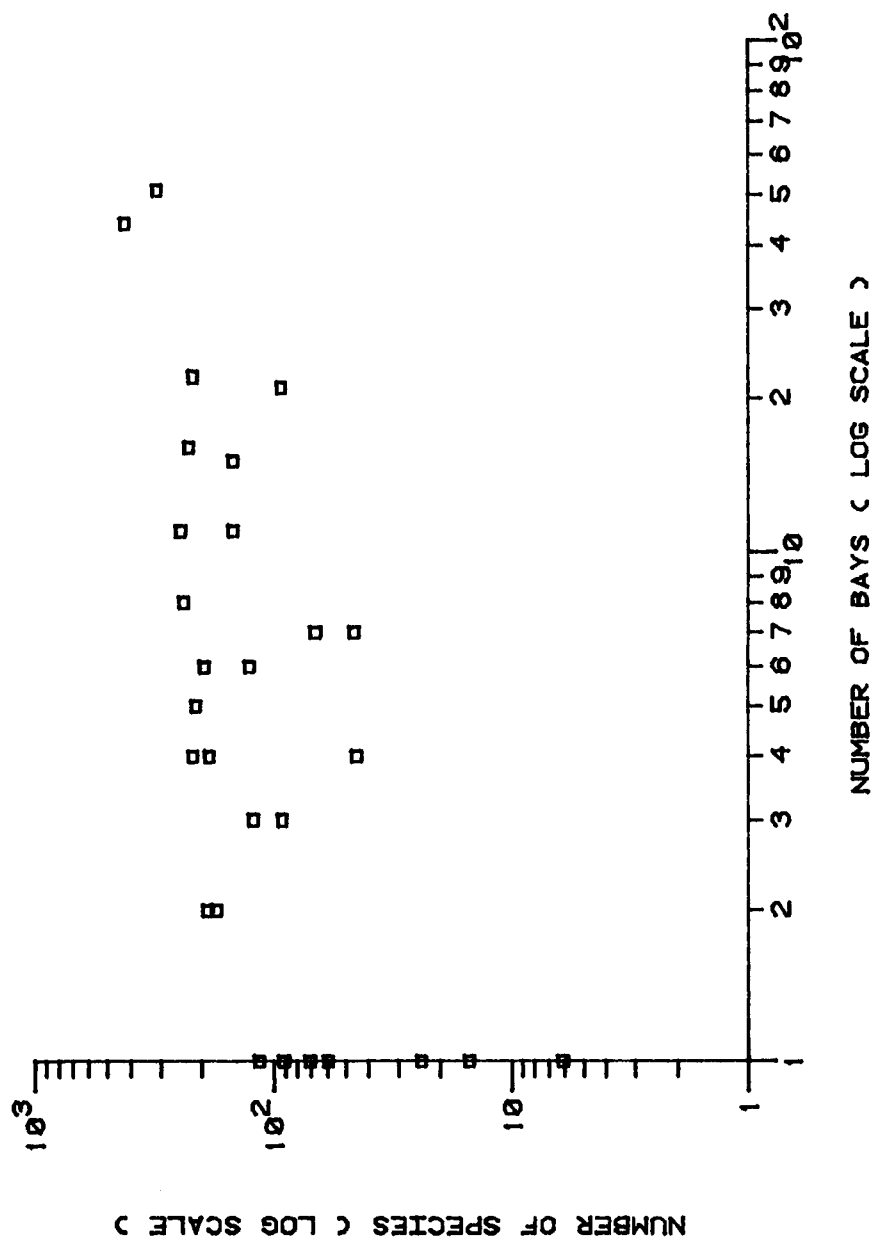


Figure 26. Relationship between the number of species of composites and the mean of the radial deviations ($r = 0.834$).

these variables and the floristic variables are different from the species-area relationships. The relationships with these factors are most linear in the log-log form. The relationships of the number of species with stream length (Figure 27) and the number of bays (Figure 28) depend on the size of an island and the topographic complexity of the island. Stream length is especially indicative of the complexity of the topography. Areas near streams and their valleys often contain vegetation which appears to be more diverse than the vegetation in the exposed areas. The number of bays is indicative of the complexity of an island's shape and the circulation patterns of the water around the island. Bays are also often the location of sand beaches which may present a more suitable temporary colonization site than the rock cliffs and large cobble beaches found on the exposed shores. Many families also show correlations between their number of species and these geographic variables (Table 5, page 76).

A pattern with increasing latitude of an area and a decreasing number of species has been described in a number of studies (Pianka 1966). Most of the correlations between latitude and the number of species on the islands in the study are not significant (Table 6). One exception to this pattern is a positive correlation ($r = 0.671$) found between latitude and the number of species of saxifrages (Figure 29). This relationship is probably due to many of the species of this family in this region being arctic and alpine (Hulten 1968).

A significant negative correlation ($r = -0.393$) between the logarithm of the number of species of orchids and the logarithm of latitude is another exception to the pattern of nonsignificance.



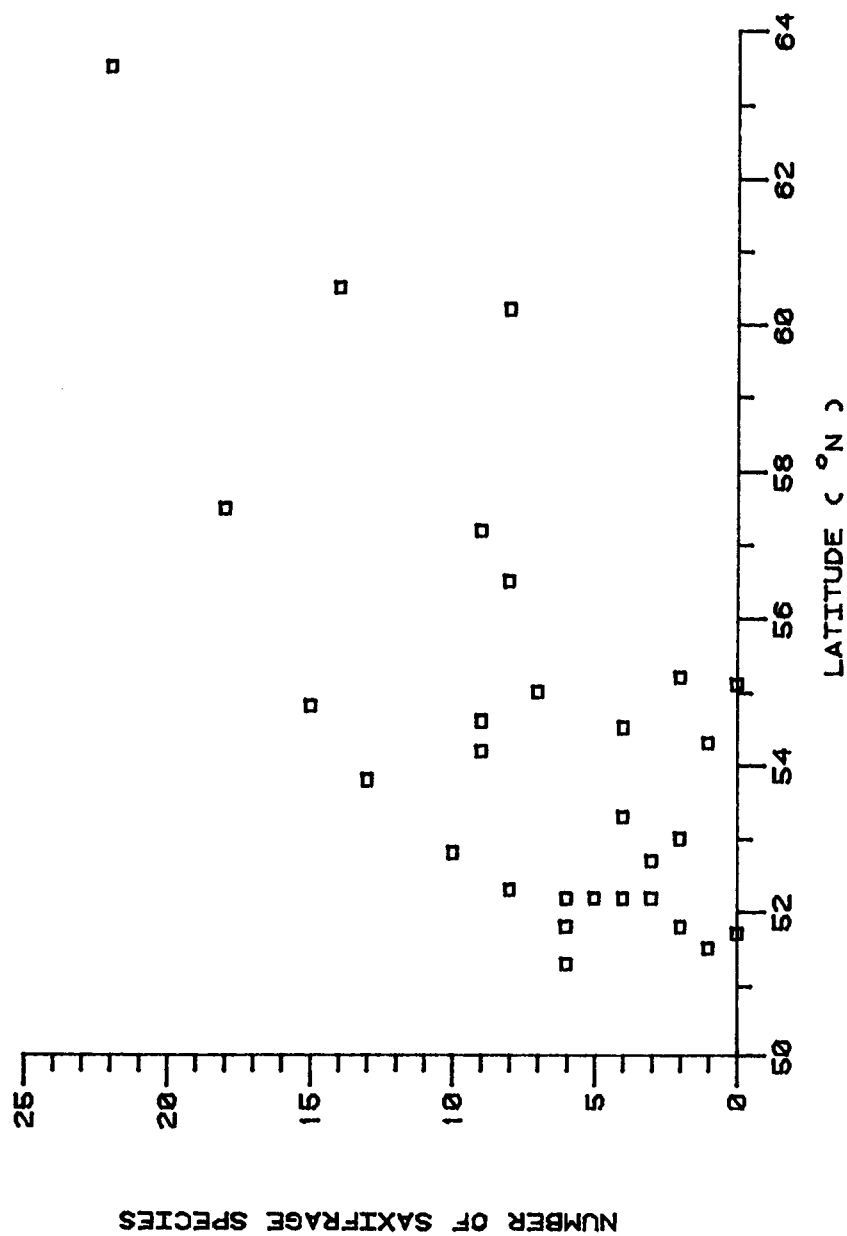


Figure 29. Relationship between the number of saxifrage species and latitude
($r = 0.671$).

This correlation is probably significant because very few species of orchids have been reported for the northern islands (two species from Nunivak and one species from St. Paul).

Latitude is also a useful substitute for distance from the northern and southern source areas. A significant negative correlation ($r = -0.788$) is observed between latitude and the proportion of species on an island which are in common with the flora of the southeastern coastal source area (Figure 30). A positive correlation ($r = 0.683$) is also found between latitude and the proportion of species in common with the flora of the Seward Peninsula source area. Both of these relationships are consistent with the concept of decreasing floristic affinity between areas separated by increasing distance. In this case, the distance between two areas is represented by the difference in latitude which is the north-south vector of distance.

Number of Species Per Area and Geologic Variables

The soil type and geologic information available for the islands in this region varies widely in detail and accuracy. In an attempt to utilize a commonly available level of detail, values for three categorical variables were determined for each of the Aleutian Islands in the data set. These categorical variables were then used to form groups of islands for analysis of variance on the number of species per area from the log-log model. The area relationship with the number of species in the log-log model was factored out to determine if differences in the number of species per area could be explained by these geologic variables. The first categorical variable was the

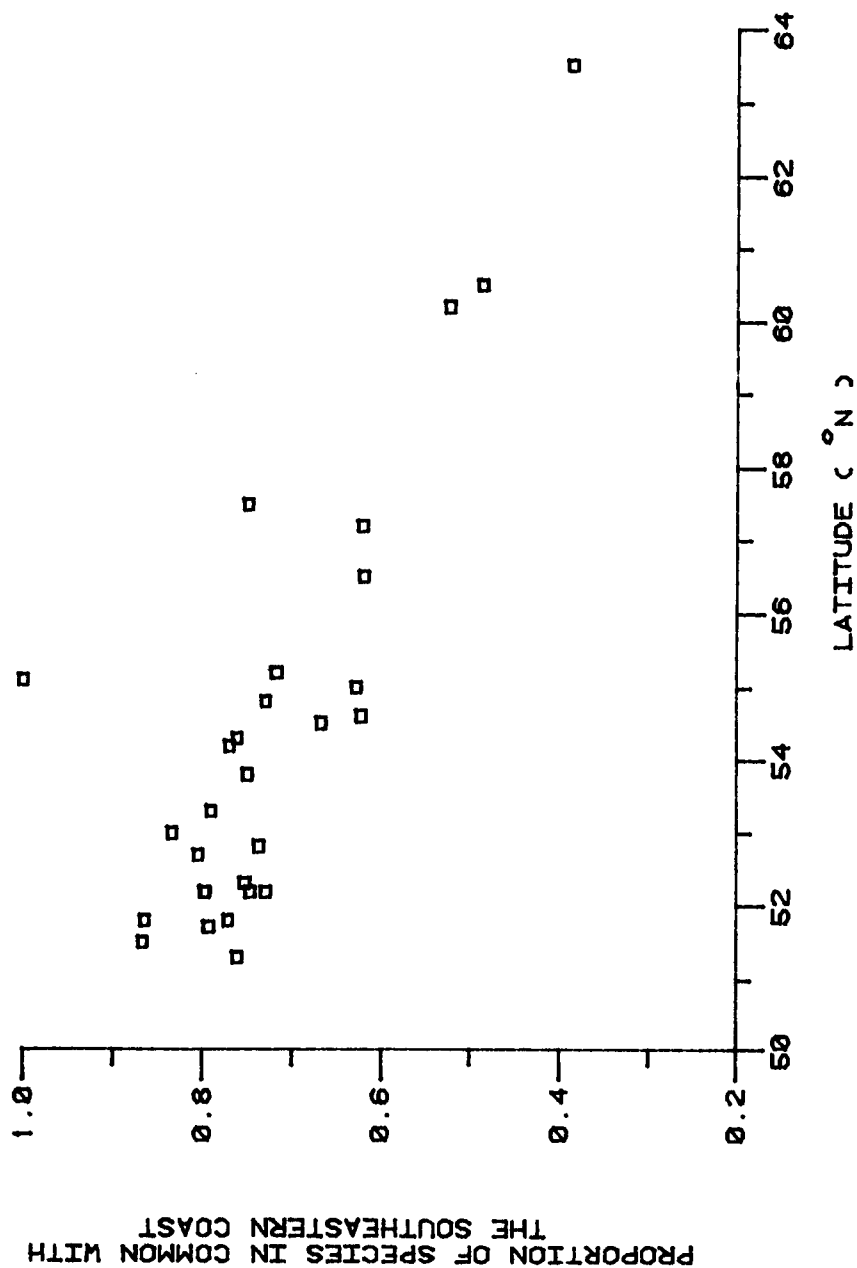


Figure 30. Relationship between the proportion of species in common with the Southeastern Coastal source area and latitude ($r = -0.788$).

general shape of the island. The shape categories used were volcanic cone, bench or terrace, and a combination of both. The analysis of variance on groups formed by this categorical variable is not significant. The presence or absence of recently active volcanoes (Coats 1950) was also used as a categorical variable to assign the islands to groups for analysis of variance on the number of species per area. This analysis of variance is also not significant. Islands were also assigned to groups by the number of geologic periods that were represented by the age of their rocks. The analysis of variance of the number of species per area was repeated and is not significant.

All of the categorical variables and the analyses performed with them are probably insufficiently refined to explain differences in the number of species per area on the islands. However, this is the level of information which is uniformly available for the Aleutian Islands in the data set. If the adequacy of the variables and analyses was accepted, then the nonsignificant results would mean that these factors do not explain variations in the number of species per area on the Aleutian Islands.

Number of Species and Isolation-Distance Effects

The isolation of an island was an element of the theory of island biogeography developed by MacArthur and Wilson (1967). The general form of the hypothesized relationship was that islands with greater isolation would have fewer species. Since the isolation of an island is difficult to measure directly, a relationship between distance and isolation is usually assumed in studies of biogeography.

Islands which are farther from source areas are assumed to be more isolated. Distances from each island to other areas were used in this study as one measure of isolation.

The relationship between distance from a source area and the total number of species was the first isolation pattern studied. The most logical source areas for the islands appeared to be the Alaska and Kamchatka Peninsulas (Figure 1, page 2). However, the major currents shown in Figure 6 (page 31) indicate that the islands are isolated from propagules from Kamchatka. The means of transport of propagules from Kamchatka to the island are not clear but may depend on other means such as man, ice rafting, or storms. Figures 31 and 32 show the relationship between the distance to these source areas and the total number of species. No pattern or correlation is observed for these relationships (Table 7). Given the linear nature of the Aleutian Island Chain and the magnitude of distance that it spans, it is surprising to observe no relationship between distance and the number of species.

The flora of each island being the net result of isolation from and exposure to the floras of several source areas on both the Asian and American continents was the second possibility considered. In order to clarify the pattern between the number of species and the distance from a source area, the number of species which were also found on a source area were counted. This count will be referred to as the number of species in common with a source area. These values were determined for all six source areas. Relationships between the number of species in common with a source area and the distance from that

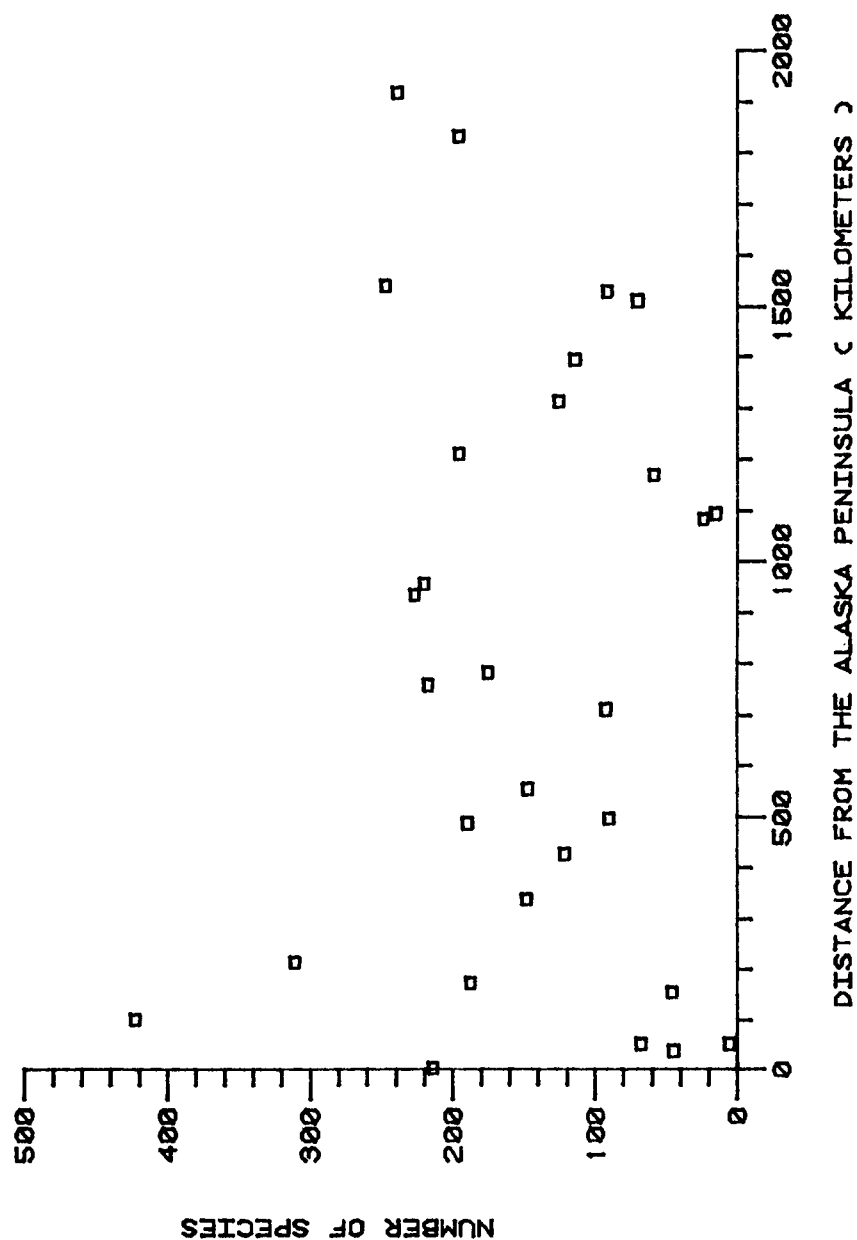


Figure 31. Relationship between the number of species and the distance from the Alaska Peninsula source area. The correlation coefficient for this relationship is not significant.

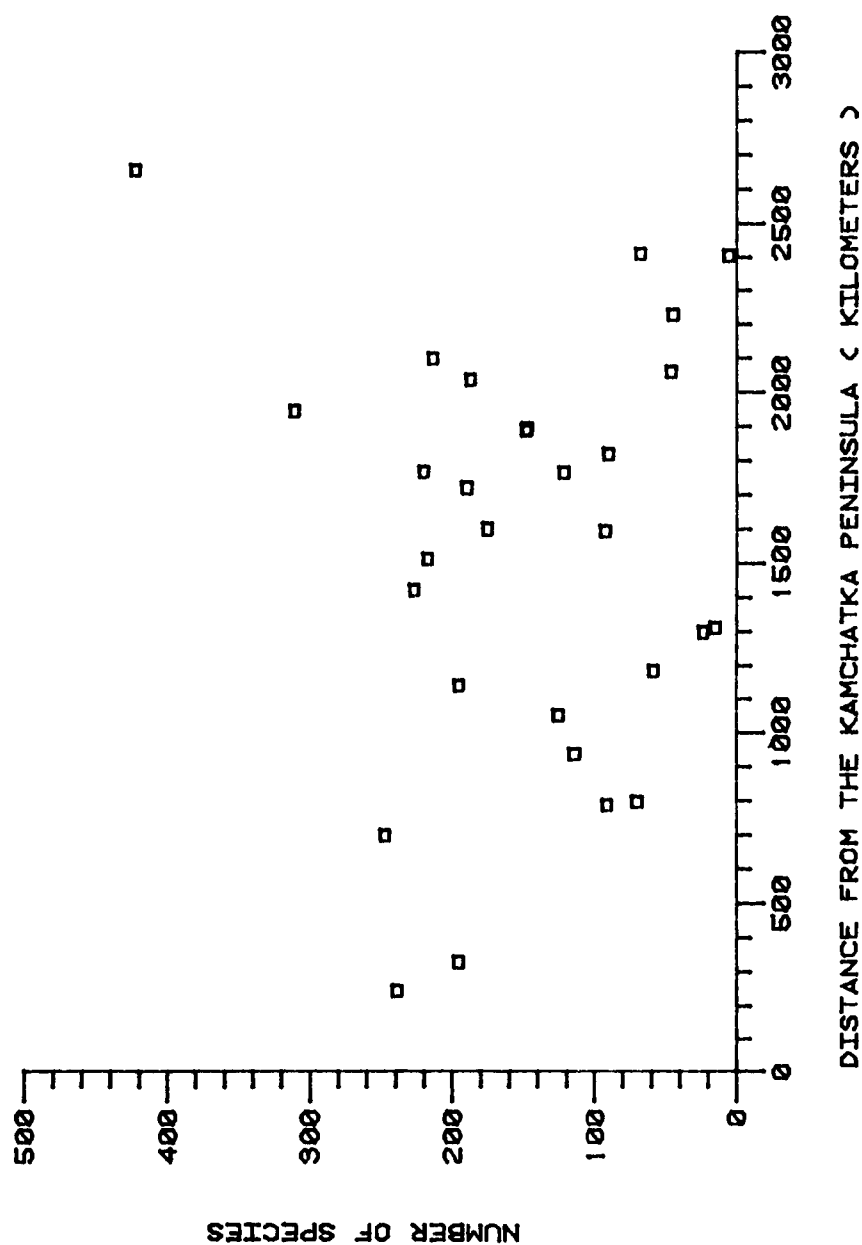


Figure 32. Relationship between the number of species and the distance from the Kamchatka Peninsula source area. The correlation coefficient for this relationship is not significant.

Table 7. Correlation coefficients between floristic variables and distance measurements.

Floristic Variables	Source Areas					
	Alaska Pen.	Kamchatka Pen.	S.E. Coast	Yukon Plain	Seward Pen.	Chukotka Pen.
Total number of species	-0.004 ^a	0.028 ^a	-0.130 ^a	-0.110 ^a	-0.181 ^a	-0.148 ^a
Number of species in common with source area	-0.079 ^a	-0.099 ^a	-0.098 ^a	-0.295 ^a	-0.464	-0.470
Proportion of species in common with source area	-0.557	-0.673	0.122 ^a	-0.493	-0.691	-0.630
Number of species restricted to source area	-0.428	-0.681	-0.314 ^a	b	-0.360 ^a	-0.628
Proportion of species restricted to source area	-0.518	-0.797	-0.104 ^a	b	-0.470	-0.353 ^a
Proportion of species restricted to source area vs. log distance	-0.398	-0.907	-0.124 ^a	b	-0.593	-0.538

Not significant, Alpha = 0.05.

None of the species restricted to the Yukon Plain source area were reported from the islands.

source area were then studied. No pattern or correlation is present in this type of relationship (Table 7). Figure 33 shows the results for the Kamchatka area as an example.

Table 8 shows that the numbers of species in common with the different source areas are correlated with each other and with the total number of species. Since some of the factors which affect the total size of the flora are independent of the island's location, the number of species in common with the source areas was divided by the total number of species. The resulting proportion was then related to the distance of the islands from the source area. After removing part of the effects of other source areas and the factors related to the total number of species on the number of species in common with a source area, a significant negative correlation ($r = -0.673$) between the proportion of species in common with a source area and the distance from the source area (Figure 34) was observed for all source areas except the southeastern coastal source area (Table 7).

Since the numbers of species in common with different source areas were correlated with one another, the accurate representation of the independent contribution of each source area to an island's flora was still questionable. The definition of the species in common with a source area still permitted a species to be defined as being related to more than one source area. To clarify the source area relationships, a more restricted specification was used to define which species on an island were related to a source area. The species on an island which were also reported on one source area and none of the other source areas were then counted for each island. This definition requires the

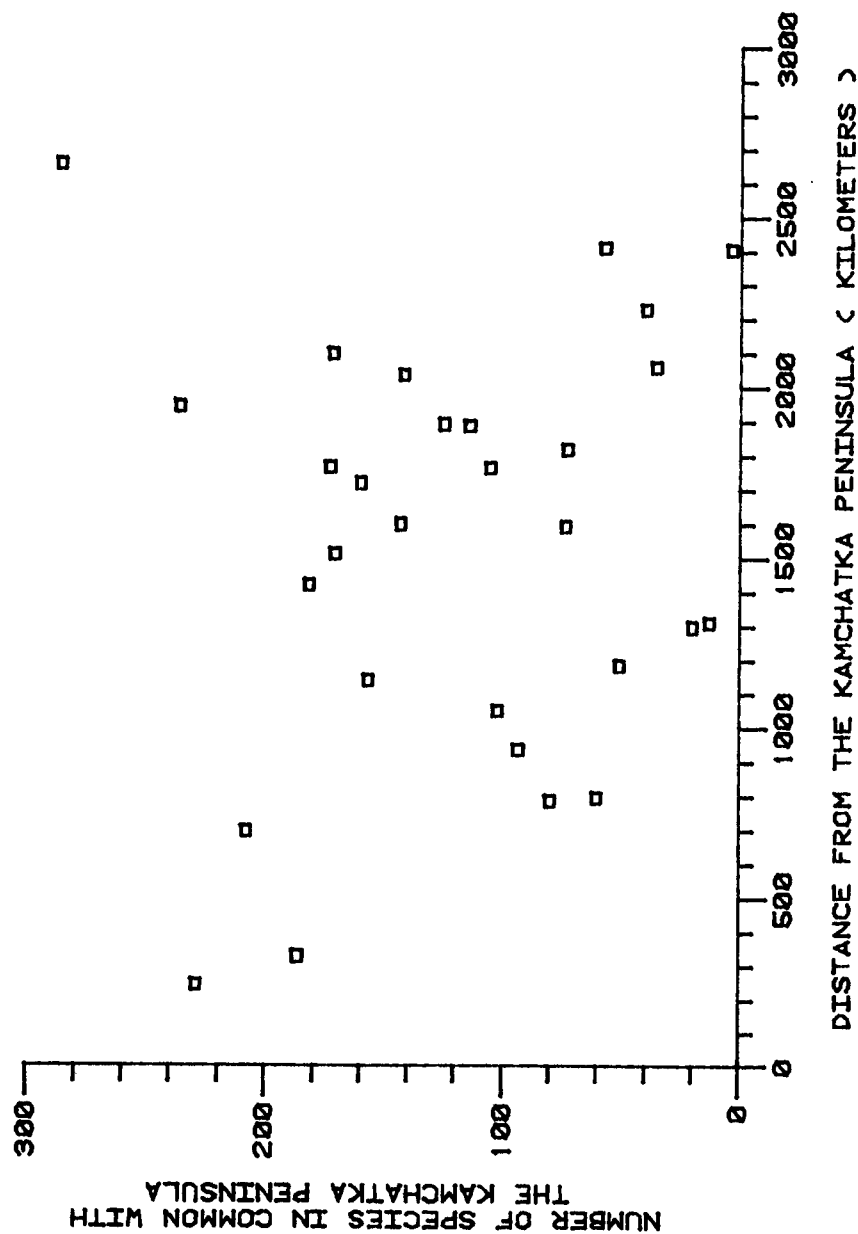


Figure 33. Relationship between the number of species in common with the Kamchatka Peninsula source area and the distance from the Kamchatka Peninsula source area. The correlation coefficient for this relationship is not significant.

Table 8. Correlation coefficients between the number of species in common with the source areas and the total number of species.

	SPNO ^a	SPAP	SPKA	SPSC	SPYU	SPSE
SPAP	0.990					
SPKA	0.983	0.964				
SPSC	0.962	0.975	0.927			
SPYU	0.942	0.922	0.944	0.827		
SPSE	0.929	0.905	0.927	0.804	0.996	
SPCH	0.906	0.879	0.911	0.766	0.992	0.996

^aVariable abbreviations:

SPNO = Number of species

SPAP = Number of species in common with the Alaska Peninsula

SPKA = Number of species in common with the Kamchatka Peninsula

SPSC = Number of species in common with the Southeastern Coast

SPYU = Number of species in common with the Yukon Plain

SPSE = Number of species in common with the Seward Peninsula

SPCH = Number of species in common with the Chukotka Peninsula.

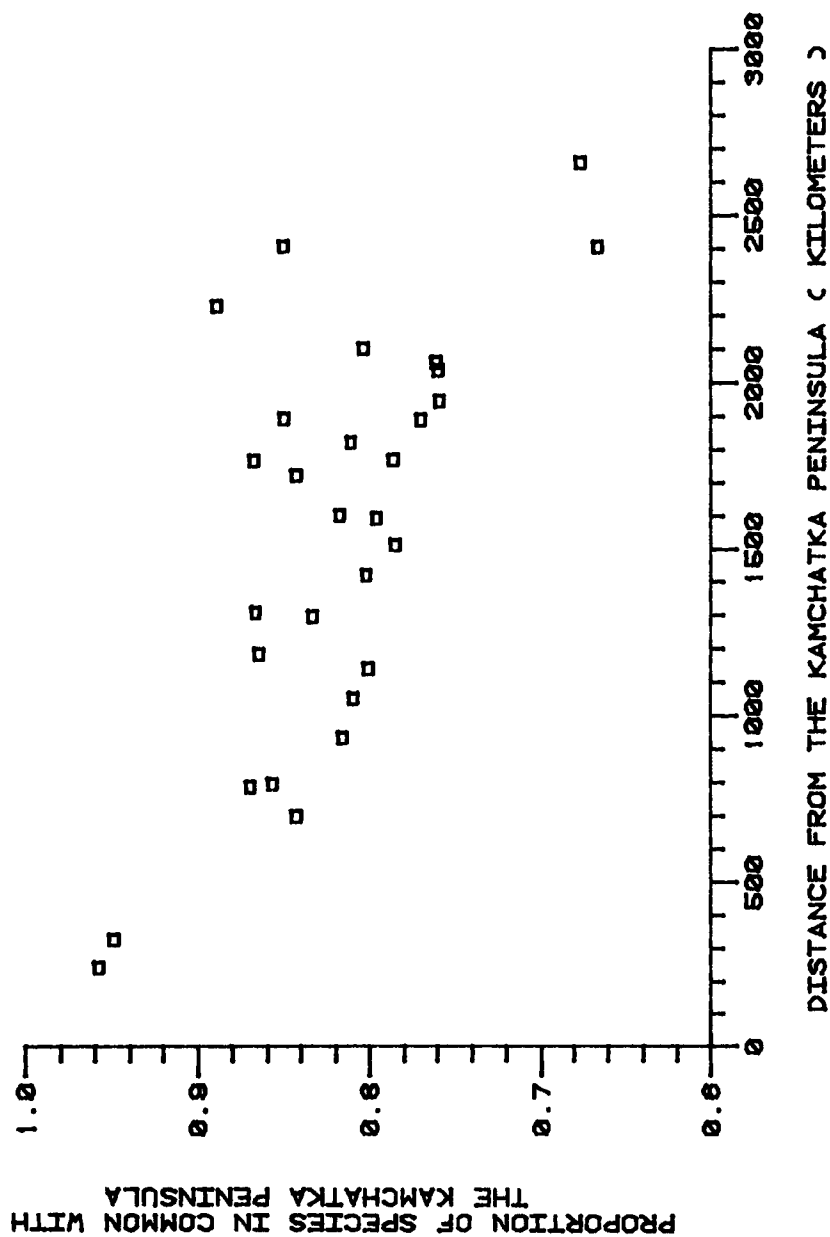


Figure 34. Relationship between the proportion of species in common with the Kamchatka Peninsula source area and the distance from the Kamchatka Peninsula source area ($r = -0.673$).

number of species being tabulated to be related to the flora of a specific source area and independent of the floras of the other source areas. The number of species which are reported from a source area and only that area is referred to as the number of species that are "restricted" to that source area. Table 9 shows that the number of species on an island restricted to a single source area on an island is correlated with the number of species in common with that source area. However, the correlations between the number of restricted species (Table 10) from the different source areas are not as strong as the correlations between the number of species in common with the source areas (Table 8). While the pattern between the restricted number of species from the Kamchatka flora is correlated ($r = 0.540$) with the number of species in common with the Kamchatka flora (Figure 35), it is interesting to note that islands with a large number of species in common with the flora of Kamchatka may or may not have a correspondingly large number of species restricted to the flora of Kamchatka.

The two species which were defined as being restricted to the Yukon Plain source area are not reported from any islands in this study. These two species are Puccinellia geniculata and Betula papyrifera. Because this area is reported as part of a possible refugia for plants during periods of glaciation (Hopkins 1972), it was expected that this source area would have more species restricted to it. Areas which are thought to be a refugia and have no "endemic" species apparently contain a flora which has successfully dispersed into at least one of the other source areas. Hypothesizing complete dispersal

Table 9. Correlation coefficients between the number of species in common with a source area and the number of species restricted to a source area.

Source Area	Correlation Coefficient
Alaska Peninsula	0.771
Kamchatka Peninsula	0.540
Southeastern Coast	0.833
Seward Peninsula	0.545
Chukotka Peninsula	0.454

Table 10. Correlation coefficients between the number of species restricted to source areas and the total number of species.

	SPNO ^a	RSAP	RSKA	RSSC	RSSE
RSAP	0.744				
RSKA	0.413	-0.107 ^b			
RSSC	0.734	0.831	0.048 ^b		
RSSE	0.566	0.787	-0.104 ^b	0.679	
RSCH	0.265 ^b	0.157 ^b	0.063 ^b	-0.134 ^b	0.200 ^b

^aVariable abbreviations:

SPNO = Number of species

RSAP = Number of species restricted to the Alaska Peninsula

RSKA = Number of species restricted to the Kamchatka Peninsula

RSSC = Number of species restricted to the Southeastern Coast

RSSE = Number of species restricted to the Seward Peninsula

RSCH = Number of species restricted to the Chukotka Peninsula.

^bNot significant, Alpha = 0.05.

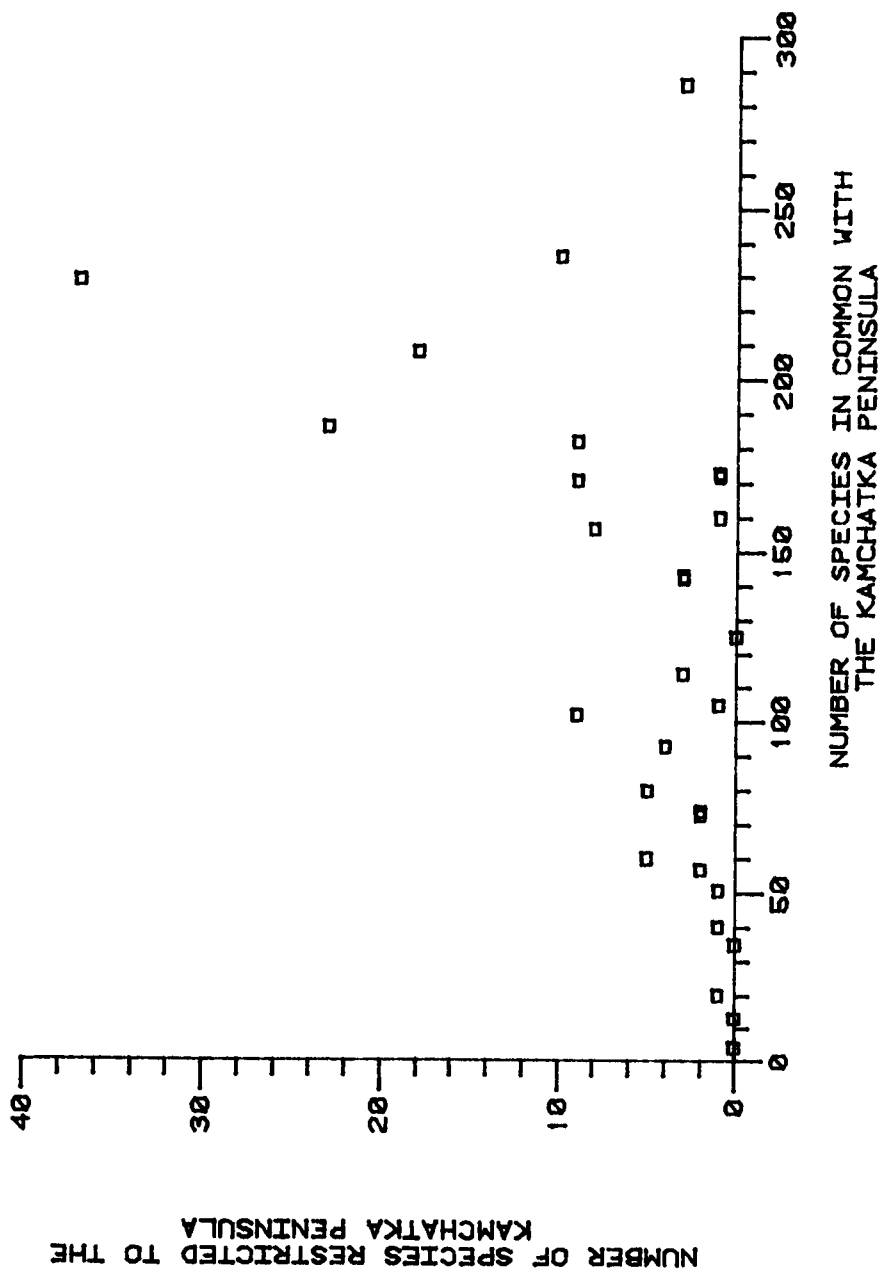


Figure 35. Relationship between the number of species restricted to the Kamchatka Peninsula source area and the number of species in common with the Kamchatka Peninsula source area ($r = 0.540$).

may not be significantly more satisfactory than stating that the flora of the area originated from all of the other source areas and has few unique or "endemic" species. An adequate explanation of this unexpected result cannot be obtained from the data available in this study.

The significant negative correlation ($r = -0.673$) between distance from Kamchatka and the number of species per island which are restricted to the Kamchatka Peninsula source area (Figure 36) could be the result of two separate isolation curves with a break in the effects of isolation occurring between the Commander and western Aleutian Islands and the remainder of the islands. This relationship also contains the influences related to the total number of species per island. While the correlation between the restricted and total number of species (Figure 37) is significant (Table 10), it is not nearly as strong as the correlation between the number of species in common with Kamchatka and the total number of species (Figure 38, Table 8). The relationship between the proportion of the total number of species which are defined as restricted to Kamchatka and the distance from Kamchatka (Figure 39) has both the effect of the variation in the total number of species and the influence of the flora of other source areas removed. When the other factors are controlled, a very clear negative correlation ($r = -0.797$) between distance and the floristic variable is observed.

Since the relationship with distance shown in Figure 39 is somewhat curved, a logarithmic transformation on distance is used to portray a linear relationship between the proportion of the species

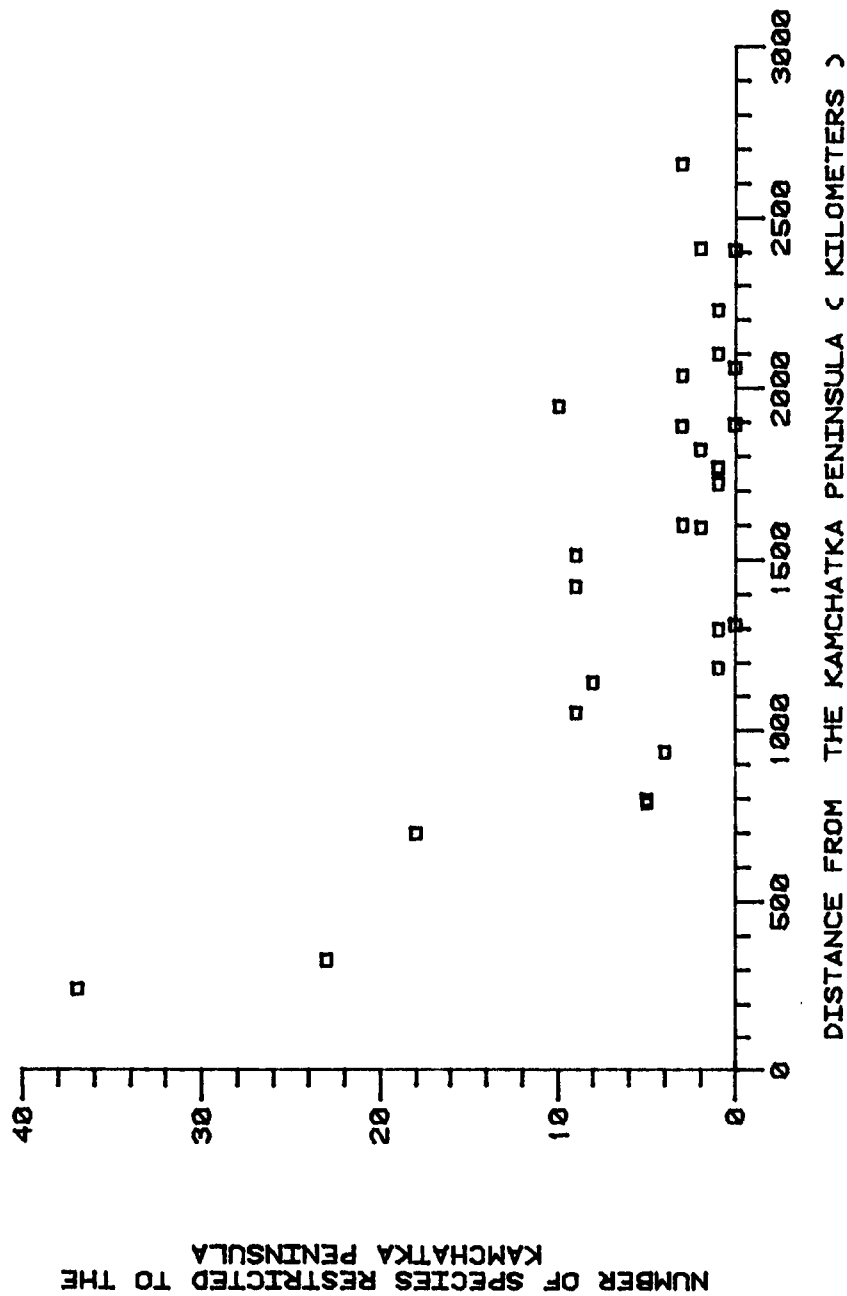


Figure 36. Relationship between the number of species restricted to the Kamchatka Peninsula source area and the distance from the Kamchatka Peninsula source area ($r = -0.673$).

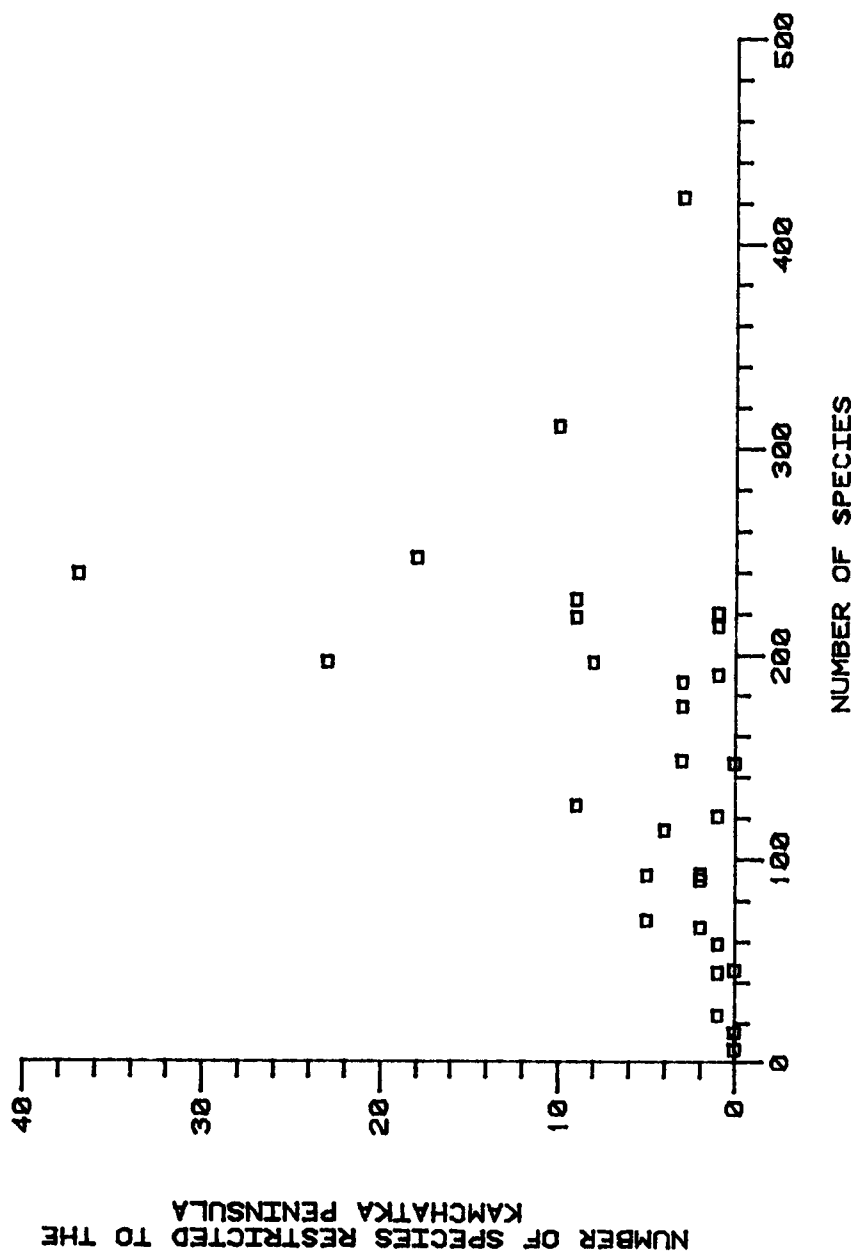


Figure 37. Relationship between the number of species restricted to the Kamchatka Peninsula source area and the total number of species ($r = 0.413$).

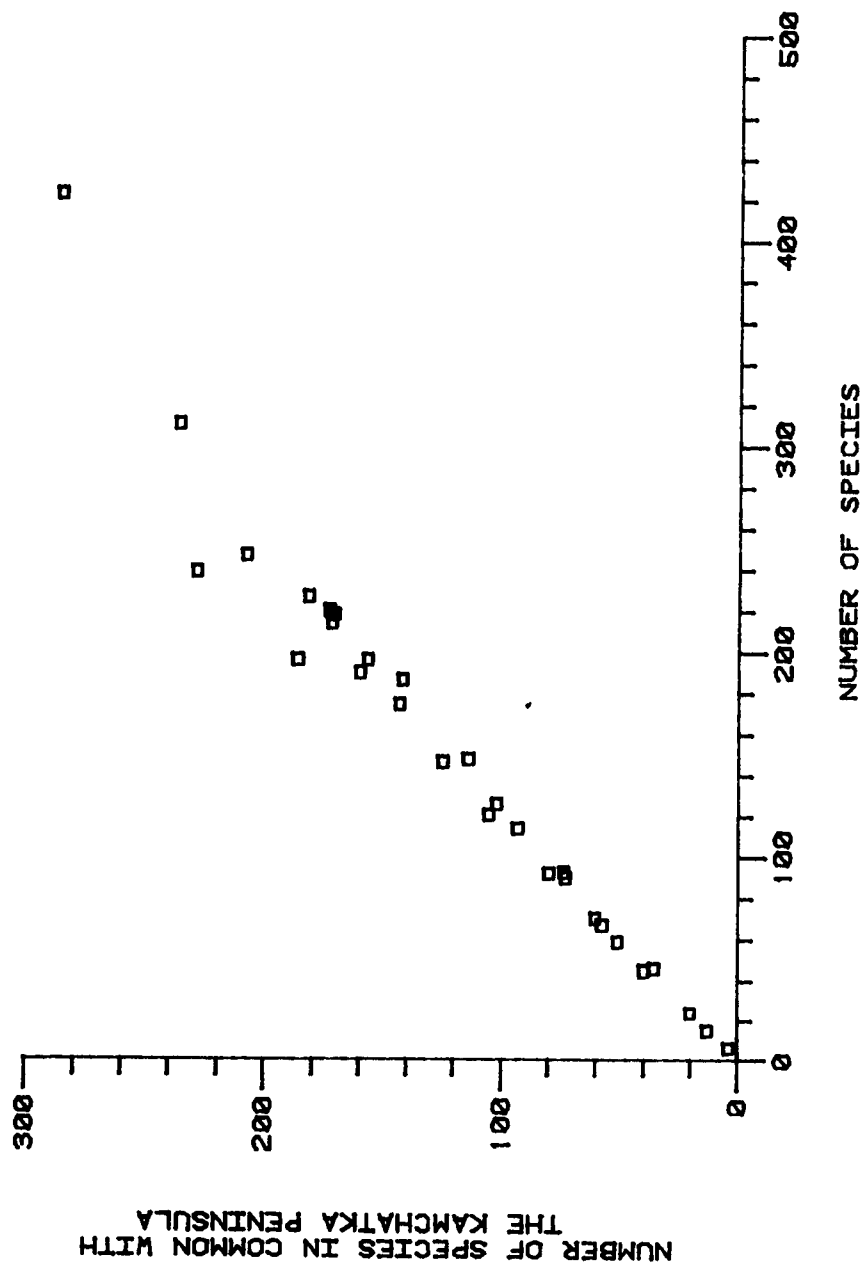


Figure 38. Relationship between the number of species in common with the Kamchatka Peninsula source area and the total number of species ($r = 0.983$).

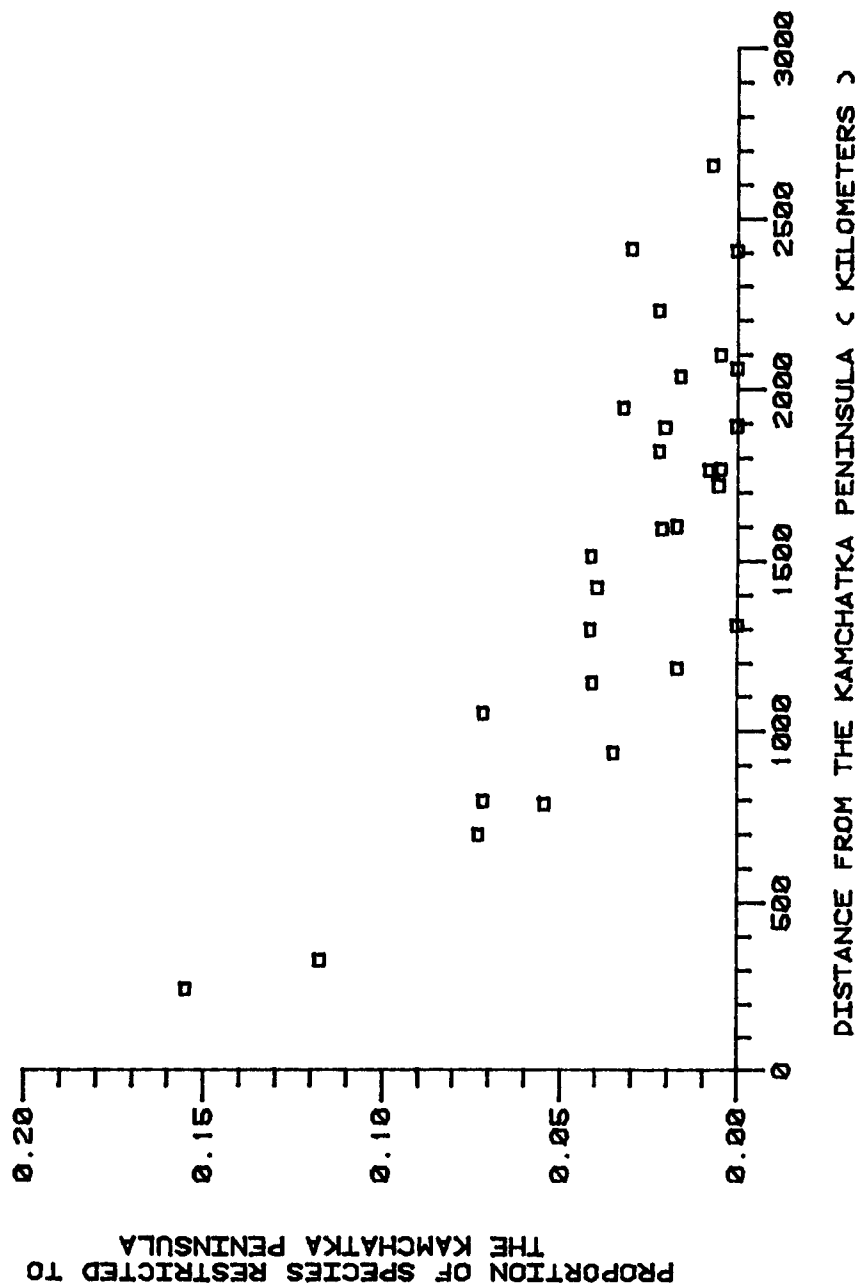


Figure 39. Relationship between the proportion of species restricted to the Kamchatka Peninsula source area and the distance from the Kamchatka Peninsula source area ($r = -0.797$).

on an island restricted to the Kamchatka source area and the distance from Kamchatka (Figure 40).

In retrospect, the failure to observe a simple relationship between the total number of species on an island and the distance of the island from one source area is not surprising. Undoubtedly several factors significantly affect the total number of species. The simultaneous action of multiple factors is a fundamental principle of ecology.

The results from the Kamchatka source area were used in this discussion because they show the clearest transition of the relationships between floristic variables and distance. The values of the number of species related to that source area are also large enough to avoid distortion of the analyses due to a large number of zeros for several islands as was observed for the values from other source areas. However, the results are surprising since the islands are isolated from Kamchatka by the major currents; man, ice rafting, and storms could be other means of transport of propagules from Kamchatka.

The patterns shown for Kamchatka are representative of the patterns observed in the other source areas except for the southeastern coastal source area. Table 7 shows that no significant correlations between these floristic variables and distance were found for that source area. Possible explanations for these nonsignificant results may be related to the fact that this source area is farther away from the islands than the other source areas. In this greater distance range, isolation may not significantly increase with increasing distance from the southeastern coastal source area. Another explanation

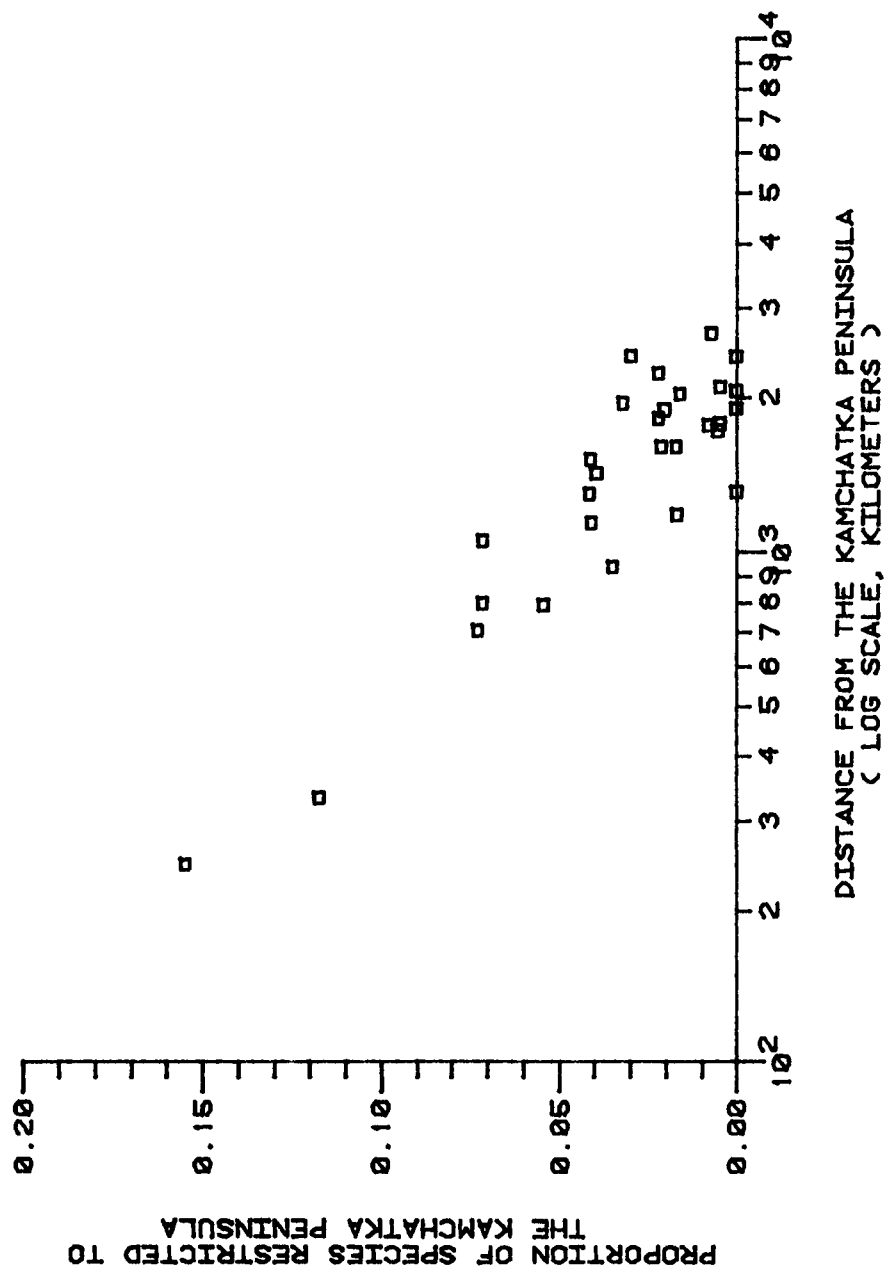


Figure 40. Relationship between the proportion of species restricted to the Kamchatka Peninsula source area and the distance from the Kamchatka Peninsula source area ($r = -0.907$, log scale).

could be that the Alaska Peninsula, which is between the southeastern coastal source area and the islands, may interact with the southeastern coastal source area in the dispersal of propagules from that area to the islands. If this were true, the observation of simple isolation from the southeastern coastal area would be obscured by this interaction.

Species-Area Relationships for "Near" and "Far" Islands

MacArthur and Wilson (1967) also hypothesized that closer islands with less isolation would have flatter species-area curves than islands farther from source areas. The smaller values of the species-area slope for less isolated islands was said to be due to the saturation of species on small islands that occurs when isolation is absent. Since the effects of the floras of islands not included in this study are not known, any decisions about the differences in isolation of the islands are simplistic. The possibility that several source areas have contributed to the flora of the islands also makes the true isolation of the islands difficult to determine. With the consideration of these limitations, the difference between the slope of the species-area curve for seven "near" islands and seven "far" islands was tested. The islands in the "near" group are Sanak through Carlisle, which are all in the eastern part of the Aleutian Island Chain (Figure 41). The islands in the "far" group are Amliia through Amchitka in the central part of the Aleutian Island Chain (Figure 41). The plot of the species-area relationships for the islands groups are shown in Figure 42. The slopes of the regression lines for these two species-area relationships are 0.337 for the

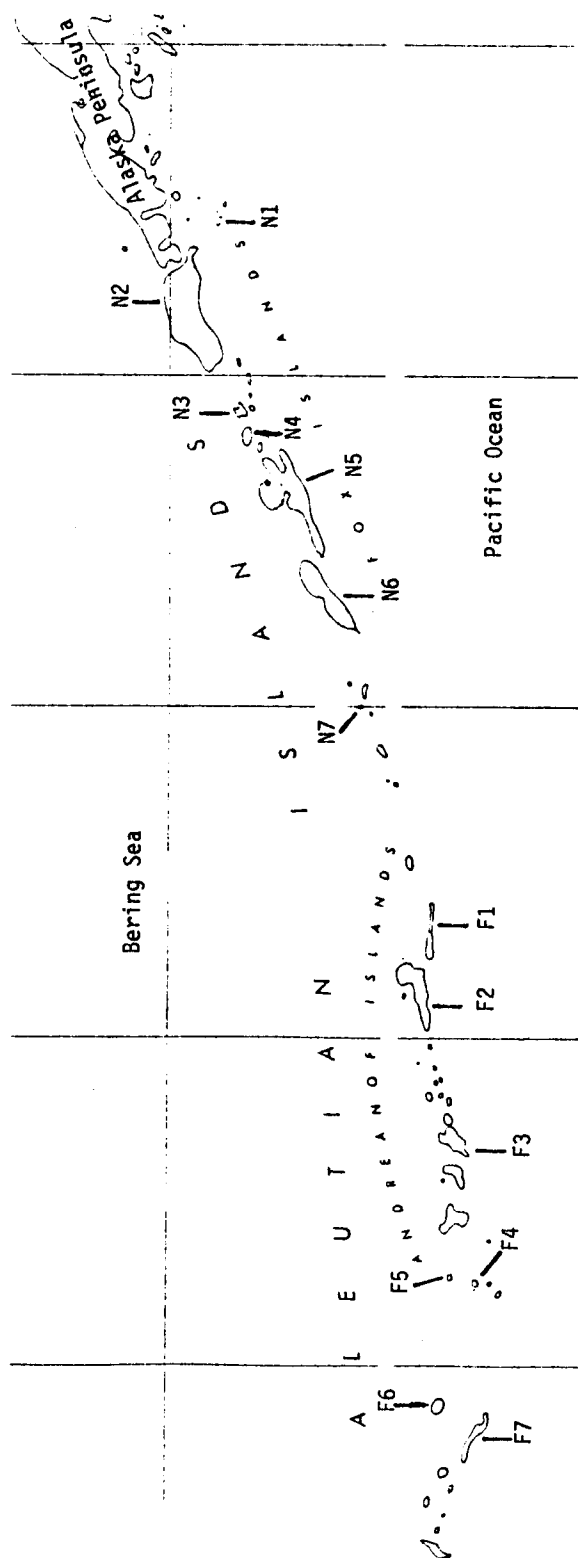


Figure 41. Location of "near" and "far" Aleutian Islands. (Map adapted from 1:10,000,000 scale World Outline Maps Series, sheet 29, Army Map Service, Corps of Engineers.) Sanak (N1), Unimak (N2), Akun (N3), Akutan (N4), Unalaska (N5), Umnak (N6), Carlisle (N7), Adak (F1), Atka (F2), Adak (F3), Kavalga (F4), Gareloi (F5), Semisopochnoi (F6), Amchitka (F7).

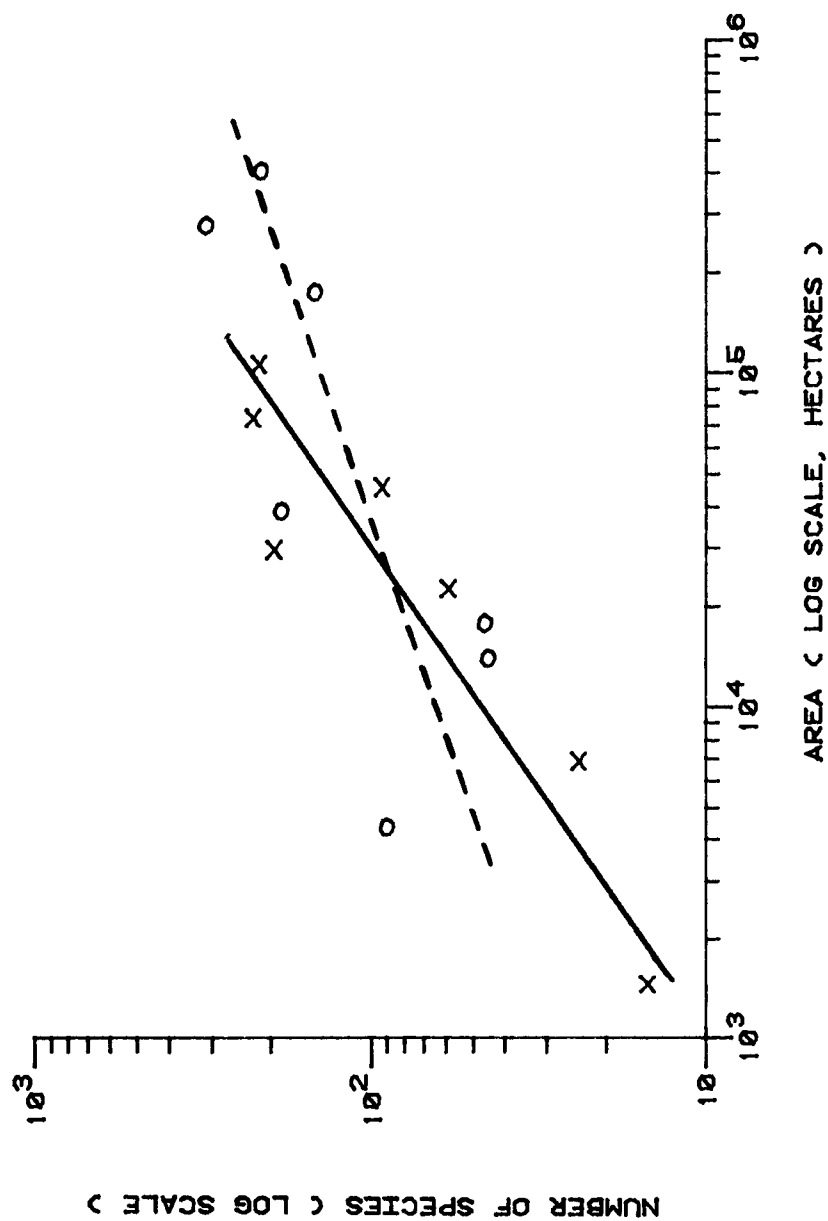


Figure 42. Species-area curves for "near" and "far" islands. (O = "near" islands, X = "far" islands; the dashed line is the regression line for the "near" islands and the solid line is the regression line for the "far" islands.)

"near" islands and 0.690 for the "far" islands. Since the ranges of the number of species and area values overlap, it is valid to test for differences. Using a t-test procedure for comparing two slopes (Zar 1974), the slopes were determined to be significantly different.

II. REPRESENTATION OF ISOLATION WITH CLUSTER ANALYSES

A negative relationship between interisland similarity and distance was described by Power (1975). Figure 43 shows a negative pattern between the interarea distance and similarity for all possible pairs of areas. This pattern is significantly correlated ($r = -0.29$). Sepkoski and Rex (1974) used cluster analysis of similarity coefficients in a biogeographic study of the faunas of rivers. This cluster analysis procedure with Jaccard's qualitative index of similarity was used to examine the pattern of island groups for various subsets of the flora. The results of the cluster analyses show pairs or groups of islands and areas which are floristically similar.

Cluster analysis is meaningful in biogeographic studies if the pairs or groups of islands derived by the analysis can be geographically identified. If isolation is important in determining the composition of the flora of an island, then the islands would be most similar to their nearest neighbors and the cluster analysis would pair the islands with their nearest neighbors or groups of other nearby islands. If the flora of the islands was not isolated, then free exchange between all parts of the region would be expected. In this case, the similarity of the floras of the islands would be influenced by factors other than geographic proximity and islands from various parts of the

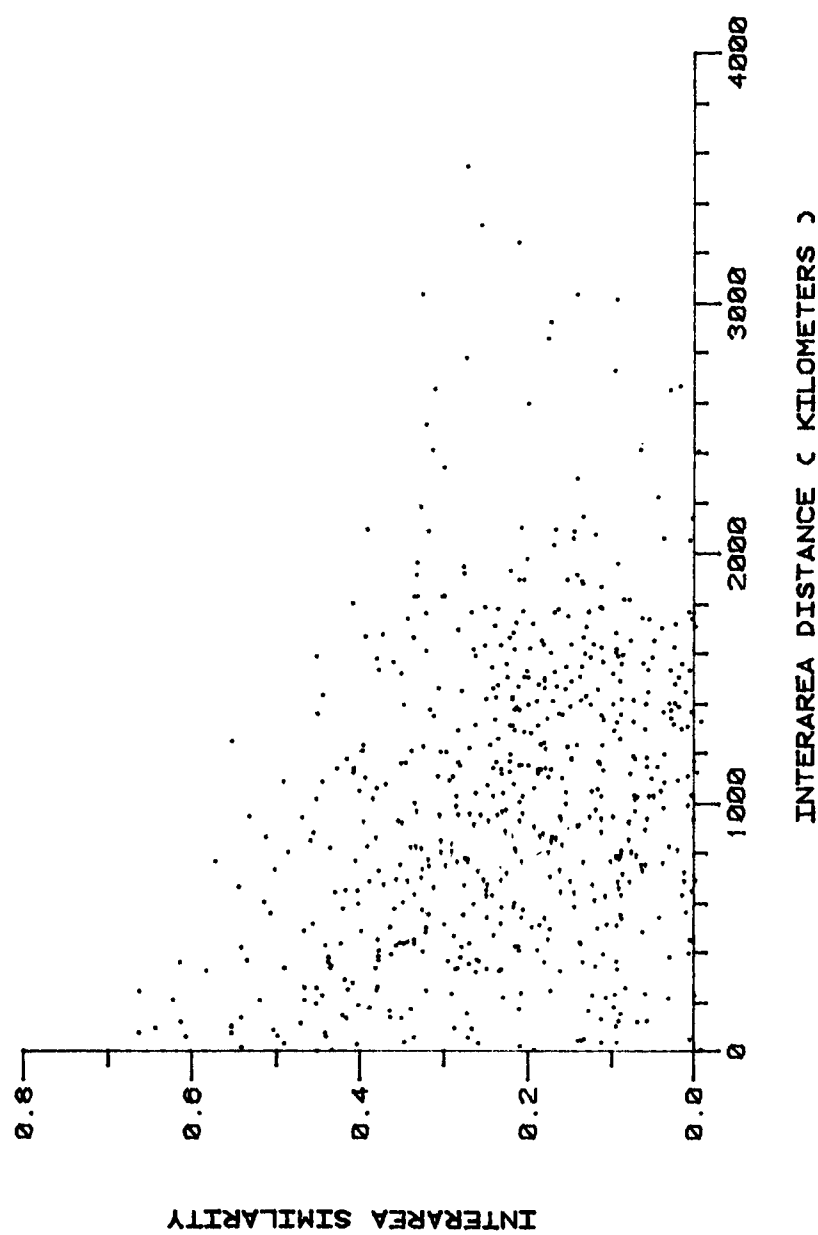


Figure 43. Relationship between interarea similarity and interarea distance
($r = -0.29$).

region would be grouped together by the cluster analysis. All of the interpretations of cluster analysis are limited by the inability to statistically test the significance of the differences in the results. The cluster analyses discussed in the section below are based on similarities calculated for the total flora and subsets of the flora of the islands.

In the cluster dendrogram of all areas with all of the species in the similarity calculations (Figure 44), several nearest neighbor pairs of islands can be seen. They include Copper and Bering, Adak and Atka, Agattu and Alaid, Buldir and Kiska, Carlisle and Amlia, St. George and St. Paul, St. Lawrence and St. Matthew, and Kavalga and Gareloi. These pairs of islands are located throughout the entire Bering Sea Region. The source areas are also grouped in a manner which is similar to their geographic location. The Alaska Peninsula and southeastern coast, and Kodiak Island form a group. The Yukon Plain and Seward Peninsula source areas are paired together and the Chukotka Peninsula is then joined to this group. Kamchatka is joined to this group of northern source areas.

A large group of interest in the dendrogram is a set of large islands just below Copper and Bering (Figure 44). It is divided into a western (Atka-Attu) and eastern (Umnak-Unimak) group. The remainder of the Aleutian Islands, which are generally smaller, form a large group which joins the group composed of the large islands and the Alaska Peninsula source area group. All of the islands in the northern part of the Bering Sea form a distinct group. This northern island group is then joined with the group composed of the northern and Asian

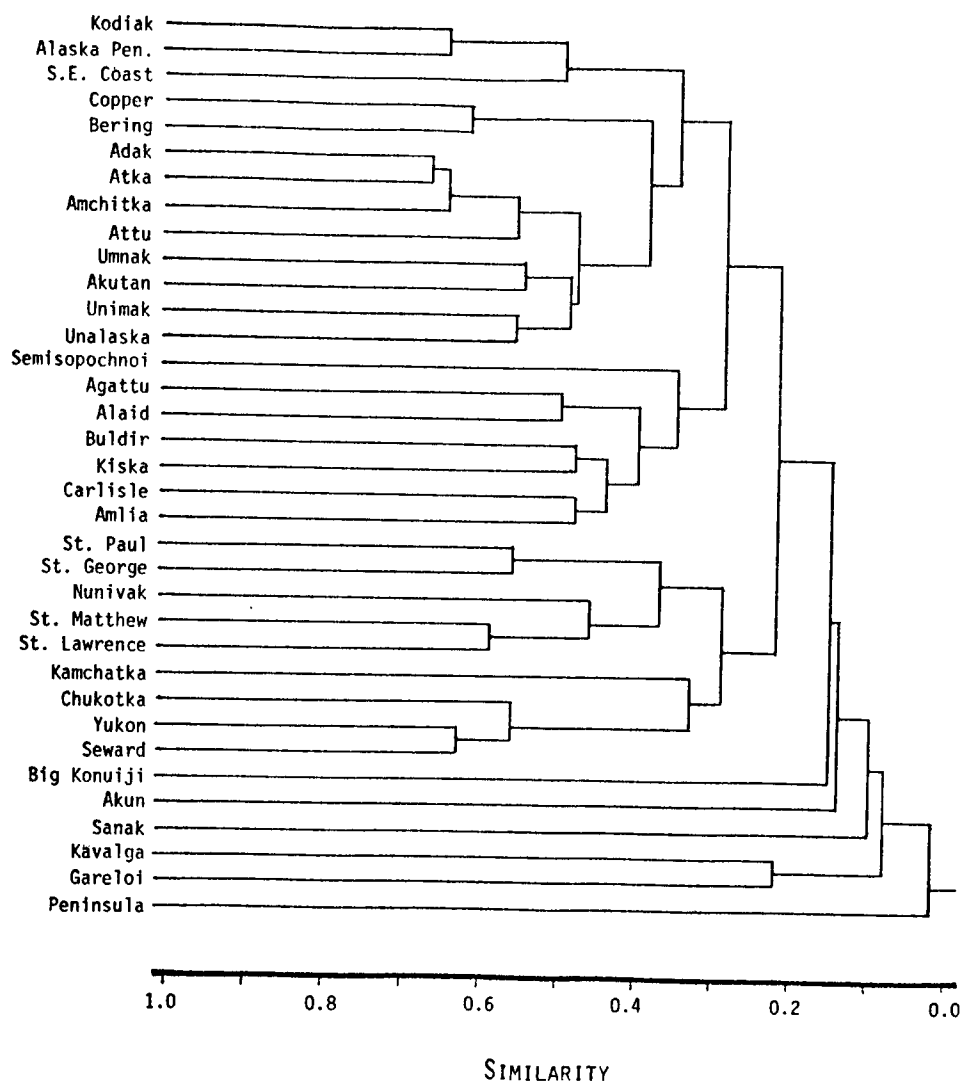


Figure 44. Dendrogram for all areas from the cluster analysis of similarity values based on the total flora.

source areas. This group of northern areas is eventually joined with the Aleutians and southern source area group.

The remainder of the islands in the dendrogram, from Big Konuiji down to Peninsula Island, all have small floras. Areas with a small number of species tend to exhibit erratic clustering patterns in this procedure. This may be an artifact of either the clustering algorithm or the calculation of the similarity coefficient. These remaining islands do not show any interpretable geographic pattern except that they are all small.

Several levels of groups are interpretable based on their geographic location. Within the Aleutian Islands, the size of the islands appears to generate a secondary level of grouping, but the region of the related groups can be identified.

This cluster analysis (Figure 44) tends to show that the Aleutian Islands are more similar to the Alaska Peninsula and the southeastern coastal area than to the Kamchatka Peninsula. This pattern of similarity is consistent with the expected results of isolation based on the current patterns in the area (Figure 6, page 31). These current patterns would tend to expose the northern Bering Sea Islands to propagules from Kamchatka and the Aleutian Islands to propagules from the southeastern coastal area and the Alaska Peninsula.

In order to determine if the pattern of geographic location was related to isolation, cluster analysis was performed with similarity values calculated for the pteridophyte flora. It was hypothesized that since this flora is dispersed by spores, it should show less regional distinction due to isolation than the general flora. Spores are

dispersed readily over long distances by wind and by floating at or near the surface of the water (Ridley 1930). The interpretation of results for this group must be tempered by the fact that the pteridophytes probably have a narrower range of environmental tolerances than the flora as a whole. Changes in the cluster pattern may be due to these limitations. However, observations in the field indicate that members of this group, especially in the genus Lycopodium, are found in a wide range of habitats.

The relationship between interarea distance and similarity still has a significant negative correlation (Figure 45), but its correlation coefficient is lower ($r = -0.08$) than the one for the whole flora. Adak and Atka, Yukon Plain and Seward Peninsula, and Nunivak and St. Matthew are the only pairs which are nearest neighbor islands in the cluster analysis of the pteridophyte flora (Figure 46). Kiska and St. Paul, Alaska Peninsula and Bering, Attu and Unalaska are examples of geographically separate areas that are paired together. None of the large cluster groupings are interpretable as geographic regions. The northern areas are split into three groups. The northern and Asian source areas are more closely related to the groups of large Aleutian islands. In contrast to the cluster analysis based on the total flora, the cluster analysis of the pteridophyte flora shows little geographic pattern. A reasonable conclusion from this type of interpretation is that this subset of the flora shows little, if any, isolation in the Bering Sea Region.

The cluster analysis was repeated for several families to determine if differences in these cluster analyses were due to the use

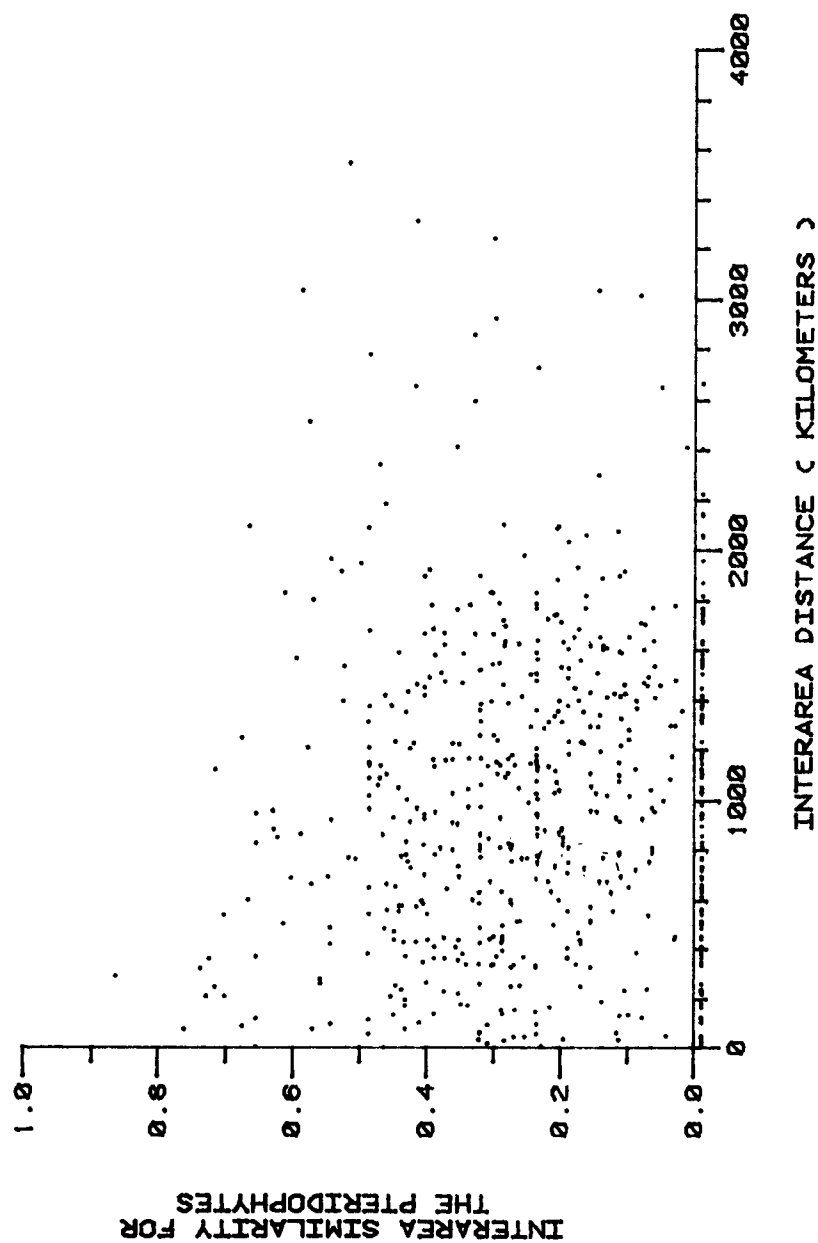


Figure 45. Relationship between interarea similarity of the pteridophytes and interarea distance ($r = -0.08$).

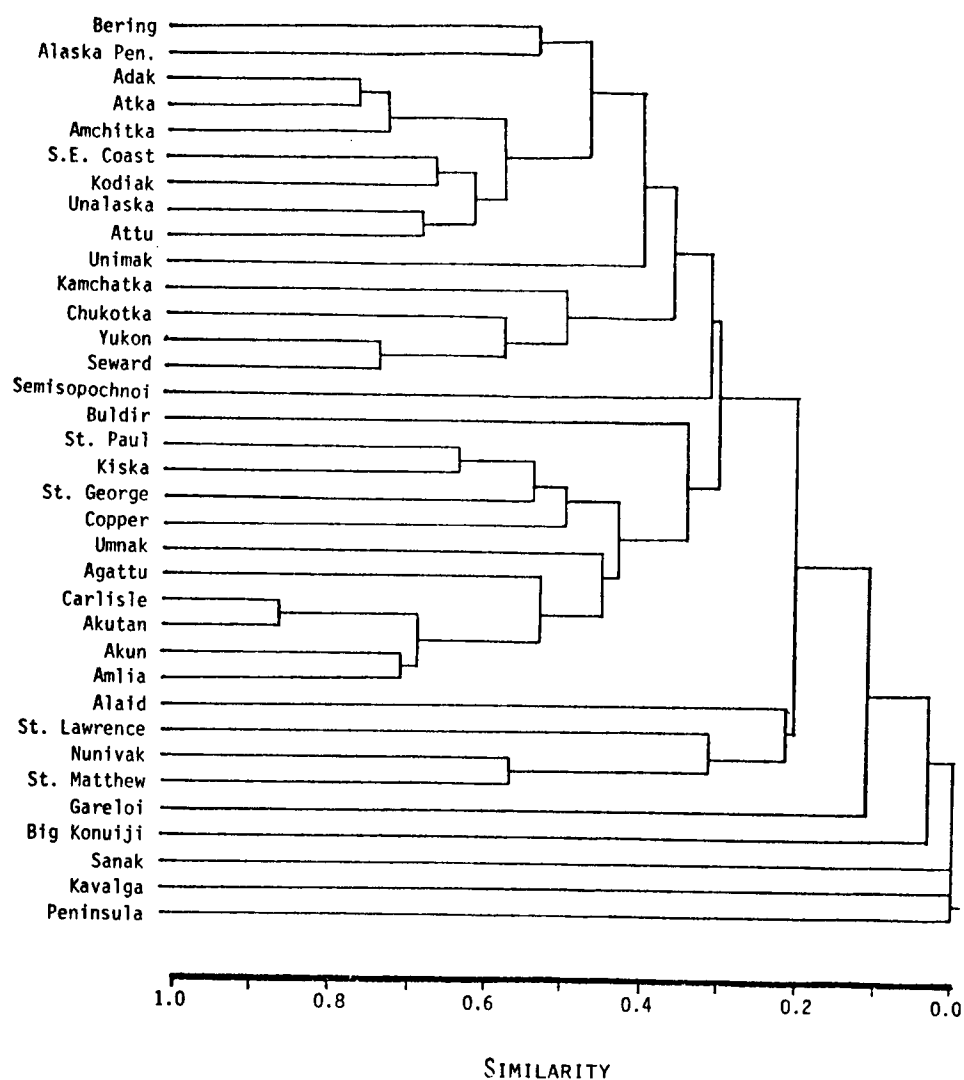


Figure 46. Dendrogram for all areas from the cluster analysis of similarity values based on the pteridophytes.

of a subset of the flora. The pattern in the cluster dendrogram based on the flora of the grass family is very similar to the one generated with the total flora (Figure 47). The Alaska Peninsula group is again clustered with the large Aleutian Islands group. The northern islands are grouped with the northern and Asian source areas. The smaller islands are also grouped together. The nearest neighbor pairs are also very similar to those in the cluster based on the total flora.

One difference in the cluster analysis of the grass family is the arrangement of the northern source areas. In the cluster of the total flora, the Yukon Plain and Seward Peninsula source areas are grouped before the Chukotka source area is added to the group. In the cluster using the grasses, the Chukotka and Seward Peninsula source areas are paired first and then the Yukon Plain source area is added to the group. This indicates that the grasses are slightly more similar across the region of the Bering Land Bridge than the overall flora. The same pattern of clustering of these source areas is also seen for the composites. The pattern for the sedges, orchids, and pteridophytes is the same as it is for the total flora. Since the results of cluster analyses are not statistically testable, it is difficult to state that these changes in pattern are significant. With this limitation, these differences in similarity patterns provide only very general clues about the groups of plants that may have been exchanged across the land bridge connection. Since the climate of the Bering Land Bridge was thought to be dry and continental (Hopkins 1972), it is reasonable to expect a greater exchange of composites and grasses than the sedges, orchids and pteridophytes, which are generally associated with wetter sites.

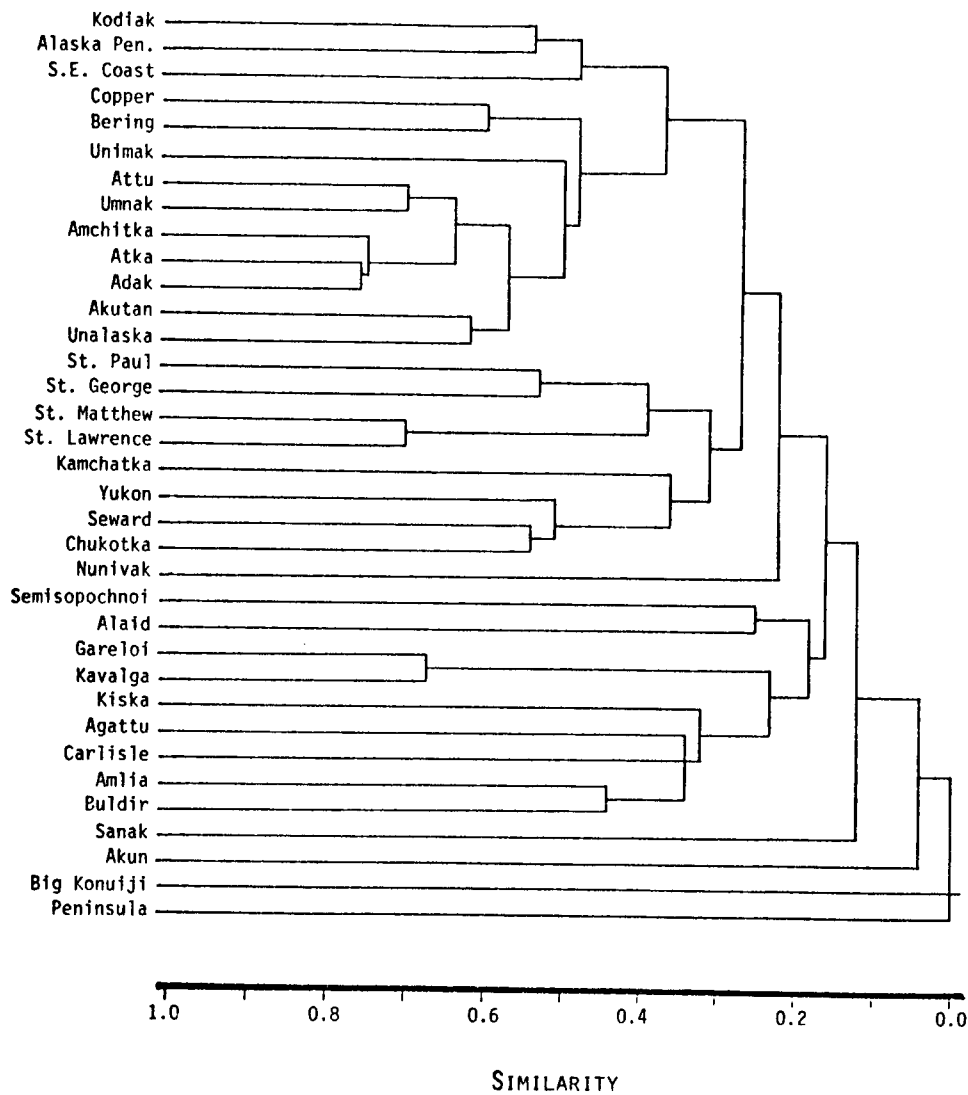


Figure 47. Dendrogram for all areas from the cluster analysis of similarity values based on the grass species.

In another attempt to determine the reality of the apparent absence of isolation observed in the pteridophyte flora, a random subset of the total flora was used in the calculation of interarea similarity values. This subset can be considered a control group that provides a first approximation of the number of nearest neighbor pairs that might be expected if the species of a floristic subset did not share any common attributes. In the cluster analysis of the random subset of species, the nearest neighbor pairs of Kodiak and Alaska Peninsula, St. Paul and St. George, Agattu and Alaid, Copper and Bering, Adak and Atka, Akutan and Unalaska, Seward Peninsula and Yukon Plain, and St. Lawrence and St. Matthew still emerge (Figure 48). This cluster analysis has eight pairs of areas which are nearest neighbors. The larger groups of islands are also geographically interpretable. This analysis contrasts with the cluster analysis of the pteridophyte flora which had only three pairs of nearest neighbors and larger groups of islands that are not geographically interpretable.

The comparison of these cluster analyses supports the conclusion that the pattern shown by the pteridophyte flora is different from the total flora and represents less geographic isolation.

The species reported from all six source areas constituted another group of species also not expected to show a clear geographic pattern. The species with extensive continental distributions were expected to have potential distributions across the islands of the entire Bering Sea Region. Therefore, these species were not expected to show regional similarities or patterns due to isolation. The number of species per island which are also reported from all of the source

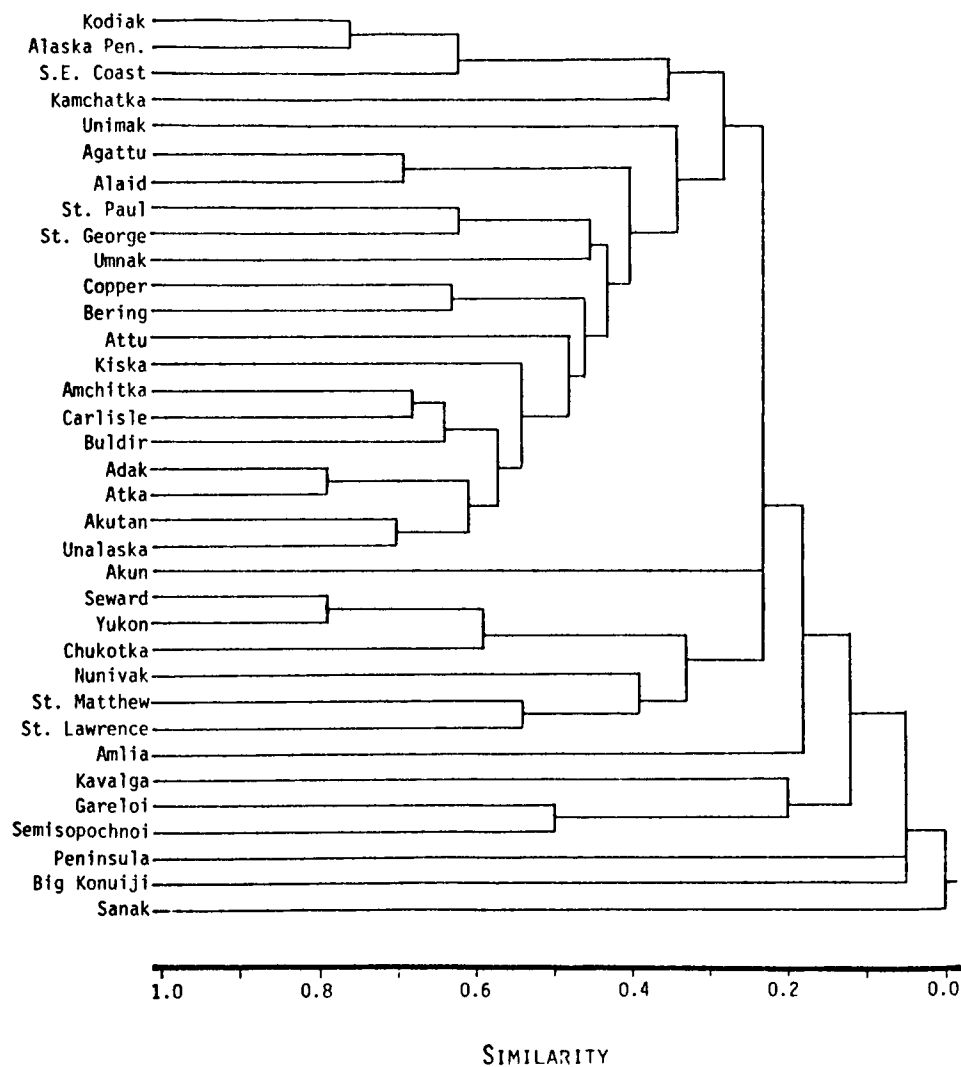


Figure 48. Dendrogram for all areas from the cluster analysis of similarity values based on a random subset of the flora.

areas is highly correlated ($r = 0.965$) with the total number of species per island (Figure 49). In contrast, the cluster analysis based on this flora (Figure 50) is different from the cluster analyses of the total flora (Figure 44, page 129). Bering and Copper, St. Matthew and St. Lawrence, Gareloi and Semisopochonoi, and Buldir and Agattu are the only four pairs of nearest neighbors. The large islands form a group similar to the one formed for the total flora. Most of the northern islands are also in a group together. Some very unusual pairs or groups also occur in this cluster analysis. Attu is in a group with Kodiak and Unalaska from the opposite end of the island chain. The Copper and Bering Island group is then joined to this group. Another unusual combination is Carlisle and Kiska Islands. These islands are dominated by volcanic topography. The size and shape attributes of the islands are more useful than location to explain the pattern of floristic similarity of the widely distributed flora.

The results of cluster analyses with the subsets of the species in common with the source area floras are similar to the results of the total flora. The analyses of the source area floras are also similar to each other.

Groups of species were also formed based on similarities of dispersal mechanism and morphology. The groups formed are listed in Table 3, page 45. Cluster analyses were performed using the species of these groups. Only two of the dispersal groups showed patterns significantly different from the other dispersal groups. These were the species with plumed seeds and those species which were not

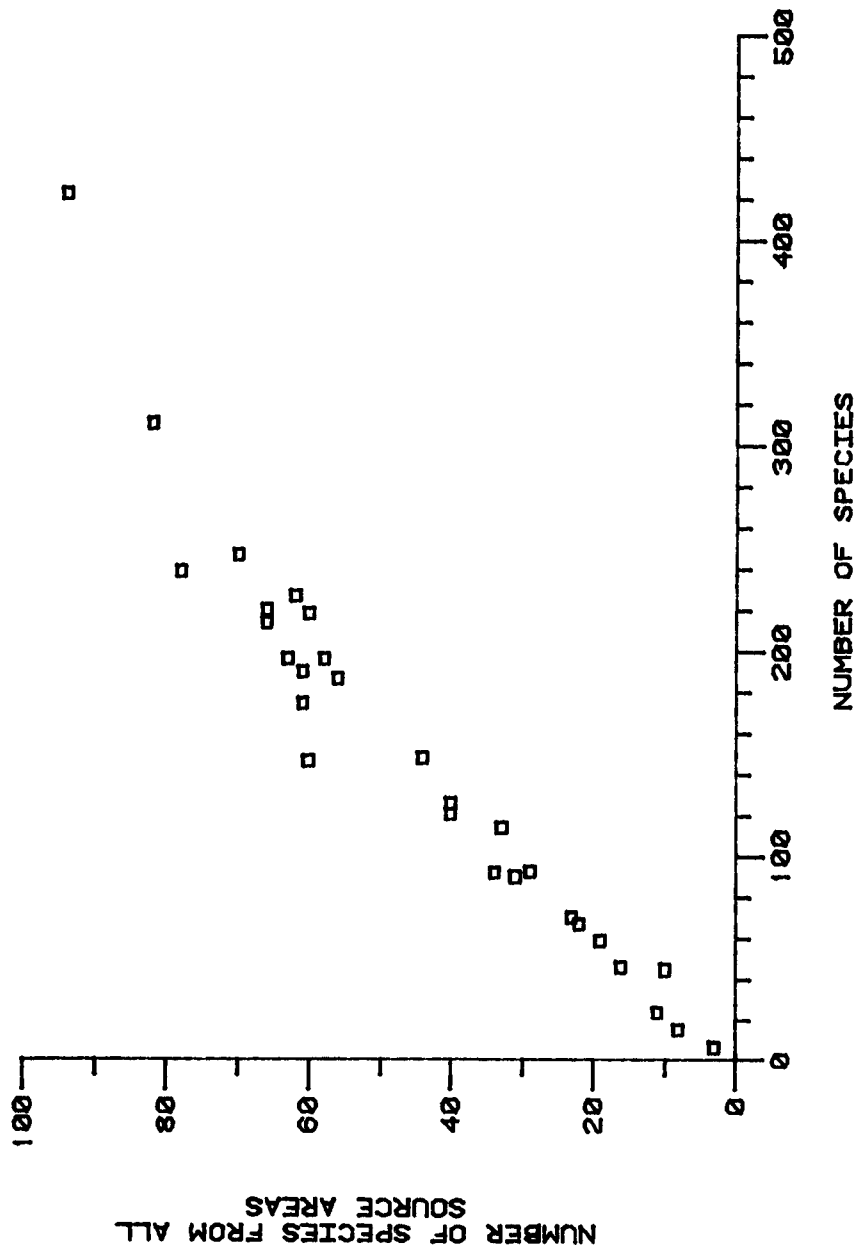


Figure 49. Relationship between the number of species from all source areas and the total number of species ($r = 0.965$).

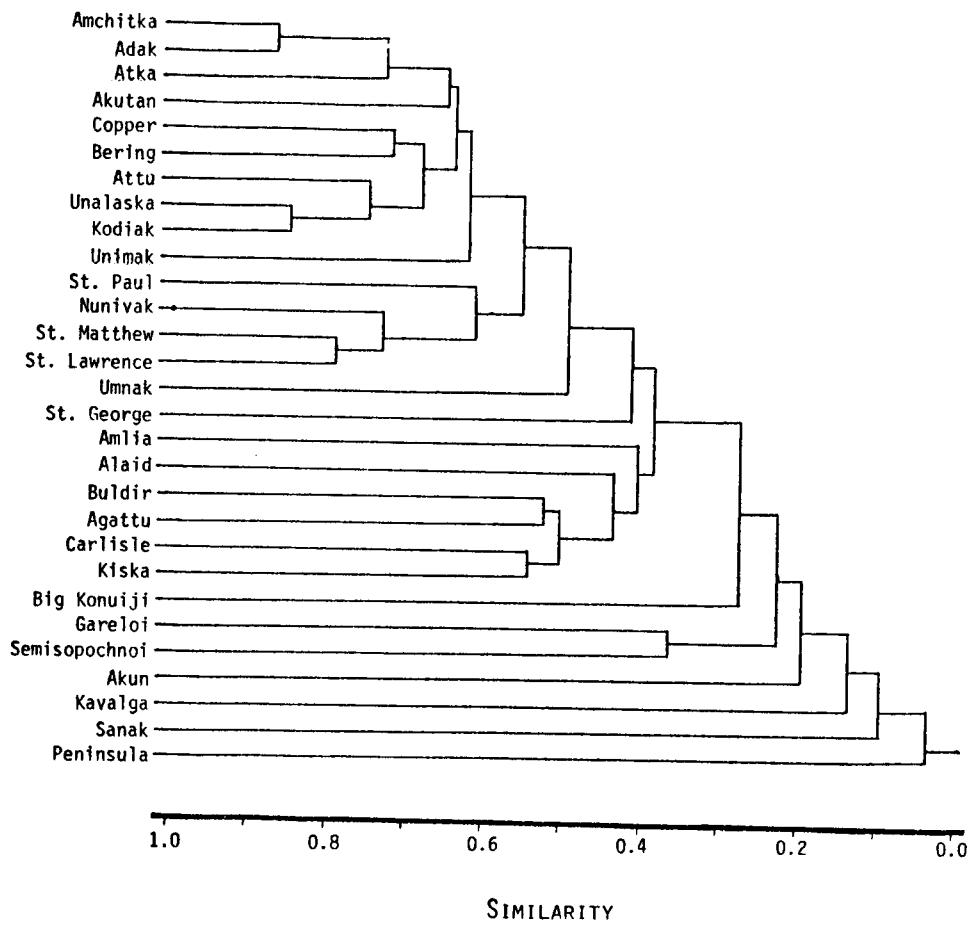


Figure 50. Dendrogram for all islands from the cluster analysis of similarity values based on the species from all of the source areas.

assigned to any dispersal group. The cluster analyses of these groups of species contain a high number of nearest neighbor pairs and larger groups that are geographically interpretable. The cluster dendrogram for the species which are not in any special dispersal group shows a pattern of floristic similarity which is very interpretable with location and size characteristics of the areas (Figure 51). The species which are not in any defined dispersal groups apparently exhibit a slightly greater isolation pattern than the total flora which contains species with adaptation for dispersal. The species with plumed seeds also apparently have a slightly greater than intermediate amount of isolation. This result was unexpected and may indicate that this mode of dispersal is not effective for long distances across water.

In summary, cluster analysis is a very useful technique for identifying the presence or absence of biogeographic patterns. The analysis appears to reveal simultaneously the influence of location and size differences on the floristic similarity of islands and groups of islands. The total flora of the islands exhibits patterns suggestive of intermediate isolation effects. The pteridophytes and species reported from all source areas show patterns that could be the result of a lower than intermediate isolation. Species without any specific dispersal mechanism appear to be more isolated than the total flora.

III. OTHER ISOLATION MEASURES

Several other geographic variables were measured and analyzed in attempts to show differences in local isolation in the Aleutian Islands.

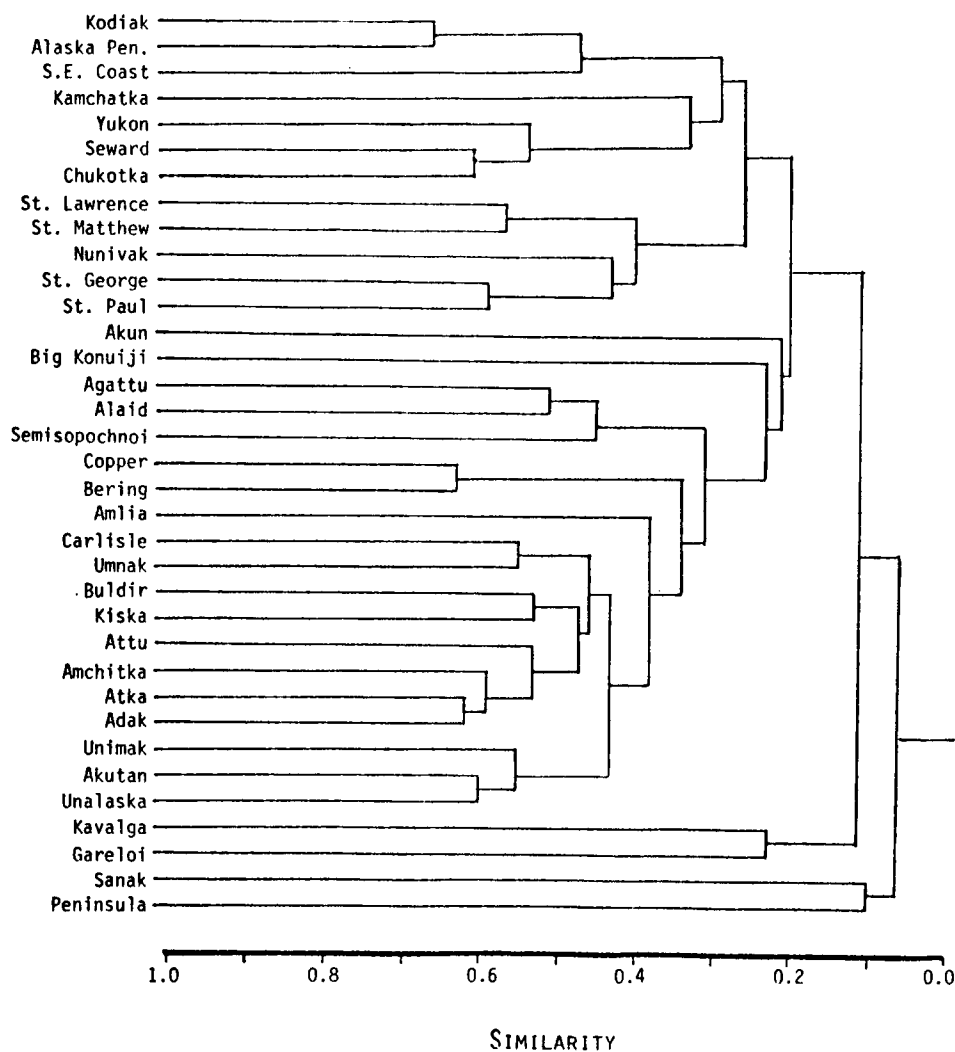


Figure 51. Dendrogram for all areas from the cluster analysis of similarity values based on the species not in any specific dispersal group.

These variables included the percentage of the island area within one kilometer of the shore, the depth and width of the largest adjacent interisland pass, the distance of the islands from the Kamchatka and Alaska Peninsula regions by way of the path of the major currents and the distance to the southern limit of winter pack ice. All of these variables were intended to reflect differences in the exposure of the islands to the water around them which might carry plant propagules to the island. The depth and width of the interisland passes are related to the volume of water flowing through the passes (Favorite 1974). These measures may also represent the isolation of an island from one of its nearest neighbors.

Distances along the major current paths were measured to determine if different species-distance relationships from those with the great-circle distances would be observed. However, the distances along the current paths are very highly correlated with the great-circle distance calculated. The distance to the pack ice limit was measured in an attempt to represent the frequency of pack ice drifting to an island. Pack ice may provide a means of rafting plant propagules to the islands.

Most of these variables are not significantly correlated with the floristic variables. An exception to this is that the percentage of the island area within one kilometer of the shore is negatively correlated with the number of species (Table 6, page 84). The percentage of the island area near the shore is also negatively correlated ($r = -0.638$) in a similar manner with the total area of an island. The correlation of the percentage of near shore area with

the number of species may be an artifact of the correlation between the percentage of near shore area and the total island area. Islands with a greater percentage of area near the shore were expected to have a larger number of species for groups which were commonly water dispersed and might remain near the shore. None of the expected positive correlations materialized for any of the floristic groups.

The variables representing the local isolation of islands are probably too simplistic to have significant bivariate relationships with the floristic variables. They are more appropriate in a multiple regression context and will be discussed further in that section.

IV. EXPECTED VERSUS OBSERVED INTERISLAND SIMILARITY

Connor and Simberloff (1978) presented methodology for calculating the expected number of species that two islands should share in common. Their methodology was used to generate this expected number of shared species for all island pairs. Similar to the results of Connor and Simberloff (1978), nearly all of the island pairs in the Bering Sea Region shared more than the expected number of species. St. Lawrence Island is the only island which shared fewer than the expected number of species with several of the other islands, and that can be explained by the fact that it is the northernmost island and is not close to any of the other islands.

Since the expected number of shared species is inversely related to the size of the pool of potentially colonizing species used for the calculations, these comparisons may not be meaningful because defining the species pool for a pair of islands in this region is difficult.

It is unlikely that all of the species in the region are a part of a pool of species which may colonize the islands. Because of the large size of this region, it is also unlikely that the total number of species found on one or more islands should be considered the species pool for the islands. Logical criteria for determining the extent of the species pool of a pair of islands are not currently developed. As a result of this limitation, the comparisons of the expected and observed number of shared species may not be conclusive for this region.

V. PROBABILITY OF SPECIES ON NEIGHBORING ISLANDS

The probabilities of species on an island in the Aleutian Island Chain also being reported from one of its two or four nearest neighbors were calculated. From the "stepping stone" hypothesis of MacArthur and Wilson (1967), these probabilities were expected to be lower for islands that are farther out the island chain. If the island chain were being colonized by propagules from both the east and west, then the probabilities were expected to be lower in the central part of the island chain. Most of the probabilities are greater than 0.85. Exceptions below this value are for species rich islands which are adjacent to relatively depauperate islands in the data set. This difference is an artifact of the depauperate islands not having a large enough number of species to contain all of the flora of the species rich island. After the artifact was acknowledged, no pattern which might be related to changes in isolation of the islands is observed across the Aleutian Island Chain.

VI. MULTIPLE REGRESSION MODELS FOR THE PREDICTION OF THE NUMBER OF SPECIES

Multiple regression techniques have been commonly used in studies of island biogeography to assess the importance of different kinds of geographic variables in developing a predictor for the number of species on islands (Simberloff 1974). Simberloff (1974) also warned against the problems involved with dependence and independence assumptions necessary for the relationships of variables in multiple regression. Biological and ecological mechanisms which support these assumed independent-dependent relationships may not be known in all cases. In this discussion, all independent (geographic) variables will be referred to as predictors of the dependent (floristic) variable. The lack of information on the mechanisms may limit the validity of these assumptions, and the interpretation of the multiple regression results in this study.

The relative value of prediction by the overall multiple regression model developed may be assessed by way of the coefficient of determination (R^2) which is proportional to the percentage of the variance of the dependent variable which is explained by the regression model (Zar 1974). The relative importance of each variable to the overall model in the context of the variables previously entered by the stepwise procedure can also be assessed on their contribution to the improvement of the overall R^2 value of the model. The following aspects of the multiple regression results are presented and interpreted:

1. The order of entry of variables by the stepwise procedure.
2. The sign of significant partial regression coefficients.
3. The R^2 value of the models composed of the different number of independent variables.
4. The significance of the overall model.

From this information, the importance of the variables to the overall model and the predictive success of the models can be assessed.

The results of multiple regression analyses are presented in tables which follow a consistent format. The independent variables are listed in the order of entry into the multiple regression model by the stepwise procedure. The first variable entered is at the left and the last is at the right. The sign of the partial regression coefficient is indicated for the variable when the coefficient is significantly different from zero. Variables that contribute more than 0.02 to the total R^2 value of the model are underlined. The value of 0.02 was selected as the criterion for this underlining because it shows which variables contribute substantially to the R^2 value of the model. This value does not have any other special importance or significance. The R^2 value under each variable name is for the model which contains the variable above it and all of the previously entered variables to the left of it.

The typical multiple regression model for predicting the number of species is shown in the first model of Table 11. This model includes measures of area, isolation (distance from source areas), habitat diversity (maximum elevation) and latitude. The R^2 values for the models indicate that area is substantially more important to the

Table 11. The results of multiple regression analyses with the total number of species as the dependent variable.

Model Number	Dependent Variable ^a	Independent Variables ^b				
		1	2	3	4	5
1	LSPNO	<u>LAREA+</u>	<u>LDKAM</u>	<u>LDALPEN</u>	LELIS	LLAT
	R ²	0.626	0.669	0.678	0.678	0.681
2	LSPNO	<u>LAREA+</u>	<u>TODI</u>	<u>TOMN</u>	TOVA	
	R ²	0.626	0.646	0.670	0.674	
3	LSPNO	<u>LAREA+</u>	<u>RRADM+</u>	RRADV		
	R ²	0.626	0.729	0.734		
4	LSPNO	<u>LAREA+</u>	<u>RRAV+</u>	RRAM		
	R ²	0.626	0.698	0.702		
5	LSPNO	<u>LAREA+</u>	<u>LDKAM</u>	TODI		
	R ²	0.626	0.677	0.685		
6	SPNO	<u>RADM+</u>	DKAM	<u>DALPEN</u>	ELIS	
	R ²	0.702	0.713	0.735	0.736	
7	SPNO	<u>RADM+</u>	TODI	DKAM	DALPEN(2) ^c	TODI
	R ²	0.702	0.721	0.727	0.735	0.742
8	LSPNO	<u>LAREA+</u>	<u>RRADM+</u>	<u>LDKAM-</u>	TODI	LDALPEN
	R ²	0.626	0.729	0.773	0.785	0.785
9	LSPNO	<u>LAREA+</u>	<u>RRAV+</u>	<u>LDKAM-</u>	TODI	LDALPEN
	R ²	0.626	0.698	0.751	0.768	0.768
10	LSPNO	<u>LSTRKM+</u>	<u>LNBAV</u>	<u>LDKAM</u>	TODI	LDALPEN
	R ²	0.439	0.489	0.516	0.529	0.532

^aDependent variable abbreviations:

LSPNO = Logarithm of the number of species

SPNO = Number of species.

Table 11 (Continued)

^bIndependent variable abbreviations:

LAREA = Logarithm of area

ELIS = Maximum elevation

LELIS = Logarithm of the maximum elevation

TOMN = Mean number of topographic lines per sample square

TOVA = Variance of the number of topographic lines per sample square

TODI = Diversity of topographic lines per sample square

RRADM = Mean of relative radial deviations

RRADV = Variance of relative radial deviations

RRAM = Mean of relative radii

RRAV = Variance of relative radii

DKAM = Distance from Kamchatka Peninsula

LDKAM = Logarithm of the distance from the Kamchatka Peninsula

DALPEN = Distance from Alaska Peninsula

LDALPEN = Logarithm of the distance from the Alaska Peninsula

LLAT = Logarithm of latitude

LSTRKM = Logarithm of the length of streams

LNBAY = Logarithm of the number of bays.

^cThe stepwise multiple regression procedure will occasionally replace a variable which was previously selected by the maximum R^2 improvement criterion when other variables have been added to the model. In this case DALPEN replaced TODI, the second variable, to form the best three variable model.

prediction by the model than the isolation and habitat diversity variables. This relationship of importance among the geographic variables is true for all measures related to area and isolation. In this typical model, the distance values are more important than the maximum elevation. The relationship of the importance of the distance and habitat diversity is not always consistent.

The second model in Table 11 provides a comparison between the topographic complexity variables in the context of the area of the island. From this model, the diversity of number of contour lines per sample square (TODI) is shown to be a slightly better predictor than the mean or variance of the number of contour lines per sample square. Based on this observation, TODI was used interchangeably for maximum elevation to represent changes in habitat diversity due to changes in topography.

The mean of the relative radial deviations is compared with the variance of the relative radial deviations in the context of area in the third model of Table 11. The relative values of these radial variables were used in order to determine the importance of these measures which are independent of the island size. The mean of the relative radial deviations increased the R^2 value of the model, after area was entered, more than any other variable. Based on these results, this representation of the complexity of the shape of the island is the best geographic variable for predicting changes in the number of species after the effect of area has been removed.

In a similar manner, the variance of the relative radii is also important in the fourth model in Table 11. In the eighth and ninth

models of Table 11, these measures of the complexity of shape are more important than the isolation and topographic diversity values in predicting the total number of species per island.

The fifth model of Table 11 includes area, isolation, and habitat diversity variables. It is representative of the results that were obtained when only one variable of each of the types of geographic variables were in the multiple regression model.

The sixth and seventh models are similar to the fifth model in Table 11. The mean of the radial deviations (RADM) was substituted for area, two distance values were included, and TODI and maximum elevation were interchanged in the initial design of these models. The untransformed values of the number of species were used in this model since the relationship between RADM and the number of species is linear (Figure 25, page 94). The variable related to size is still a more important predictor of the number of species than the isolation and topographic diversity variables. Comparison of the R^2 values of these two models indicates that TODI is a slightly better predictor than maximum elevation.

Variables that are independent of the size of an island and represent the complexity of the island shape (RRADM and RRAV) were added to the above type of model to form the eighth and ninth models in Table 11. These variables representing the shape of the islands are more important than isolation and topographic diversity variables. The eighth model resulted in the best overall R^2 values for predicting the total number of species per island. The results of this model also show the coefficient for the distance to the Kamchatka peninsula is

significant and negative. The sign of this variable supports the distance pattern described by MacArthur and Wilson (1967).

In the last model presented in Table 11, the total length of streams and the number of bays were substituted for area as a representation of the size and shape of the islands. Comparison of the R^2 values of this model with others indicates that this substitution does not improve the ability of the model to predict the total number of species.

From the results of multiple regression with the total number of species as the dependent variable, several consistent patterns were observed. The size of the island is always the most important predictor of the number of species on an island. The result could support the equilibrium model of MacArthur and Wilson (1967). Since data on immigration and extinction are not available, specific acceptance or rejection of the equilibrium model cannot be made from the results of this study. Some other mechanism may result in larger islands having a greater number of species. The results of sampling small areas in the vegetation types of this region indicate the presence of log-log species-area relationships (McCord and Clebsch 1980). That sampling also suggests the presence of a lognormal distribution for the frequency of occurrence of species. Preston (1962) and May (1975) reported that that type of distribution may also explain the observed overall species-area relationship. Biological and ecological mechanisms for those patterns of species distribution are not known.

The complexity of the shape of the island is secondary to the size of the island for predicting the number of species on an island.

In the Aleutians, differences both in the number of plant communities and total number of species can be seen between areas with different complexity of shape. Open areas are more exposed to the action of the winds which can remove snow and soil. Drainage patterns and soil types are also simpler in these open areas than in the valleys of the dissected landscape. Changes in these environmental factors probably constitute the mechanism underlying the relationship observed between the number of species and the complexity of the shape of the island.

Measures of isolation appear to follow size and complexity of island shape in importance for predicting the number of species per island. Given the size of this region, it is surprising that isolation is not more important in predicting the number of species. The presence of multiple source areas and absence of isolation from nearby islands not included in the data set or the analyses may have an effect on the accurate observation and understanding of isolation phenomena.

The maximum elevation and topographic diversity variables are the least important type of geographic variable used for predicting the number of species per island. The vegetation of the region does not show the clear pattern of changing plant communities between different elevations such as can be observed in the vegetation of other mountain systems. A decrease in the density and size of plants, with eventual complete elimination of the plants, can be observed at higher elevations. On the scale of whole islands, as was used in this study, the change across elevation is apparently of minor importance in determining the total number of species per island. The results of these multiple regressions indicate that changes in the shape of the landscape are

more important than the overall difference in elevation of the islands for predicting differences in the number of species due to differences in habitat diversity.

The multiple regression models presented in Table 12 represent the results of attempts to predict the number of species related to the Alaska and Kamchatka Peninsula source areas. After the effect of other source areas on the number of species was partially removed, isolation measures (distance to the source areas) were expected to become more important in these models. This expected result is not found in the first two models for the number of species in common with the source areas. In the prediction of the number of restricted species from the source areas, the distance measures are more important. The importance of area is reduced. Even though area and shape (RRADM) remain more important than distance, the contribution of distance to the overall R^2 value of the model is greater than in models for the total number of species. These multiple regression results, in a manner similar to the correlation analyses, substantiated that isolation is a complex phenomenon which is difficult to adequately represent and interpret. Once again, topographic diversity continued to remain the least important predictor of number of species from source areas.

In an attempt to improve the representation of the isolation of an island, models using the percentage of area near the shore, depth and width of the interisland pass, distance from source areas along current paths, and distance to pack ice limits were tested. Since the current path values and interisland pass measures were determined for only the Aleutian Islands, the other Bering Sea Islands were not included

Table 12. The results of multiple regression analyses with the number of species related to source areas as the dependent variable.

Model Number	Dependent Variable ^a	Independent Variables ^b			
		1	2	3	4
1	LSPAP	<u>LAREA+</u>	<u>RRADM+</u>	<u>TODI</u>	LDALPEN
	R ²	0.626	0.718	0.743	0.748
2	LSPKA	<u>LAREA+</u>	<u>RRADM</u>	<u>LDKAM-</u>	TODI
	R ²	0.610	0.716	0.779	0.784
3	LRSAP	<u>LAREA+</u>	<u>RRADM+</u>	<u>LDALPEN</u>	TODI
	R ²	0.359	0.432	0.502	0.514
4	LRSKA	<u>LAREA+</u>	<u>LDKAM-</u>	<u>RRADM+</u>	<u>TODI+</u>
	R ²	0.276	0.475	0.612	0.638

^aDependent variable abbreviations:

LSPAP = Logarithm of the number of species in common with the Alaska Peninsula

LSPKA = Logarithm of the number of species in common with the Kamchatka Peninsula

LRSAP = Logarithm of the number of species restricted to the Alaska Peninsula

LRSKA = Logarithm of the number of species restricted to the Kamchatka Peninsula.

^bIndependent variable abbreviations:

LAREA = Logarithm of area

RRADM = Mean of relative radial deviations

TODI = Diversity of the number of topographic lines per sample square

LDALPEN = Logarithm of the distance from the Alaska Peninsula

LDKAM = Logarithm of the distance from the Kamchatka Peninsula.

in these models. The species in common with the Kamchatka and Alaska Peninsula source areas were used in these models since the current paths represent the distance from these areas. Representative results from this type of model are presented in Table 13. The representation of isolation was not improved. The only significant models depend mainly on the percentage of near shore area and occasionally on the width of the interisland pass. The relationship observed with the percentage of near shore area and the number of species is similar to a relationship between near shore area and total island area. Similar to the correlation results, these relationships are probably an artifact of the geometry of the island.

When the percentage of near shore area was replaced by the length of mapped streams and number of bays, the models including the variables representing local isolation are significant (Table 13). In these models, distances along the current paths are equivalent to the great-circle distances to the source areas. The width of the interisland pass is consistently important in the models that included the length of mapped streams and number of bays. It is interesting to note that the coefficient of the width of the interisland pass is negative. The width of the interisland pass was originally included in the analyses to represent the volume of water going through that part of the island chain. A larger volume of water was expected to be related to an increased exposure of the island to plant propagules being carried in the water. This expected relationship is opposite of the one observed. An alternate interpretation of the effect of the width of the pass is that a greater width may actually represent greater

Table 13. The results of multiple regression analyses with independent variables representing local isolation and the number of species related to the source areas as the dependent variable.

Model Number	Dependent Variable ^a	Independent Variables ^b				
		1	2	3	4	5
1	SPAP	<u>PNSA-</u>	<u>WPAS</u> /// ^c	DCURE	DPI	DPAS
	R ²	0.309	0.345	(0.384) ^d	(0.412)	(0.415)
2	SPKA	<u>PNSA-///</u>	WPAS	DCURW	DPI	DPAS
	R ²	0.209	(0.305)	(0.390)	(0.401)	(0.401)
3	LSPAP	<u>LSTRKM+</u>	<u>LWPAS-</u>	<u>LDCURE</u>	<u>LDPAS</u>	LNBA
	R ²	0.528	0.586	0.645	0.670	0.674
4	LSPKA	<u>LSTRKM+</u>	<u>LWPAS-</u>	<u>LDCURW-</u>	<u>LDPAS</u>	LNBA
	R ²	0.509	0.556	0.663	0.714	0.715

^aDependent variable abbreviations:

SPAP = Number of species in common with the Alaska Peninsula

SPKA = Number of species in common with the Kamchatka Peninsula

LSPAP = Logarithm of the number of species in common with the Alaska Peninsula

LSPKA = Logarithm of the number of species in common with the Kamchatka Peninsula.

^bIndependent variable abbreviations:

PNSA = Percentage of area near the shore

WPAS = Width of adjacent interisland pass

DCURE = Distance along current path from Alaska Peninsula Region

DCURW = Distance along current path from Kamchatka Peninsula Region

DPAS = Depth of adjacent interisland pass

DPI = Distance to pack ice limit

LSTRKM = Logarithm of the width of the adjacent interisland pass

LDCURE = Logarithm of the width of the adjacent interisland pass from the Alaska Peninsula Region

LDCURW = Logarithm of the distance along the current path from the Kamchatka Peninsula Region

LDPAS = Logarithm of the depth of the adjacent interisland pass

LNBA = Logarithm of the number of bays.

^c/// follows the last variable entered with the total model remaining significant.

^dR² values for nonsignificant regression models are enclosed in parentheses.

local isolation of the island from its nearest neighbor. It is also possible that a greater volume of water moving past the island may result in the direction of the water movement being more perpendicular to the path from one island to the next. This pattern of water movement could result in the increasing width of the interisland pass being an increasingly effective barrier to dispersal.

The multiple regression models presented in Table 14 provide a comparison between the number of species in all source areas and the number of species related to only one source area. The variables related to size are still the most important and are followed by isolation and topographic variables. In contrast to similar models used to predict the total number of species, the distance variables make consistent contributions to the R^2 values of the model. The model containing variables representing isolation is more successful than the ones for species related to a specific source area. This result suggests that the distribution of species common to all source areas are affected more by the local isolation characteristics such as the width of the interisland pass, than the species from specific source areas.

Several multiple regression models are presented in Table 15 using the number of species from the grass family as the dependent variable. The results obtained from this family are generally representative of other families analyzed. The order of importance of the variables is the same as that observed in the models for all of the species. The R^2 values are generally lower in the models for the grass family than in the models for all species. The lower R^2

Table 14. The results of multiple regression analyses with the number of species from all source areas as the dependent variable.

Model Number	Dependent Variable ^a	Independent Variables ^b				
		1	2	3	4	5
1	ALSSP	<u>RADM+</u>	<u>DKAM</u>	<u>DALPEN</u>	ELIS	
	R ²	0.617	0.642	0.682	0.688	
2	ALSSP	<u>PNSA-</u>	<u>DCURE</u>	<u>WPAS///^c</u>	<u>DPI</u>	<u>DPAS</u>
	R ²	0.294	0.324	0.411	(0.435) ^d	(0.437)
3	LALSSP	<u>LSTRKM+</u>	<u>LWPAS</u>	<u>LDCURE</u>	<u>LDPAS</u>	LNBay
	R ²	0.460	0.515	0.673	0.717	0.723

^aDependent variable abbreviations:

ALSSP = Number of species from all source areas.

LALSSP = Logarithm of the number of species from all source areas.

^bIndependent variable abbreviations:

RADM = Mean of the radial deviations

DKAM = Distance from Kamchatka Peninsula

DALPEN = Distance from Alaska Peninsula

ELIS = Maximum elevation

PNSA = Percentage of area near the shore

DCURE = Distance along the current path from Alaska Peninsula Region

WPAS = Width of the adjacent interisland pass

DPI = Distance to pack ice limit

DPAS = Depth of adjacent interisland pass

LSTRKM = Logarithm of the length of mapped streams

LWPAS = Logarithm of the width of the adjacent interisland pass

LDCURE = Logarithm of the distance along the current path from the Alaska Peninsula Region

LDPAS = Logarithm of the depth of the adjacent interisland pass

LNBay = Logarithm of the number of bays.

^c/// follows the last variable entered with the total model remaining significant.

^dR² values for nonsignificant regression models are enclosed in parentheses.

Table 15. The results of multiple regression analyses with the number of grass species as the dependent variable.

Model Number	Dependent Variable ^a	Independent Variables ^b			
		1	2	3	4
1	LSPF25	<u>LAREA+</u>	<u>LDKAM</u>	<u>RRADM</u>	TODI
	R ²	0.468	0.535	0.572	0.581
2	LSPF25	<u>LAREA+</u>	<u>RRAV+</u>	<u>LDKAM-</u>	TODI
	R ²	0.468	0.552	0.662	0.625
3	SPF25	<u>RADM+</u>	DKAM	<u>DALPEN</u>	ELIS
	R ²	0.567	0.581	0.663	0.667

^aDependent variable abbreviations:

LSPF25 = Logarithm of the number of species in the grass family

SPF25 = Number of species in the grass family.

^bIndependent variable abbreviations:

LAREA = Logarithm of area

LDKAM = Logarithm of the distance from Kamchatka Peninsula

RRADM = Mean of the relative radial deviations

TODI = Diversity of the number of topographic lines per sample square

RRAV = Variance of the relative radii

RADM = Mean of the radial deviations

DKAM = Distance from Kamchatka Peninsula

DALPEN = Distance from Alaska Peninsula

ELIS = Maximum elevation.

values may be due to the relatively few species in the one family which results in a variable with an increased variance due to relatively larger changes from one value to the next.

The orchid family is an exception to the general pattern observed for other families. The analyses with the number of species of orchids as the dependent variable were performed using data from only the Aleutian Islands since a latitudinal effect was found in the bivariate relationships. The models predicting the number of species of orchids depend more strongly on variables related to topographic diversity than the ones for the total flora (Table 16). The shape of the island when represented by the number of bays and the mean of the relative radial deviations is also more important to the prediction of the number of species of orchids. A partial explanation of the mechanism underlying these results can be obtained from the distribution pattern of these species. Observations in the field indicate that orchids, particularly members of the genus Platanthera, are distributed across a wide range of habitats. However, the infrequent species of orchids such as Cypridedium guttatum on Adak are usually found in relatively protected locations in small valleys. This pattern of distribution may explain the increased importance of topographic complexity in predicting the number of orchid species.

The last model presented in Table 16 for the orchids is essentially the same as the third one except that it includes measures of the local isolation of the islands. While the model remains statistically significant for all of the variables, the variables related to local isolation of the island do not greatly improve the R^2 value or the predictive value of the model.

Table 16. The results of multiple regression analyses with the number of orchid species as the dependent variable.

Model Number	Dependent Variable ^a	Independent Variables ^b							
		1	2	3	4	5	6	7	8
1	LSPF32	<u>LAREA+</u>	<u>RRADM+</u>	<u>TODI</u>	LDALPEN				
	R ²	0.461	0.640	0.675	0.676				
2	SPF32	<u>RADM+</u>	<u>DKAM</u>	TODI	DALPEN				
	R ²	0.606	0.660	0.668	0.670				
3	LSPF32	<u>LNBAV+</u>	<u>LDKAM</u>	<u>TODI</u>	<u>LDALPEN</u>	LSTRKM			
	R ²	0.606	0.664	0.708	0.739	0.739			
4	LSPF32	<u>LNBAV+</u>	<u>LDCURW</u>	<u>TODI</u>	<u>LDPI</u>	LPNSA	LWPAS	LDPAS(5) ^c	LPNSA
	R ²	0.606	0.664	0.706	0.733	0.734	0.734	0.734	0.735

^aDependent variable abbreviations:

LSPF32 = Logarithm of the number of species in the orchid family

SPF32 = Number of species in the orchid family.

^bIndependent variable abbreviations:

LAREA = Logarithm of area

RRADM = Mean of the relative radial deviations

TODI = Diversity of the number of topographic lines per sample square

LDALPEN = Logarithm of the distance from the Alaska Peninsula

RADM = Mean of the radial deviations

Table 16 (Continued)

DKAM	= Distance from the Kamchatka Peninsula
DALPEN	= Distance from the Alaska Peninsula
LNBA	= Logarithm of the number of bays
LDKAM	= Logarithm of the distance from the Kamchatka Peninsula
LSTRKM	= Logarithm of the length of streams
LDCURW	= Logarithm of the distance along the current path from the Kamchatka Peninsula Region
LDPI	= Logarithm of the distance to the pack ice limit
LPNSA	= Logarithm of the percentage of near shore area
LWPAS	= Logarithm of the width of the adjacent interisland pass
LDPAS	= Logarithm of the depth of the adjacent interisland pass.

^cThe stepwise procedure of multiple regression replaced LPNSA with LDPAS when the best six variable model was formed.

Several multiple regression models were constructed to predict the number of species in the different dispersal groups. The results of these models are similar for the different dispersal groups and the same as those of the analyses of the total number of species. The similarities are probably related to correlations observed between the number of species in the dispersal groups and the total number of species.

Exceptions to this pattern of similarity were found in models composed of independent variables which are related to the attributes associated with water on the islands. The model predicting the number of species which are found in aquatic or wet habitats has higher R^2 values than the same model for other dispersal groups (Table 17). The model for the graminoid plants with rhizomes is representative of the other dispersal groups (Table 17). The differences in these models are not necessarily related to differences in the dispersability of these groups, but may be related to differences in the prediction of the number of species in these groups by the length of mapped streams. The improved prediction of the number of species of aquatic plants by the length of mapped streams is not surprising since it can be considered representative of the size of the area of the aquatic habitats. In this perspective, this relationship is another form of the overall species-area relationship.

The dispersal group containing species which are dispersed by spores is another exception to the pattern of similarity among the multiple regression models for the dispersal groups. Topographic diversity is the most important variable in this model (Table 17).

Table 17. The results of multiple regression analyses with the number of species in selected dispersal groups as the dependent variables.

Dependent Variable ^a	Independent Variables ^b				
	1	2	3	4	5
LDIS7	<u>LSTRKM+</u>	<u>LWPAS-</u>	<u>LDCURE-</u>	LDPAS	LNBAY
R ²	0.634	0.722	0.860	0.869	0.869
LDIS9	<u>LSTRKM+</u>	<u>LDCURE-</u>	<u>LWPAS-</u>	LDPAS	LNBAY
R ²	0.461	0.529	0.655	0.674	0.680
LDIS1	<u>TODI+</u>	<u>LAREA+</u>	<u>LDKAM</u>	<u>RRADM</u>	LDALPEN
R ²	0.365	0.551	0.616	0.665	0.665
LDIS4	<u>LAREA+</u>	<u>RRADM+</u>	<u>LDKAM-</u>	<u>TODI</u>	LDALPEN
R ²	0.349	0.460	0.552	0.601	0.607

^aDependent variable abbreviations:

LDIS1 = Logarithm of the number of species with spore dispersal

LDIS4 = Logarithm of the number of species with fleshy fruits

LDIS7 = Logarithm of the number of species from aquatic or wet habitats

LDIS9 = Logarithm of the number of species of graminoid plants with rhizomes.

^bIndependent variable abbreviations:

LSTRKM = Logarithm of the length of mapped streams

LDCURE = Logarithm of the distance along the current path from the Alaska Peninsula Region

LWPAS = Logarithm of the width of the adjacent interisland pass

LDPAS = Logarithm of the depth of the adjacent interisland pass

LNBAV = Logarithm of the number of bays

TODI = Diversity of the number of topographic lines per sample square

LAREA = Logarithm of area

LDKAM = Logarithm of the distance from the Kamchatka Peninsula

RRADM = Mean of relative radial deviations

LDALPEN = Logarithm of the distance from the Alaska Peninsula.

The importance of topographic diversity for predicting this dispersal group is not thought to be related to differences in the dispersal of this group. Observations in the field indicate that many species of ferns in this group are found in protected sites located on steep slopes and in small valleys. The topographic diversity variable was intended to represent the aspects of the topography which are related to the occurrence of these areas. The model for the species with dispersal by spores contrasts with the model for the dispersal group of species with fleshy fruits (Table 17) which is similar to the models for the other species groups.

In summary, the multiple regression analyses indicate that the order of importance of the geographic variables for the prediction of the number of species is:

1. Variables related to the size of an island
2. Complexity of island shape
3. Isolation and distance variables
4. Topographic diversity

For certain subsets of species, such as orchids and the water associated dispersal group, other factors such as topographic diversity and geographic attributes related to water may be slightly more important.

Variables related to size are thought to be related to the number of species through either an equilibrium model such as the one proposed by MacArthur and Wilson (1967) or possibly a fundamental lognormal frequency distribution for the occurrence of species. However, evidence presented in this study is not sufficient for a definitive statement on the ecological mechanism responsible for the consistent relationship between the size of the island and its number of species.

Increased complexity of island shape is described as being related to an increase in the number of species per island because it represents an increased number of habitats. These habitats differ primarily in microclimate and number of soil types.

For some subsets of the flora, the effect of isolation is observed when it is represented by the distance to source areas. The effect of isolation is only of minor importance to the prediction of the total number of species. The importance of isolation is slightly increased for subsets of the flora that are related to the source areas.

Variables representing topographic diversity have a significant but minor role in predicting the number of species per island. These variables may be unimportant because their level of resolution is poor. The absence of a clear transition of plant communities in this region may also explain the relative unimportance of this factor.

VII. INTER-TAXONOMIC CORRELATIONS

One of the original objectives of this study was to determine if differences were observed in the biogeographic relationships for different families. The results of the analyses for the families showed that the biogeographic patterns are all similar to one another and the same as the patterns of the total number of species. In the process of performing the analyses, the number of species in most of the families analyzed were discovered to be highly correlated with each other and with the total number of species. Values of the correlation coefficients are shown in Table 18 for representative

Table 18. Correlation coefficients between the number of species in selected families.

	SPNO ^a	SPF25	SPF26	SPF32	SPF69	SPF80
SPF25	0.935					
SPF26	0.945	0.910				
SPF32	0.700	0.657	0.556			
SPF69	0.792	0.624	0.638	0.692		
SPF80	0.921	0.848	0.795	0.668	0.767	
SPF89	0.922	0.774	0.827	0.634	0.891	0.877

^aVariable abbreviations:

SPNO = Number of species

SPF25 = Number of grass species

SPF26 = Number of sedge species

SPF32 = Number of orchid species

SPF69 = Number of heath species

SPF80 = Number of figwort species

SPF89 = Number of composite species.

families. Figures 15 (page 77) and 52 display the nature of the relationship between these variables.

These inter-taxonomic relationships were initially thought to be interesting and useful since it might be possible to analyze biogeographic patterns with a subset of the flora which is easily collected, such as the composites. A review of the published literature revealed that this type of result had not been previously reported. This literature review also revealed that no result that was remotely similar had ever been reported. A correlation between the number of species in the different strata of a forest community (herbs, shrubs, and trees) (for example, Del Moral 1972) is the only result similar to the taxonomic correlations reported here. However, the vegetation of the Aleutian Islands does not have distinct strata.

Without the benefit of previous interpretation of similar results, an attempt will be made to offer possible explanations for these results. Additional analyses revealed that random subsets of the flora, which are approximately equal to the size of a family, are also highly correlated with the total number of species and the number of species in families. The occurrence of correlations from random subsets of the flora suggests that using families as subsets of the flora is equivalent to a random subset. This equivalence indicates that there is nothing different or nonrandom about the number of species from a family per island. Instead of the taxonomic correlations being indicative of nonrandom or family specific results that are biogeographically meaningful, they are part of the biogeographic pattern that is expected when the numbers of species in families do not change differentially.

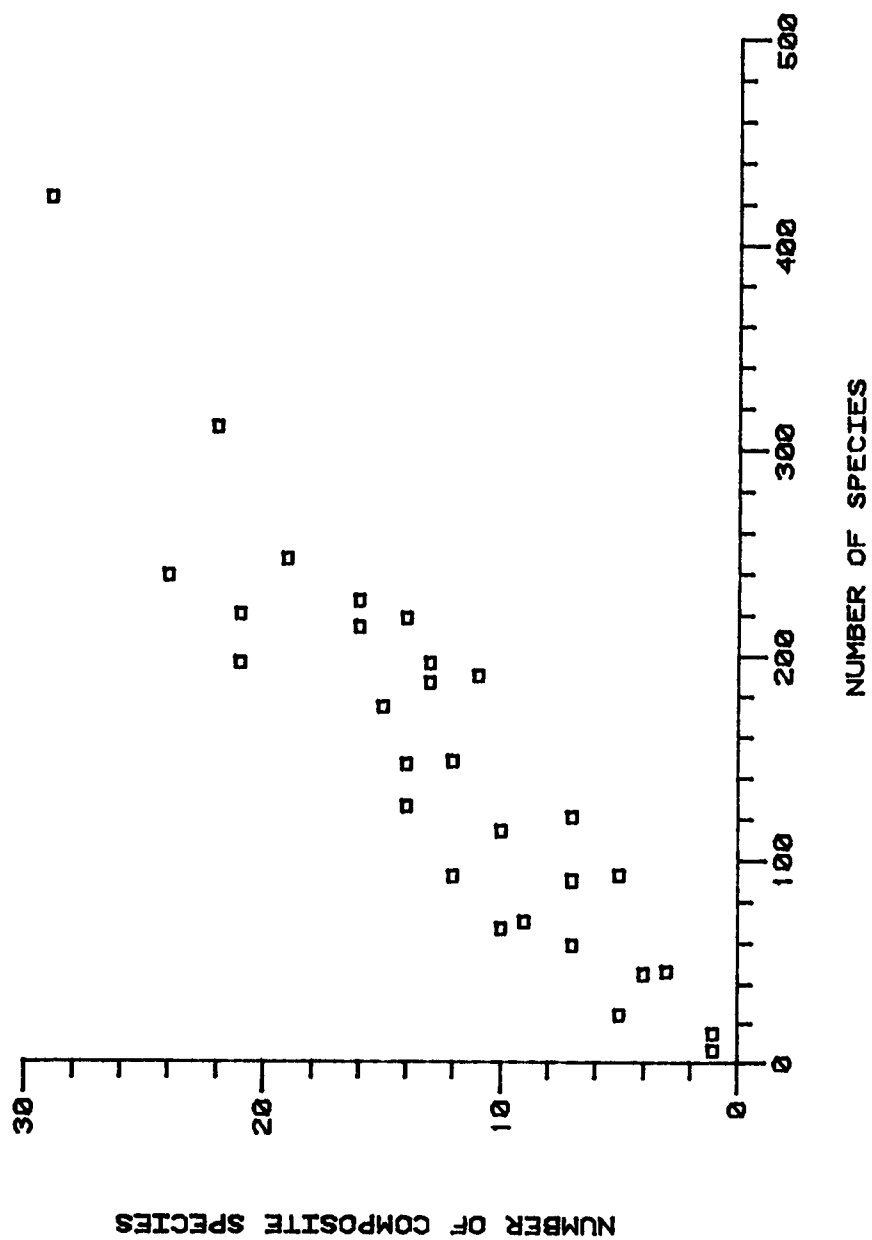


Figure 52. Relationship between the number of species of composites and the total number of species ($r = 0.922$).

When the expected pattern due to randomness is the correlated result, then uncorrelated relationships may be expected from nonrandom phenomena. An investigation of the uncorrelated family groups did not reveal any consistent pattern of deviation from the expected correlation for any island or group of islands. Therefore, it is not possible to offer any general hypotheses based on geographic characteristics that explain the presence or absence of taxonomic correlations.

Observations in the field did not reveal any family specific patterns of distribution for the different plant communities. Each community appeared to have species from each of the more diverse families such as grasses, sedges, and composites. This widespread distribution of plant families across a range of community types also tends to support the concept of a family being similar to a random subset of species of the flora of this region.

All of the above discussion is related to the number of species per family. These comments do not necessarily mean that the composition of species found on an island for each family is random. The cluster analyses did show that there are some differences in compositional similarities between the families.

Since results like these taxonomic correlations have not been previously reported from other areas, I do not know if these results are unique to the Bering Sea Region or the maritime tundra vegetation. If such uniqueness were demonstrated, then it would be very interesting to hypothesize and test explanations for this uniqueness. Possible explanations for the existence of such a unique pattern might be due to the unusual climate and geography of the area. These ideas are

only conjectures and are intended to indicate what information needs to be known before a better understanding of the taxonomic correlations can be obtained.

CHAPTER 7

SUMMARY

The theory of island biogeography developed by MacArthur and Wilson (1967) was used to examine biogeographic patterns in the vascular flora on islands in the Bering Sea Region. The basic relationships between the number of species and the size, indices of environmental heterogeneity, and isolation of the islands were studied. Those relationships were also examined for families, groups of species defined by type of dispersal, and subsets of the flora that were related to the mainland source areas.

The floristic data for 29 islands and six source areas in the Bering Sea Region were compiled primarily from the published works of Hultén. Information from recent collections in the Aleutian Islands was also added to the floristic data set.

Geographic variables included area, maximum elevation, distance to source areas and other islands, and latitude. Measures of topographic complexity were synthesized from samples of the number of contour lines per unit area on topographic maps. Indices of the size and complexity of island shape were developed from radial measurements of the islands. The size and shape of an island were also represented by the number of bays and total kilometers of mapped streams. The depth and width of interisland passes, percentage of near shore area, distance along current paths and distance to the limit of pack ice were used to represent the local isolation of the Aleutian Islands.

The relationships between the floristic and geographic variables were analyzed with correlation and multiple regression. Patterns in the floral similarity of islands were examined with cluster analysis.

The log-log species-area relationship observed for the vascular flora on the islands of the Bering Sea Region was similar to the relationship predicted by the theory of island biogeography developed by MacArthur and Wilson (1967). The species-area relationship of this study was also similar to ones observed in other studies (for examples, see Amerson 1975, Power 1972, Simpson 1974, Connor and McCoy 1979). Species-area relationships similar to the one observed for the total flora were also obtained when the number of species per family were analyzed.

Because data on immigration and extinction rates are not available for the flora of this area, it was not possible to know if the observed species-area relationship was due to the equilibrium model proposed by MacArthur and Wilson or to the "canonical" result of a lognormal distribution of species abundance or to some other cause. A significant correlation between the number of families and the number of species on the islands suggested that a "canonical" distribution may be present. While the presence of this type of distribution can mathematically explain the occurrence of species-area relationships, the biological or ecological explanations of the species-area relationships are still not known.

The maximum elevation of an island was used as an index of environmental heterogeneity of an island. Correlations between the number of species and maximum elevation were either weak or not

significant. The absence of a distinct change in plant communities across changes in elevation was thought to be an explanation of the nonsignificance of this result.

Indices of topographic complexity were developed in an attempt to more adequately represent changes in the environmental heterogeneity of the islands. In general, the correlations between these indices and the number of species were similar to the correlations between the number of species and maximum elevation.

Geographic variables that were synthesized from radial measurements to represent the size and shape of the islands were also positively correlated with the number of species on an island. The mean and variance of the radii were positively correlated with the number of species. These relationships were partially dependent on a relationship between the magnitude of the radii and the size of an island.

The mean of the radial deviations was the only geographic variable with a correlation coefficient greater than the one for the species-area relationship. The size of the island and the complexity of its shape were both represented by the mean of the radial deviations. The difference between this variable and the area of the islands was probably due to the mean of the radial deviations representing additional environmental heterogeneity that is related to the shape of an island. The shape of an island was thought to influence the environmental heterogeneity through the pattern of the soils, topography, and local climate.

The number of bays and total length of streams were positively correlated with the number of species. These variables were intended

to be another representation of the size and complexity of the shape of an island. They were also correlated with the area of the island.

Differences in the number of species per area were not explained by categorical variables of the geological attributes of the islands. The nonsignificance of these results may be due to the unrefined nature of the variables (for example, the presence or absence of recently active volcanoes). Another interpretation of these results is that the geological attributes have not had a recent effect on the number of species per area on an island.

The isolation of an island was represented by the distance to mainland source areas. Correlations between the total number of species and the distance to the source areas were not significant. When the proportion of species related to the flora of a source area was used in the analyses of isolation, significant negative correlation coefficients with the distance to the source areas were found. The significance of this type of relationship was apparently due to the removal of the effects of other source areas and the total number of species on an island from the floristic variable. The negative correlation coefficients between the distance variables and this floristic variable were similar to the relationships expected from MacArthur and Wilson (1967). Hultén (1963), Tatewaki (1963a) and Lindroth (1963) also observed in this region a pattern of decreasing influence of the flora of a mainland area with increasing distance from the mainland area.

A steeper species-area curve for "far" islands than "near" islands was another biogeographic pattern obtained by this study. This type of relationship was also predicted by the theory developed by

MacArthur and Wilson. They explained this pattern by hypothesizing differences in the immigration rate of islands with different isolation. Information on the immigration rates of the flora to the islands in this region is not available. Even though it was not possible to describe the mechanism for the observed difference in the species-area curves, it is fair to conclude that the equilibrium model could explain the similarities between the observed and predicted results.

Regional patterns in the floristic similarities of the islands were observed from the results of cluster analyses. The results of cluster analyses indicated that the floras of neighboring areas were more similar than areas from different parts of the region. This was interpreted as evidence for isolation between the parts of the Bering Sea Region. A significant negative correlation between interisland similarity and interisland distance also supported the presence of a pattern of isolation across the region. Terborgh (1973), Power (1975), and Connor and Simberloff (1978) have also reported similar relationships from other areas.

The results of cluster analyses of species with long range dispersal ability showed a pattern of floristic similarity that was not geographically interpretable. The results were interpreted to indicate a lower degree of isolation for this group. The pteridophytes were examined as an example of a group of species with long range dispersal ability.

Cluster analyses also indicated that the flora of the Aleutian Islands tends to be more similar to the flora of the North American source areas than the Asian source areas. This conclusion supported

the designation of Hult  n's Line as a phytogeographic division between the Aleutian and Commander Islands (Tatewaki 1963b).

The results of multiple regression analyses indicated that the area of an island was the most important type of geographic variable used in the prediction of the number of species. As was stated earlier for the correlation results, the mechanism underlying this species-area relationship is not known, but a relationship between area and environmental heterogeneity may account for part of it.

Geographic variables that were synthesized from relative values of the radial measurements were the next most important type of variable in the multiple regression models. The variables that were based on the relative radial measurements represent differences in the complexity of the shape of the islands that were not related to size. The complexity of the shape of an island was interpreted to be related to additional environmental heterogeneity of an island that was not related to its size.

Distance from the source areas and maximum elevation or topographic diversity were the remaining types of geographic variables that were important in the prediction of the number of species with multiple regression models. In general, the distance variables were more important than maximum elevation. In studies of island biogeography in tropical and temperate areas (for examples, see Amerson 1975, Simpson 1974, Johnson et al. 1968), elevation has been more important than distance variables in multiple regression models. The unimportance of elevation in the analyses of the islands in the Bering Sea Region may be due to the absence of a significant pattern of floristic change across elevations.

The width and depth of interisland passes, percentage of near shore area, distance along current paths, and distance to the pack ice limit were also used in multiple regression models to represent the local isolation of the Aleutian Islands. The width of the adjacent interisland pass was the most important of the local isolation variables. It often had a significant negative partial regression coefficient. Larger widths of the interisland passes were interpreted to be related to greater isolation of an island from a neighboring island.

Significant positive correlations between the number of species in families and the total number of species were observed in this study. The biogeographic significance of these correlations is not known. Explanations of these correlations may include the geography and climate of the area.

In summary, the results of this study do not directly prove or disprove the equilibrium model developed by MacArthur and Wilson in their theory of island biogeography. However, geographic variables related to the size, environmental heterogeneity, and isolation of an island can be used to predict the number of species on islands in the Bering Sea Region. The relationships between the floristic and geographic variables were also similar to the ones used in the development of the theory of island biogeography.

CHAPTER 8

RECOMMENDATIONS FOR FUTURE RESEARCH

In the past, one of the limitations on studies of the biogeography of the flora of the islands in the Bering Sea Region was the lack of information on the distributions of the species (Hultén 1960). This limitation is now less severe, but many of the islands are still floristically unknown. The biogeographic interactions between these islands are also unknown. Since the geography of the Aleutian Island Chain provides an excellent opportunity to study the floristic patterns resulting from the exchange of species along a long, linear series of islands, it would be very useful to obtain more floristic information.

If enough floristic information could be obtained, the Aleutians also present an excellent opportunity to use computer simulation to study the effects of islands for which the flora is not known. Computer simulations could also be useful for studying hypotheses related to the size and spacing of areas, differential dispersal ability of the species of the flora, and the biogeographic interactions of species on the scale of whole islands.

The thorough collection of the flora of all of the islands in a segment of the island chain could also provide a better understanding of the true isolation of the islands. However, the interpretation of the biogeography of this set of islands would still be limited by the knowledge of the ecology of the species in the flora. Some of the differences in the floras may be due to differences in the soils, local

climate, and recent geologic history of the islands. A better understanding of the mechanisms that can explain the observed relationship between the number of species and topographic diversity and complexity of the island shape would also improve the interpretation of biogeographic patterns.

The equilibrium model of the theory of island biogeography was described as functioning through a dimension of time. Because of this time dimension, knowledge of the history of the flora of the Aleutian Islands would improve the understanding of the biogeography of the flora. From palynological studies, it might be possible to answer the following questions:

1. What is the age of the present flora?
2. Was it changed or removed during the Pleistocene glaciations?
3. If the flora was removed, how rapidly did it return?
4. What was the pattern of the species composition during the period of recolonization?

This study has assumed that the composition of the flora is close to equilibrium. However, palynological studies on the islands could provide some of the information needed to evaluate the validity of this assumption.

Knowledge of the mechanisms that can explain the observed biogeographic patterns would contribute substantially to the interpretation of island biogeography. Species-area relationships have been commonly observed. The occurrence of this type of relationship for a large number of areas and taxa must indicate that some fundamental phenomenon occurs in almost all areas. Preston (1962) and May (1975) suggested that species-area relationships are due to the lognormal

distribution of species abundance. An explanation of the occurrence of this type of distribution of abundance would certainly provide a basis for understanding changes in the number of species of different areas. It could also lead to a better understanding of the significance of the number of species and its relationship to other ecosystem attributes such as stability, complexity, etc. Personal observations of the plant communities on islands of different sizes indicate that similar communities on smaller islands have fewer species. I interpret these observations to mean that the mechanisms affecting the species-area relationships for whole islands also appear to have some effect on the number of species at the community level.

While the geographic variables used in this study can explain a large portion of the variation in the number of species, it would be useful to know what other environmental factors are related to the number of species in an area. The identification of other factors is probably important for understanding the biogeography of subsets of the flora. Knowledge of the factors that change the biogeographic relationships of different groups of species could lead to a more comprehensive understanding of biogeography.

The isolation of an island is probably the least understood biogeographic concept. This includes not only the quantitative representation of the isolation of an island, but also the differences in the effectiveness of isolation on species with different dispersal mechanisms. The frequency of the dispersal of plants between islands is undescribed. The differences in the dispersal ability of plants through the air and on the water are also unknown. Because the

concepts of immigration and isolation are major aspects of the theory of island biogeography, more information on dispersal is very important.

In summary, more information on the past and present distributions of the plant species in the Aleutian Islands is needed. A better knowledge of the ecology of the plant species in this region is also important for interpreting future biogeographic studies of this region. The documentation of biological and ecological mechanisms that can explain the observed biogeographic patterns, in either the Aleutian Islands or any other area, is certainly essential to an improved understanding of biogeography and ecology.

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APPENDIX

APPENDIX

FLORISTIC, GEOGRAPHIC, AND DISPERSAL DATA

Table A-1. Species presence/absence data for islands and source areas.

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
ABIES GRACILIS	J....	6
ACER GLABRUM	B...	6
ACHILLEA BOREALIS	.AAAAAAD.KKAFAAA..P.BBB...A.BBB.	0
ACHILLEA PTARMICA	AA.....A...	0
ACHILLEA SIBIRICA	AA.....A.B..	0
ACONITUM DELPHINIFOLIUM	.AAAAA.....P.BBBBBBA.BBBB	0
ACONITUM FISHERI	J....	0
ACONITUM MAXIMUM	.AAAAA.....AAAAA.....AA...	0
ACTAEA ERYTHROCARPA	J....	0
ACTAEA RUBRA	B....AJBB..	0
ADIANTUM PEDATUM	...A.....A...B.....B...	1
ADOXA MOSCHATELLINA	BB.	4
AGROPYRON BOREALE	B...B	5
AGROPYRON MACROURUM	BB.	9
AGROPYRON MUTABILE	J....	5
AGROPYRON PAUCIFLORUM	B....BCB.B.	5
AGROPYRON SUBSECUNDUM	R...	5
AGROPYRON TURCZANINOWII	J....	5
AGROSTIS ALASKANA	.A.AAAA.AE...HA...AC...BBB...A.B...	5
AGROSTIS BOREALIS	...AAA..AE...H..A.AA...B....AABBB.	5
AGROSTIS CLAVATA	B....	5
AGROSTIS EXARATA	.A.AAA..AE...H.F..A...B....AJB...	5
AGROSTIS SCABRA	AA..A.....B....A.BB.B	5
AGROSTIS STOLONIFERA	B.B.	9
AGROSTIS TRINNII	B.BB.	9
ALLIUM SCHOENOPRASUM	B....BJRBBB	0
ALLIUM STRICTUM	J....	0
ALLIUM VICTORIALIS	A.....A...	0
ALNUS CRISPA	.A..A.....B....AABBBB	0
ALNUS FRUTICOSA	J....	0
ALNUS INCANA	BJ....	0
ALOPECURUS AEGUALIS	.A.....AE...A.....BBB...AARB..	9
ALOPECURUS ALPINUS	AE...A...AAAA...BBBBB.A.BBB	9
AMELANCHIERA FLORIDA	A.B...	4
AMERORCHIS ROTUNDIFOLIA	B.	2
ANAPHALIS MARGARITACEA	.A.AAA..AA...AAF.AAAA..B....AAB...	3

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
ANDROMEDA POLIFOLIA	AA..B..BBBAABBB	0
ANDROSACE ALASKANA	B.....	0
ANDROSACE CHAMAEJASME	.A.AAA.....A..P.BBBBBBAA.BBB	0
ANDROSACE FILIFORMIS	B...B	0
ANDROSACE SEPTENTRIONALIS	J..BB	0
ANEMONE DIBILIS	J....	0
ANEMONE DICHOTOMA	J....	0
ANEMONE DRUMMONDII	BBB	0
ANEMONE MULTIFIDIA	R...	0
ANEMONE NARCISSIFLORA	.AAAA.AAAOK.AAFAAAAP.B..BBBAABBB	0
ANEMONE NEMOROSA	J....	0
ANEMONE PARVIFLORA	B.....AA.BBB	0
ANEMONE RICHARDSONII	AA..A...A.....AAA..BB.BBBAA.BBB	0
ANGELICA GENUFLEXA	.A.....A.A..B.....AAB...	0
ANGELICA LUCIDA	...AAAA.AAOKKAFAAA.A..BBBBBBAABBB	0
ANTENNARIA DIOICA	AA...AA...A.A.....A....	3
ANTENNARIA FRIESIANA	BB.BBC	0
ANTENNARIA ISOLEPIS	B.....	0
ANTENNARIA MONOCEPHALA	AA.AAAA.A....A.....P.BB.BBBAA.R.BB	0
ANTENNARIA PALLIDA	AAA...H.....B....A.B...	3
ANTENNARIA ROSEA	B.....	0
ANTHRISCUS NEMOROSA	J....	0
APARGIDIUM BOREALE	B...	3
APHRAGMUS ESCHSCHOLTZIANUS	.A..A...A...A...A.....A...B.	0
AGUILEGIA FORMOSA	B...	0
ARABIS ARENICOLA	BB	0
ARABIS HIRSUTA	...AA...A.....P.B.....AAB...	8
ARABIS LYRATA	.A.AAA.AA.....AA..BB.BB.AABBB	0
ARABIS PENDULA	J....	0
ARABIS STELLARI	AA.....A....	0
ARCTAGROSTIS LATIFOLIA	.A.....BB.BBAA.BBB	9
ARCTERICA NANA	A.....A....	0
ARCTOPHILA FULVA	A...BBBBBAARBB	9
ARCTOSTAPHYLOS ALPINA	.A..A.....AAP.B..BBBAA.BBB	4
ARCTOSTAPHYLOS RUBRA	BBB	4
ARCTOSTAPHYLOS UVA-URSI	...AA.....B.....	4
ARENARIA CAPILLARIS	B....	0
ARENARIA CHAMISSONIS	BB	0
ARENARIA LONGIPEDUNCULATA	BC	0
ARNERIA MARITIMA	AAA.A.....P.BBB..BAA.BBB	0
ARNICA ALPINA	B	3
ARNICA AMPLEXICAULIS	B.....B.B...	0

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
ARNICA CHAMISSONIS	.A..AA.....B....A.B...	3
ARNICA FRIGIDA	BBB	0
ARNICA LATIFOLIA	P.B.....B...	3
ARNICA LESSINGII	.A.AA.....P.B..BBBAARB	3
ARNICA UNALASCHCENSIS	...AAAAAAA.KKAFAAAAA...BB.B..A...	3
ARTEMISIA ALASKANA	B.	0
ARTEMISIA ALEUTICA	A.....	0
ARTEMISIA ARCTICA	.A.AA.....AAAP.BBBBBAABBB	0
ARTEMISIA BOREALIS	A.....BAA.BBB	0
ARTEMISIA FURCATA	AA.....BB.A..BB	0
ARTEMISIA GLOBULARIA	.A..A.....BB.BBA...BB	0
ARTEMISIA GLOMERATA	B.B..BB	0
ARTEMISIA LACINIATIFORMIS	B...	0
ARTEMISIA SENJAVINENSIS	BB	0
ARTEMISIA STELLERIANA	J...	0
ARTEMISIA TILESII	.A.AA...E.....A...BBB.BB.B.BBB	0
ARTEMISIA UNALASKENSIS	...AA...A....AF.AAAA.....A...	0
ARTEMISIA URSORUM	J...	0
ARTEMISIA VERLITORUM	J...	0
ARUNCUS SYLVESTER	A...B....AAB...	0
ASPLENIUM VIRIDE	B...	1
ASTER ALPINUS	B...	3
ASTER JUNCIFORMIS	B....	0
ASTER SIBIRICUS	.A..A.....A..BB...BARBBB	3
ASTER SUBSPICATUS	...A.....A..P.B.....B...	3
ASTRAGALUS ABORIGINUM	BBB	0
ASTRAGALUS ALPINUS	...A.....B.ARB	0
ASTRAGALUS AMERICANUS	B..B...	0
ASTRAGALUS EUCOSMUS	B..B.	0
ASTRAGALUS POLARIS	A..BB.	0
ASTRAGALUS ROBBINSII	R...	0
ASTRAGALUS SCHELICHOWII	J...	0
ASTRAGALUS UMBELLATUS	BBB.J.BBB	0
ATHYRIUM DISTENTIFOLIUM	BB..B	1
ATHYRIUM FILIX-FEMINA	..AAAAAAA.KKAFF.AAAA..BBB...ABBB.	1
ATRIPLEX ALASKENSIS	B.....B...	0
ATRIPLEX DRYMARIOIDES	B.....B...	0
ATRIPLEX GWELINI	B.....JB	0
AVENA PLANICULMIS	J...	5
AVENA SATIVA	B.....J...B	5
AVENA STRIATA	J...	5
BARBAREA ORTHOCERAS	.A.AAAA.AD.....AA...B....AABBBB	0

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
BECKMANNIA ERUCAEFORMIS	B.B.B	5
BELLIS PERENNIS	A....D.....	3
BETULA ERMANI	AA.....A....	6
BETULA KENAIICA	B.....B..BB.	6
BETULA NANA	AA..B..BBBAARBB	6
BETULA OREGONA	B...	6
BETULA PAPYRIFERA	B..	6
BETULA PLATYPHYLLA	J....	6
BIDENS RADIATA	J....	0
BLECHNUM SPICANT	AE.....B.....B...	1
BOSCHNIAKIA ROSSICA	B.....BBBBB.	0
BOTRYCHIUM BOREALE	.A..A.....K....A...B.....AR..B	1
BOTRYCHIUM LANCEOLATUM	.A.....A...B.....AA....	1
BOTRYCHIUM LUNARIA	.A..A...E...HA...A.A..BB...AAB.BB	1
BOTRYCHIUM MULTIFIDUM	.A..A...E.....A....	1
BOTRYCHIUM VIRGINIANA	A.....	1
BOYKINA RICHARDSONII	BB.	0
BRAYA BARTLETTIANA	B.	0
BRAYA HUMILIS	B.	0
BRAYA PILOSA	B.	0
BRAYA PURPURASCENS	BB	0
BROMUS CILIATUS	B.....B.....	5
BROMUS COMMUTATUS	BB.....	5
BROMUS HORDEACEUS	B.....B..R.B.	5
BROMUS INERMIS	B..R.B.	9
BROMUS MARGINATUS	B.	5
BROMUS PACIFICUS	B...	5
BROMUS PUMPELLIANUS	BBRBBB	9
BROMUS RICHARDSONII	B....	5
BROMUS SITCHENSIS	...AAA.AAD...H.F..AA.....A.B...	5
BROMUS TECTORUM	B.....B.	5
BRYANTHUS GMELINI	AA.....A....	0
BUPLEURUM TRIRADIATUM	B.BBB	6
CACALIA AURICULATA	AFAAAAA.....A....	3
CACALIA HASTATA	J....	0
CAKILE EDENTULA	B.....B...	0
CALAMAGROSTIS CANADENSIS	AA.AAA..AD...H....AAA..BB...BAABBB	9
CALAMAGROSTIS DESCHAMPSIODES	A.....BB..BBAB.BB	9
CALAMAGROSTIS HOLMII	B...B.....B	9
CALAMAGROSTIS INEXPANSA	...AAA.....B.....AA..B.	9
CALAMAGROSTIS LAPONICA	D.....BBB	9
CALAMAGROSTIS NEGLECTA	B.BB.	9

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
CALAMAGROSTIS NUTKAENSIS	...AAA.AAD...AAF..A.....JB...	9
CALAMAGROSTIS PURPURASCENS	.A.AAA..A.....AA...B....AA..BB	5
CALAMAGROSTIS SACHALINENSIS	J....	5
CALLA PALUSTRIS	B....	7
CALLITRICHE ANCEPS	.A.....H...AA...B....AA...C	0
CALLITRICHE HERMAPHRODITICA	A.....A.....A.....A....	6
CALLITRICHE VERNA	.A.....A..A..B....CAABBBB	0
CALTHA BIFLORA	B...	0
CALTHA LEPTOSEPALA	B.....A.B...	7
CALTHA NATANS	BJ.BB.	7
CALTHA PALUSTRIS	.A.AAA.AAD...AA....AA..B.BBBBBABBBB	7
CALYSO BULBOSA	B...	2
CAMPANULA CARNOSA	J....	0
CAMPANULA CHAMISSONIS	...AAAA.AA...A....A..A..B.....A....	0
CAMPANULA LASIOCARPA	AAAAAA..AA.K.AAF..AAP.BBB...AA.BBB	0
CAMPANULA LATISEPALA	PB.....B.B...	0
CAMPANULA UNIFLORA	...AA.....B..B....BBB	0
CARDAMINE ANGULATA	B...	8
CARDAMINE BELLIDIFOLIA	.A.AAA..AE...H....A....BBBBBBAA.BBB	8
CARDAMINE HYPERBOREA	B....BB	8
CARDAMINE MICROPHYLLA	B.B..BB	8
CARDAMINE PENNSYLVANICA	R...	8
CARDAMINE PRATENSIS	...AAA..A.....AAP.BBBBBBAABBBB	8
CARDAMINE PURPUREA	B.B..BBB	8
CARDAMINE REGELIANA	A.....A....	8
CARDAMINE TENUIFOLIA	J....	8
CARDAMINE UMBELLATA	.A.AAAAAA..KAFAAAAAAP.BBBBBBAABBBB	8
CAREX AMBLYOLEPIS	J....	5
CAREX AMBLYORHYNCHA	B	5
CAREX ANTHOXANTHEA	.A.AAAAAA...A.F.AA....BBBB...B..B	9
CAREX APPENDICULATA	A.....A....	5
CAREX AQUATILIS	.A.....D.....BBBBBBBAABBBB	9
CAREX ATROFUSCA	BBB	5
CAREX AUGUSTINOMIEZII	J....	5
CAREX BICOLOR	.A.....B	9
CAREX BIGELOWII	A....H.....AA.BBB	9
CAREX BONANZENSIS	B....	5
CAREX BRUNNESCENS	B....BBR...	5
CAREX BUXBAUMII	BJB...	9
CAREX CANESCENS	...A.....B....AAB.B.	5
CAREX CAPILLARIS	J...B	5
CAREX CAPITATA	BB	5

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
CAREX CHORDORRHIZA	B...BB.....	9
CAREX CIRCINNATA	.A.AAAAAA...AAF..A...B....A.B...	5
CAREX DIANDRA	B....	9
CAREX DIOCIA	AE..KH....A.....AA.B.B	9
CAREX DISPERMA	B.....JB...	5
CAREX DRYMOPHILA	J....	5
CAREX ECHINATA	...B.....J....	5
CAREX ELEUSINOIDES	B...B	5
CAREX ENANDERI	...A....E....F.....B.....B...	5
CAREX FLAVA	R...	5
CAREX GARBERI	R...	9
CAREX GLACIALIS	BB	5
CAREX GLAREOSA	.A..A...E....F...A..BBBB.BAA.BBB	5
CAREX GLOBULARIS	J....	5
CAREX Gmelini	...A..G.....AAA..BBB...AABBBB	5
CAREX GRACILIS	J....	5
CAREX HAKKODENSIS	J....	5
CAREX HELEONASTES	B....	5
CAREX HOLOSTOMA	B	9
CAREX JACOBI-PETERI	C...B.	5
CAREX KELLOGGII	AA..AA..AE...A...AAA..BB...A.B...	5
CAREX KIRGANICA	J....	5
CAREX KRAUSEI	C	5
CAREX LACHENALII	BBBBBB.B.BBB	5
CAREX LAEVICULMIS	B....BBB...	5
CAREX LAPPONICA	B.B...	5
CAREX LASIOCARPA	B....	9
CAREX LAXA	J....	9
CAREX LEPTALEA	B....B.R...	5
CAREX LIMOSA	JR...	9
CAREX LIVIDA	A...B....CAJB...	9
CAREX LOLIACEA	B....	5
CAREX LONGEROSTRATA	J....	5
CAREX LUGENS	BBB	9
CAREX LYNGBYAEI	.A.AAA.AAD...A.F.AAAA..BBBB..AABBBB	9
CAREX MACKENZIEI	BB....BBBB.	5
CAREX MACLOVIANA	...A.....A..B....AAB...	5
CAREX MACROCEPHALA	B....BBB...	9
CAREX MACROCHAETA	AA.AAAAAA.KKAFAAAA..BBBBB.AAB..B	9
CAREX MAGELLANICA	J....	5
CAREX MARITIMA	B...B....BB	9
CAREX MEDIA	BBB	5

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
CAREX MELANOCARPA	B	9
CAREX MEMBRACEA	BB...BBB	9
CAREX MERTENSII	B....B.B...	5
CAREX MICHAUXIANA	J....	5
CAREX MICROGLOCHIN	B.	9
CAREX MIDDENDORFFII	J....	5
CAREX MISANDRA	BB.B.BBB	5
CAREX NARDINA	BB	5
CAREX NESOPHILA	.A.....A...A...BBB.BBAA.BBB	9
CAREX NIGRICANS	.A.AA.A.AE.....AA..B....A.B...	9
CAREX OEDERI	JB...	5
CAREX PALLIDA	J....	5
CAREX PAUCIFLORA	J..B.....JB...	5
CAREX PEDIFORMIS	J....	5
CAREX PETRICOSA	C	9
CAREX PHYLLomenica	B...	5
CAREX PLURIFLORA	.A.AA.AAAA...AAFAAA...BBB...A.B...	9
CAREX PODOCARPA	B.....BBB	9
CAREX PYRENAICA	...A....E.....A..BBB...AAB..B	9
CAREX RAMENSKII	...B.....BB.BB.B.BB.	9
CAREX RARIFLORA	B.B.BBB	9
CAREX RHYNCHOPHYSA	B....	9
CAREX ROSTRATA	BBB...	9
CAREX ROTUNDATA	B.B.BBB	9
CAREX RUESANENSIS	J....	5
CAREX RUPESTRIS	BB	9
CAREX SAXATILIS	.A..AA.AAA...A...A...BB.B.BAJRBBB	9
CAREX SCHMIDTII	J....	5
CAREX SCIRPOIDEA	B...B.B.BBB	9
CAREX SCITA	J....	5
CAREX SITCHENSIS	B...	9
CAREX SPECTABILIS	A...BB..B..AB...	9
CAREX STENANTHA	J....	5
CAREX STYLOSA	...A....E...A...A.A..A...AABBBB	5
CAREX SUBSPATHACEA	B...BBB	5
CAREX TENUIFLORA	B....B....	5
CAREX TOLMIEI	J....	5
CAREX TRAIZISCANA	J....	5
CAREX TUMINENSIS	J....	5
CAREX URSINA	B	5
CAREX VAGINATA	AA.....A..BB	9
CAREX VERNA	A.....A....	5

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
CAREX WILLIAMSII	B...B	5
CASSIOPE LYCOPODIODES	AAAAAAAAA..KAF.AAAA..B....AAB..B	0
CASSIOPE MERTENSIANA	B...	0
CASSIOPE STELLERIANA	.A.AA.....A..B....AAB..B.	0
CASSIOPE TETRAGONA	B.B.J.BBB	0
CASTILLEJA CAUDATA	B....BBB	0
CASTILLEJA ELEGANS	BB	0
CASTILLEJA HYETOPHILA	B...	0
CASTILLEJA HYPERBOREA	B..BBB	0
CASTILLEJA MINIATA	B...	0
CASTILLEJA PARVIFLORA	B...	0
CASTILLEJA UNALASCHENSIS	.AAAAA.....H....A..P.BB...AJB...	0
CATABROSA AQUATICA	B....	9
CERASTIUM ALEUTICUM	...A...A....AAF..A....BB.....	0
CERASTIUM ARVENSE	B.....B..B	0
CERASTIUM BEERINGIANUM	.A.AAAAAA...A....A.P.BBBBBBABB	0
CERASTIUM FISCHERIANUM	...AAAAAAA..HAF...AA..BB..BB.ABB..B	0
CERASTIUM JENISEJENSE	BB.	0
CERASTIUM MAXIMUM	A.....A....	0
CHAMAECYPARIS NOOTKATENSIS	B...	0
CHAMAEDAPHNE CALYCVLATA	J.BB.	0
CHENOPODIUM GLAUCUM	B....	0
CHRISTOLIA PARRYOIDES	B...B	0
CHRYSANTHEMUM ARTICUM	KKAFAAAAA.PBBBBBBAABBB	0
CHRYSANTHEMUM BIPINNATUM	BB.	0
CHRYSANTHEMUM INTEGRIFOLIUM	E.....J..BB	0
CHRYSOSPLENIUM KAMTSCHATICUM	AA.....A...B	0
CHRYSOSPLENIUM RIMOSUM	J....	0
CHRYSOSPLENIUM TETRANDRUM	.A..A.....A...B.B.BBAJRBBB	0
CHRYSOSPLENIUM WRIGHTII	.AAAA...A.....F..A....BB.BBAA..BB	0
CICUTA DOUGLASII	B.....B...	0
CICUTA MACKENZIEANA	A..B..	0
CICUTA VIROSA	A.....A....	0
CIMICIFUGA SIMPLEX	J....	0
CINNA LATIFOLIA	.B.....BBB...	5
CIRCAEA ALPINA	.A.....B....AAB...	3
CIRSIIUM KAMTSCHATICUM	AAAAA.....A....	3
CLADOTHAMNUS PYROLAEFLORUS	B...	0
CLAYTONIA ACUTIFOLIA	BB.B.BBB	0
CLAYTONIA ARCTICA	A...HA...A.....BC.A....	0
CLAYTONIA CHAMISSOI	.AA.AA.....A...B....A.B...	8
CLAYTONIA PARVIFOLIA	B...	0

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
CLAYTONIA SARMENTOSA	BBBBBBAA.BBB	0
CLAYTONIA SCAMMANIANA	B.....	0
CLAYTONIA SIBIRICA	.AAAAA.GAO.KAAFAAAAA..B....A.B...	0
CLAYTONIA TUBEROSA	BB.B.BBB	0
CLEMATIS ALPINA	J....	0
CLEMATIS FUSCA	J....	0
CLINTONIA UNIFLORA	B...	0
CNIDIUM AJANENSE	AA.....A...B	0
CNIDIUM CNIDIFOLIUM	BB.	9
COCHLEARIA OFFICINALIS	.A.AAAA.AA...A.F.AAAAP.BBBBBBAABBB	0
COELOGLOSSUM VIRIDE	...A...AE...A...A.AP.B....AAB.BB	2
COLPODIUM FULVUM	J....	5
COLPODIUM WRIGHTII	BB	5
CONIOSELINUM CHINENSE	..AAAAA.AA...HAFA.AAA..BBBB.BAABBB.	0
COPTIS ASPLENIIFOLIA	B...	0
COPTIS TRIFOLIA	..AAAAA.AA...KAAFAAAAA..B....AAB.B.	0
CORALLORRHIZA MACULATA	B...	2
CORALLORRHIZA PATENS	J....	2
CORALLORRHIZA TRIFIDA	A.....ARBB.	2
CORNUS CANADENSIS	A.....H.F...A.....AJBBB.	4
CORNUS SUECICA	.A.AAA..GA..KAA.AAAAAP.BBBBBBAABBB	4
CORYDALIS AMBIGUA	J....	0
CORYDALIS PAUCIFLORA	BB.BBBBB.BBB	0
CRASSULA AQUATICA	B.....	0
CRATAEGUS CHLOROSARCA	J....	0
CREPIS CHRYSANTHA	B....	3
CREPIS NANA	BB	3
CRYPTOGRAMMA CRISPA	..A.A.....A...B....AAB.B.	1
CRYPTOGRAMMA STELLERI	BC	1
CYPRIPEDIUM GUTTATUM	A...A.....A..P.B....A...	2
CYPRIPEDIUM MACRANTHUM	J....	2
CYPRIPEDIUM PASSERINUM	B.	2
CYSTOPTERIS FRAGILIS	.AAAAA.AA...AA...A...BBB...AABBB	1
CYSTOPTERIS MONTANA	B.....B.BC	1
DACTYLORRHIZA ARISTATA	A.AAAAAA...AA.AAAAAP.B..B..AA....	2
DANTHONIA INTERMEDIA	D.....BB...	5
DAPHNE KAMTSCHATICA	J....	0
DELPHINIUM BRACHYCENTRUM	A.....B.A..BB	0
DELPHINIUM GLAUCUM	BB.	0
DESCHAMPSIA ALPINA	H.....	5
DESCHAMPSIA BERINGENSIS	AA.AAAAAE...A.F.AAAA..BBB.B.AABB..	5
DESCHAMPSIA CAESPITOSA	.A.AAAA.AE...AA...A...BB..BBABBB	5

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
DESCHAMPSIA PUMILA	B....B	5
DESCURAINIA SOPHIOIDES	J.BBB	0
DIANTHUS REPENS	B.BBB	0
DIAPENSIA LAPPONICA	H....AA..B....BAA.BBB	0
DICENTRA PEREGRINA	J....	0
DODECATHEON FRIGIDUM	BBB	0
DODECATHEON JEFFRYI	B...	0
DODECATHEON PULCHELLUM	B....B.B...	0
DOUGLASIA OCHOTENSIS	BB...BB	0
DRABA ALEUTICA	A....HA...AA....B.....B	0
DRABA ALPINA	B...B....BB	0
DRABA AUREA	B....	0
DRABA BARBATA	B	0
DRABA BOREALIS	.A.AAAAAA.....F..AAAP.BBB.BBAA..BB	0
DRABA CAESIA	B.	0
DRABA CHAMISSONIS	B	0
DRABA CINEREA	J...B	0
DRABA ESCHSCHOLTZII	BB	0
DRABA EXALATA	B.	0
DRABA FLADNIZENSIS	A.....B...BB...BB	0
DRABA HIRTA	J..BB	0
DRABA HYPERBOREA	..AAAAA.....KAAF.AA..P.BBB.B...B...	0
DRABA KANTSCHATICA	B.....A...B	0
DRABA LACTEA	...A.....B...B.A..BB	0
DRABA LONGIPES	B.	0
DRABA MACROCARPA	B....BB	0
DRABA MAXIMA	B.....R...	0
DRABA MEMOROSA	...B.....J....	0
DRABA NIVALIS	...A..A.....B....A..B.B	0
DRABA PILOSA	BB	0
DRABA PSEUDOPILSODA	BB...BB	0
DRABA STENOLOBA	...A.....A.....R...	0
DRABA STENOPETALA	B...B.B	0
DRABA SUBCAPITATA	B	0
DROSER A ANGELICA	B.....AB...	2
DROSER A ROTUNDIFOLIA	...A....E.....AAAP.B....AABBBB	2
DRYAS INTEGRIFOLIA	B...BBB	0
DRYAS OCTOPETALA	AA.....P.B..BBBAA.BBB	3
DRYOPTERIS DIALATA	...A...AE..KAAFA.AAA..BBB...AABBB.	1
DRYOPTERIS FRAGRANS	B.BBB	1
DUPONTIA FISCHERI	BB.BB...BBB	9
ECHINOPANAX HORRIDUM	B.....B...	4

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
ELATINE HYDROPIPER	J....	0
ELATINE TRIANDRA	J....	0
ELEOCHARIS ACICULARIS	J....	5
ELEOCHARIS KAMTSCHATICA	A.....ABB.B	9
ELEOCHARIS NITIDA	B....B....	9
ELEOCHARIS PALUSTRIS	A..B....AB...	9
ELEOCHARIS QUINQUEFLORA	D.....B....	9
ELEOCHARIS UNIGLUMIS	B....	9
ELYMUS ARENARIUS	.A.AA.AAAADKKAAFAAAAA..BB..BBABBBB	9
ELYMUS GLAUCUS	R...	9
ELYMUS HIRSUTUS	A.....B...	9
ELYMUS INTERIOR	B...B	9
ELYMUS SIBIRICUS	J....	9
EMEPTUM NIGRUM	.AAAAA.....KAAFAAAAA..BB..BBABBBB	4
EPILOBIUM ANAGALLIDIFOLIUM	.A.AA...GD.....A....BBB.B.AAB.BB	3
EPILOBIUM ANGUSTIFOLIUM	.AAAAA..AD....A...A.A..BB.B..AABBBB	3
EPILOBIUM BEHRINGIANUM	.A..AAAAA..KAAFAAAAA..BBB.B.AAB...	0
EPILOBIUM DAVURICUM	B..BB	3
EPILOBIUM GLANDULOSUM	A...AA..AA...HA..AAAA..B....ABB...	3
EPILOBIUM HORNEMANNII	...AA...AE.....AAA..BB....AABBBB	3
EPILOBIUM LACTIFLORUM	G.....R...	0
EPILOBIUM LATIFOLIUM	.A.AAA..A.....AAA..B..BBBAABBBB	0
EPILOBIUM LEPTOCARPUM	A...A.....B....A.R...	3
EPILOBIUM LUTEUM	.AAAAA.....B....A.B...	0
EPILOBIUM PALUSTRE	B....CBRRBBB	0
EPILOBIUM SERTULATUM	.AAAA..A...H....AA..BB..B.AA.BB.	0
EPIPACTIS PAPILLOSA	J....	2
EPIPOGON APHYLLUM	J....	2
ERUISETUM ARVENSE	.AAAAA.....KAA..AAAA..BBBBBBAABBBB	1
ERUISETUM FLUVIATILE	A..B....BAARBBB	1
ERUISETUM HIEMALE	A.A.....A....	1
ERUISETUM PALUSTRE	B.BB.BBC	1
ERUISETUM PRATENSE	F...A...B....BARBBBC	1
ERUISETUM SCIRPOIDES	B.BB..B.BBB	1
ERUISETUM SILVATICUM	A....B..AA.BB.	1
ERUISETUM VARIEGATUM	...A...AE.....A.....AB.BB	1
ERIGERON ACRIS	AA.....AA....	3
ERIGERON ERIOCEPHOLUS	B	0
ERIGERON HUMILIS	AAA.....A..BB	3
ERIGERON HYPERBOREUS	BB.	0
ERIGERON PEREGRINUS	.AAAAA...AD.KKAAFAAAAA..B....AJB...	3
ERIOPHORUM ANGUSTIFOLIUM	.A.AAA...D...H....AA..B...NBAABBBB	3

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
ERIPHORUM BRACHYANTHERUM	BC	3
ERIPHORUM GRACILE	B....	3
ERIPHORUM RUSSEOLUM	A..AA...GE...HA...A...B..BBBAABBB	3
ERIPHORUM SCHEUCHZERI	.A.....D.....A..B...CAA..BB	3
ERIPHORUM VAGINATUM	J..BB.	3
ERITRICHUM ARETIODES	BB	0
ERITRICHUM CHAMISSONIS	BB..BBA...BB	0
ERITRICHUM PECTINATUM	J....	0
ERITRICHUM VILLOSUM	B...B	0
ERYSIMUM HIERACIFOLIUM	J....	0
ERYSIMUM PALLASII	B..B.	0
EUPHARSIA MOLLIS	A..AA..AA...H...AAAP..B....AAR...	0
EUTREMA EDWARDSII	B..BB..B.BBB	0
FAURIA CRISTA-GALLI	B...	0
FESTUCA ALTAICA	A...AE.....B..B..AA.BBB	5
FESTUCA BRACHYPHYLLA	.A..AA..AA...AA...A.A..BB..BBABBBB	5
FESTUCA OVINA	C....	5
FESTUCA RUBRA	AA.AAAAAAAK.AAF.AAAA..BBBB.BAABBBB	9
FESTUCA SUBULATA	B...	5
FILIPENDULA KAMTSCHATICA	A.....A....	0
FILIPENDULA PALMATA	J....	0
FIMBRISTYLIS ANNUA	J....	5
FRAGARIA CHILDENSIS	.A.AAA..AE.....B.....B...	4
FRITILLARIA CAMSCHATCENSIS	.A.AAAA.AA..KA.FAAAAA..BBB...AAB...	8
GAGEA LUTEA	J....	0
GALIUM APARINE	...AAA.AAE...H...AA..P.B....A.B...	0
GALIUM BOREALE	B....BB.BBB	0
GALIUM BRANDEGEI	BB.	0
GALIUM KAMTSCHATICUM	A.....A.....AA....	0
GALIUM RUTHENICUM	J....	0
GALIUM TRIFIDUM	A...AA..AA...A.F..AAAP.BB...AABB.B	0
GALIUM TRIFLORUM	.A.AA.....P.B....AAB...	0
GAULTHERIA MIGUELIANA	A.....A....	4
GENTIANA ALEUTICA	.A.AA....E...HAF..A...B.....	2
GENTIANA ALGIDA	.A..A....E.....P..BBBBBAA.BBB	2
GENTIANA AMARELLA	.AAAAA..AE...H.F..A.....B...	2
GENTIANA AURICULATA	AAA.....C.A...B	2
GENTIANA DOUGLASIANA	B...	2
GENTIANA GLAUCA	A..BBBBBBAA.BBB	2
GENTIANA PLATYPETALA	B.....B...	2
GENTIANA PROPINGUA	BBB	2
GENTIANA PROSTRATA	A.....B....AA.BBB	2

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
GENTIANA TENELLA	B....B.BBB	2
GERANIUM ERIANTHAM	.AAAAA.AA..KAAFAAAAA..BBB...AABB.B	3
GEUM ALEPPICUM	B....	0
GEUM CALTHIFOLIUM	AA.AAAAAA..KAAFAAAAAP.B...B.AAB...	3
GEUM GLACIALE	B.B..BB	3
GEUM MACROPHYLLUM	.A.AAA..AA..KA.F..AAAP.B....AAB...	0
GEUM PENTAPETALUM	A...AA...AA.....A....	0
GEUM ROSSII	.A.AAA.AAA...AF..AAA..BBBB.AA.BBB	0
GEUM SELINIFOLIUM	J....	0
GEUM STRICTUM	A.....A....	0
GLAUX MARITIMA	B...	0
GLEHNIA LITTORALIS	B.....B...	9
GLYCERIA BOREALIS	R...	0
GLYCERIA LITHUANICA	J....	5
GLYCERIA MAXIMA	B....	5
GLYCERIA NATANS	J....	5
GLYCERIA PAUCIFLORA	B...	9
GOODYERA OBLONGIFOLIA	B...	2
GOODYERA REPENS	J....	2
GYMNADENIA CAMTSCHATICA	J....	2
GYMNOCARPIUM DRYOPTERIS	...A...A..KA...AA.A..B....AABBBB	1
GYMNOCARPIUM ROBERTIANUM	B	1
HALENIA CORNICULATA	J....	0
HAMMARBYA PALUDOSA	B....	2
HEDYSARUM ALPINUM	RBB.	0
HEDYSARUM HEDYSAROIDES	C.B..BB	0
HEDYSARUM MACKENZII	BC	0
HENIEROCALLIS HIDDENDORFFII	J....	0
HERACLEUM LANATUM	.A.AAAA.AADKKAFAAAAA..B....AABBB.	0
HEUCHERA GLABRA	.A.....P.B....A.B....	0
HIERACIUM GRACILE	A.....A.....B....A.B...	3
HIERACIUM SCABRIUSCULUM	B....	0
HIERACIUM TRISTE	AA.AAAAAA..KAAFAAAAAP.B....AABB..	3
HIERACIUM UMBELLATUM	J....	3
HIEROCHOLE ALPINA	A.....A.A..B..BBBAA.BBB	5
HIEROCHOLE ODORATA	.A.AAA..AE...AA...AAA..ABB...AAB.BB	9
HIEROCHOLE PAUCIFLORA	BB..B.B.BBB	9
HIPPURIS MONTANA	.A.AA....E...H.F..A.....B...B...	0
HIPPURIS TETRAPHYLLA	A....BBBBBAABBBB	7
HIPPURIS VULGARIS	.A.AA..AAD..KA...AAAA..BBBBBBAABBBB	7
HONCKENYA PEPOIDES	.AAAAA.AA..KAAF.AAAP.BBBBBBAABBBB	0
HORDEUM BRACHYANTHERUM	AA.AAA..AA...H....A.A..BB....AABBB.	5

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
HORDEUM JUBATUM	B.B....BR.BB	5
HORDEUM VULGARE	...B.....B....R...	5
HYPERICUM GEBLERI	J....	0
HYPERICUM KAMTSCHATICUM	J....	0
IMPATIENS NOLI-TANGERE	BB...	8
INULA BRITANNICA	J....	0
IRIS SETOSA	.A..A..AAD...HA...AAP.BB.B..AABBBB	8
ISOETES MURICATA	.A..A...AE...A...A.A..BBB...BAB...	1
ISOETES TRUNCATA	D.....B.....B...	1
JUNCUS ALPINUS	A.....B....CAJRB..	9
JUNCUS ARCTICUS	.A.AAAAAA..KAFAAAAA..BB.B..AAB.BB	9
JUNCUS ARTICULATUS	BB...	9
JUNCUS BERINGENSIS	J....	5
JUNCUS BIGLUMIS	B..B.....BBB.BB.B.BBB	5
JUNCUS BUFONIUS	B.....JB..B	5
JUNCUS CASTANEUS	.A.AA..A.....AA..BB.BBBAARBBB	9
JUNCUS DRUMMONDII	...A..A.....A...B....A....	9
JUNCUS EFFUSUS	B...	8
JUNCUS ENSIFOLIUS	...AA..AAD...A..A.....A.B...	9
JUNCUS FALCATUS	...AA..AD.....A.....B...	9
JUNCUS FAURIENSIS	J....	5
JUNCUS FILIFORMIS	B.B...BB...	9
JUNCUS LESCHENAUTII	B...B	5
JUNCUS MERTENSIANUS	.A.AA..BA...A.AAA...B....A.B...	9
JUNCUS OREGANUS	B.....B...	5
JUNCUS PROMINENS	J....	5
JUNCUS STYGIUS	JB...	5
JUNCUS TENUIS	R...	5
JUNCUS TRIGLUMIS	.A...A.AAE...H.....B....AJRBBB	5
JUNIPERUS COMMUNIS	BB.B.	0
KOBRESIA MYOSUROIDES	B.B.BBB	5
KOBRESIA SIBIRICA	B	5
KOBRESIA SIMPLICIUSCULA	BBB	9
KOELERIA GRACILIS	J....	5
KOENIGIA ISLANDICA	.A..AA...E...HAF...AAA..BBB..BAA.BBB	2
KYLLINGIA BREVIFOLIA	J....	5
LAGOTIS GLAUCA	.AAAAA.....AAAAAP.BBBBBBAA.BBB	0
LAPPULA DEFLEXA	J....	0
LAPPULA MYOSOTIS	JR...	0
LARIX DAURICA	J....	6
LATHYRUS MARITIMUS	.A.AAA..AA..KAA.AAAAAP.BB.BBBAABBBB	8
LATHYRUS PALUSTRIS	...A...AE...AA...A.A..B.....AABB...	8

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
LEDUM PALUSTRE	A...A.....AAA..B..BBBAABBB	6
LEMNA MINOR	J....	7
LEMNA TRISULCA	B....	7
LEPTARRHENA PYROLIFOLIA	.A.AA...AA..KHA.....AJB...	0
LEBQUERELLA ARCTICA	B....	0
LIGUSTICUM MUTELLINOIDES	BBBBB.BBB	0
LIGUSTICUM SCOTICUM	.A.AAA.AAA..KAFAAAAA..BBBB..AABBB.	0
LILIUM DAVURICUM	J....	8
LILIUM MEDEOLOIDES	J....	8
LIMOSELLA AQUATICA	AD...H.....J...B.....J..B.	0
LINNAEA BOREALIS	...AAAAAA...AAFAAAAA..B...BAABBB	0
LISTERA BOREALIS	B...	2
LISTERA CAURINA	B...	2
LISTERA CONVALLARIOIDES	A...GD.....A.A.....	2
LISTERA CORDATA	.A.AAAAAA...AAF.AAAA..B....AABB..	2
LLOYDIA SEROTINA	.A.AA...AE.....BB.BBBAA.BBB	0
LLOYDIA TRIFLORA	J....	0
LOBELIA SESSILIFOLIA	J....	0
LOISELEURIA PROCUMBENS	.A.AAAA.AA...AAFAAAAA.P.B..BBBAABBB	4
LOLIUM MULTIFLORUM	...B.....B..B.	9
LOMATOGONIUM CARINTHIACUM	J....	0
LOMATOGONIUM ROTATUM	J.BBC	0
LONICERA CHAMISSOI	J....	0
LONICERA COERULEA	A.....A....	4
LONICERA INVOLUCRATA	B...	4
LUETKEA PECTINATA	B.....A.B...	0
LUPINUS ARCTICUS	BB.	0
LUPINUS NODTKATENSIS	..AAAAAAA.KKAA.AAA....BBBB..B.B...	0
LUZULA ARCUATA	AA.AAA.AAE..KAA.A.AAA..BBB.BBAABBB	5
LUZULA CONFUSA	B...BBB	9
LUZULA MULTIFLORA	.A.AAAAAAAK.AAF.AAAA..BB....AABBB	5
LUZULA OLIGANTHA	J....	5
LUZULA PALLESCENS	J....	5
LUZULA PARVIFLORA	.A.AAAAAA.KKAFF.AAAA..BBBB..AABBB	9
LUZULA RUFESCENS	AA.....A.B.C	5
LUZULA SPICATA	A.....B.....A.R...	5
LUZULA TUNDRICOLA	B.BBBBBBBB...BBF.B....BBBBBBB..BBB	5
LUZULA WAHLENBERGII	A..AA.A.AA...AA...A....B..BBBAABBB	5
LYCOPODIUM ALPINUM	.AAAA.A.AD..KAFF..AAA..BB.BB.AABBB	1
LYCOPODIUM ANNOTINUM	.AAAAAAA...AAFAAAAA..BB..B.AABBB.	1
LYCOPODIUM CLAVATUM	.A.AA.A.AD.KKAFF..A.A..B....BABBB	1
LYCOPODIUM COMPLANATUM	B.BB.	1

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
LYCOPODIUM OBSCURUM	A.....A....	1
LYCOPODIUM SABINAEFOLIUM	...AA...AA...AAF...AAA.....AAB...	1
LYCOPODIUM SELAGO	..AAA.AAAA...AAFAAAAA..BBBBBBAABBB	1
LYCOPUS UNIFLORUS	B....	0
LYSICHITON AMERICANUM	B.....JB...	0
LYSIMACHIA THYRSIFLORA	A...B....AAR...	0
MAIANTHEMUM DILATATUM	A...HA.AAAAA.....AAB...	4
MALACHIUM AQUATICUM	J....	0
MALUS FUSCA	B...	4
MATTEUCCIA STRUTHIOPTERIS	B....	1
MAXALIS MONOPHYLLA	A.....A...B....AB...	2
MECODIUM WRIGHTII	B...	1
MELANDRIUM AFFINE	B.....B..BB	6
MELANDRIUM APETALUM	.A.AA.....A...BB..BB.A.BBB	6
MELANDRIUM BRACHYPETALUM	J....	0
MELANDRIUM MACROSPERMUM	BB.	0
MELICA NUTANS	J....	5
MELICA SUBULATA	A.....A.B...	5
MENTHA ARVENSIS	BBB.B	0
MENYANTHES TRIFOLIATA	A.....A..B....AABBB.	0
MENZIESIA FERRUGINEA	R...	0
MERTENSIA KAMZATICA	B....	6
MERTENSIA MARITIMA	.AA.A...AE..KA..A.AAA..BBBBBBAABBB	4
MERTENSIA PANICULATA	BB.	0
MERTENSIA RIVULARIS	J....	0
MILIMUM EFFUSUM	J....	7
MINULUS GUTTATUS	AAAAAAAAAD..KNAF..A...PBB...A.B...	0
MINUARTIA ARCTICA	.A..A.....BB...AA.B.B	0
MINUARTIA BIFLORA	A.....A..B	0
MINUARTIA MACROCARPA	.A.....AA..BBBB.BAA.BBB	0
MINUARTIA OBTUSILOBA	BB...BBB	0
MINUARTIA ROSSII	B.....BBB	0
MINUARTIA RUBELLA	.A.....A...B....A..BB	0
MINUARTIA STRICTA	B	0
MINUARTIA VERNA	J....	0
MINUARTIA YUKONESIS	B	0
MITELLA PENTANDRA	B.....B...	0
MOHRINGIA LATERIFLORA	A.AAAA...D...IA...AAA..B....AABBB	0
MONESES UNIFLORA	B.....BBB.BB	0
MONOTROPA HYPOPHYTIS	B...	0
MONTIA FONTANA	...AAAA.A...H.F..AAA.PBBB..BAABBB	0
MULGEDIUM SIBIRICUM	J....	3

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
MYOSOTIS ALPESTRIS	A.....B..B.BBB.BBB	0
MYRICA GALE	B.....BBBB..	4
MYRIOPHYLLUM SPICATUM	AAD...A...ALAA.....ARBB.	7
MYRIOPHYLLUM VERTICILLATUM	C....	7
NUPHAR POLYSEPALUM	.A..A.....A...B....A.BB..	7
NUPHAR PUMILUM	J....	0
NYMPHACEA TETRAGONA	B....	7
OENANTHE SARMENTOSA	B...	0
OPHIOGLOSSUM VULGATUM	A.....A....	1
OROBANCHE FASCICULATA	B....B....	0
OSMORHIZA CHILENSIS	...A.....B...	0
OSMORHIZA PURPUREA	B.....B...	0
OXALIS ACETOSELLA	J....	0
XYCOCCUS MICROCARPUS	A.....A.A..B..B..AABBBB	4
XYCOCCUS PALUSTRIS	BB...	0
XYCOCCUS QUADRIPETALUS	AA.....A....	4
XYGRAPHIS GLACIALIS	A.A.....AA..BB	0
XYRIA DIGYNA	AA.AA...AA...H.F..AAP.BB.BBBABBBB	6
XYTROPIS ARCTICA	B.	0
XYTROPIS BOREALIS	J..BB	0
XYTROPIS CAMPESTRIS	R.BB	0
XYTROPIS ERECTA	J....	0
XYTROPIS KAMTSCHATICA	J....	0
XYTROPIS LITORALIS	J....	0
XYTROPIS LONGIPES	J....	0
XYTROPIS MAYDELLIANA	BBB.BBB	0
XYTROPIS MERTENSIANA	BB	0
XYTROPIS NIGRESCENS	B..BBBB.BBB	0
XYTROPIS REVOLUTA	B....	0
XYTROPIS RUBICAUDEX	J....	0
XYTROPIS VISCIDA	B..B..	0
PAPAVER ALASKANUM	.A.AAAA.....HA.....BBB.BBA.....	8
PAPAVER ALBOROSEUM	C.....B....	8
PAPAVER LAPPONICUM	B	8
PAPAVER MACOUNII	B..BB...BB.	8
PAPAVER WALPOLEI	BB	8
PARNASSIA FIMBRIATA	R...	8
PARNASSIA KOTZEBUEI	.A.AAA..AD...AA...A...B..BBBA.RBBB	2
PARNASSIA PALUSTRIS	A.....AAA.....ARBBB	8
PARRYA NUDICAULIS	.A..A.....A.....BBBAA.BBB	6
PEDICULARIS ANGENA	B	8
PEDICULARIS CAPITATA	.A.AA.....B...BBAA.BBB	8

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
PEDICULARIS CHAMISSONIS	.A..AA.AAA..KAA.AAAAA.....AA....	8
PEDICULARIS ERIOPHORA	A.....A....	8
PEDICULARIS KANEI	.A..A.....P.BBBBBBAABBB	8
PEDICULARIS LABRADORICA	B....BB.BBB	8
PEDICULARIS LANGSDORFFII	.A.AA.....BB.BBBAA.BBB	8
PEDICULARIS LAPPONICA	J....	8
PEDICULARIS OEDERI	A.....BB.BBBAAABBB	8
PEDICULARIS ORNITHORHYNCHA	B...	8
PEDICULARIS PARVIFLORA	B.BA..BBB	8
PEDICULARIS RESUPINATA	J....	8
PEDICULARIS RUBINSKII	J....	8
PEDICULARIS SUDETICA	.A.AA.....AA..B.BBBAA.BBB	8
PEDICULARIS VERTICILLATA	.A.AAA.....A...BBBBBBAABBB	8
PEDICULARIS VILLOSA	B	8
PETASTIES FRIGIDUS	AA..GAO.KH....AA..B..BBBAA.BBB	3
PETASTIES HYPERBOREUS	BB.B..B.BBBB	3
PHALARIS ARUNDINACEA	BB...	0
PHIPPSIA ALGIDA	BB.BB...BBB	5
PHIPPSIA CONCINNA	B.....	9
PHLEUM COMMUTATUM	.A.AAA.AAA..KAAF.AAAA..BBBB..AAB...	5
PHLOX SIBIRICA	BBC	0
PHRAGMITES COMMUNIS	J....	5
PHYLLODOCE ALEUTICA	.A.AA.A.AE..K.AF..AAA..B....AAB...	0
PHYLLODOCE COERULEA	GAA.....B.A.BBB	0
PHYLLOSPADIX SCOULERI	B...	7
PHYSOCARPUS CAPTIATUS	B...	0
PICEA GLAUCA	B.	6
PICEA JEZOENSIS	J....	6
PICEA SITCHENSIS	D..H.....B....B.B...	6
PICRIS HIERACIODES	G.....A.A.....A....	3
PINGUICULA VILLOSA	A.....B....AABBB.	0
PINGUICULA VULGARIS	...AA.AAAA..AAFA.A..P.B....AAB.B.	4
PINUS CONTORTA	B...	6
PINUS PUMILA	J....	6
PLAGIOBOTHRYIS ORIENTALIS	A..A.....A..B....AA....	0
PLANTAGO CAMTSCHATICA	AA.....A....	0
PLANTAGO MACROCARPA	A.....GD...H.F..G...PB....AAB...	0
PLANTAGO MARITIMA	A..A...H.....B....A.BBBC	0
PLATANThERA CHORISIANNA	A...AE...HA..AA.....AB...	2
PLATANThERA CONVALLARIEFOLIA	AAAAAAAAAA.KKAFAAAAA..B....AA..B.	2
PLATANThERA DILATATA	.A.AAA..AD...A.F..A.AP.BB....AAB...	2
PLATANThERA DITMARIANA	J....	2

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
PLATANThERA HYPERBOREA	GD.....JR...	2
PLATANThERA OBTUSATA	B..B....BB.	2
PLATANThERA OLIGANTHA	A.....A...	2
PLATANThERA PARVULA	J....	2
PLATANThERA SACCATA	...A...G.....B...	2
PLATANThERA TIPULOIDES	A...H...A.A.....A...	2
PLATANThERA UNALACHENSIS	...A.....B...	2
PLEUROSPerMUM URALENSE	J....	0
POA ALPIGENA	AA.....AARBBB	5
POA ALPINA	AAGE...A....J.....JRBBB	5
POA ARCTICA	GD...H.F..AAA..BBBBBBAABBBB	9
POA BRACHYANTHERA	B.....B....	5
POA BRACTEOSA	J....	5
POA EMINENS	.A.AAA...E...H...AAAA..BB.BBBAABBBB	9
POA EYERDAMII	B.....	9
POA GLAUCA	B.....A.BBB	5
POA HISPIDULA	.A.AAAAAA...AA.AAA.A..B....A.R...	9
POA LANATA	.A..A.....H.....AAR.BB	9
POA LEPTOCOMA	D.....B.B...BB...	5
POA MACROCALYX	AA.AA...K...A.AAA.....AABB..	9
POA MALACANTHA	..AAAA.AAEA..AA..AAAA..B...BB.A..BB	9
POA MEMORALIS	A...A.....AAR...	5
POA OCCIDENTALIS	J....	5
POA PALUSTRIS	...A.....B....AAB.C.	9
POA PAUCISPICULA	B...BBB.R.BB	5
POA PSEUDOABBREVIATA	B.....B.....B	5
POA RADULA	J....	5
POA STENANTHA	.A.AA..AAA.....B....A.B...	5
POA TRIVIALIFORMIS	J....	5
POA TURNERI	...AA..AAA...AA...A.....	9
PODAGROSTIS AEGUIVALIS	...A.....B...	5
PODAGROSTIS THURBERIANA	...AA.....B...	5
POLEMONIUM ACUTIFLORUM	.AAAAA..A.....AA.PBBBBBBAARBBB	0
POLEMONIUM BOREALE	B.B..B...BB	0
POLEMONIUM HUMILE	A.....A....	0
POLEMONIUM PULCHERRIMUM	B.....B...B	0
POLYGONUM AMPHIBIUM	BRB..	0
POLYGONUM BISTORTA	B.BBBB.BBB	0
POLYGONUM CAURIANUM	A..BB.	0
POLYGONUM CONVULVULUS	J....	0
POLYGONUM FOWLERI	B.....B...	0
POLYGONUM PENNSYLVANICUM	B.....B.B...	0

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
POLYGONUM THUNBERGII	J....	0
POLYGONUM TRIPTEROCARPUM	B...B	0
POLYGONUM VIVIPARUM	.AAAAAAAAA..AAFAAAAAP.BBBBBBABB	0
POLYPODIUM VULGARE	.A..AA..AE..KH....A..P.B....AAB...	1
POLYSTICHUM ALEUTICUM	AE.....A.....A....	1
POLYSTICHUM BRAUNII	F..A.A.....AB...	1
POLYSTICHUM LONCHITIS	A....E.....AA.....AB...	1
POLYSTICHUM MUNITUM	B...	1
POPULUS BALSAMIFERA	B....B..BB.	3
POPULUS QUAEVOLENS	J....	3
POPULUS TREMULOIDES	B....	3
POTAMOGETON ALPINUS	.A..A.....A....B....AAB...	7
POTAMOGETON BERCHTOLDI	B....BBR...	7
POTAMOGETON EPIHYDRUS	A....B.....B...	7
POTAMOGETON FILIFORMIS	.A..A..GA.....A....BB....ARB	7
POTAMOGETON FRIESII	B....	7
POTAMOGETON GRAMINEUS	A..B....ABB...	7
POTAMOGETON MAACKIANUS	J....	7
POTAMOGETON NATANS	BB...	7
POTAMOGETON NODOSUS	J....	7
POTAMOGETON OBTUSIFOLIUS	J....	7
POTAMOGETON PANORMITANUS	J....	7
POTAMOGETON PECTINATUS	D.....BR...	7
POTAMOGETON PERFOLIATUS	.A..AA..A.....A..B....ARB...	7
POTAMOGETON PRAELONGUS	D.....A....B.....A..B.	7
POTAMOGETON SUBSIBIRICUS	B...	7
POTAMOGETON VAGINATUS	AE...H.....B.....RBB.	7
POTAMOGETON ZOSTERIFOLIUS	BR...	7
POTENTILLA BIFLORA	BB	0
POTENTILLA EGEDII	..A.A....E...A.F.A.AA..BBBBBBA	0
POTENTILLA ELEGANS	BB	0
POTENTILLA FRAGIFORMIS	B...B	0
POTENTILLA FRUTICOSA	J.BBB	0
POTENTILLA HOOKERIANA	B..B...B	0
POTENTILLA HYPARCTICA	A....A.FA...A..BBBBBA..BBB	0
POTENTILLA NIVEA	BR..B	0
POTENTILLA PALUSTRIS	AAA.A.....AAA..BBBBBBA	0
POTENTILLA PULCHELLA	A.....B	0
POTENTILLA STOLONIFERA	AA.....A....	0
POTENTILLA UNIFLORA	B.BBB.B.BBB	0
POTENTILLA VAHLIANA	N....BB.	0
POTENTILLA VILLOSA	.A.AAAAAA.KKAFAAAAAP.BBBBBBAJB	0

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
POTENTILLA VIRGULATA	B.	0
PRENANTHES ALATA	...AAA.....B...B.B...	3
PRIMULA BOREALIS	BBB...BBB	0
PRIMULA CUNEIFOLIA	.A.AAAAAA.KKAFAAAAAAP.B..B..AA.BBB	0
PRIMULA EGALIKSENSIS	...A.....A.RBBB	0
PRIMULA FARINOSA	J..B.	0
PRIMULA NIVALIS	J...	0
PRIMULA SIBIRICA	B.BBB	0
PRIMULA STRICTA	B.	0
PRIMULA TSCHUKTSCHORUM	.A..A..A.....A..P.BBBBBBAA.BBB	0
PRUNELLA VULGARIS	...AA.A.AD.....AAA.....AB...	0
PTERIDIUM AQUILINUM	BB...	1
PUCCINELLIA ANGUSTATA	B	5
PUCCINELLIA BOREALIS	BB.	5
PUCCINELLIA GENTICULATA	B..	5
PUCCINELLIA GLABRA	B.....	5
PUCCINELLIA GRANDIS	B...	5
PUCCINELLIA HAUPTIANA	B.B.B	5
PUCCINELLIA HULTENII	B.....B...	5
PUCCINELLIA KAMTSCHATICA	B.....BB...	5
PUCCINELLIA LANGEANA	AAA.E...A.FA.....BBBBB.A..BB	5
PUCCINELLIA NUTKAENSIS	...A.....B....A.B...	5
PUCCINELLIA PHYRGANODES	B.....RBBB	9
PUCCINELLIA PUMILA	B.....CB...	5
PULSATILLA PATENS	B....	3
PYROLA ASARIFOLIA	.A.AA...E...H...A.A..B....AARBBB	0
PYROLA CHLORANTHA	B....	0
PYROLA GRANDIFLORA	B...BBB	0
PYROLA MEDIA	AA.....A...	0
PYROLA MINOR	.A..AA..AEA..H.FA.AAAP.BB.BB.AARBBB	0
PYROLA SECUNDA	B.....BBB..	0
RANUNCULUS ACRIS	...A.....B.....JB...	0
RANUNCULUS AURICOMUS	A.....J...	0
RANUNCULUS BONGARDI	.A..A.....A..P.B....AJB...	0
RANUNCULUS CONFEROIDES	B.....B.R...	0
RANUNCULUS COOLEYAE	B...	0
RANUNCULUS CYMBALARIA	P....B..BBB.	0
RANUNCULUS ESCHSCHOLTZII	.A.AAAAAA....F..AAA..BBB...AAB..B	0
RANUNCULUS GELIDUS	A....	0
RANUNCULUS GLACIALIS	B...BB	0
RANUNCULUS GHELINI	B.BBB	0
RANUNCULUS GRANDIS	E....FA..AA.....	0

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
RANUNCULUS HYPERBOREUS	.A.....HAF...AAP.BBBBBBAA.BBB	0
RANUNCULUS LAPPONICUS	BB...BBB	0
RANUNCULUS MACOUNII	B.....	0
RANUNCULUS NIVALIS	B.BBB...BBB	0
RANUNCULUS OCCIDENTALIS	..AAAAAAOKKAAF..A.A.....B...	0
RANUNCULUS ORTHORHYNCHUS	B...	0
RANUNCULUS PACIFICUS	B...	0
RANUNCULUS PALLASII	BBBB.B.BBB	0
RANUNCULUS PEDATIFIDUS	BB	0
RANUNCULUS PYGMAEUS	BB.BB.B.BBB	0
RANUNCULUS REPTANS	.A..AA.AAD...AA...A...BBB...AABB..	0
RANUNCULUS SCCELERATUS	B.BB.	0
RANUNCULUS SUBSIMILIS	J....	0
RANUNCULUS SULPHUREUS	A...A.....AA...BBBBB.A..BB	0
RANUNCULUS TRICHOPHYLLUS	.A.AAA.AAD...A...A...BB...AAB...	7
RANUNCULUS TURNERI	BB....C	0
RHINANTHUS MINOR	.A.AA.AAAA...HAF...AAA..B....AJBB..	8
RHODODENDRON CAMTSCHATICUM	AAAAAAAAA...KHAF.AAAAP.B....AA..BB	6
RHODODENDRON CHRYSANTHUM	AA.....A...	6
RHODODENDRON LAPPONICUM	BB	6
RHYNCHOSPORA ALBA	JB...	9
RIBES BRACTEOSUM	B...	4
RIBES HUDSONIANUM	B..B..	4
RIBES LACUSTRE	B.B...	4
RIBES LATIFOLIUM	J....	4
RIBES LAXIFLORUM	B...	4
RIBES TRISTE	BRBBB	4
ROMANZOFFIA SITCHENSIS	B....B.B...	0
ROMANZOFFIA UNALASCHCENSIS	.A.AAA.....P.B....A....	0
RORIPPA HISPIDA	A.BB.	0
RORIPPA ISLANDICA	A.....A..B....A.BB..	0
ROSA ACICULARIS	J..B.	0
ROSA DAVURICA	J....	0
ROSA NUTKANA	A.....B.....B...	4
RUBUS ARCTICUS	.A.AA..AAA...AAF...AAP.BBB.BBAABBBB	4
RUBUS CHAMAEMORUS	.A.AA....E...AAFAAAAA..BBBBBBBAAABBB	4
RUBUS IDAEUS	B....	4
RUBUS PARVIFLORUS	B...	4
RUBUS PEDATUS	B....A.B...	4
RUBUS SPECTABILIS	.A.AA....E.....P.B....A.B...	4
RUMEX ARCTICUS	H.....A..B..BBBBAA.BBB	0
RUMEX FENESTRATUS	.A.AAA.AGE...A.F..A...B...N.A.B...	0

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
RUMEX GRAMINIFOLIUS	.A.....B....AA.BBB	0
RUMEX SIBIRICUS	B.B..	0
RUMEX TRANSTORIUS	A.....B....A.B...	0
RUPPIA SPIRALIS	A..A.....A..BB....AAB...	7
SAGINA CRASSICAULIS	...AA.A.AE...A.F.AA...B....AB...	0
SAGINA INTERMEDIA	.A.AAAAAA...HAF..A.A..BBBB.BA.BBBB	0
SAGINA LITORALIS	J....	0
SAGINA OCCIDENTALIS	A....E...H.....	0
SAGINA SAGINOIDES	...A....E.....B....AAB..B	0
SAGITTARIA NATANS	J....	7
SALIX ALAXENSIS	.A..A.....A..B....AARBBB	3
SALIX ARBUSCULOIDES	B..BB.	3
SALIX ARCTICA	.AAAAA.AA.KKAAF..AAA..BB.BBBAABBBB	3
SALIX ARCTOLITORALIS	B.	3
SALIX BARCLAYI	.A.AA....D.....AA..B....AJRB..	3
SALIX BOGANIDENSIS	R..B	3
SALIX CHAMISSONIS	B.B.BB.	3
SALIX COMMUTATA	B.....B.R...	3
SALIX CYCLOPHYLLA	.A.AAAA.AE.K.A..A.A....B.BBBA..BB.	3
SALIX DEPRESSA	B....BBB...	3
SALIX FUSCESCENS	AA..B..BBBAA.BBB	3
SALIX GLAUCA	B.....B.....B..B..BB.BBB	3
SALIX GMELINI	J....	3
SALIX HASTATA	B..BB	3
SALIX HULTENII	J....	3
SALIX KRYLOVII	B	3
SALIX LANTA	BBB	3
SALIX LONGIPETIOLATA	J....	3
SALIX MACROLEPIS	J....	3
SALIX MYRTILLIFOLIA	A....	3
SALIX NIPHOCLEADA	B.....B.	3
SALIX NUMMULARIA	B	3
SALIX OVALIFOLIA	G.....B.B..BBB	3
SALIX PARALLELINERVIS	J....	3
SALIX PENTANDRA	J....	3
SALIX PHLEBOPHYLLA	G.....B.B.BBB	3
SALIX POLARIS	D..A....A....BBBAA.BBB	3
SALIX PULCHRA	.A..A.....BBBBA.BBB	3
SALIX RECTICULATA	AA.AAAA.....AAA..BB.BBBAABBB	3
SALIX REPTANS	BB..B	3
SALIX ROTUNDIFOLIA	.A.AAAA.AA..KA....A..B..BBBA..BBB	3
SALIX SACHALINENSIS	J....	3

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
SALIX SCOULERIANA	B....B.B...	3
SALIX SITCHENSIS	B....B.B...	3
SALIX SPHENOPHYLLA	B..BB	3
SALIX STOLONIFERA	...AA.....B....A.B...	3
SALIX TSCHUKTSCHORUM	J...B	3
SAMBUCUS RACEMOSA	.A..A.....B....AAB...	4
SANGUISORBA MENZIESII	B.B...	0
SANGUISORBA OFFICINALIS	B..B.	0
SANGUISORBA STIPULATA	.A.AAA...E.....P.B...B.A.BB..	0
SANGUISORBA TENUIFOLIA	J....	0
SAUSSUREA AMERICANA	R...	3
SAUSSUREA ANGUSTIFOLIA	B..BBB	3
SAUSSUREA NUDA	A.....AA....B...A.BBB	3
SAUSSUREA RIEDERI	J....	0
SAUSSUREA TILESII	A.....B...B	3
SAUSSUREA VISCIDA	BB...BB	3
SAXIFRAGA ASCENDENS	B.	0
SAXIFRAGA ALEUTICA	AA....AFAAA.....	0
SAXIFRAGA BRACTEATA	.A.AAAAAAA.KAAAAAA..BBBBBBAAR.BB	0
SAXIFRAGA BRONCHIALIS	AA..A.....A.AAA..BB.BBBAA.BBB	0
SAXIFRAGA CAESPITOSA	.A.AAA.....B...BBA.R.BB	0
SAXIFRAGA CERNUA	B.B.J.BB.	0
SAXIFRAGA DAVURICA	B.B..BB	0
SAXIFRAGA ESCHSCHOLTZII	B...BB..BB	0
SAXIFRAGA EXILIS	B...BB.	0
SAXIFRAGA FERRUGINEA	B....A.B...	0
SAXIFRAGA FLAGELLARIS	B...BBB.BB.	0
SAXIFRAGA FOLIOLOSA	...A....E...H.....BBBBAA.BBB	0
SAXIFRAGA FUSCA	J....	0
SAXIFRAGA HIERACIFOLIA	BBBBBBB.BBB	0
SAXIFRAGA HIRCULUS	AA..A.....H....AA..BBB.BBAA.BBB	0
SAXIFRAGA LYALLII	B....A.B...	0
SAXIFRAGA MERKII	J....	0
SAXIFRAGA MERTENSIANA	B.....B...	0
SAXIFRAGA NIVALIS	...AA.....B..B.BAAR.BB	0
SAXIFRAGA NUDICAULIS	B...BBB	0
SAXIFRAGA OPPOSITIFOLIA	.A..A.....AA..BB..BBAAR.BB	0
SAXIFRAGA PUNCTATA	.A..AAAAE...AAF.AA.AP..B..BBAABBBB	0
SAXIFRAGA REFLEXA	BB.	0
SAXIFRAGA RIVULARIS	.A.....AE.....F..A....B...BBAAB.BB	0
SAXIFRAGA SERPHYLLIFOLIA	AA.AA.....AA..BBB.BBAA.BBB	0
SAXIFRAGA SPICATA	B...BB.	0

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
SAXIFRAGA TRICUSPIDATA	R...	0
SAXIFRAGA UNALASCHCENSIS	.A.AA..AA.....A...AA...BBBBBAA..BB	0
SCHEUCHZERIA PALUSTRIS	B...	0
SCHIZACHNE PURPURASCENS	B....	5
SCIRPUS JAPONICUS	J....	5
SCIRPUS MARGARITACEUS	J....	5
SCIRPUS MARITIMUS	J....	5
SCIRPUS MICROCARPUS	B.....BB...	9
SCIRPUS TABERNAEMONTANI	J....	5
SCIRPUS VALIDUS	BB...	9
SCUTELLARIA GALERICULATA	B....	0
SEDUM AIZOON	J....	0
SEDUM ROSEA	.A.....B...BBBBABBBB	2
SEDUM TELEPHIUM	J....	0
SEDUM VERTICILLATUM	J....	0
SELAGINELLA SELAGINOIDES	...A...AA...H.F..A...B.....AB.BC	1
SELAGINELLA SIBIRICA	...A.....BB	1
SENECIO ATROPURPUREUS	BB.B.BBB	0
SENECIO CANNABIFOLIUS	AAA.....A...	3
SENECIO CONGESTUS	B.BBB.BBB	3
SENECIO CONTENMINUS	B.	0
SENECIO FUSCATUS	B..B	0
SENECIO HYPERBOREALIS	C	3
SENECIO LUGENS	B....B..BB.	3
SENECIO MALAISEI	J....	0
SENECIO PSEUDO-ARNICA	.A.AAA..AA.KKAFAAAAAAP.BBBBBBAAABBB	3
SENECIO RESEDIFOLIUS	AA.....P.B..BBBAA.BBB	3
SENECIO TRIANGULARIS	B....B.B...	0
SENECIO YUKONESIS	B.....BB.	3
SIBBALIDA PROCUMBENS	.A.AA...AA...AAFAAAAA..BBB.B.AABBB	6
SILENE ACAULIS	.A.AA...AE.....AA..BBB..BACR.BB	6
SILENE LATIFOLIA	J....	0
SILENE REPENS	B....	0
SILENE STENOPHYLLA	B	0
SISYRINCHIUM LITORALE	A.....B....A.B...	0
SIUM SAUVE	B....	9
SMELOWSKIA CALYCINA	BBB	0
SOLIDAGO LEPIDA	.A...A.....B....A.B...	0
SOLIDAGO MULTIRADIATA	AAA.A.A.AE....A..AACA..B..B.BAABBBB	3
SORBARIA SORBIFOLIA	J....	0
SORBUS KAMTSCHATCENSIS	J....	0
SORBUS SAMBUCIFOLIA	AAAAA.....A...	4

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
SORBUS SCOPULINA	B.	4
SORBUS SITCHENSIS	B.....B.B...	4
SPARGANIUM ANGUSTIFOLIUM	...A.....A.....B.....ABBB.	7
SPARGANIUM HYPERBOREUM	.A..A...AD...A...AAAA..B.....AABBB.	7
SPARGANIUM MINIMUM	A.....AB...	6
SPARGANIUM MULTIPEDUNCULATUM	J.B..	7
SPERGULARIA CANADENSIS	B.....B...	0
SPIRAEA BEAUVERDIANA	B..B..BB.BBB	0
SPIRAEA DOUGLASII	B...	0
SPIRAEA MEDIA	J....	0
SPIRANTHES ROMANZOFFIANA	.A..A.....B.....A.B...	2
SPIRODELA POLYRHIZA	J....	0
STACHYS PALUSTRIS	B...	0
STACHYS RIEDERI	J....	0
STELLARIA CLAYCANTHA	.A..AAA.AA..KAAFAAAAA..BB.B..AABB..	0
STELLARIA CRASSIFOLIA	AP.BBB..B.ABBBB	0
STELLARIA CRISPA	...AA.....F..A...B.....A.B...	0
STELLARIA EDWARDSII	B.....BB.	0
STELLARIA FENZLII	J....	0
STELLARIA HUMIFUSA	...A.....F..A...BBBB.BAABBBB	0
STELLARIA LAETA	B...B.	0
STELLARIA LONGIFOLIA	BR...	0
STELLARIA LONGIPES	BBB	0
STELLARIA NONANTHA	B..B...B.	0
STELLARIA RADIAN	A.....A...	0
STELLARIA RUSCIFOLIA	.A.AA..AAE...H...A...BB...AA..B.	0
STELLARIA SITCHANA	.A.AA..AAE...H...A...B.....A.B.B.	0
STELLARIA UMBELLATA	B...	0
STREPTOPUS AMPLEXIFOLIUS	...AAAAAA...AAFAAAAA..BBB..AABB..	4
STREPTOPUS ROSEUS	B...	4
STREPTOPUS STREPTOPOIDES	B...	4
SUAEDA DEPRESSA	B...	0
SUBULARIA AQUATICA	A.....H...A...B.....AAR...	0
SWERTIA PERENNIS	...A.....A.....A.B...	0
SWERTIA TETRAPETALA	J....	0
TARAXACUM ALASKANUM	B.B..B.	3
TARAXACUM ALBESCENS	J....	3
TARAXACUM CERATOPHORUM	BB..BBBBBBB.	3
TARAXACUM DILUTUM	J....	3
TARAXACUM EVITTATUM	J....	3
TARAXACUM MULLENII	J....	3
TARAXACUM HYPARCTICUM	B.....B	3

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
TARAXACUM KAMTSCHATICUM	A.....BBBAA.BBB	3
TARAXACUM LACERUM	BB.	3
TARAXACUM LATERITIUM	B....BB	3
TARAXACUM LATISQUAMEUM	J....	3
TARAXACUM LEPTOCERAS	J....	3
TARAXACUM MALAISEI	J....	3
TARAXACUM OFFICINALE	D...H.....B....B.B...	3
TARAXACUM PERLATESCENS	J....	3
TARAXACUM PHYMATOCARPUM	BC	3
TARAXACUM PLATYCERAS	J....	3
TARAXACUM PSEUDOGLABRUM	J....	3
TARAXACUM RUBIGINANS	J....	3
TARAXACUM RUFUM	J....	3
TARAXACUM TRIGONOLOBUM	.A.AAAA.AE...AAFAAAAAP.B.....AA....	3
TELLIMA GRANDIFLORA	.A.....B.....A.B...	0
THALICTRUM ALPINUM	B....BBB.BBB	6
THALICTRUM AQUILEGIFOLIUM	J....	6
THALICTRUM MINUS	A.....AA.....A....	6
THALICTRUM SPARSIFLORUM	B.....AARB..	0
THELYPTERIS LIMBOSPERMA	A...AA...A...AA...B.....AB...	1
THELYPTERIS PHEGopteris	.A..AA..AA...AA...AA...BBB...AABBB.	1
THERMOPSIS FABACEA	J....	0
THLASPI ARVENSE	A....B.....AA..B.	0
THUJA PLICATA	B...	0
THYMUS SERPYLLUM	J....	0
TIARELLA TRIFOLIATA	B...	0
TIARELLA UNIFOLIATA	B...	0
TOFIELDIA COCCINEA	.A.AAAAAAA.A...AAAA..B....AABBBB	0
TOFIELDIA GLUTINOSA	B...	0
TOFIELDIA PUBILLA	AJ.BBB	0
TOLMIEA MENZIESII	B...	0
TRICHOPHORUM ALPINUM	B....	3
TRICHOPHORUM CAESPITOSUM	A...AE...HA..AAAA..B....AABBBB	3
TRICTIUM AESTIVUM	B.....	5
TRIENTALIS EUROPAEA	.A.AAAAAA.KKAFAAAAAAP.BBBBB.AABBBB	0
TRIGLOCHIN MARITIMUM	B.....B.B..B	0
TRIGLOCHIN PALUSTRIS	A.....A..B....AABBBB	0
TRILLIUM PALLASII	A.....A....	0
TRIPLEUROSPERMUM PHAEOCEPHALUM	B....BBB	0
TRisetum CERNUm	B...	5
TRisetum SIBIRICUM	B.BB.	9
TRisetum SPICATUM	.A.AAA.AAA...A..A.AAA..BB.BBBBAABBBB	5

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
TROLLIUS MEMBRANOSTYLIS	J....	0
TROLLIUS RIEDERIANUS	A...AA.....A....	0
TSUGA HETEROPHYLLA	B...	0
TSUGA MERTENSIANA	B...	0
TYPHA LATIFOLIA	B....	3
URTICA ANGUSTIFOLIA	J....	0
URTICA GRACILIS	B....B.R...	0
URTICA LYALLII	H.....B.....B...	0
URTICA PLATYPHYLLA	AA.....A....	0
URTICULARIA INTERMEDIA	BR...	0
UTRICULARIA MINOR	A.....B.....AAR..C	0
UTRICULARIA VULGARIS	B....BBB	0
VACCINIUM ALASKENSIS	B...	4
VACCINIUM CASEPITOSUM	B...	4
VACCINIUM OVALIFOLIUM	...AA...E.....AAA..B....AJB...	4
VACCINIUM PARVIFOLIUM	B...	4
VACCINIUM PRAESTANS	J....	4
VACCINIUM ULIGINOSUM	.A.AAAAAA...AALAAA.A..B....AABBB	4
VACCINIUM VITIS-IDAEA	.A..A.AAAA...AA.AAAAA.BBBBBBAABBB	4
VAHLODEA ATROPURPUREA	.A.AAA..AE...A....AAA..BBB...AB...	5
VALERIANA CAPITATA	AA..A.....BBBBBBAA.BBB	3
VALERIANA SITCHENSIS	B...	0
VERATRUM ALBUM	AAA.....A..BB	0
VERATRUM VIRIDE	B....A.B...	0
VERONICA AMERICANA	A...AD...A.F.AAAA.....AAB...	0
VERONICA GRANDIFLORA	AAE...AAFA.AAA.....A....	0
VERONICA SCUTELLATA	B....	0
VERONICA STELLERI	.A.AAAAAA...KAFA.AAAP.BB...AA....	0
VERONICA WORMSKJOLDII	.A..A...AD.....G....B....A.B.B.	0
VIBURNUM EDULE	B....B.BBB.	4
VICIA GIGANTEA	B...	0
VIOLA ADUNCA	B.....R...	0
VIOLA AVATSCHEWENSIS	J....	0
VIOLA BIFLORA	A...B..B.BAA.BB.	0
VIOLA CRASSA	J....	0
VIOLA CRASSICORNIS	J....	0
VIOLA EPIPSILA	AAA..BBBBBBAABBB	0
VIOLA GLABELLA	G.....B....B.B...	0
VIOLA HULTENII	J....	0
VIOLA KOMAROVII	J....	0
VIOLA LANGSDORFFI	.A.AAAAAA...AAFAAAAA..BBBBB.AABBB.	0
VIOLA SELKIRKII	A..P.....A....	0

Table A-1 (Continued)

Species Name ^a	Presence/Absence Code ^b	Dispersal Code ^c
WILHELMIA PHYODES	BB.J.BBB	0
WOODSIA ALPINA	B.BBB	1
WOODSIA GLABELLA	B.BBB	1
WOODSIA ILVENSIS	B.BBB	1
ZANICHELLIA PALUSTRIS	BB.B.	7
ZOSTERA MARINA	.A..A.....A..B.....AABBBB	7
ZYGADENUS ELEGANS	BB.	0

^aThe species in this table are organized alphabetically. Because this table was printed by the computer, underlining and the use of lower case were not available. In normal type, the name should be underlined and only the genus name is capitalized.

^bThe presence/absence code indicates the reported presence of the species on the islands and source areas. One letter has been used for the references of each reported presence. A period represents that the species has not been reported for that island or area. The order of areas from left to right is the Aleutian, Commander, Shumagin, Pribilof, and Northern Bering Sea Islands, and the six source areas. In specific, the order and position from left to right is as follows: Sanak (1), Unimak (2), Akun (2), Akutan (4), Unalaska (5), Umnak (6), Carlisle (7), Adak (8), Atka (9), Adak (10), Kavalga (11), Gareloi (12), Semisopochnoi (13), Amchitka (14), Kiska (15), Buldir (16), Alaid (17), Agattu (18), Attu (19), Copper (20), Bering (21), Big Konuiki (22), Peninsula (23), Kodiak (24), St. Paul (25), St. George (26), Nunivak (27), St. Matthew (28), St. Lawrence (29), Alaska Peninsula source area (30), Kamchatka Peninsula source area (31), Southeastern Coastal source area (32), Yukon Plain source area (33), Seward Peninsula source area (34), and Chukotka Peninsula source area (35). The letter used to represent the presence of a species indicates the source of the information. The reference codes are as follows: A = Hultén (1960), B = Hultén (1968), C = Hultén (1973), D = Hein (1976), E = Clebsch et al. (1975), F = Byrd (1976), G = York (1950), H = Amundsen (1977), I = Williams and Schulmeister (1977), J = Hultén (1928-1930), K = Day and Early (1977), L = Martin (1970), M = Rodstrom (1976), N = Klein (1959), O = Day (1978), P = Moe and Day (1977), Q = Williams (1977), R = Alaback (1975).

^cDispersal code: 0 = not assigned to other dispersal groups, 1 = spores, 2 = very small seeds, 3 = seeds with plumes, 4 = seeds in fleshy fruit, 5 = caespitose, graminoid plants without extensive rhizomes, 6 = seeds with wings, 7 = plants found in wet or aquatic habitats, 8 = seeds in capsule, 9 = graminoid plants with extensive rhizomes.

Table A-2. Numbers of species per island for the total flora and selected families.

Island Name	Number of Species ^a										
	1	2	3	4	5	6	7	8	9	10	11
Sanak	45	6	3	3	1	0	4	3	2	1	4
Unimak	214	22	14	4	11	8	15	12	8	11	16
Akun	46	1	0	2	2	1	1	2	2	2	3
Akutan	187	25	10	4	12	10	9	10	8	8	13
Unalaska	311	35	18	13	16	14	13	14	12	14	22
Umnak	148	22	8	4	6	9	4	6	4	6	12
Carlisle	90	8	5	3	6	5	2	2	6	3	7
Amlia	93	14	6	3	5	3	4	4	4	4	5
Atka	218	29	13	9	10	12	8	9	7	8	14
Adak	227	31	19	9	12	5	6	12	7	8	16
Kavalga	15	3	0	0	1	0	1	0	0	0	1
Gareloi	24	2	1	1	0	0	0	1	0	0	5
Semisopochnoi	59	4	1	1	2	2	2	3	3	2	7
Amchitka	196	27	14	6	11	6	6	9	5	8	13
Kiska	126	12	5	5	6	3	6	8	7	4	14
Buldir	114	9	7	3	8	4	5	9	5	4	10
Alaid	70	6	2	2	1	1	3	6	3	4	9
Agattu	92	8	5	4	3	3	3	6	5	3	12
Attu	247	24	14	10	11	12	10	10	10	10	19
Copper	196	20	9	3	9	8	9	11	13	9	21
Bering	239	20	16	8	10	6	7	14	17	9	24
Big Konuiji	67	0	0	4	3	6	2	7	3	6	10
Peninsula	6	0	0	0	0	0	0	0	0	0	1
Kodiak	423	42	38	9	21	18	18	19	13	12	29
St. Paul	190	27	17	1	14	10	9	9	1	9	11
St. George	121	19	11	0	8	6	8	8	1	3	7
Nunivak	147	10	8	2	8	7	8	9	7	8	14
St. Matthew	175	17	10	0	6	13	14	13	5	7	15
St. Lawrence	220	22	20	0	11	14	22	11	7	8	21

^aThe number of species from left to right is as follows:
 Total (1), Grasses (2), Sedges (3), Orchids (4), Pinks (5),
 Mustards (6), Saxifrages (7), Roses (8), Heaths (9), Figworts (10),
 Composites (11).

Table A-3. Species assigned to dispersal group 1, spores.^a

Species Name	Species Name
<u>Adiantum pedatum</u>	<u>Gymnocarpium robertianum</u>
<u>Asplenium virgide</u>	<u>Isoetes muricata</u>
<u>Athyrium distentifolium</u>	<u>Isoetes truncata</u>
<u>Athyrium filix-femina</u>	<u>Lycopodium alpinum</u>
<u>Blechnum spicant</u>	<u>Lycopodium annotinum</u>
<u>Botrychium boreale</u>	<u>Lycopodium clavatum</u>
<u>Botrychium lanceolatum</u>	<u>Lycopodium complanatum</u>
<u>Botrychium lunaria</u>	<u>Lycopodium obscurum</u>
<u>Botrychium multifidum</u>	<u>Lycopodium sabinaefolium</u>
<u>Botrychium virginiana</u>	<u>Lycopodium selago</u>
<u>Cryptogramma crista</u>	<u>Matteuccia struthiopteris</u>
<u>Cryptogramma Stelleri</u>	<u>Mecodium Wrightii</u>
<u>Cystopteris fragilis</u>	<u>Ophioglossum vulgatum</u>
<u>Cystopteris montana</u>	<u>Polypodium vulgare</u>
<u>Dryopteris dilatata</u>	<u>Polystichum aleuticum</u>
<u>Dryopteris fragrans</u>	<u>Polystichum Braunii</u>
<u>Equisetum arvense</u>	<u>Polystichum lonchitis</u>
<u>Equisetum fluviatile</u>	<u>Polystichum munitum</u>
<u>Equisetum hiemale</u>	<u>Pteridium aquilinum</u>
<u>Equisetum palustre</u>	<u>Selaginella selaginoides</u>
<u>Equisetum pratense</u>	<u>Selaginella sibirica</u>
<u>Equisetum scirpoides</u>	<u>Thelypteris limbosperma</u>
<u>Equisetum silvaticum</u>	<u>Thelypteris phegopteris</u>
<u>Equisetum variegatum</u>	<u>Woodsia alpina</u>
<u>Gymnocarpium dryopteris</u>	<u>Woodsia glabella</u>
	<u>Woodsia ilvensis</u>

^aDispersal information for the species was obtained from Hultén (1968) and personal observations.

Table A-4. Species assigned to dispersal group 2, very small seeds.

Species Name	Species Name
<u>Amerorchis rotundifolia</u>	<u>Goodyera oblongifolia</u>
<u>Calyso bulbosa</u>	<u>Goodyera repens</u>
<u>Coeloglossum viride</u>	<u>Gymnadenia camtschatica</u>
<u>Corallorrhiza maculata</u>	<u>Hammarbya paludosa</u>
<u>Corallorrhiza patens</u>	<u>Koenigia islandica</u>
<u>Corallorrhiza trifida</u>	<u>Listera borealis</u>
<u>Cypripedium guttatum</u>	<u>Listera caurina</u>
<u>Cypripedium macranthum</u>	<u>Listera convallarioides</u>
<u>Cypripedium passerinum</u>	<u>Listera cordata</u>
<u>Dactylorhiza aristata</u>	<u>Maxalis monophylla</u>
<u>Drosera anglica</u>	<u>Parnassia Kotzebuei</u>
<u>Drosera rotundifolia</u>	<u>Platanthera Chorisiana</u>
<u>Epipactis papillosa</u>	<u>Platanthera convallariifolia</u>
<u>Epipogon aphyllum</u>	<u>Platanthera dilatata</u>
<u>Gentiana aleutica^a</u>	<u>Platanthera Ditmariana</u>
<u>Gentiana algida^a</u>	<u>Platanthera hyperborea</u>
<u>Gentiana amarella^a</u>	<u>Platanthera obtusata</u>
<u>Gentiana auriculata^a</u>	<u>Platanthera oligantha</u>
<u>Gentiana Douglasiana^a</u>	<u>Platanthera parvula</u>
<u>Gentiana glauca^a</u>	<u>Platanthera saccata</u>
<u>Gentiana platypetala^a</u>	<u>Platanthera tipuloides</u>
<u>Gentiana propinqua^a</u>	<u>Platanthera unalachensis</u>
<u>Gentiana prostrata^a</u>	<u>Sedum rosea</u>
<u>Gentiana tenella^a</u>	<u>Spiranthes Romanzoffiana</u>

^aDispersal information for these species was obtained from Ridley (1930). Dispersal information for the other species was obtained from Hultén (1968) and personal observations.

Table A-5. Species assigned to dispersal group 3, seeds with plumes.^a

Species Name	Species Name
<u>Anaphalis margaritacea</u>	<u>Populus suaveolens</u>
<u>Antennaria dioica</u>	<u>Populus tremuloides</u>
<u>Antennaria pallida</u>	<u>Prenanthes alata</u>
<u>Apargidium boreale</u>	<u>Pulsatilla patens</u>
<u>Arnica alpina</u>	<u>Salix alaxensis</u>
<u>Arnica Chamissonis</u>	<u>Salix arbusculoides</u>
<u>Arnica latifolia</u>	<u>Salix arctica</u>
<u>Arnica Lessingii</u>	<u>Salix arctolitoralis</u>
<u>Arnica unalaschcensis</u>	<u>Salix Barclayi</u>
<u>Aster alpinus</u>	<u>Salix boganiensis</u>
<u>Aster sibiricus</u>	<u>Salix Chamissonis</u>
<u>Aster subspicatus</u>	<u>Salix commutata</u>
<u>Bellis perennis</u>	<u>Salix cyclophylla</u>
<u>Cacalia auriculata</u>	<u>Salix depressa</u>
<u>Circaea alpina</u>	<u>Salix fuscescens</u>
<u>Circium kamtschaticum</u>	<u>Salix glauca</u>
<u>Crepis chrysantha</u>	<u>Salix Gmelini</u>
<u>Crepis nana</u>	<u>Salix hastata</u>
<u>Dryas octopetala</u>	<u>Salix Hultenii</u>
<u>Epilobium anagallidifolium</u>	<u>Salix Krylovii</u>
<u>Epilobium angustifolium</u>	<u>Salix lanta</u>
<u>Epilobium davuricum</u>	<u>Salix longipetiolata</u>
<u>Epilobium glandulosum</u>	<u>Salix macrolepis</u>
<u>Epilobium Hornemannii</u>	<u>Salix myrtillofolia</u>
<u>Epilobium leptocarpum</u>	<u>Salix niphoclada</u>
<u>Erigeron acris</u>	<u>Salix Nummularia</u>
<u>Erigeron humilis</u>	<u>Salix ovalifolia</u>
<u>Erigeron peregrinus</u>	<u>Salix parallelinervis</u>
<u>Eriophorum angustifolium</u>	<u>Salix pentandra</u>
<u>Eriophorum brachyantherum</u>	<u>Salix phlebophylla</u>
<u>Eriophorum gracile</u>	<u>Salix polaris</u>
<u>Eriophorum russeolum</u>	<u>Salix pulchra</u>
<u>Eriophorum Scheuchzeri</u>	<u>Salix reticulata</u>
<u>Eriophorum vaginatum</u>	<u>Salix reptans</u>
<u>Geranium erianthum</u>	<u>Salix rotundifolia</u>
<u>Geum calthifolium</u>	<u>Salix sachalinensis</u>
<u>Geum glaciale</u>	<u>Salix Scouleriana</u>
<u>Hieracium gracile</u>	<u>Salix sitchensis</u>
<u>Hieracium triste</u>	<u>Salix sphenophylla</u>
<u>Hieracium umbellatum</u>	<u>Salix stolonifera</u>
<u>Mulgedium sibiricum</u>	<u>Salix tschuktschorum</u>
<u>Petasties frigidus</u>	<u>Saussurea americana</u>
<u>Petasties hyperboreus</u>	<u>Saussurea angustifolia</u>
<u>Picris hieracioides</u>	<u>Saussurea nuda</u>
<u>Populus balsamifera</u>	<u>Saussurea Tilesii</u>

Table A-5 (Continued)

Species Name	Species Name
<u>Saussurea viscida</u>	<u>Taraxacum lacerum</u>
<u>Senecio cannabifolius</u>	<u>Taraxacum lateritium</u>
<u>Senecio congestus</u>	<u>Taraxacum latisquameum</u>
<u>Senecio hyperborealis</u>	<u>Taraxacum leptoceras</u>
<u>Senecio lugens</u>	<u>Taraxacum Malaisei</u>
<u>Senecio pseudo-arnica</u>	<u>Taraxacum officinale</u>
<u>Senecio resedifolius</u>	<u>Taraxacum perlatescens</u>
<u>Senecio yukonesis</u>	<u>Taraxacum phymatocarpum</u>
<u>Solidago multiradiata</u>	<u>Taraxacum platyceras</u>
<u>Taraxacum alaskanum</u>	<u>Taraxacum pseudoglabrum</u>
<u>Taraxacum albescens</u>	<u>Taraxacum rubiginans</u>
<u>Taraxacum ceratophorum</u>	<u>Taraxacum rufum</u>
<u>Taraxacum dilutum</u>	<u>Taraxacum trigonolobum</u>
<u>Taraxacum evittatum</u>	<u>Trichophorum alpinum</u>
<u>Taraxacum Hultenii</u>	<u>Trichophorum caespitosum</u>
<u>Taraxacum hyparcticum</u>	<u>Typha latifolia</u>
<u>Taraxacum kamtschaticum</u>	<u>Valeriana capitata</u>

^aDispersal information for the species was obtained from Hultén (1968) and personal observations.

Table A-6. Species assigned to dispersal group 4, seeds in fleshy fruits.

Species Name	Species Name
<u>Adoxa moschatellina</u> ^a	<u>Ribes laxiflorum</u>
<u>Amelanchiera florida</u>	<u>Ribes triste</u>
<u>Arctostaphylos alpina</u>	<u>Rosa nutkana</u>
<u>Arctostaphylos rubra</u>	<u>Rubus arcticus</u>
<u>Arctostaphylos uva-ursi</u>	<u>Rubus chamaemorus</u>
<u>Cornus canadensis</u>	<u>Rubus idaeus</u>
<u>Cornus suecica</u>	<u>Rubus parviflorus</u>
<u>Echinopanax horridum</u>	<u>Rubus pedatus</u>
<u>Emeptrum nigrum</u>	<u>Rubus spectabilis</u>
<u>Fragaria chiloensis</u>	<u>Sambucus racemosa</u>
<u>Gaultheria Migueliana</u>	<u>Sorbus sambucifolia</u>
<u>Loiseleuria procumbens</u>	<u>Sorbus scopulina</u>
<u>Lonicera coerulea</u>	<u>Sorbus sitchensis</u>
<u>Lonicera involucrata</u>	<u>Streptopus amplexifolius</u>
<u>Maianthemum dilatatum</u>	<u>Streptopus roseus</u>
<u>Malus fusca</u>	<u>Streptopus streptopoides</u>
<u>Mertensia maritima</u>	<u>Vaccinium alaskensis</u>
<u>Myrica Galea</u> ^a	<u>Vaccinium casepitosum</u>
<u>Oxycoccus microcarpus</u>	<u>Vaccinium ovalifolium</u>
<u>Oxycoccus quadripetalus</u>	<u>Vaccinium parvifolium</u>
<u>Pinguicula vulgaris</u>	<u>Vaccinium praestans</u>
<u>Ribes bracteosum</u>	<u>Vaccinium uliginosum</u>
<u>Ribes hudsonianum</u>	<u>Vaccinium vitis-idaea</u>
<u>Ribes lacustre</u>	<u>Viburnum edule</u>
<u>Ribes latifolium</u>	

^aDispersal information for these species was obtained from Ridley (1930). Dispersal information for the other species was obtained from Hultén (1968) and personal observations.

Table A-7. Species assigned to dispersal group 5, caespitose, graminoid plants without extensive rhizomes.^a

Species Name	Species Name
<u>Agropyron boreale</u>	<u>Carex globularis</u>
<u>Agropyron mutabile</u>	<u>Carex Gmelini</u>
<u>Agropyron pauciflorum</u>	<u>Carex gracilis</u>
<u>Agropyron subsecundum</u>	<u>Carex hakkodensis</u>
<u>Agropyron Turczaninowii</u>	<u>Carex heleonastes</u>
<u>Agrostis alaskana</u>	<u>Carex Jacobi-Peteri</u>
<u>Agrostis borealis</u>	<u>Carex Kelloggii</u>
<u>Agrostis clavata</u>	<u>Carex kirganica</u>
<u>Agrostis exarata</u>	<u>Carex Krausei</u>
<u>Agrostis scabra</u>	<u>Carex Lachenalii</u>
<u>Avena planiculmis</u>	<u>Carex laeviculmis</u>
<u>Avena sativa</u>	<u>Carex lapponica</u>
<u>Avena striata</u>	<u>Carex leptalea</u>
<u>Beckmannia erucaeformis</u>	<u>Carex loliaceae</u>
<u>Bromus ciliatus</u>	<u>Carex longerostrata</u>
<u>Bromus commutatus</u>	<u>Carex Mackenziei</u>
<u>Bromus hordeaceus</u>	<u>Carex macloviana</u>
<u>Bromus marginatus</u>	<u>Carex magellanica</u>
<u>Bromus pacificus</u>	<u>Carex media</u>
<u>Bromus Richardsonii</u>	<u>Carex Mertensii</u>
<u>Bromus sitchensis</u>	<u>Carex Michauxiana</u>
<u>Bromus tectorum</u>	<u>Carex Middendorffii</u>
<u>Calamagrostis purpurascens</u>	<u>Carex misandra</u>
<u>Calamagrostis sachaliensis</u>	<u>Carex nardina</u>
<u>Carex amblyolepis</u>	<u>Carex Oederi</u>
<u>Carex amblyorhyncha</u>	<u>Carex pallida</u>
<u>Carex appendiculata</u>	<u>Carex pauciflora</u>
<u>Carex atrofusca</u>	<u>Carex pediformis</u>
<u>Carex Augustinowiczii</u>	<u>Carex phyllomenica</u>
<u>Carex bonanzensis</u>	<u>Carex ruesanensis</u>
<u>Carex brunnescens</u>	<u>Carex Schmidtii</u>
<u>Carex canescens</u>	<u>Carex scita</u>
<u>Carex capillaris</u>	<u>Carex stenantha</u>
<u>Carex capitata</u>	<u>Carex stylosa</u>
<u>Carex circinnata</u>	<u>Carex subspathacea</u>
<u>Carex disperma</u>	<u>Carex tenuiflora</u>
<u>Carex drymophila</u>	<u>Carex Tolmiei</u>
<u>Carex echinata</u>	<u>Carex traiziscana</u>
<u>Carex eleusinoides</u>	<u>Carex tuminensis</u>
<u>Carex Enanderi</u>	<u>Carex ursina</u>
<u>Carex flava</u>	<u>Carex verna</u>
<u>Carex glacialis</u>	<u>Carex Williamsii</u>
<u>Carex glareosa</u>	<u>Cinna latifolia</u>

Table A-7 (Continued)

Species Name	Species Name
<u>Colpodium fulvum</u>	<u>Luzula Wahlenbergii</u>
<u>Colpodium Wrightii</u>	<u>Melica nutans</u>
<u>Danthonia intermedia</u>	<u>Melica subulata</u>
<u>Deschampsia alpina</u>	<u>Phippsia algida</u>
<u>Deschampsia beringensis</u>	<u>Phleum commutatum</u>
<u>Deschampsia caespitosa</u>	<u>Phragmites communis</u>
<u>Deschampsia pumila</u>	<u>Poa alpigena</u>
<u>Eleocharis acicularis</u>	<u>Poa alpina</u>
<u>Festuca altaica</u>	<u>Poa brachyanthera</u>
<u>Festuca brachyphylla</u>	<u>Poa bracteosa</u>
<u>Festuca ovina</u>	<u>Poa glauca</u>
<u>Festuca subulata</u>	<u>Poa leptocoma</u>
<u>Fimbristylis annua</u>	<u>Poa nemoralis</u>
<u>Glyceria lithuanica</u>	<u>Poa occidentalis</u>
<u>Glyceria maxima</u>	<u>Poa paucispicula</u>
<u>Glyceria natans</u>	<u>Poa pseudoabbreviata</u>
<u>Hierochloa alpina</u>	<u>Poa radula</u>
<u>Hordeum brachyantherum</u>	<u>Poa stenantha</u>
<u>Hordeum jubatum</u>	<u>Poa trivialiformis</u>
<u>Hordeum vulgare</u>	<u>Podagrostis aequivalis</u>
<u>Juncus beringensis</u>	<u>Podagrostis Thurberiana</u>
<u>Juncus biglumis</u>	<u>Puccinellia angustata</u>
<u>Juncus bufonius</u>	<u>Puccinellia borealis</u>
<u>Juncus Fauriensi</u>	<u>Puccinellia geniculata</u>
<u>Juncus Leschenaultii</u>	<u>Puccinellia glabra</u>
<u>Juncus oreganus</u>	<u>Puccinellia grandis</u>
<u>Juncus prominens</u>	<u>Puccinellia Hauptiana</u>
<u>Juncus stygius</u>	<u>Puccinellia Hulténii</u>
<u>Juncus tenuis</u>	<u>Puccinellia kamschatkica</u>
<u>Juncus triglumis</u>	<u>Puccinellia Langeana</u>
<u>Kobresia myosuroides</u>	<u>Puccinellia nutkaensis</u>
<u>Kobresia sibirica</u>	<u>Puccinellia pumila</u>
<u>Koeleria gracilis</u>	<u>Schizachne purpurascens</u>
<u>Kyllingia brevifolia</u>	<u>Scirpus japonicus</u>
<u>Luzula arcuata</u>	<u>Scirpus margaritaceus</u>
<u>Luzula multiflora</u>	<u>Scirpus maritimus</u>
<u>Luzula oligantha</u>	<u>Scirpus Tabernaemontani</u>
<u>Luzula pallescens</u>	<u>Trisetum aestivum</u>
<u>Luzula rufescens</u>	<u>Trisetum cernuum</u>
<u>Luzula spicata</u>	<u>Trisetum spicatum</u>
<u>Luzula tundricola</u>	<u>Vahlodea atropurpurea</u>

^aDispersal information for the species was obtained from Hultén (1968) and personal observations.

Table A-8. Species assigned to dispersal group 6, seeds with wings.

Species Name	Species Name
<u>Abies gracilis</u>	<u>Parrya nudicaulis</u>
<u>Acer glabrum</u>	<u>Picea glauca</u>
<u>Betula Ermani</u>	<u>Picea jezoensis</u>
<u>Betula kenaica</u>	<u>Picea sitchensis</u>
<u>Betula nana</u>	<u>Pinus contorta</u>
<u>Betula oregona</u>	<u>Pinus pumila</u>
<u>Betula papyrifera</u>	<u>Rhododendron camtschaticum</u>
<u>Betula platyphylla</u>	<u>Rhododendron chrysanthum^a</u>
<u>Bupleurum triradiatum</u>	<u>Rhododendron lapponicum^a</u>
<u>Callitriche hermaphrodita</u>	<u>Sibbaldia procumbens^a</u>
<u>Larix dahurica</u>	<u>Silene acaulis^a</u>
<u>Ledum palustre^a</u>	<u>Sparganium minimum</u>
<u>Melandrium affine</u>	<u>Thalictrum alpinum^a</u>
<u>Melandrium apetalum</u>	<u>Thalictrum aquilegifolium^a</u>
<u>Mertensia kamczatica</u>	<u>Thalictrum minus^a</u>
<u>Oxyria digyna</u>	

^aDispersal information for these species was obtained from Ridley (1930). Dispersal information for the other species was obtained from Hultén (1968) and personal observations.

Table A-9. Species assigned to dispersal group 7, plants found in wet or aquatic habitats.

Species Name	Species Name
<u>Calla palustris</u>	<u>Potamogeton Maackianus</u>
<u>Caltha leptosepala</u>	<u>Potamogeton natans</u>
<u>Caltha natans</u>	<u>Potamogeton nodosus</u>
<u>Caltha palustris</u> ^a	<u>Potamogeton obtusifolius</u>
<u>Hippuris tetraphylla</u>	<u>Potamogeton panormitanus</u>
<u>Hippuris vulgaris</u>	<u>Potamogeton pectinatus</u>
<u>Lemna minor</u>	<u>Potamogeton perfoliatus</u>
<u>Lemna trisulca</u>	<u>Potamogeton praelongus</u>
<u>Milium effusum</u>	<u>Potamogeton subsibiricus</u>
<u>Myriophyllum spicatum</u>	<u>Potamogeton vaginatus</u>
<u>Myriophyllum verticillatum</u>	<u>Potamogeton zosterifolius</u>
<u>Nuphar polysepalum</u>	<u>Ranunculus trichophyllus</u>
<u>Nymphacea tetragona</u>	<u>Ruppia spiralis</u>
<u>Phyllospadix Scouleri</u>	<u>Sagittaria natans</u>
<u>Potamogeton alpinus</u>	<u>Sparganium angustifolium</u>
<u>Potamogeton Berchtoldi</u>	<u>Sparganium hyperboreum</u>
<u>Potamogeton epihydrus</u>	<u>Sparganium multipedunculatum</u>
<u>Potamogeton filiformis</u>	<u>Zanichellia palustris</u>
<u>Potamogeton Friesii</u>	<u>Zostera marina</u>
<u>Potamogeton gramineus</u>	

^aDispersal information for this species was obtained from Ridley (1930). Dispersal information for the other species was obtained from Hultén (1968) and personal observations.

Table A-10. Species assigned to dispersal group 8, seeds in capsules.

Species Name	Species Name
<u>Arabis hirsuta</u>	<u>Papaver Macounii</u>
<u>Cardamine angulata</u>	<u>Papaver Walpolei</u>
<u>Cardamine bellidifolia</u>	<u>Parnassia fimbriata</u>
<u>Cardamine hyperborea</u>	<u>Parnassia palustris</u>
<u>Cardamine microphylla</u>	<u>Pedicularis anoena</u>
<u>Cardamine pennsylvanica</u>	<u>Pedicularis capitata</u>
<u>Cardamine pratensis</u>	<u>Pedicularis Chamissonis</u>
<u>Cardamine purpurea</u>	<u>Pedicularis eriophora</u>
<u>Cardamine Regelliana</u>	<u>Pedicularis Kanei</u>
<u>Cardamine tenuifolia</u>	<u>Pedicularis Labradorica</u>
<u>Cardamine umbellata</u>	<u>Pedicularis Langsdorffii</u>
<u>Claytonia Chamissoi</u>	<u>Pedicularis lapponica</u>
<u>Fritillaria camschatcensis</u>	<u>Pedicularis Dederi</u>
<u>Impatiens noli-tangere</u>	<u>Pedicularis ornithorhyncha</u>
<u>Iris setosa</u>	<u>Pedicularis parviflora</u>
<u>Lathyrus maritimus</u>	<u>Pedicularis resupinata</u>
<u>Lathyrus palustris</u>	<u>Pedicularis Rubinskii</u>
<u>Lilium davuricum^a</u>	<u>Pedicularis sudetica</u>
<u>Lilium medeoloides^a</u>	<u>Pedicularis verticillata</u>
<u>Papaver alaskanum</u>	<u>Pedicularis villosa</u>
<u>Papaver alboroseum</u>	<u>Rhinanthus minor</u>
<u>Papaver lapponicum</u>	

^aDispersal information for these species was obtained from Ridley (1930). Dispersal information for the other species was obtained from Hultén (1968) and personal observations.

Table A-11. Species assigned to dispersal group 9, graminoid plants with extensive rhizomes.^a

Species Name	Species Name
<u>Agropyron macrourum</u>	<u>Carex pyrenaica</u>
<u>Agrostis stolonifera</u>	<u>Carex Ramenskii</u>
<u>Agrostis Trinnii</u>	<u>Carex rariflora</u>
<u>Alopecurus aequalis</u>	<u>Carex rhynchophysa</u>
<u>Alopecurus alpinus</u>	<u>Carex rostrata</u>
<u>Arctagrostis latifolia</u>	<u>Carex rotundata</u>
<u>Arctophila fulva</u>	<u>Carex rupestris</u>
<u>Bromus inermis</u>	<u>Carex saxatilis</u>
<u>Bromus Pumpellianus</u>	<u>Carex scirpoidea</u>
<u>Calamagrostis canadensis</u>	<u>Carex sitchensis</u>
<u>Calamagrostis deschampsoides</u>	<u>Carex spectabilis</u>
<u>Calamagrostis Holmii</u>	<u>Carex vaginata</u>
<u>Calamagrostis inexpansa</u>	<u>Catabrosa aquatica</u>
<u>Calamagrostis Lapponica</u>	<u>Cnidium cnidifolium</u>
<u>Calamagrostis neglecta</u>	<u>Dupontia Fischeri</u>
<u>Calamagrostis nutkaensis</u>	<u>Eleocharis kamtschatica</u>
<u>Carex anthoxanthea</u>	<u>Eleocharis nitida</u>
<u>Carex aquatilis</u>	<u>Eleocharis palustris</u>
<u>Carex bicolor</u>	<u>Eleocharis quinqueflora</u>
<u>Carex Bigelowii</u>	<u>Eleocharis uniglumis</u>
<u>Carex Buxbaumii</u>	<u>Elymus arenarius</u>
<u>Carex chordorrhiza</u>	<u>Elymus glaucus</u>
<u>Carex diandra</u>	<u>Elymus hirsutus</u>
<u>Carex dioica</u>	<u>Elymus interior</u>
<u>Carex Garberi</u>	<u>Elymus sibiricus</u>
<u>Carex holostoma</u>	<u>Festuca rubra</u>
<u>Carex lasiocarpa</u>	<u>Glehnia littoralis</u>
<u>Carex laxa</u>	<u>Glyceria pauciflora</u>
<u>Carex limosa</u>	<u>Hierochloa odorata</u>
<u>Carex livida</u>	<u>Hierochloa pauciflora</u>
<u>Carex lugens</u>	<u>Juncus alpinus</u>
<u>Carex Lyngbyaei</u>	<u>Juncus arcticus</u>
<u>Carex macrocephala</u>	<u>Juncus articulatus</u>
<u>Carex macrochaeta</u>	<u>Juncus castaneus</u>
<u>Carex maritima</u>	<u>Juncus Drummondii</u>
<u>Carex melanocarpa</u>	<u>Juncus effusus</u>
<u>Carex membranacea</u>	<u>Juncus ensifolius</u>
<u>Carex microglochin</u>	<u>Juncus falcatus</u>
<u>Carex nesophila</u>	<u>Juncus filiformis</u>
<u>Carex nigricans</u>	<u>Juncus Mertensianus</u>
<u>Carex petricosa</u>	<u>Kobresia simpliciuscula</u>
<u>Carex pluriflora</u>	<u>Lolium multiflorum</u>
<u>Carex podocarpa</u>	<u>Luzula confusa</u>

Table A-11 (Continued)

Species Name	Species Name
<u>Luzula parviflora</u>	<u>Poa palustris</u>
<u>Phippsia concinna</u>	<u>Poa Turneri</u>
<u>Poa arctica</u>	<u>Puccinellia phryganodes</u>
<u>Poa eminens</u>	<u>Rhynchospora alba</u>
<u>Poa Eyerdamii</u>	<u>Scirpus microcarpus</u>
<u>Poa hispidula</u>	<u>Scirpus validus</u>
<u>Poa lanata</u>	<u>Sium saue</u>
<u>Poa macrocalyx</u>	<u>Trisetum sibiricum</u>
<u>Poa malacantha</u>	

^aDispersal information for the species was obtained from Hultén (1968) and personal observations.

Table A-12. Numbers of species in the dispersal groups.

Island Name	Number of Species Per Dispersal Group ^a								
	1	2	3	4	5	6	7	8	9
Sanak	0	3	11	0	8	2	0	1	4
Unimak	12	10	26	12	19	6	9	14	22
Akun	7	3	5	2	1	1	0	1	1
Akutan	8	7	21	12	20	5	4	12	22
Unalaska	25	20	35	19	33	8	10	18	29
Umnak	6	7	18	6	20	2	3	9	16
Carlisle	7	3	11	6	9	1	0	4	9
Amlia	5	3	6	6	12	1	5	4	15
Atka	17	11	24	10	25	5	8	10	27
Adak	22	15	29	14	29	5	9	8	28
Kavalga	0	0	1	0	1	0	0	0	3
Gareloi	2	1	5	0	1	0	0	0	4
Semisopochnoi	8	1	9	3	2	1	1	4	6
Amchitka	16	10	21	12	23	5	6	9	23
Kiska	11	8	16	11	10	2	1	7	13
Buldir	10	6	10	8	10	3	0	3	10
Alaid	3	2	10	11	4	1	0	4	7
Agattu	5	5	13	9	4	2	3	4	13
Attu	24	16	25	14	19	5	10	13	26
Copper	10	6	26	14	15	10	4	10	18
Bering	18	12	31	16	20	11	9	10	19
Big Konuiji	1	6	9	6	0	2	0	6	0
Peninsula	0	0	0	0	0	0	0	0	0
Kodiak	23	18	49	23	55	11	17	17	38
St. Paul	12	5	14	7	21	4	4	13	30
St. George	7	3	6	6	16	2	3	7	19
Nunivak	5	6	23	8	9	4	3	12	13
St. Matthew	6	4	21	8	14	6	3	12	16
St. Lawrence	3	6	28	8	18	7	3	16	28

^aDispersal groups: 1 = spores, 2 = very small seeds, 3 = seeds with plumes, 4 = seeds in fleshy fruits, 5 = caespitose, graminoid plants without extensive rhizomes, 6 = seeds with wings, 7 = plants found in wet or aquatic habitats, 8 = seeds in capsules, 9 = graminoid plants with extensive rhizomes.

Table A-13. Numbers of species per island that are related to source areas.

Island Name	SPAPA	SPKA	SPSC	SPYU	SPSE	SPCH	RSAP	RSKA	RSSC	RSSE	RSCH	ALSSP
Sanak	43	40	30	28	26	29	0	1	0	0	0	10
Unimak	200	172	156	129	139	133	2	1	3	0	1	66
Akun	41	35	35	27	32	26	0	0	3	0	0	16
Akutan	157	142	144	99	113	99	2	3	8	0	0	56
Unalaska	253	236	233	162	176	159	3	10	13	0	0	82
Umnak	129	114	117	83	85	78	2	3	6	0	0	44
Carlisle	78	73	75	52	53	49	1	2	2	0	0	31
Amlia	79	74	74	49	54	48	0	2	1	0	0	29
Atka	170	171	164	114	125	112	1	9	7	0	2	60
Adak	173	182	175	117	126	113	0	9	8	0	0	62
Kavalga	12	13	13	11	12	12	0	0	1	0	0	8
Gareloi	20	20	19	18	19	15	0	1	1	0	0	11
Semisopochnoi	53	51	51	33	35	30	0	1	3	0	0	19
Amchitka	159	157	149	111	114	99	1	8	5	0	1	58
Kiska	101	102	94	67	70	65	1	9	2	0	3	40
Buldir	92	93	91	61	63	58	0	4	5	0	0	33
Alaid	62	60	51	41	42	32	0	5	0	0	0	23
Agattu	77	80	74	53	53	48	0	5	1	0	0	34
Attu	186	208	182	120	134	119	1	18	9	0	1	70
Copper	145	186	122	117	121	117	0	23	0	0	1	63
Bering	168	229	150	135	139	134	0	37	1	0	0	78
Big Konuiji	60	57	48	40	42	40	1	2	3	0	0	22
Peninsula	6	4	6	3	3	3	0	0	0	0	0	3
Kodiak	333	286	317	209	227	202	7	3	28	2	0	94
St. Paul	152	160	118	138	152	145	2	1	1	0	2	61
St. George	98	105	75	91	96	94	1	1	1	0	0	40
Nunivak	126	125	77	133	141	132	0	0	0	0	0	60
St. Matthew	130	143	85	140	160	154	1	3	2	0	1	61
St. Lawrence	145	173	85	172	206	201	2	1	0	1	4	66

Table A-13 (Continued)

aVariable abbreviations:

SPAP = Number of species in common with the Alaska Peninsula source area
 SPKA = Number of species in common with the Kamchatka Peninsula source area
 SPSC = Number of species in common with the Southeastern Coastal source area
 SPYU = Number of species in common with the Yukon Plain source area
 SPSE = Number of species in common with the Seward Peninsula source area
 SPCH = Number of species in common with the Chukotka Peninsula source area
 RSAP = Number of species restricted to the Alaska Peninsula source area
 RSKA = Number of species restricted to the Kamchatka Peninsula source area
 RSSC = Number of species restricted to the Southeastern Coastal source area
 RSSE = Number of species restricted to the Seward Peninsula source area
 RSCH = Number of species restricted to the Chukotka Peninsula source area
 ALSSP = Number of species reported from all six source areas.

Table A-14. Geographic characteristics of islands: area, maximum elevation, topographic diversity, and measurements of shape.

Island Name	AREA ^a	AOI	ELIS	TOMN	TOVA	TODI	RAM	RAV	RADM	RADV
Sanak	13990	13800	530	1.12	0.15	0.38	24.5	135.8	5.38	56.5
Unimak	404000	310200	2856	1.29	1.99	1.53	131.3	3627.0	17.55	428.5
Akun	17770	15280	818	1.88	1.25	1.44	29.1	169.5	6.00	68.8
Akutan	38560	29500	1294	2.48	1.45	1.58	41.4	153.7	6.22	42.8
Unalaska	275600	176500	2036	3.18	2.15	1.78	107.2	5660.0	29.61	1823.0
Umnak	174800	86300	2109	1.75	2.11	1.66	83.5	3806.0	23.38	1003.0
Carlisle	4337	2330	1609	3.86	3.38	1.91	16.0	3.7	1.16	1.2
Amlia	45580	38640	615	2.31	1.23	1.49	40.0	1270.0	14.38	467.7
Atka	106000	55990	1479	2.45	1.96	1.71	57.1	3270.0	21.50	944.0
Adak	73220	63690	1181	1.78	1.47	1.57	58.3	905.0	13.22	212.7
Kavalga	1464	1464	96	0.35	0.23	0.37	7.6	24.0	1.83	7.4
Gareloi	6865	3162	1572	4.01	2.69	1.87	18.5	5.0	1.27	1.6
Semisopchnoi	22670	16670	1221	2.84	2.97	1.83	33.9	18.6	3.00	7.3
Amchitka	29550	29550	365	0.66	0.70	1.08	28.3	1389.0	13.94	716.2
Kiska	28160	23200	1220	2.11	1.78	1.64	32.3	574.7	9.83	250.4
Buldir	1990	176	614	3.51	1.72	1.46	9.7	5.7	1.11	1.5
Alaid	594	594	202	1.08	1.17	1.20	4.8	7.8	1.22	1.4
Agattu	22470	21520	634	1.41	1.95	1.35	30.3	270.2	6.00	66.6
Attu	90570	61770	868	3.45	3.14	1.74	65.2	577.4	15.44	212.4
Copper	27220	NAb	494	NA	NA	NA	NA	NA	NA	NA
Bering	172000	NA	671	NA	NA	NA	NA	NA	NA	NA
Big Konuiji	9123	8486	572	3.26	1.42	1.54	18.5	161.5	6.72	68.8
Peninsula	156	156	304	3.66	0.33	0.57	3.3	0.8	0.33	0.3
Kodiak	897400	312700	1360	2.78	2.51	1.85	212.6	5844.0	42.61	1088.0
St. Paul	17800	17800	203	1.39	0.24	0.67	21.5	103.5	4.50	30.1
St. George	8900	8900	308	1.07	0.60	0.74	18.0	138.0	3.72	20.3
Nunivak	359000	359000	253	0.57	0.37	0.85	143.2	1355.0	16.94	328.8
St. Matthew	28700	2650	459	1.19	1.10	1.37	30.8	859.5	10.77	376.0
St. Lawrence	456800	435100	631	0.23	0.45	0.57	136.6	7429.0	31.61	2749.0

Table A-14 (Continued)

^aAbbreviations and units for measurements:

AREA = Area of island (hectares)
 A01 = Area between 0 and 1000 ft. elevation (hectares)
 ELIS = Maximum elevation (meters)
 TOMN = Mean of topographic contour lines (# contour lines/sample square)
 TOVA = Variance of topographic contour lines (# contour lines/sample square)
 TODI = Topographic diversity (# contour lines/sample square)
 RAM = Mean of the radii (0.25 kilometers)
 RAV = Variance of the radii (0.25 kilometers)
 RADM = Mean of the radial deviations (0.25 kilometers)
 RADV = Variance of the radial deviations (0.25 kilometers).

^bTopographic maps with 200 ft. contour lines and 1:250,000 scale were not available for the Commander Islands.

Table A-15. Relative radial measurements and other measures of island shape and geology.

Island Name	RRAM ^a	RRAV	RRADM	RRADV	NBAY	STRKM	PNSA	VA	NRA	CDTP	LAT
Sanak	0.424	0.040	0.093	0.017	3	50	40	0	1	1	54.5
Unimak	0.597	0.075	0.080	0.009	4	551	9	1	2	3	54.8
Akun	0.714	0.046	0.107	0.013	6	15	43	1	2	2	54.3
Akutan	0.709	0.043	0.107	0.011	3	46	28	1	1	2	54.2
Unalaska	0.420	0.087	0.116	0.028	50	403	22	1	2	2	53.8
Umnak	0.345	0.065	0.097	0.017	10	1845	15	1	3	2	53.3
Carlisle	0.941	0.013	0.069	0.004	0	1	45	1	1	2	53.0
Amlia	0.308	0.075	0.111	0.028	20	130	36	0	1	1	52.2
Atka	0.429	0.185	0.162	0.053	21	321	28	1	2	3	52.3
Adak	0.584	0.091	0.132	0.021	15	211	32	0	3	3	51.8
Kavalga	0.401	0.067	0.096	0.020	0	0	73	0	2	1	51.5
Gareloi	0.842	0.010	0.058	0.003	0	17	48	1	1	2	51.7
Semisopochnoi	0.917	0.014	0.081	0.005	0	54	23	1	1	2	51.8
Amchitka	0.218	0.082	0.107	0.042	5	187	48	0	2	1	51.3
Kiska	0.421	0.097	0.128	0.042	5	100	34	1	2	3	52.2
Buldir	0.886	0.047	0.101	0.013	0	11	69	0	1	2	52.7
Alaid	0.405	0.054	0.102	0.010	0	4	100	0	1	1	52.7
Agattu	0.552	0.089	0.109	0.022	2	100	33	0	2	3	52.5
Attu	0.502	0.034	0.119	0.013	10	170	23	0	3	2	52.8
Copper	NAb	NA	NA	NA	5	NA	NA	NA	NA	NA	54.6
Bering	NA	NA	NA	NA	7	NA	NA	NA	NA	NA	55.0
Big Konuiji	0.440	0.092	0.160	0.039	6	4	82	NA	NA	NA	55.2
Peninsula	0.560	0.022	0.056	0.010	0	0	100	NA	NA	NA	55.1
Kodiak	0.746	0.072	0.150	0.013	43	2840	16	NA	NA	NA	57.5
St. Paul	0.899	0.180	0.188	0.052	1	0	48	NA	NA	NA	57.2
St. George	0.514	0.113	0.106	0.017	2	2	48	NA	NA	NA	56.5
Nunivak	0.672	0.030	0.080	0.007	14	1376	9	NA	NA	NA	60.2
St. Matthew	0.514	0.239	0.180	0.104	1	184	40	NA	NA	NA	60.5
St. Lawrence	0.427	0.073	0.099	0.027	3	1492	10	NA	NA	NA	63.5

Table A-15 (Continued)

^aAbbreviations and units for measurements:

RRAM = Mean of the relative radii
 RRVA = Variance of the relative radii
 RRADM = Mean of the relative radial deviations
 RRADV = Variance of the relative radial deviations
 NBAY = Number of bays
 STRKM = Length of mapped streams (kilometers)
 PNSA = Percentage of near shore area
 VA = Recent volcanic activity (Yes = 1, No = 0)
 NRA = Number of geologic periods of rock types
 CDTTP = Topographic shape code (1 = terrace or bench shape, 2 = volcanic cone or mountain,
 3 = volcanic cone plus bench)
 LAT = Latitude (degrees north).

^bNNA = Not available or not applicable.

Table A-16. Distance to source areas.

Island Name	DALPEN ^a	DKAM	DSEC	DYUK	DSEW	DCHU
Sanak	37	2228	1587	734	1147	1743
Unimak	3	2101	1701	676	1075	1633
Akun	155	2060	1746	761	1147	1658
Akutan	174	2037	1764	773	1154	1655
Unalaska	215	1947	1805	805	1167	1618
Umnak	340	1889	1932	881	1231	1639
Carlisle	496	1820	2087	977	1291	1607
Amliia	710	1595	2299	1131	1400	1590
Atka	758	1512	2343	1137	1385	1535
Adak	935	1422	2517	1261	1468	1506
Kavalga	1095	1308	2669	1386	1561	1507
Gareloi	1084	1298	2655	1366	1537	1482
Semisopochnoi	1170	1186	2732	1416	1563	1449
Amchitka	1213	1140	2780	1475	1624	1499
Kiska	1314	1054	2861	1491	1586	1393
Buldir	1396	939	2924	1549	1627	1352
Alaid	1511	796	3017	1616	1658	1299
Agattu	1528	789	3039	1642	1687	1327
Attu	1538	702	3039	1633	1666	1289
Copper	1833	331	3243	1790	1724	1129
Bering	1919	245	3317	1923	1778	1142
Big Konuiji	51	2411	1355	691	1123	1723
Peninsula	51	2405	1366	696	1126	1706
Kodiak	98	2658	949	607	973	1832
St. Paul	490	1721	1894	555	816	1208
St. George	428	1766	1879	588	877	1284
Nunivak	554	1894	1602	57	469	1110
St. Matthew	783	1601	1916	454	506	834
St. Lawrence	955	1771	1711	189	134	63

^aAbbreviations and units for measurements:

DALPEN = Distance from the Alaska Peninsula (kilometers)

DKAM = Distance from the Kamchatka Peninsula (kilometers)

DSEC = Distance from the Southeastern Coast (kilometers)

DYUK = Distance from the Yukon Plain (kilometers)

DSEW = Distance from the Seward Peninsula (kilometers)

DCHU = Distance from the Chukotka Peninsula (kilometers).

Table A-17. Local isolation measurements for the Aleutian Islands.

Island Name	DCURE ^a	DCURW	DPAS	WPAS	DPI
Sanak	710	2502	46	26	185
Unimak	941	2333	48	20	73
Akun	942	2328	91	7	149
Akutan	1049	2291	85	6	162
Unalaska	1049	2291	58	8	185
Umnak	1228	2023	200	71	239
Carlisle	1343	1930	183	9	323
Amlia	1531	1751	121	30	473
Atka	1672	1559	47	9	478
Adak	1808	1460	60	13	565
Kavalga	1901	1355	67	14	680
Gareloi	1925	1321	1155	110	639
Semisopochnoi	2064	1186	1155	110	684
Amchitka	1996	1253	1155	110	725
Kiska	2237	1023	200	101	742
Buldir	2354	916	843	118	806
Alaid	2514	774	108	35	842
Agattu	2540	786	106	50	871
Attu	2566	711	108	35	856

^aAbbreviations and units for measurements:

DCURE = Distance along the current path from Alaska Peninsula Region (kilometers)

DCURW = Distance along the current path from Kamchatka Peninsula Region (kilometers)

DPAS = Depth of adjacent interisland pass (meters)

WPAS = Width of adjacent interisland pass (kilometers)

DPI = Distance to the pack ice limit (kilometers).

TABLE A-18. Correlation coefficients between geographic variables.

	AREA ^a	ELIS	NBAY	STRKM	TODI	TOVA	TOWN	RAM	RAV	RADM	RADV	RRAM	RRAV	RADM	RDALPEN	DKAM	DCURE
ELIS	0.353																
NBAY	0.627 ^b	0.365															
STRKM	0.894 ^b	0.275	0.523 ^b														
TODI	0.127	0.676 ^b	0.364	0.101													
TOVA	0.132	0.666 ^b	0.239	0.097	0.901 ^b												
TOWN	-0.112	0.356	0.187	-0.165	0.640 ^b	0.675 ^b											
RAM	0.963 ^b	0.426 ^b	0.654 ^b	0.875 ^b	0.179	0.161	-0.147										
RAV	0.813 ^b	0.451 ^b	0.643 ^b	0.756 ^b	0.113	0.092	-0.160	0.825 ^b									
RADM	0.862 ^b	0.399 ^b	0.776 ^b	0.830 ^b	0.222	0.152	-0.127	0.896 ^b	0.925 ^b								
RADV	0.621 ^b	0.271	0.531 ^b	0.603 ^b	0.005	-0.017	-0.209	0.653 ^b	0.938 ^b	0.828 ^b							
RRAM	0.051	0.110	-0.159	-0.025	0.237	0.372	0.425 ^b	-0.004	-0.231	-0.260	-0.330						
RRAV	-0.034	-0.108	0.102	-0.048	-0.067	-0.265	-0.325	-0.022	0.132	0.177	0.154	-0.240					
RADM	0.090	-0.160	0.274	0.064	0.093	-0.110	-0.135	0.074	0.117	0.274	0.113	-0.134	0.843 ^b				
RADV	-0.148	-0.203	0.016	-0.124	-0.056	-0.263	-0.251	-0.130	0.051	0.109	0.154	-0.313	0.905 ^b	0.774 ^b			
DALPEN	-0.274	-0.316	-0.275	-0.254	0.093	0.190	-0.089	-0.294	-0.240	-0.227	-0.099	-0.011	-0.046	-0.354	0.028		
DKAM	0.380 ^b	0.244	0.295	0.405 ^b	-0.130	-0.217	0.075	0.400 ^b	0.337	0.329	0.204	0.029	0.013	0.045	-0.028	-0.970 ^b	
DCURE	-0.431	-0.480 ^b	-0.291	-0.283	0.090	0.201	0.073	-0.426	-0.409	-0.312	-0.312	0.086	-0.038	0.134	0.020	0.992 ^b	-0.996 ^b
DCURW	0.442	0.487 ^b	0.310	0.278	-0.073	-0.192	-0.064	0.439	0.419	0.320	0.322	-0.090	0.043	-0.127	-0.020	-0.994 ^b	0.995 ^b

^aVariable abbreviations:

AREA = Area of the island

ELIS = Maximum elevation

NBAY = Number of bays

STRKM = Length of mapped streams

TODI = Diversity of number of contour lines per sample square

TOVA = Variance of number of contour lines per sample square

TOWN = Mean of number of contour lines per sample square

RAM = Mean of radii

RAV = Variance of radii

RADM = Mean of radial deviations

RADV = Variance of radial deviations

RRAM = Mean of relative radii

RRAV = Variance of relative radii

RRADM = Mean of relative radial deviations

RRADV = Variance of relative radial deviations

DALPEN = Distance from Alaska Peninsula

DKAM = Distance from Kamchatka Peninsula

DCURE = Distance along current path from Alaska Peninsula Region

DCURW = Distance along current path from Kamchatka Peninsula Region.

^bSignificant, Alpha = 0.05.

VITA

Raymond A. McCord was born in Tulsa, Oklahoma on April 10, 1952. He attended elementary schools in Tulsa, Oklahoma; Jackson, Tennessee; Omaha, Nebraska; Champaign, Illinois; and Elkins, West Virginia; and was graduated from Carthage Community High School, Carthage, Illinois in May 1970. Starting October 1970, he attended Robert Morris College, Carthage, Illinois and then transferred to Western Illinois University where in March 1974 he received a Bachelor of Science, with a major in Botany.

One quarter of graduate work at Western Illinois University was completed in the Spring of 1974 before he came to the Graduate Program in Ecology at The University of Tennessee, Knoxville in the Fall of 1974. While at The University of Tennessee, Knoxville, he was a Graduate Research Assistant in Ecology and worked on a Master of Science Degree in Ecology. This degree was awarded in December of 1976.

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