AN ISLAND BIOGEOGRAPHIC STUDY OF SUBALPINE FOREST ISLANDS

by

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B.Sc., University of Calgary, 1978

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in the Department
of
Geography

SIMON FRASER UNIVERSITY

1981

APPROVAL

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Title of Thesis/Project/Extended Essay

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ABSTRACT

The plant ecology of the forest "islands" in a subalpine region of the northern Cascade Mountains of Washington State was examined in the framework of equilibrium island biogeographic theory. Regression analyses were used to relate the number of vascular plant species present in a forest island with several habitat and environmental variables. Particular emphasis was placed on island area as a predicting variable. Additionally, an ordination of common species was used to separate groups of similar forest islands in order to expose variables affecting only a portion of the forest islands sampled. The possiblity of time affecting species diversity through climatic and tree canopy changes, was examined by analysing island ages. The island ages were inferred from dates obtained by tree coring.

Island area was found to have a significant correlation with species number. This is consistent with equilibrium theory. However, the effects of area appear to be expressed through changes in habitat diversity, a factor inconsistent with equilibrium theory. As well, the correlation between area and species diversity, though significant, is not strong, limiting the relationships' biolcgical predictability. It appears that the forest islands may be in a continual state of nonequilibrium due to the harshness of the high altitude environment and the continually changing effects of the tree canopy. The

nonequilibrium condition would explain the poor species-area relationship.

ACKNOWLEDGEMENTS

Oh to acknowledge the world and still seek brevity in numbers and in words. I must first of all thank my supervisor Dr. Ian Hutchinson, committee member Brian Sagar and Dr. Robert Brooke who served as my external examiner. As well I am grateful to Dr. Fulton Fisher for his thoughts in the early going, to Charles Raddon, Resource Assistant of the Glacier Ranger District for his help in the conduction of field work and to the Natural Sciences and Engineering Research Council for financial support by providing a scholarship.

I am grateful to Anne, Chris, Tom, Ken, Bernard and many others for both intellectual and nonintellectual entertainment during my stay at SFU. I must especially give a big thankyou to Helen and Steve. and finally, three big hearty cheers to W.t.P.

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I. Objectives

The alpine timberline regions of the world have presented biologists with a major area of study. This major vegetation boundary, representing the upper limit of forest growth in mountainous regions, has been separated into two types in Europe (Tranquillini, 1979). A forest in one case may end abruptly as a smooth continuous treeline. In this instance the separation between closed forest and open alpine zone lacks a discernible ecotone. In the second form, the subalpine forest breaks up into a patchy parkland across a broad ecotone. Within this transition zone both the forest clumps and individual trees are reduced in stature with increasing elevation until only krummholtz trees remain. Walter (1968) proposes that shade-tolerant species generally form sharp timberlines, while light-demanding produce open stands within a wide transition zone in the European Alps.

In western North America, particularly in the Pacific Northwest, where timberlines and alpine regions are largely untouched by man, a sharp timberline boundary is absent. Here a wide ecotone with a mosaic of forest clumps and alpine meadows exists. An uneven pattern of snow accumulation, by affecting the length of the growing season, is thought to be the major reason for the presence of a wide transition zone (Brink, 1959; Brooke, 1965; Franklin et al., 1971; Lowery, 1972). The forest clumps appear to be located on raised ground in the meadows, and have a longer snow-free season (Brink, 1959; Brooke, 1965; Lowery, 1972). It appears that tree survival is only possible in locations which become free of snow early. Wardle (1974) provides two possible explanations for the importance of the length of the growing season. In attempting to explain tree limits he hypothesises that in order for trees to survive there must be adequate time for new shoots to ripen if they are to tolerate the winter cold and dessication. In addition there must be a sufficient temperature sustained in the leaves to permit growth. Because the length of the growing season influences both the ripening period and the period during which there is sufficient temperature for growth, a variable which influences the growing season must influence tree survival. This variable is the accumulation of snow. Trees are able to survive on rises which become free of snow early but not in depressions where snow accumulates and lingers late into the summer months.

Trees at subalpine timberlines are characterised by a very slow growth rate and sporadic reproduction. This is to be expected for plants growing at the limit of their survival capabilities. While this is also true of trees within forest clumps, tree groups have a definite ecological advantage over isolated individuals (Tranquillini, 1979). A tree group produces more favorable growing conditions by creating its own moderated microclimate (Tranquillini, 1979). This was demonstrated in the Cascade Mountains of North America by Lowery (1972) who, through a detailed analysis of two forest clumps found that the tree ages and growth rates were highest in the center of the clumps. It is at the center that one would expect the moderation of climatic extremes to be the greatest. Lowery (1972) used his observations to develop a hypothesis for the development of the forest clumps. A forest clump initially begins with the establishment of a few seedlings. As these trees modify the meadow microclimate, the rate of snow melt is accelerated and the growing season extended (Franklin et al., 1971). The acceleration of snow melt is the result of a combination of snow melting while it is retained on the tree canopy and reradiation of absorbed solar energy from the dark colored bark and leaves. In addition, the snow which falls from the tree tends to fall away from the tree stem. All of these factors create a snow melt crater around the tree (Lowery, 1972). The extension of the growing season allows new seedlings to become established and the forest clumps develop.

Lowery's hypothesis is not the only explanation for the development of the forest clumps. Other possibilities include the development of tree colonies through vegetative reproduction or the germination of seeds deposited in caches by birds and animals. A further explanation may be that certain forest clumps develop en masse from a major invasion of alpine meadows by tree seedlings. Major invasions of seedlings have been observed in the Olympic and Cascade Mountains of North America (Brink, 1959; Franklin et al., 1971; Lowery, 1972) but the development of these seedlings into forest groups has not been followed. The noted major invasion of seedlings appears to have occurred during a period of mild winters in the late 1920's and early 1930's (Brink, 1959; Franklin et al., 1971).

The presence of distinct forest clumps raises several questions concerning the makeup of the subalpine forest vegetation. If one accepts the hypothesis that the pattern of snow accumulation controls tree growth, then the same factor likely also affects the understory forest vegetation. The understory must also be influenced by the presence of the tree canopy. Is the floristic composition of the forest understory influenced mainly by topographic variables such as slope, aspect, elevation and the effects of avalanches, streams and snowpatches or are biological factors more important? These biological factors relate specifically to the effects of the tree canopy on the understory. Furthermore, what are the effects on the understory through time as the trees grow and produce a fuller canopy?

The fragmentation of the forest may also influence the understory. What is the effect of the size and changes in the size of the forest clumps? What is the effect of the isolation of the forest clumps and is there any limitation to the interchange of species between them? Finally, does the manner in which the forest clumps are established affect the understory? For example, it is possible that a forest clump which has gradually developed over time will influence the understory in a different manner than when the canopy develops en masse.

In this study I intend directing the research towards answering several of these questions. I will examine the influences of slope, aspect and elevation on the composition of the understory. The influence of common but specialised subalpine habitats such as avalanche slopes, stream edges and snow patches will be included in the study. Any changes in the understory which can be related to the age of the trees will also be examined. The age of the trees is taken as an estimate of the length of time the understory has been influenced by the tree canopy. The effects of forest clump size and isolation are to be examined and related to the species diversity of the vegetation of the forest clumps. In addition I will attempt to include a measure of habitat richness in explaining species diversity. I will not be able to document any change in the species composition of the forest clumps with their development because this would require a long term ongoing study. However, I will look at the age distribution of the trees within the tree clumps in an attempt to discover the manner in which they developed. The theoretical framework in which I will examine these questions is the equilibrium theory of island biogeography, originally developed for oceanic islands but applicable to subalpine forest clumps by extension.

The apparent insularity of the subalpine forest clumps suggests that an analytical approach similar to that used in many island biogeographic studies is appropriate. By correlating species diversity with island size, isolation, age and a number of environmental variables, the answers to these questions may be found.

Within this framework the general objectives of the thesis are:

1. To produce an explanation for variations in the species diversity of the subalpine forest islands, with particular attention paid to island area.
2. To conduct a detailed analysis of the vegetation composition of the forest islands at the time of sampling. The forest islands with similar composition will be grouped into classes and the similarities of these groupings explored.
3. To examine the ages of the subalpine forest islands and speculate on any effects of island age on species diversity. The possible modes of forest island formation will also be considered.

The study will be conducted on the vegetation of the subalpine parkland in the Northern Cascade Mountains of Washington State.

The applicability of the equilibrium theory to the study and the history of its development are examined in the next chapter. In Chapter Three I discuss the fieldwork methodology and the data analysis. The fourth chapter will present and discuss the results obtained leading to the conclusions in Chapter Five.

II. Island Biogeographic Theory

Subalpine Forest Habitats and Insularity

A visual characteristic of subalpine forest clumps is that they often resemble islands in the subalpine meadows. Specific reference to such features as islands is made by both Tranquillini (1979) and MacArthur and Wilson (1967). MacArthur and Wilson regard insularity as a universal feature of all natural habitats and refer to habitats isolated within another as 'habitat islands'. The meaning of "island" in a biological context therefore goes beyond the common connotation of land enveloped by water and includes terrestrial habitat discontinuities. The subalpine forest clumps represent an excellent example of such discontinuity. However, the biological definition of an island must take into account the behavior of the members of the community. Organisms which readily disperse as propagules or adults across habitat barriers do not recognise the insularity of the habitat which we perceive. The habitat discontinuities which produce the island boundaries are also often biologically indistinct. This complication is produced by species which occupy both the habitat island and the barrier.

This situation may also exist with islands of the standard definition, but it probably occurs more frequently in the case of habitat islands.

Many of the questions I raised in Chapter One are related to the assumptions of the equilibrium theory of island biogeography developed by MacArthur and Wilson (1967). The manner in which they studied oceanic islands is similar to the approach I will adopt here. The size and isolation of the islands are key elements. Preston (1960, 1962) and MacArthur and Wilson (1963, 1967) developed a hypothesis to explain observed variations in species diversity. They proposed that the species number reached an equilibrium condition where the immigration of new species to an island balances the local extinction of species on the island. Although there is a turnover of species on the island, the total number of species remains the same. The rate of immigration to an island is seen to be dependent on the distance of the island from the species source pool and independent of island area. Extinction rates are considered as being inversely proportional to the species population size, which is in turn proportional to area (MacAthur and Wilson, 1967). Considering only the effects of area, small islands should have smaller population sizes and therefore higher extinction rates than larger areas. More species would then be present on large islands than small islands.

Other hypotheses have been developed to explain the relationship between area and diversity. Williams (1964) developed a habitat-diversity hypothesis which proposes that as the amount of area sampled increases, new habitats with new species are sampled. Area is therefore simply a surrogate measure of habitat diversity, as Abele (1974) demonstrated in his work on marine crustaceans. However, Simberloff (1976a), in examining immigration and species turnover rates on mangrove islands, showed that area has an effect independent of habitat diversity.

A third hypothesis ignores biological processes such as population dynamics and specialised habitat utilisation and regards any observed area-diversity relationship as purely a sampling artifact (Connor and McCoy, 1979). Greater effort is put into sampling large areas and more species are found.

Development of the Equilibrium Theory

The examination of the biota of island microcosms has been particularly fruitful for the development of ecological and evolutionary theory. The development of the Darwin-Wallace theory of evolution by natural selection is closely linked with the work of the former in the Galapagos and the latter in Indonesia. Darwin abandoned his view that the Galapagos Islands were a small separate world when he noted the similarity between species present on the Galapagos Islands and those in different habitats in South America. This similarity, along with the lack of species similarity with climatically and geologically similar islands and the differences between different islands in the Galapagos group, led Darwin to believe that the islands were colonised by long distance dispersal followed by natural selection in unlike physical and biotic environments (Darwin, 1859).

Modern theories of island biogeography tend to follow Darwin in looking at the processes of migration and evolution (Sauer, 1969). The natural history framework has been to examine the habitats and dispersal of local species in the diverse habitats which make up an island. Research using this method has often explained similarities and differences between islands themselves (eg. Carlquist, 1967). A second approach in analysing island biota involved plotting the number of species per island as a function of some common characteristic of the islands, usually area. It is from these diversity-area plots that the new field of biogeography developed. MacArthur and Wilson's (1967) equilibrium theory became its foundation.

MacArthur and Wilson began the development of equilibrium theory by using Preston's (1963) treatment of island area and equilibrium species number. Preston suggested that isolated areas have an equilibrium species number related to the number of species the island can support. At equilibrium there is a balance in the addition of new species through immigration and evolution and the loss of species by extinction. The graphical model presented by MacArthur and Wilson relates immigration and extinction rates to the number of species present. A high species number produces lower immigration rate and a higher extinction rate. High species numbers limit the number of new colonists and thereby lower the immigration rate. The extinction rate is also high due to low population sizes. The equilibrium species number is taken as the number at the intersection of the immigration and extinction curves. Immigration rates are also high on near islands and extinction rates low on large islands. Therefore there will be more species on near large islands than on remote small islands. MacArthur and Wilson (1967) then discuss the importance of differences in species dispersal, demography and ecological niches, the effects of stepping-stone islands, the strategy of colonisation and evolutionary changes following colonisation with regards to their theory.

Several assumptions are implicit in the equilibrium theory. These basic assumptions are:

1. the number of species on an island is constant through time, but there is a constant turnover of species
2. the immigration rate to an island is an inverse function of species number
3. the extinction rate is an exponential function of species number

4. for any species number, the immigration rate is dependent on island isolation
5. for any species number, the extinction rate is dependent on island area
6. equilibrium species number is therefore a function of island area and isolation

MacArthur and Wilson (1967) suggested the use of the power function: $S=cA^z$, where S equals the species number, A the area and c and z are the coefficient and exponent respectively, to mathematically express the species-area relationship at equilibrium. Attempts to define the biological meaning of the coefficient and particularly the exponent are numerous in the literature. The exponent z is the slope of the log species/log area regression line that is used to approximate the power function. This indicates the rate at which species accumulate with increments of area (Connor and McCoy, 1979). The value of z has been remarkably constant for most demonstrated species-area relationships. Preston (1962) predicted a canonical value of 0.262 but because of possible sampling errors accepted values in the range of 0.17 to 0.33 as possible values for z. MacArthur and Wilson (1967) accepted values of between 0.20 and 0.35. However, Connor and McCoy (1979) feel that with the abundance of z values between 0.20 and 0.40 a correlation between species number and area without a functional relationship is often indicated. A regular occurrence of slope values in this range may be an expected characteristic of any regression system with a high correlation coeficient (r) value and a relatively small range in the dependent variable compared to the independent variable (Connor and McCoy, 1979).

There have been several explanations for observed deviations in the slope value from the expected range. Preston (1960) attributes higher values to an increase in habitat diversity and lower values to the sampling of nonisolated areas. MacArthur and Wilson (1967) proposed that for nonisolated areas the range in slope should be in the range of 0.12 to 0.19. This decreased slope value would be the result of the many transient species that would be encountered in nonisolated areas. The transient species would flood small sampling areas and depress the slope of the curve (MacArthur and Wilson, 1967). Therefore, it is the rate at which species diversity increases with area that differs between island and continental areas, with islands representing an isolated and continents a nonisolated situation.

This transient hypothesis has gained much acceptance, but it is not without critics. Connor and McCoy (1979) claim that many of the isolate/nonisolate comparisons may not be valid due to a lack of sufficient overlap in area ranges. They also point out a number of studies where low slope values have been obtained for true isolates.

Studies of distant archipelagos have also produced contradictions in these circumstances. MacArthur and Wilson

(1967) predicted that the slope of the species-area curve should be higher because isolation restricts the number of transients which are present. This hypothesis has often been contradicted. Schoener (1976), in particular, has shown that the slope decreases with isolation in many instances.

While the understanding of the exponent has retreated from being generally agreed upon to a more questionable position, the coefficient has never been fully studied or explained. Haas (1975) attributes the lack of discussion to the large amount of variation that the coefficent exhibits. MacArthur and Wilson (1967) considered the coefficient to depend greatly on population density and the innate species diversity of the given taxon. They claim that c should be smaller in resource-poor regions where the total number of organisms in the taxon is less. Increased isolation should also cause a decrease in the value of c (MacArthur and Wilson, 1967). Problems in explaining the coefficient are produced by the dependence of c on the scale used in measuring area (Connor and McCoy, 1979).

The use of the power function has gained general but not universal acceptance as the empirical model used to explain the species area relationship (Gould, 1979). Other models, however, have also been applied. In early work the empirical model

$$S = \log k + z(\log A)$$

received a lot of attention from plant ecologists. Other possibilities besides the power function should therefore be tested when analysing species-area data. Connor and McCoy (1979) tested 100 published data sets by fitting the log species/log area (power funtion), species/log area (empirical), log species/area and species/area regressions to them. They concluded that there was no single best fit model. For a particular model the most appropriate species-area model can only be determined empirically.

Island Biogeographic Review

Oceanic Island Studies

The research published in support of or to criticise the equilibrium theory appears to be concentrated in a number of areas. Comprehensive reviews have been compiled by Simberloff (1974) and Gilbert (1980). The majority of studies examined oceanic islands but a few were conducted using habitat islands. In reviewing the literature special attention will be paid to habitat island and botanical studies because they are more directly related to this thesis.

Criticism of many of the assumptions of the equilibrium theory were quickly brought from biogeographers rooted in the natural history tradition of biogeography. Sauer (1969) raised several valid criticisms. His overall opinion was that the equilibrium model suffers from extreme oversimplification because it treats islands as a whole with little attention paid to internal habitat diversity and because species are treated interchangeably without considering genetic and geographic diversity. More specifically, Sauer finds fault in the assumptions that immigration and extinction rates vary as a function of the number of species present. The number of species present only set a limit on the potential new immigrants which remain in a fixed pool and the number of species which could become extinct. The actual rates fall anywhere between zero and this upper ceiling. Criticism is also pointed at the assumption that distance affects only the immigration rate and not the pool of species capable of reaching an island or extinction rates and that size affects only extinction rates and not immigration rates. Actually, the larger the island the greater the chance of a propagule hitting it. The closer the island is to the source of propagules the greater the chance of continual immigration preventing extinction. Therefore, remoteness and size only loosely correlate with immigration and extinction rates (Sauer, 1969).

The bulk of the research involves only the demonstration of the species-area relationship. MacArthur and Wilson (1967) appropriately cited several examples in support of their theory. However, they may have been carefully selecting their examples to include only special cases which gave a good fit to the species-area curve (Gilbert, 1980). In his survey of the literature, Gilbert (1980) claimed to find only one study, that of Diamond and Mayr (1976), which showed area as the exclusive predictor of species number. More commonly a measure of isolation is included (eg. Weisman and Rentz, 1976; Hamilton and Armstrong, 1965). Johnson and Simberloff (1974) found that the number of plant species on British islands correlated with the number of soil types, log of latitude, log area and log of the number of soil types in that order. In addition the number of soil types was correlated with area. Three studies have used the flora of the Galapagos Islands and have come to very different conclusions. Johnson and Raven (1973) found elevation the best predictor of species number, Simpson (1974) found only area, (especially Pleistocene area) correlated with species number, and finally Connor and Simberloff (1979) concluded that the number of collecting trips explained the most diversity variation.

A second major thrust in island biogeographic research came from examining the reduction of species number due to a reduction in island area (eg. Diamond 1971, 1972, 1974; Terborgh 1974; Willcox, 1978). These studies have attempted to show this relaxation effect on, for example, land-bridge islands which have become isolated due to increases in sea levels following the Pleistocene deglaciation. However, the long relaxation times mean that climatic and geologic changes have likely taken place, changing the equilibrium number (Abbott and Grant, 1976). As well, the findings of Willcox (1978) have been disputed because of problems in the methodology, especially in determining island age (Faeth and Connor, 1979). Simberloff (1976a) provided the only direct experimental evidence on the effects of area changes when he removed portions of red mangrove islands and watched the change in species number. However, his findings did not support the equilibrium theory.

The third and perhaps only true test of the equilibrium theory involves observing species turnover and therefore the effects of immigration and extinction. The most extensive work along these lines were the defaunation experiments of Simberloff and Wilson (Simberloff and Wilson, 1969, 1970; Wilson and Simberloff, 1969; Simberloff, 1969). They intially found good support for the equilibrium theory but Simberloff (1976b) has since re-examined the data and concluded that the true rates of turnover are very low. The initially calculated high turnover rates were accounted for by a 'pseudoturnover' produced by transients to the islands (Simberloff, 1976b). Lack (1970) found a similar base of criticisms when he noted the large numbers of nonbreeding birds present on a number of island groups.

An alternate method of attempting to analyse turnover rates comes from the establishment of permanent vegetation plots. Holland (1978) studied plots marked in a hardwood forest and concluded that the number of species present remained constant but that there was a continuous rearrangement of species in small quadrats. However, his plot size may have been of such a small size as to overestimate turnover.

Habitat Island Studies

The proposition that theories of insularity should be applicable to discontinuities in the habitat as well as land-water breaks has been tested in a number of different settings. Cave dwelling arthropods were studied by Calver et al. (1973) and Vuilleumier (1973). However, the first study seemed to be plagued by problems in determining area and the second appeared to give scant support to the equilibrium theory (Gilbert, 1980). Both Vuilleumier (1970) and Mauriello and Roskoski (1974) examined data on birds living in the Paramos islands of South America and concluded that area and the distance to the species source pool were the best predictors of species number. Simpson (1974) studied the flora of the same islands and concluded that Pleistocene area was the best predictor of species diversity. Johnson (1975) studied boreal birds and concluded that a measure of habitat diversity rather than area was the best predictor. Brown (1971) found that area had an effect on the number of mammals living on mountain tops in the Sierra Nevada and Rocky Mountains. The equilibrium theory was even applied to arthropods living on single plants. The idea was introduced by Janzen

(1968, 1973) and has been applied by Brown and Kodric-Brown (1974) and Seifert (1975).

Well documented examples have been the application of the equilibrium theory to numbers of breeding birds in woods. Again, not all have found consistent results (Gilbert, 1980). Examples include the works of Whitcomb et al. (1976), Moore and Hooper (1975) and Helliwell (1976).

In both oceanic and habitat island studies the majority of research has been in analysing species-area relationships. A statistically good fit of the power function should not be taken as verification of the equilibrium model. To examine the assumptions of immigration and extinction rates the turnover of species through time must be measured. In the few studies were this has been attempted contradictory results have been found. Therefore, the only assumption which can be tested with a lack of turnover data is the relationship between island area and isolation and species diversity. Such studies should not attempt to falsify nor verify the equilibrium model but use its treatment of islands as functional units as a basis for the study.

The study of the subalpine forest clumps will treat the forest clumps as functional units. By examining the characteristics of the islands as a whole explanations for variations in species diversity will be sought. Island size and isolation, variables important in the equilibrium theory, will be tested for their predicting capabilities. Other environmental variables, in particular elevation, will be included with the variables tested as will a measure of the habitat diversity of the islands. The floristic composition of the habitat islands will be examined to assess similarities between them. If islands are too different biologically, differences between species assemblages may overshadow any functional difference between islands in explaining species diversity.

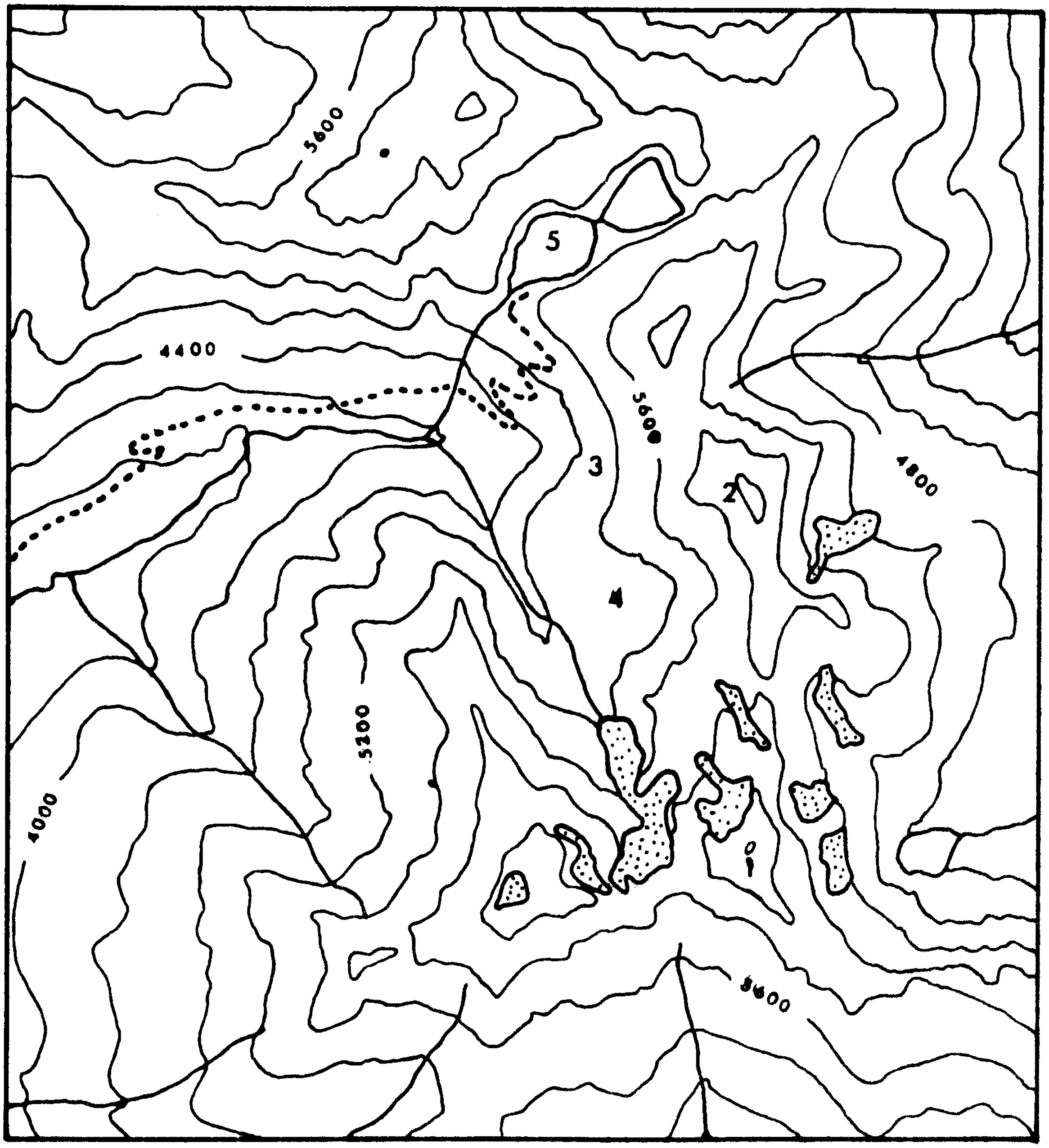
III. Methodology

Study Area

The area chosen for study is located on the northwest slope of Goat Mountain (2100 meters) in Mount Baker National Forest, Washington. Field data were collected from a small basin and the enclosing ridges. Figure 3.1 shows a map of the study area. Elevations range from 1500 meters in the basin to 2000 meters on the ridges. Geologically the area consists of volcanic bedrock which outcrops over much of the area. A small glacier is present on the north slope of Goat Mountain and a series of recessional moraines are deposited across the basin floor.

Forest islands are present on all of the ridges up to an elevation of approximately 2000 meters. In the basin itself the forest islands are only present as small individual trees. Field work was conducted on all of the ridges except the west ridge where the steepness of slope prevented sampling. Forest islands in the basin were also sampled.

FIG. 3.1 - GOAT MOUNTAIN STUDY AREA



KEY

••• Road

— Stream

▨ Glacier

1 Goat Mountain
2 East Ridge
3 North Ridge
4 Basin
5 Twin Lakes

0 Scale 1 Mi.

Contour Interval
- 400 ft.

Field Studies

During July and August of 1979 information on the physical and vegetational characteristics of selected forest islands was collected. The forest islands studied were selected to give as wide a variety of sizes and locations as possible. Factors used to select forest islands for study include accessibility and ease of sampling of the terrain where the forest island is located, and the number of forest islands similar in size and location. Forest islands which were very difficult to get to and/or sample were not included as were those where similar forest islands had been already repeatedly sampled. In total 101 forest islands were selected. These ranged in size from 0.5 to 582.1 square meters and had an elevational range of 1486 to 1976 meters above sea level. The boundary of a forest island was defined as the edge of the tree canopy of a distinct cluster of trees. It did not include seedlings scattered away from the actual cluster although some larger, solitary trees were included as forest islands.

The physical properties measured were those that would allow the forest islands to be separated into specific habitat types. All measurements were made in U.S. units and then converted into metric units. Elevation, slope, aspect, distance to the two nearest forest islands, and area were measured. Elevation readings were taken with a Thommen 3B5.01.2 altimeter.

Slope and aspect were measured with a Sokkisha compass. The slope readings were taken to approximate the average slope that a forest was on. Distances to the nearest two forest islands were measured to record the degree of isolation. A hundred foot chain was used and measurements were taken to the nearest foot. The area of the islands was estimated by measuring the maximum width and maximum length with the hundred foot chain. By taking into account the shape of the islands and applying the correct geometric formula, the area was calculated. Possible shapes included circular, ellipsoidal, tear-shaped, 'L'-shaped and rectangular.

Two further physical characteristics were recorded. These were a count of the number of distinct habitats found in a forest island and an estimation of the soil moisture. Habitat type was included to separate between the very distinct growing conditions and soil moisture was estimated to distinguish between the the lush moist areas and the sparser dry sites. Possible types of habitats include:

1. very exposed rock ridges
2. moist cracks in rocks
3. morainal debris
4. stream edges
5. avalanche slopes
6. areas of open meadows
7. areas of seepage or depressions where water collects

8. small rises in the ground without extreme exposure

An index for estimating soil moisture was established with four levels. The criteria it was based on were:

1. Hydric - seepage sites from snowpatches which linger well into the summer and areas along water channels
2. Mesic - slopes with north aspects, wetter easterly and westerly slopes and avalanche slopes
3. Xeric - southerly slopes and exposed westerly slopes
4. Very Xeric - very exposed slopes and ridge tops

The vegetational analysis involved censusing the species composition of the forest islands and stem coring to determine the age of the oldest trees. The total number of vascular plant species and the name of each species were recorded. Sample specimens were collected and pressed for later identification in the laboratory. The tree, or trees, which appeared to be the oldest were cored. Usually the tree which was the largest was assumed to be the oldest.

A more detailed study of the age distributions for a subset of the forest islands was also undertaken. The islands studied were chosen to obtain a representative cross-section of island types with preference given to those islands where regeneration was evident. Along two perpendicular transects running through the center of the forest islands every tree was cored or a cutting was taken, if the tree was too small to core. The trees were cored as close to the ground as possible. The height of the trees sampled was either measured directly or measured through triangulation using a compass. Finally the distance and direction along the transects were recorded for each tree.

Laboratory Study

In the lab the plant samples were identified. Terminolcgy used was that of Hitchcock, Cronquist, Ownbey and Thompson(1969). The tree cores and cuttings were aged using a stereo-microscope. The raw ages were then adjusted to take into account the coring height. These adjustments made use of growth rates calculated for those forest islands used in the detailed age study. Growth rates were calculated for those trees with a coring height that was not more than 0.25 meters by dividing the tree height by the number of tree rings. If the coring height was greater than zero, the coring height was subtracted from the tree height. Average growth rates were obtained for each species for each forest island. If trees were present which appeared to be stunted, their growth rates were averaged separately. For each tree with a coring height greater than zero the coring height was divided by the average growth rate for that species. The result was added to the raw age to give the final adjusted age. For those forest islands where no growth rates were calculated, the average growth rate used was that calculated for the selected forest island whose physical characteristics most closely resembled those of the forest island under study.

Regression Analysis

An explanation for the variations in species diversity was sought using a series of regressional analyses. All regressions utilized the BMDP biomedical computer programs (Brown, 1977).

In the initial stage of the analysis a stepwise multiple regression was conducted. The number of species was the dependent variable. Island area, the number of habitats, slope, elevation, the distances to the nearest two forest islands, aspect and the age of the oldest tree were used as independent variables. Two regressions were run and none of the variables were transformed. The first regression included all of the independent variables but the second excluded habitat number from the analysis. A third multiple regression was then conducted to assess the relationships of the variables, excluding species number, to habitat diversity..

The second stage of the analysis involved using a series of simple linear regressions to determine the best fit of the four possible combinations of untransformed and logarithmically transformed variables in explaining variations in species number. In this analysis area was used as the independent variable and species number as the dependent variable.

After this initial analysis was complete the data were examined to determine if a better fit could possibly be achieved. This involved examining the environmental data of every forest island with very large residuals from the predicted line, to assess if any similarities existed between islands. If any patterns existed, certain forest islands could validly be excluded or the data subdivided. In accordance with this a number of forest islands were excluded and simple regressions rerun. In this analysis area and the number of habitats were the independent variables and no transformations were made.

The effects of island age on the species diversity and area of the forest islands were then analysed. A linear regression of species number versus island age was conducted with species number as the dependent variable. When it appeared that a second or third degree polynomial model would provide a better fit of the data, these were tested. Finally the data was subdivided by age into two groups. Those forest islands with trees older than 200 years and those with trees exclusively younger than 200 years old were put into separate groups. Again simple linear regressions were run using no transformations and both dependent variables.

Ordination

To determine if there were any distinct groupings of forest islands based on their vegetational composition, the forest islands were ordered multidimensionally using Bray-Curtis ordination techniques. These are described by Mueller-Dombois and Ellenberg (1974). In this technique the forest stands are placed in a multidimensional space geometrically, based on their degree of similarity, and vegetation clusters are then subjectively delimited.

The ordination process begins with the calculation of similarity indices for every forest island pair. The index used was that developed by Sorenson (1948):

$$IS = 2c / (A+B) \times 100$$

where IS is the similarity index, c is the number of species in common between two sample areas, A is the total number of species present in one area and B is the total number of species present in the second area. Because similarity indices, when used in ordination calculations place the most similar stands farthest apart, indices of dissimilarity are substituted. The index of dissimilarity is simply 100 minus the index of similarity.

The first ordination or the the linear sequence of the forest islands is constructed along the x-axis using the two least similar stands as the axis endpoints. To avoid problems resulting from using too dissimilar stands, any endpoint of the x-axis or any subsequent axis must show a similarity of at least 50 percent with at least three other forest islands (Swan and Dix, 1966). The length of any axis is the dissimilarity between the two endpoints.

The remaining stands are then positioned along the x-axis by their dissimilarity to the two endpoints. Their relative position is determined by using the Pythagorean theorem which was rewritten by Beals (1960) in the form:

$$x = (L + (dA) - (dB))/2L$$

In the equation, L is the length of the axis, dA is the dissimilarity from the first endpoint and dB is the dissimilarity from them second endpoint. The relative position , x, is measured from the first endpoint.

To get a better geometric approximation of the similarity of the forest islands, they were separated into a second dimension with the construction of a y-axis. The first endpoint of the y-axis was chosen for its dissimilarity from both x-endpoints. This dissimilarity is based on the calculation of an e-value. The formula for calculating e is:

$$e = dA - x .$$

The first y-endpoint is choosen as that stand with the highest e-value provided it falls within the mid 50 percent range of the x-axis (Newsome and Dix, 1968). The second endpoint is that stand with the lowest similarity with the first endpoint. It also must be within 10 percent of the position of the first y-endpoint on the x-axis (Meuller-Dombois and Ellenberg, 1974). This is to keep the y-axis as perpendicular with the x-axis as possible. The forest islands are then positioned along the y-axis using Beals formula. The positions of the islands along both axes can now be plotted and groupings made.

To align the forest islands in a third dimension a z-axis is constructed. The first endpoint on the z-axis should be the island which has the greatest dissimilarity from both the x- and y-endpoints. This is determined as the forest island with the highest value for e + e , with e calculated in the same manner as e . This endpoint must be within the mid 50 percent range of both the x- and y-axis (Newsome and Dix, 1968). The second z-endpoint is that stand which is the most dissimilar to the first end-point. Again the forest islands are positioned along the z-axis using Beals formula. Two further plots can be obtained, z/x and z/y.

Forest Age Analysis

All of the tree ages were analysed to detect any concentrations over time which would indicate a spurt of tree establishment in the area. The ages were plotted along a time series from zero to 200 years before present. Frequency of occurrence was plotted as the y-variable. The ages were smoothed with a five year moving average before plotting.

The data from those forest islands which were more intensely sampled for tree ages was plotted to show position and ages of the trees. These plots were then subjectively examined for any patterns in the distribution of ages, any evidence of regeneration and the possibility of expansion of the forest islands.

IV. Results

In this chapter an explanation for variations in species diversity is sought. The habitats of the forest islands are initially described with important variables and characteristics noted. The exploratory multiple regression investigation into these variables' relationships to species diversity is discussed. This is followed by a more detailed discussion of the species-area relationship, its deficiencies and the reasons for the deficiencies. Throughout the chapter the usefulness of the equilibrium model is considered culminating with the concluding statement on its appropriateness.

Description of Forest Island Habitats

The forest islands studied are located on the northern slopes of Goat Mountain and on the eastern and northern ridges surrounding the central basin. A few forest islands were also sampled in the basin itself. The pattern of snow accumulation is probably the most important variable influencing tree location. Trees are present is areas which became free of snow early. In addition to the apparent primary control of snow depth on tree location, the morphology of the trees themselves varies with elevation, aspect and slope steepness. On the northern slope of Goat Mountain and on the eastern ridge the trees are strung out along the ridge tops and clustered in groups on steep, rocky slopes. On the ridge crests the trees are very twisted and stunted. Here they spread out laterally as if clinging to the edge of the cliff.

The northern ridge, with a gentler slope, had trees restricted to topographical rises in the meadows. These rises become free of snow early in the summer while the surrounding depressions remain covered with snow. It was not until late July that these depressions, along with avalanche slopes and the basin itself became free of snow. The ridges and higher locations were free of snow by late June.

On this northern ridge the forest islands can be subjectively divided into two groups. On the highest rises are the largest and oldest trees and therefore presumably the oldest forest islands. The largest trees in these forest islands are approximately 200 to greater than 700 years old. Often dead and broken trees are present. The second group of forest islands are much younger, usually with trees less than 125 years old. These forest islands are found in less pronounced rises in the meadows. This suggests that a period of milder winters may have occurred within the last 125 years which allowed these trees to become established. Overall, it appears that trees will grow in almost any location with suitable physical conditions. They do not appear to be restricted in any way by other forms of vegetation.

Within the basin itself the forest islands are often restricted to single trees which are much younger than the oldest trees on the ridges. The trees are very scattered and are located on the recessional moraines. As the distance of the moraines from the glacier increases the trees present on them increase in age and stature. This suggests a gradual colonization of the basin during a period of climatic moderation which may have produced the glacial retreat from the basin. Trees present on the youngest of the moraines show minimum ages of 22 to 39 years indicating that they were most likely established during the relatively warm climatic period between 1920 and 1950 (Mathews, 1951; Hubley, 1956). Minimum ages for trees on older moraines range from 48 to 101 years indicating a gradual invasion of the basin after the last large glacial advance which ended approximately 300 years b.p. (Mathews, 1951). The smaller trees in the basin may develop with time into larger forest islands similar to those present on the ridges.

The makeup of the subalpine forest in the study area consists exclusively of subalpine fir (<u>Abies lasiocarpa</u>) and mountain hemlock (<u>Tsuga mertensiana</u>). Pacific silver fir (<u>Abies amabilis</u>) and Alaska-cedar (<u>Chamaecyparis nootkatensis</u>) were found by Lowery (1972) on an adjacent mountain but were absent as trees in the study area. The occasional presence of

Alaska-cedar as a shrub in the study area was noted, however. Of the two dominant trees, subalpine fir has been found to be the most prevalent in drier sites with high radiation exposures, such as very steep, high elevation, south-facing slopes (Lowery, 1972). Mountain hemlock is found primarily on mesic sites which tend to be less inclined and have more northerly exposures (Lowery, 1972). In the study area mountain hemlock appears to be the dominant tree in most of the forest islands. It is usually the largest tree in the islands and is present in 96 percent of all the islands studied. On the west-facing easterly ridge mountain hemlock is the sole tree in most of the higher elevation forest islands. In locations where subalpine fir and mountain hemlock are present together, they are often found growing within inches of each other. In these situations the mountain hemlock tree is larger and older. These findings contradict those of Lowery (1972) who found that subalpine fir predominated in the center of the forest clumps.

A number of the species present in the understory of the forest islands are also common in the nearby meadows. Of these, Vaccinium deliciosum, Cassiope mertensiana, Phyllodoce empetriformis, and Luetkea pectinata were found in 85, 83, 91 and 78 per cent of the forest islands respectively. They were also very common in the meadows. In many instances these species dominate the understory of the forest islands. Obviously the habitat ranges must overlap to include both meadow and forest conditions. This habitat overlap probably reduces the isolation of the forest islands for the understory species.

Localised plant communities are found in special habitats. These include Mimulus lewisii, Epilobium latifolium and Epilobium glandulosum-dominated streambed and seepage-area communities. Veratrum viride, Erythronium grandiflorum and Viola glabella are common on avalanche slopes. Pioneering species on the moraines and rock outcrops include Penstemon davidsonii, Antennaria alpina, Phlox hendersonii and several Saxifraga species. These species were only present in the forest islands if their special habitat happened to occur there.

The variables determining the species composition and diversity of the forest islands appear to be complex. Snow accumulation pattern, slope, aspect, and elevation appear to be very important controls on the location and physiognomy of the trees themselves. The understory vegetation appears to be strongly influenced by the floristic characteristics of the surrounding meadow vegetation, the presence of localised habitats and the suitability of the substrate to support vegetation. The variables which influence tree location and form also play strong roles in determining the type of meadow vegetation, the placement of localized habitats and site productivity. The vegetation should then be treated as a whole. Community characteristics rather than the distribution of individual species will therefore be the primary focus of the following discussion.

Multiple Regression Results

The results of the multiple regression analysis of species diversity to the independent variables (area, aspect, forest island age, habitat diversity, elevation and island isolation) are given in Table 4.1. The only two variables shown as significant by the regression are habitat number and elevation.

The absence of area as a significant predictor of species number in the multiple regression analysis appears to be due to the inter-relationship between the habitat diversity and area variables. When habitat diversity is removed from the multiple regression, area becomes the only significant variable related to species number. It is therefore apparent that habitat number and area are explaining almost exactly the same variation in species number. A multiple regression to show the relationship of habitat diversity to the other independent variables indicates that area explains 55 percent of the variation in habitat number (Table 4.2). A graph of this relationship is shown in Figure 4.1. The other two significant variables, age and the index of isolation explain only a further three percent of the variation each. These two variables, although statistically significant, are of very little use in predicting habitat number.

Table 4.1 - Results of multiple regression analysis used to explain variations in species number

Independent Variable	R	R-squared	Increase in R-squared
No. of habitats	0.6208	0.3854	0.3854
Elevation	0.6673	0.4453	0.0599

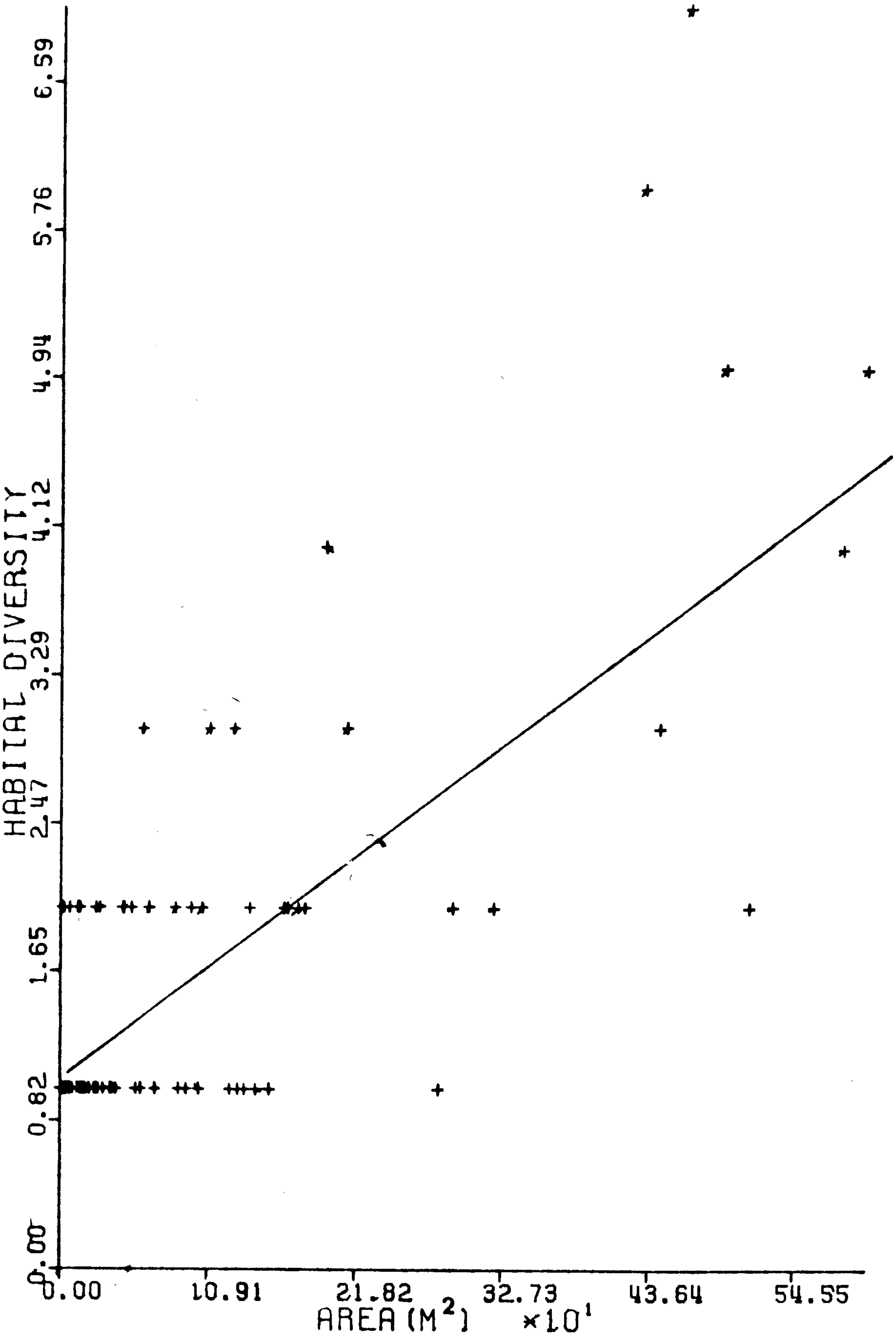
Table 4.2 - Results of multiple regression analysis used to explain variation in habitat number

Independent Variable	R	R-squared	Increase in R-squared
Area	0.7408	0.5488	0.5488
Island age	0.7588	0.5757	0.0269
Distance (1)	0.7761	0.6024	0.0266

The failure of area as a predictor can therefore be explained by its covariation with habitat diversity. Reasons for the absence of other variables are not as apparent. Elevation and isolation, in particular might also have been expected to have a higher correlation with species diversity.

Elevation was found to be the second most important variable explaining species diversity from the multiple regression results. However, it only explained an additional six

FIG. 4.1 - HABITAT DIVERSITY-AREA RELATIONSHIP



percent of the variation in species number on top of the explanation provided by habitat. An increase in elevation might be expected to correspond with a decrease in species number as a result of the increasingly harsh environment. However this does not appear to be occurring. Many of the plant species have an altitudinal range at least equal to the range of the forest islands sampled. It therefore appears that there are few species removed with an increase in altitude, or that in those situations where species are not able to survive, they are replaced by new species which could. Any effects of decreasing species diversity corresponding to elevational increases may only show up if a larger elevation range is sampled, which might have to extend almost to the limits of the alpine region. Interestingly, elevation did not explain any of the variation in habitat diversity. This may be interpreted as further support for the idea that the elevational range sampled represents only a small increase in environmental stress.

Isolation does not appear to be important in predicting any of the variation in species number. The reason may be that the distance to the nearest forest island may not be a good measure of the isolation of the forest island. There seems to be a habitat overlap of many of the meadow species into the forest islands. It appears that only the two tree species, several of the tall shrubs and species in localized habitats are potentally isolated. Of these the species present in localized habitats are more dependent on the presence or absence of their habitat than isolation. It is also likely that the tree species, in particular, and possibly many of the understory species have seed-dispersal distances which are greater than distances between patches of suitable habitat. For example, the seeds of *Abies lasiocarpa*, are predominantly dispersed by wind. Seed may be carried for several hundred meters away from the parent stand within one generation. Such long distance disperal is aided by the high degree of exposure in the subalpine areas. Therefore, isolation may only be important on very isolated islands on the ridges or the moraines, particularly at high-altitudes, where vegetative reproduction is common. These forest islands are usually sparsely populated but this sparseness may also be due to the poor quality of the habitat rather than to isolation.

Island Area and Species Diversity

The poor correlation of area to species number through the effects of habitat, is the second complication in need of discussion. Because only the nontransformed linear model had been tested the three possible logarithmic transformations were also tested. These linear regresssions of species number to area also showed that area only explained a small amount of the total variation in species diversity (Table 4.3). Although all of the correlations obtained were statistically significant, R-squared

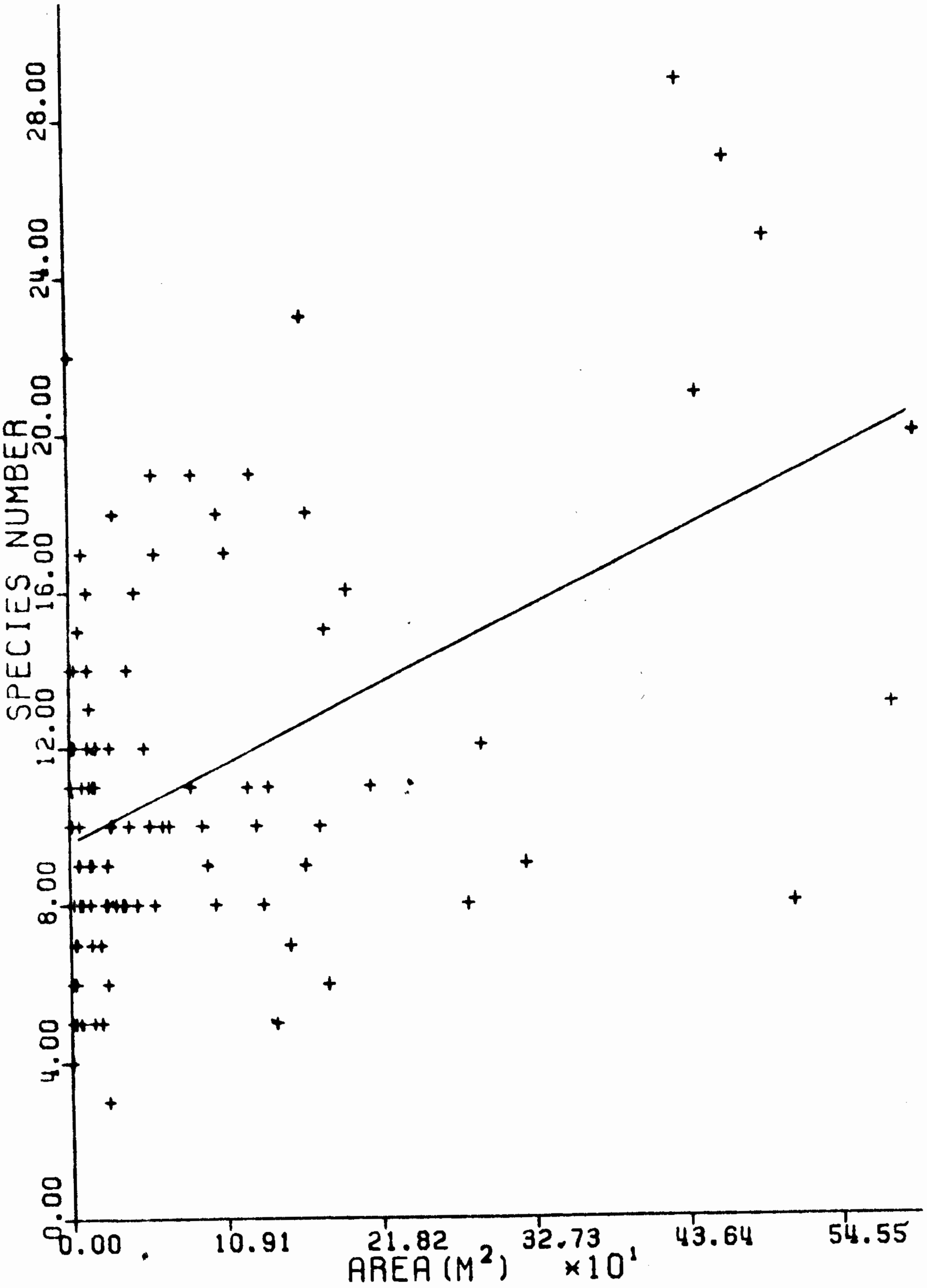
Table 4.3 - Linear analysis of the number of species versus area

Type of transformation	R	R-squared	F-ratio	Prob.
species/area	0.4636	0.2149	27.10	0.0000
log species/area	0.3899	0.1520	17.75	0.0001
species/log area	0.3494	0.1221	13.77	0.0003
log species/log area	0.3230	0.1043	11.53	0.0010

values were low. Of the four regressions tested, the nontransformed model still produced the best results. Here, area explained 21 percent of the variation in species number. A plot of this regression is shown in Fig. 4.2. The double logarithmic regression, which is commonly used to approximate the power function in the equilibrium model explained only 10 percent of the variation. It therefore must be concluded that the power function is an inappropriate model to explain the floristic composition of the subalpine forest islands.

To explain the poor correlation of area to species number a number of variables were further examined. The relationship between habitat and area, and the fact that habitat predicted slightly more of the variation in species number than area, suggests that habitat should be further examined. As well, a more detailed look at the age of the forest islands may be useful.

FIG. 4.2 - SPECIES-AREA RELATIONSHIP



Forest Island Habitats

In the initial multiple regression analysis the number of habitats explained 38 percent of the variation in species number and was statistically significant. The relatively low R-squared value results from the large residuals found in areas of low habitat diversity (Fig. 4.3). These residuals may be the result of the differences in species diversity per habitat type showing up in the total species number to a greater degree in forest islands with only a few habitat types represented. With a large habitat diversity, the relative species diversities would be averaged and therefore produce a more predictable result. Supportive evidence comes from examining those forest islands thought to be restricted to one habitat type (Table 4.4). In the four different types of habitats the average species number ranges from approximately six to fourteen. These differences are probably due to the exclusion of many of the understory species by environmental conditions. The presence of a late-lying snow pack on the avalanche slopes or exposed morainal debris may reduce the competition from many of the heath plants and allow a greater diversity of specialist plants to grow. There would, therefore, be an increase in the species diversity in sites where the heath plants were excluded. However, where just two different habitat types are represented in the same forest

FIG. 4.3 - SPECIES NUMBER-HABITAT DIVERSITY RELATIONSHIP

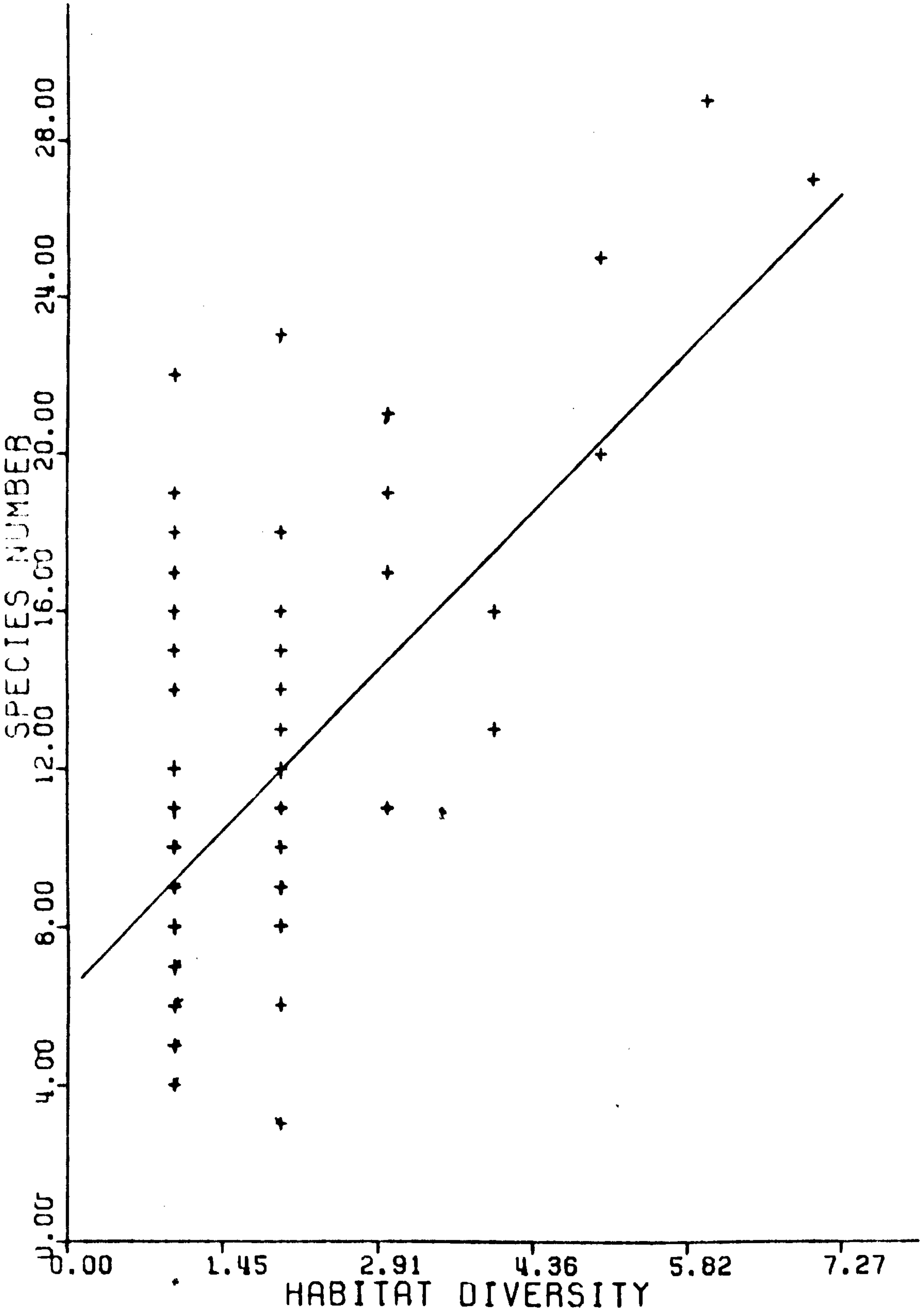


Table 4.4 - Average species diversity for forest islands restricted to one habitat type

Habitat Type	X Species No.	S.E.	Island No.	Range
Rock ridges	5.8	0.44	6	5-8
Morainal debris	13.3	1.41	7	10-22
Avalanche slopes	14.3	1.56	4	9-17
Rises in meadow	9.6	0.42	41	4-18

Table 4.5 - Average species diversity for forest islands with two habitat types

Habitat Type	X Species No.	S.E.	Island No.	Range
Rises in meadow/ Moist rock cracks	11.1	0.92	15	8-18
Open meadows/ Rises in meadow	11.6	1.84	7	8-23
Avalanche slopes/ Moist rock cracks	11.0	----	2	10-12
Rock ridges/ Moist rock cracks	10.0	1.56	6	3-15

island, the range in average species diversity is only from ten to twelve, (Table 4.5). While this generalisation fails to consider many factors it does suggest that an averaging in species number occurs with an increase in the number of habitat types present.

The habitat characteristics of individual and groups of islands were then examined to determine if a reason for the poor fit of both the species-area and species habitat regressions could be found. A number of attempts were made to examine and modify the data set to produce a better but still valid fit for the regression model. The initial approach was to examine the habitat information for those forest islands with extreme residuals from the regression line. This examination was made for both the habitat/species number and the area/species number regressions. In both instances, the same forest islands were usually examined. While it was found that several forest islands might be validly excluded, no single or group of features seemed to characterise those forest islands examined.

Examples of those forest islands which showed unique features included forest islands which had extremely dense canopy cover. This feature is probably the explanation for the depauperate flora which these forest islands showed. Another possible reason for lower species numbers than expected could be the result of the forest island being located in an unusually harsh environment in conjunction with extreme isolation. Islands located on rock cliffs where the surrounding vegetation cover was very sparse exemplify this condition.

Several of those forest islands with a much higher species number than expected could be explained by the presence of a combination of a large number of highly diverse habitats. For example, the presence of small streams or pools of standing water adjacent to or within a forest island greatly increases the number of species present. However, many of the deviations on both sides of the regression line are not readily explainable. The exclusion of those forest islands whose large residuals can be explained did not increase the fit of the regression line. This unexpected occurence may be because the small increase in the fit of the regression line was compensated for by the decrease in degrees of freedom which accompanied the decrease in size of the data set. Therefore, all of the forest islands were kept in the data set.

The similarity of the forest islands based on common floristic species was then examined. This allowed groupings of similar islands to be made. When the habitat types for these groups are compared discrepancies in the habitat classification may be shown. As well, distinct clusterings of one or more groups of islands away from the remainder may indicate that certain islands should be separated out. This examination was conducted through the use of an ordination based on similarity indices calculated for island pairs. The similarity indices allowed the islands to be arranged along three axes according to the rules outlined in Chapter 3.

The calculation of similarity indices for the forest islands showed a number of forest island pairs with zero similarity. This indicates that they have no species in common. All of these forest islands failed to show a similarity of greater than fifty percent with at least three other forest islands. This eliminated them as endpoints for the ordination axis. The forest island pair with the lowest similarity but the required associated similarities were forest islands 63 and 78. These two islands showed ten percent similarity. Therefore the length of the x-axis was 90 units. Forest islands 43 and 45 were chosen as the endpoints for the y-axis. They showed a similarity of 25 percent, producing an axis 75 units long. The z-axis endpoints were forest islands 11 and 63 with a length of 82 units.

The three possible plots of these three axes are shown in Figures 4.4 to 4.6. In these plots the forest islands are subjectively divided into two groups based on the types of habitats present. This separation is most clearly shown on the x/y and y/z plots. The first group contains all of those forest islands made up of any combination of only the following data types:

1. very exposed rock ridges
2. moist cracks in rock faces

3. small rises in the ground without extreme exposure

The second group contains forest islands which have at least one of the following habitat types present in its boundaries:

1. morainal debris
2. stream edges
3. avalanche slopes
4. areas of open meadows
5. areas of seepage or depressions which collect water

This grouping subdivides the habitat types by certain common features. Group one includes relatively common habitat types whereas those in group two are relatively rare. As well, those habitat types in group two are more likely to be associated with a very distinctive and perhaps richer flora. These distinctive floras would explain the way the group two forest islands are not clustered in the plot although they are separated from the group one islands.

The species composition of the two forest island groups is very similar in terms of the most common species. Tables 4.6 and 4.7 lists the species present in greater than twenty percent of the forest islands of the two groups and their percentage occurence. The same seven species have the highest percentage occurences in both groups. The difference between the two groups is shown by the greater number of species present in group two forest islands and the greater variability of the flora.

FIG. 4.4 - FOREST ISLAND ORDINATION - X/Y AXES

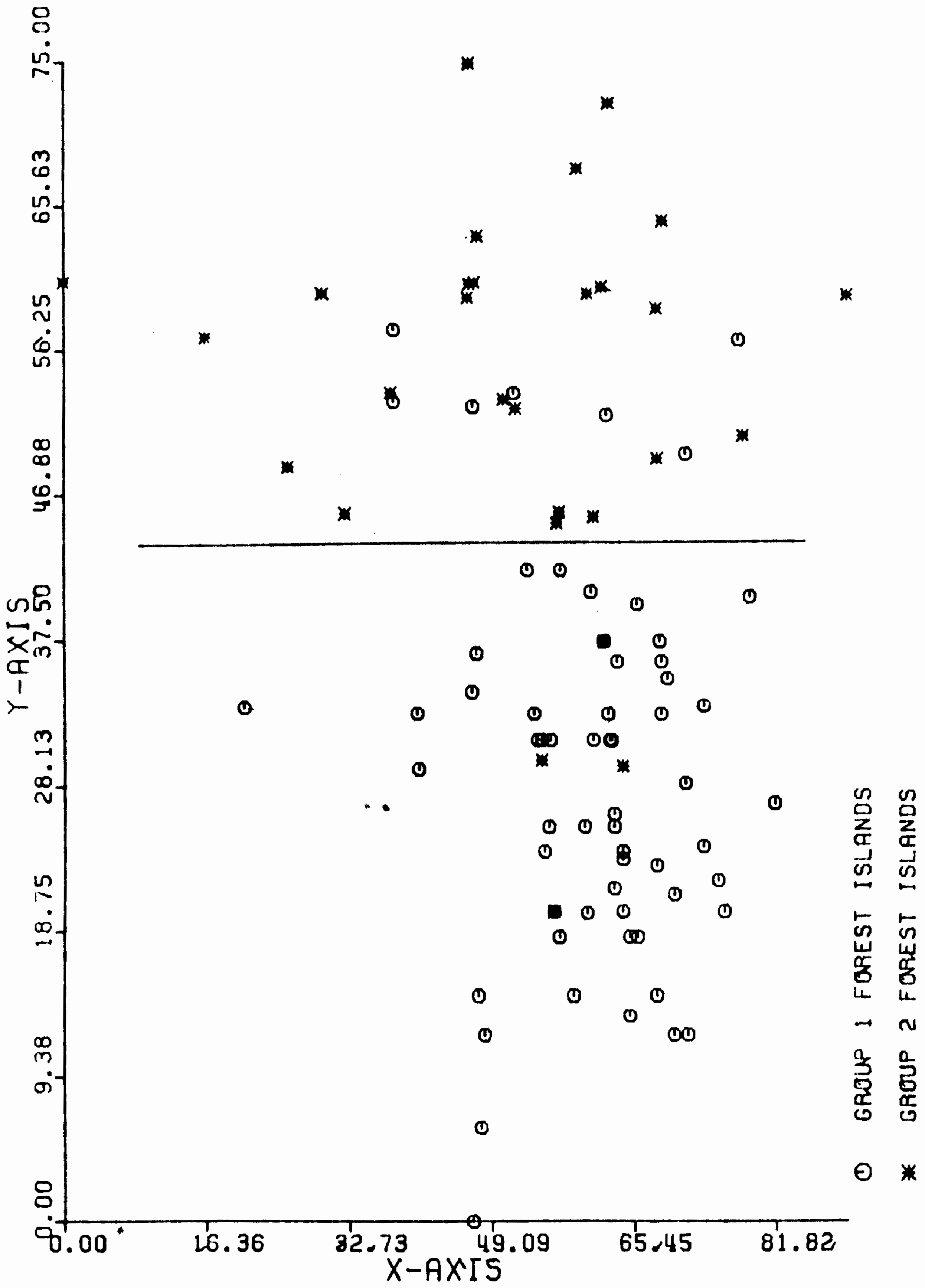


FIG. 4.5 - FOREST ISLAND ORDINATION - X/Z AXES

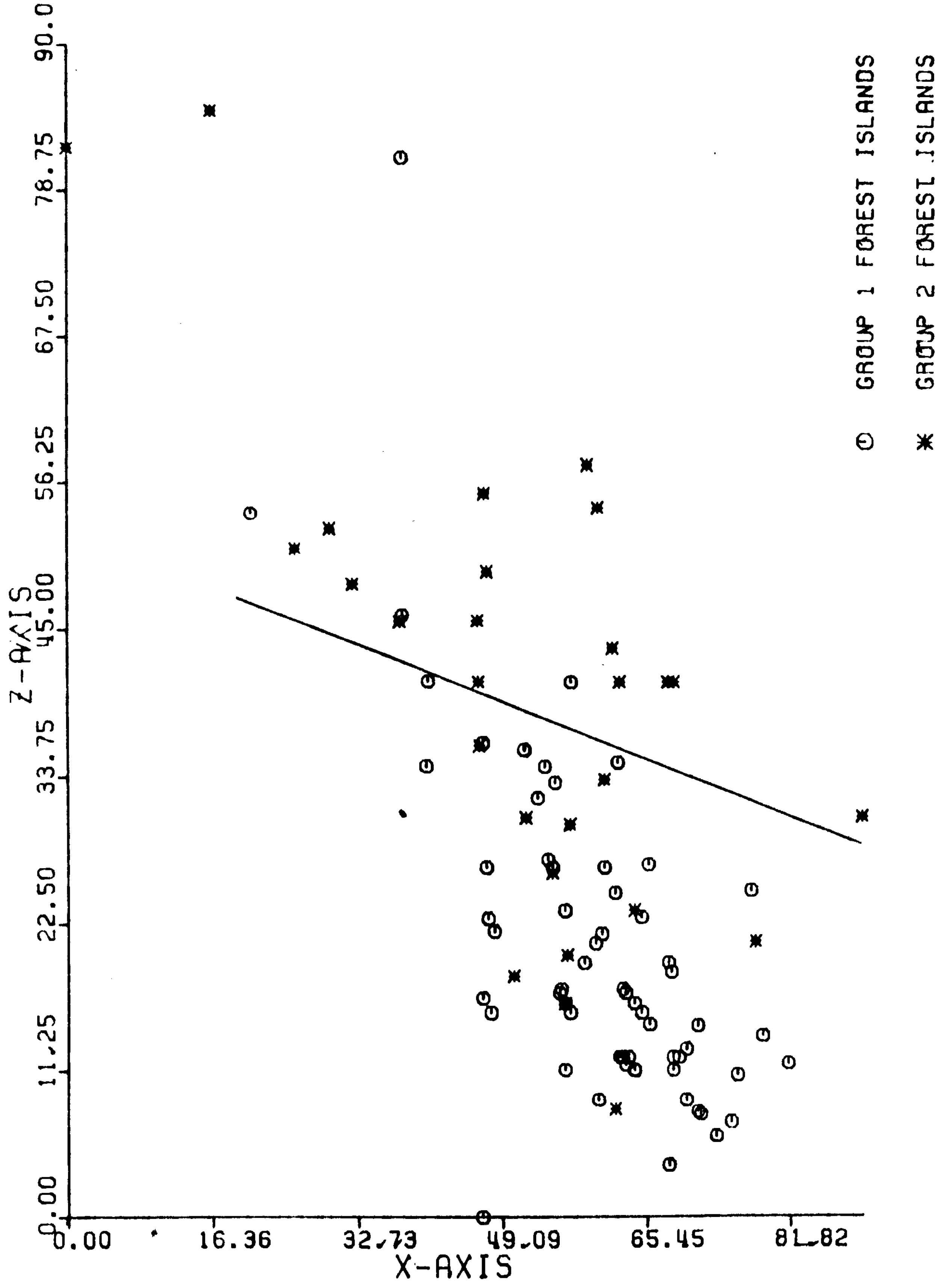


FIG. 4.6 - FOREST ISLAND ORDINATION - Y/Z AXES

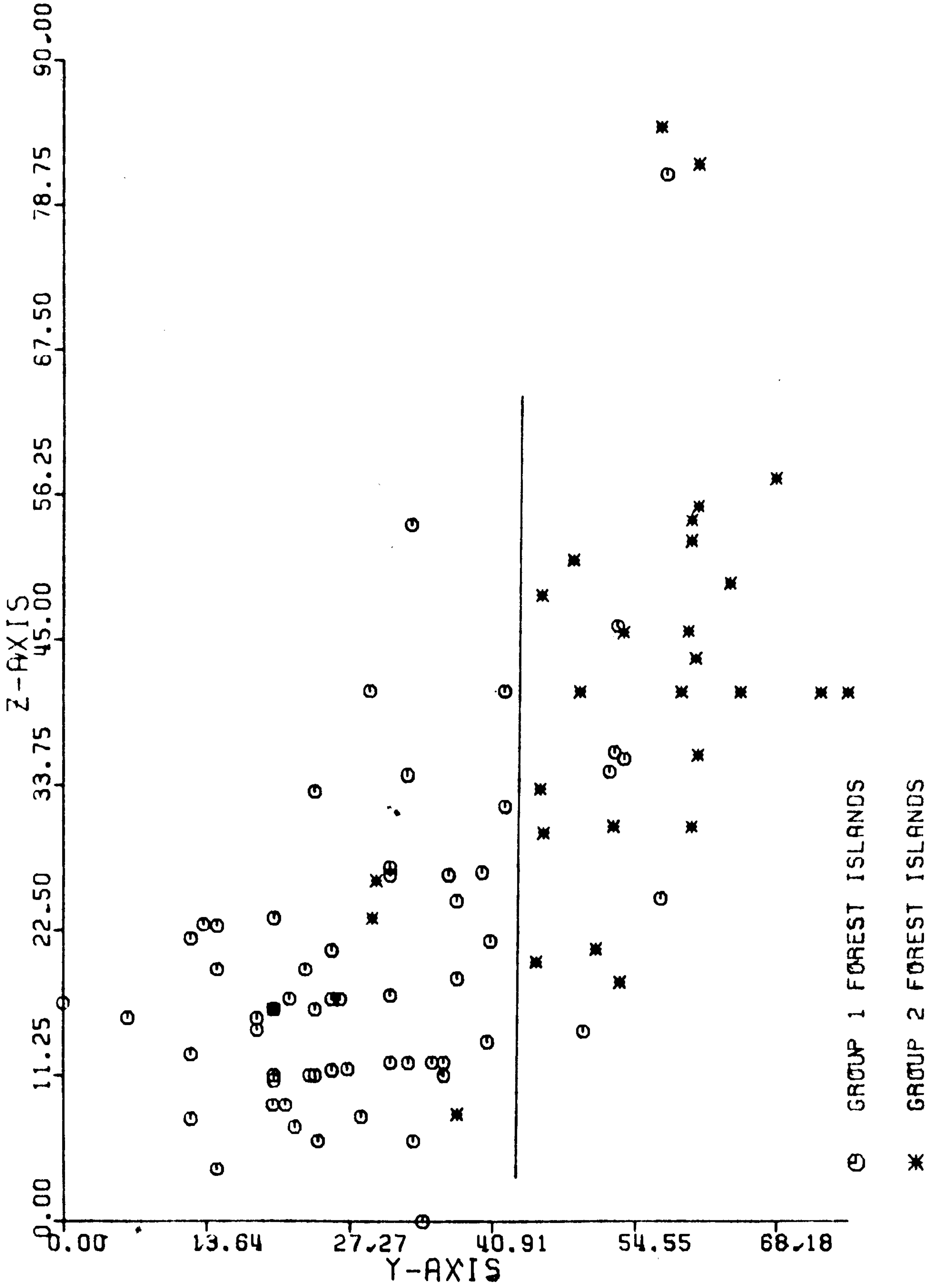


Table 4.6 - Group 1 Forest Islands - 53 species total

Species Name	Percentage Occurence
Phyllodoce empetriformis	98.6
Tsuga mertensiana	94.3
Cassiope mertensiana	94.3
Vaccinium deliciosum	91.4
Leutkea pectinata	77.1
Abies lasiocarpa	75.7
Vaccinium membranaceum	61.4
Vaccinium ovalifolium	38.6
Alnus crispa	27.4
Sorbus scopulina	25.7
Deschampsia atropurpurea	21.4
Rhododendron albiflorum	21.4

Table 4.7 - Group 2 Forest Islands - 75 species total

Species Name	Percentage Occurence
Tsuga mertensiana	96.7
Leutkea pectinata	80.6
Phyllodoce empetriformis	74.2
Abies lasiocarpa	67.7
Cassiope mertensiana	58.1
Erigeron acris	58.1
Vaccinium membranaceum	54.8
Valeriana sitchensis	51.6
Arnica latifolia	41.9
Polygonum bistortoides	38.7
Erigeron aureus	32.2
Trisetum spicatum	32.2
Luzula hitchcockii	29.0
Mitella breweri	25.8
Rhododendron albiflorum	22.6
Potentilla flabellifolia	22.6
Saxifraga ferruginea	22.6
Rubus pedatus	22.6
Deschampsia atropurpurea	22.6

The separation of the forest islands into two groups by the ordination process lends a little credibility to the habitat type classification system. However, it did not provide any insight into strengthening the species-area correlation. Species versus area regressions for these two groups provide R-squared values of 0.0257 for group one and 0.1999 for group two. This decrease in explanation could be due to the separation of habitat. With the number of habitat types partially explaining species diversity the separation of forest islands with a low number of habitat types into group one and those with numerous habitats into group two could have the same effect as isolating a single habitat. For a single habitat type there was no correlation of species number with area and there is no correlation between species number and area for the two groups.

Forest Island Age

The age of the subalpine forest was analysed in two ways. First, the maximum age of the trees in each forest island was used as an indication of the age of the island. The ages of the forest islands were then used in an attempt to explain species diversity. Second, the tree ages were used to assess the amount of tree regeneration and possible expansions of the forest islands. This information will be employed to discuss the equilibrium state of the forest islands.

Initially there appeared to be no relationship between island age and species number. A linear regression for these variables showed zero correlation between the two variables. An examination of the plot of this regression (Fig. 4.7) indicated that a second or third polynomial regression may produce a better relationship. This was not the situation, however, as neither of these regressions showed a relationship of greater than three percent. Therefore there was no direct effect of age on species number. However, by subdividing the data set into older and younger forest islands the correlations between species number and island area and species number and habitat were altered. Because a natural break occurred in the list of tree ages between the ages of approximately 150 to 200 years, the 200 year mark was taken as the dividing line. Included in the older age group were those forest islands composed only of younger trees but where large dead trees or stumps indicated a greater age. The results of the linear regression analyses using these two data sets are shown in Table 4.8 and plots of the species-area relationships are shown in Figures 4.8 and 4.9. When these results were compared to those for the undivided data set the species/habitat relationships were very similar but the species/area relationships showed big differences. For those forest islands aged less than 200 years there is an improvement in the species/area relationship. However, for the forest islands aged greater than 200 years, there is a large decrease

FIG. 4.7 - SPECIES NUMBER-FOREST ISLAND AGE RELATIONSHIP

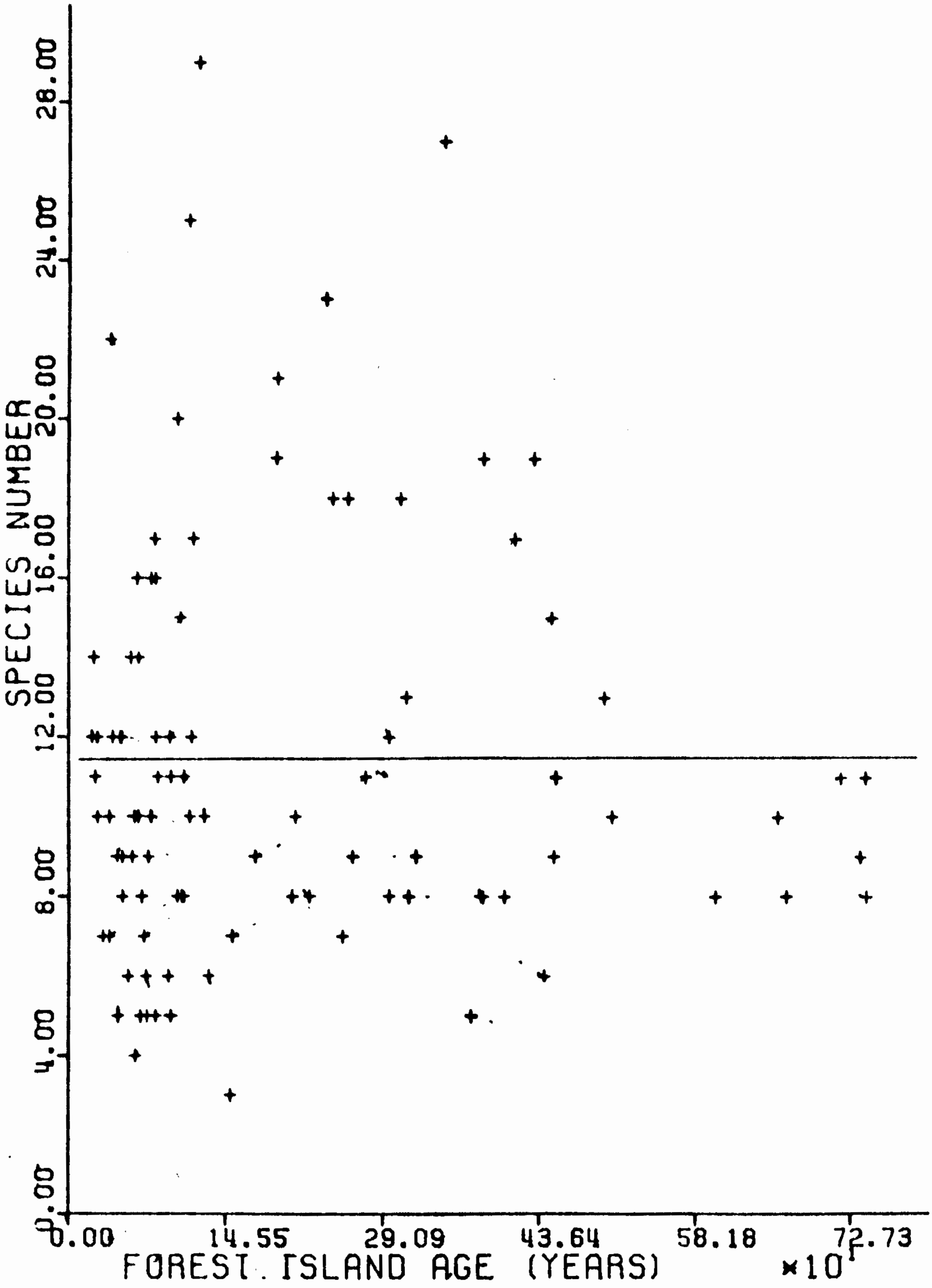


FIG. 4.8 - SPECIES NUMBER-AREA RELATIONSHIP - YOUNGER ISLANDS

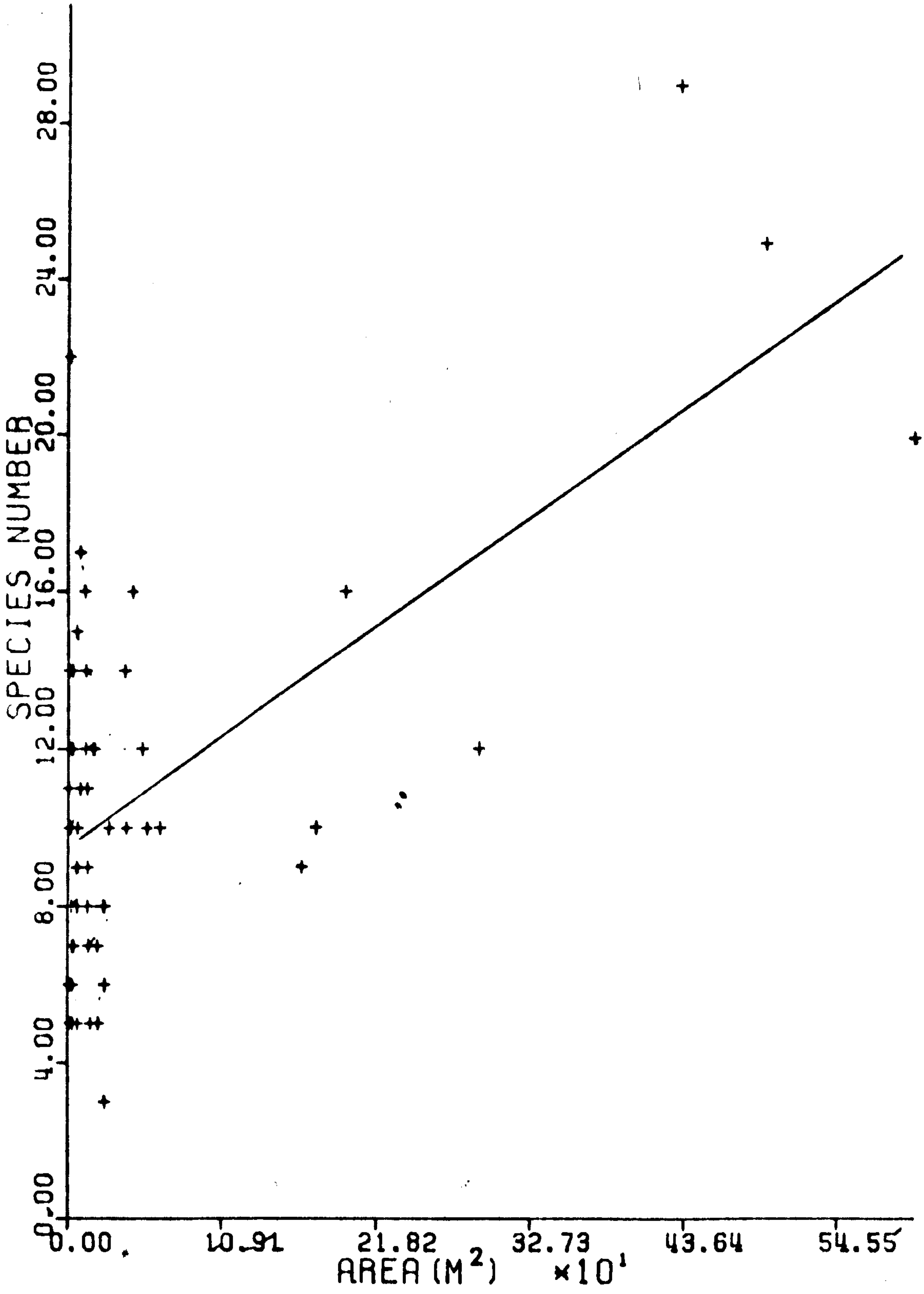


FIG. 4.9 - SPECIES NUMBER-AREA RELATIONSHIP - OLDER ISLANDS

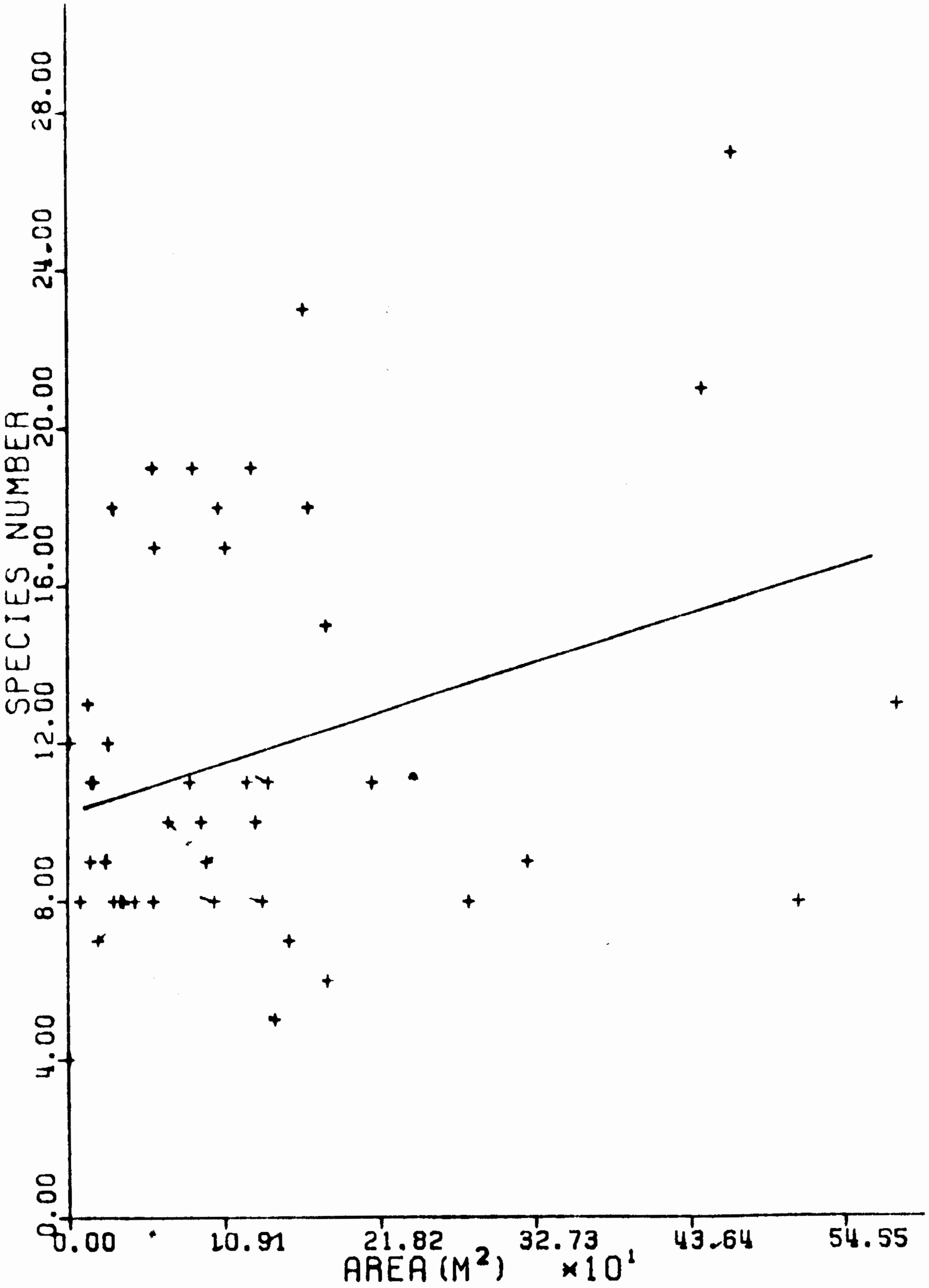


Table 4.8 - Regression analysis for the data set divided by forest island age

Type of regression	R	R-squared	F-ratio	Prob.
a) Forest islands less than 200 years				
species/habitat	0.6383	0.4674	37.12	0.0000
species/area	0.6153	0.3786	32.90	0.0000
b) Forest islands greater than 200 years				
species/habitat	0.5937	0.3567	23.84	0.0000
species/area	0.2887	0.0834	3.91	0.0544

in the fit of the regression line so that it is no longer statistically significant at the 95 percent level. This indicates that for the younger forest island there is a stronger relationship between species number and area. For the older islands, area appears to have little influence on species number. This may be due to the influence of the canopy cover and over a longer period of time as the trees get larger with age.

The development of a forest island may induce a sequence of events. As the tree seedlings are often invading meadow rather than bare ground a certain number of species will be present when the forest island is intially recognizable. Such a situation would not occur in the case of trees initially colonizing a bare patch of ground. such as a moraine. In the meadow situation few changes in species number could occur until the tree canopy develops enough to begin affecting the environment beneath it. During this development stage any change in the species composition would be due to a turnover in the meadow species. With the development of the tree canopy, the local extinction rate of the meadow species and the immigration rate of new species should increase. With the maturation of the forest the effects of shading and the modification of the forest floor may show a decrease in diversity, resulting from the removal of species which cannot tolerate the new conditions. There is also the possibility of a decreasing rate of establishment due to the poorer habitat beneath the canopy. This would also produce a decrease in species diversity with the aging of the forest.

The plot of species number versus age (Fig. 4.7) showed several interesting features. The graph can possibly be divided into three general domains. The first area includes those forest islands aged less than 200 years. These are the forest islands which showed a slight increase in the correlation between species number and area. With the exception of five forest islands their range in species number is between 4 and 17 species with the majority having less than 12 species. The five exceptions can be explained. The forest island with a very low species number has an uncommonly dense tree canopy and almost no understory. Three of the four forest islands with large species numbers also have a large number of habitat types present within them. This would tend to increase the species diversity of these islands. The final forest island is a small island located near a stream in the basin. The presence of many species common to stream edges increases its species number. With the exception of these five forest islands, in the remaining forest islands the characteristics of the alpine meadow or the harshness of newly colonized ground would be present.

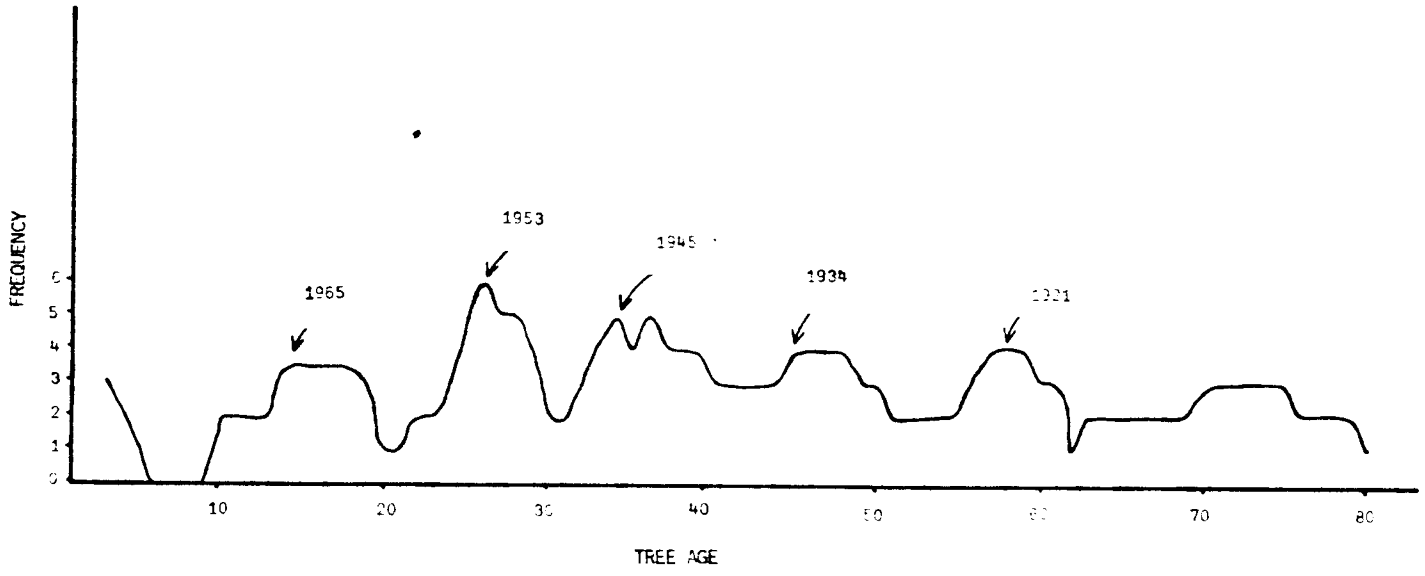
The second group are those forest islands with ages between 200 and 600 years. The species numbers in these islands fluctuates widely. This is possibly the time when the effects of the forest canopy are beginning to be felt and a turnover in species is occurring in an unpredictable manner.

The third group includes seven forest islands with ages over 600 years. The species numbers for these islands are clustered between 8 and 12. These could possibly be only those species with very broad habitat ranges. The species present in the very old forest islands are usually composed of very common species present in most islands and often found in the meadows.

Tree Age Analysis

The analysis of the age of the forest is important because it allows the state of regeneration and the possible equilibrium

Fig. 4.10 - Five Term Moving Average of Tree Ages



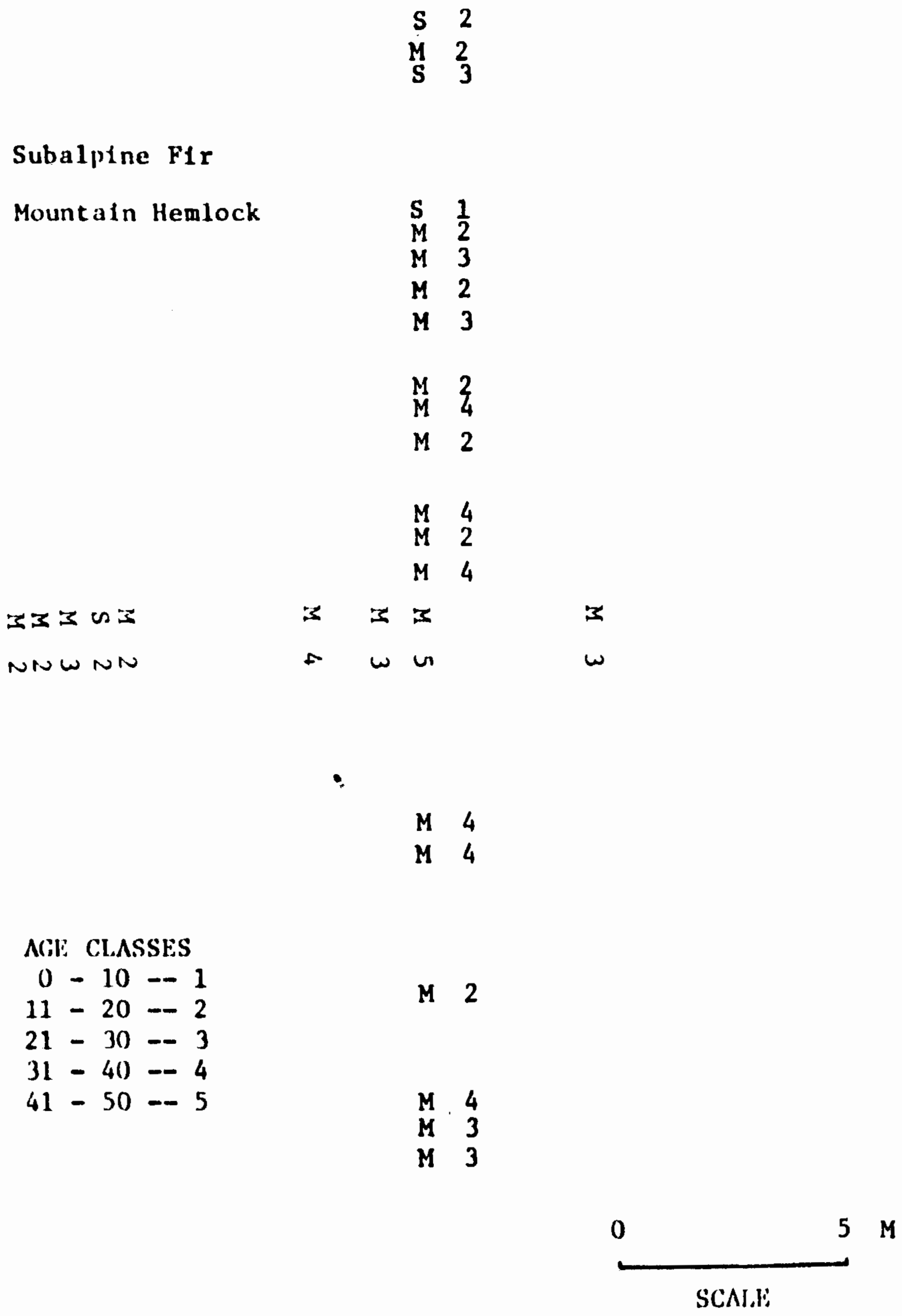
of the forest islands to be assessed.

Tree regeneration appears to be most successful in areas of lower elevation and less exposure. This is evident from the general lack of younger trees in the higher and/or exposed sites. When the complete list of tree ages was smoothed with a five year moving average, the establishment of tree seedlings appears to be irregularly spaced over time (Figure 4.10). Periods of seedling establishment appear to be present in the early 1960's, 1950's, 1940's, 1930's, 1920's. There is no temporal pattern visible before this, presumably due to the combined action of unequal tree survival, and coring and aging errors.

A number of forest islands were subjected to more intensive age sampling. When the positions and ages of the trees were plotted, several characteristics emerge. These are summarised in Table 4.9. Two different types of forest islands are present. Some forest islands contained a mixture of old and young trees while others showed large numbers of evenly-aged young trees. Figures 4.11 and 4.12 show characteristic examples of these two types of forest islands.

One of the common features exhibited by the forest islands was the lack of concentric age groupings with the oldest trees near the center and the youngest at the perimeters. This has previously been found (Lowery, 1972) and was used to explain the development of the forest islands. In those forest islands

FIG. 4.11 - TREE AGE DISTRIBUTION - FOREST ISLAND 11



S - Subalpine Fir

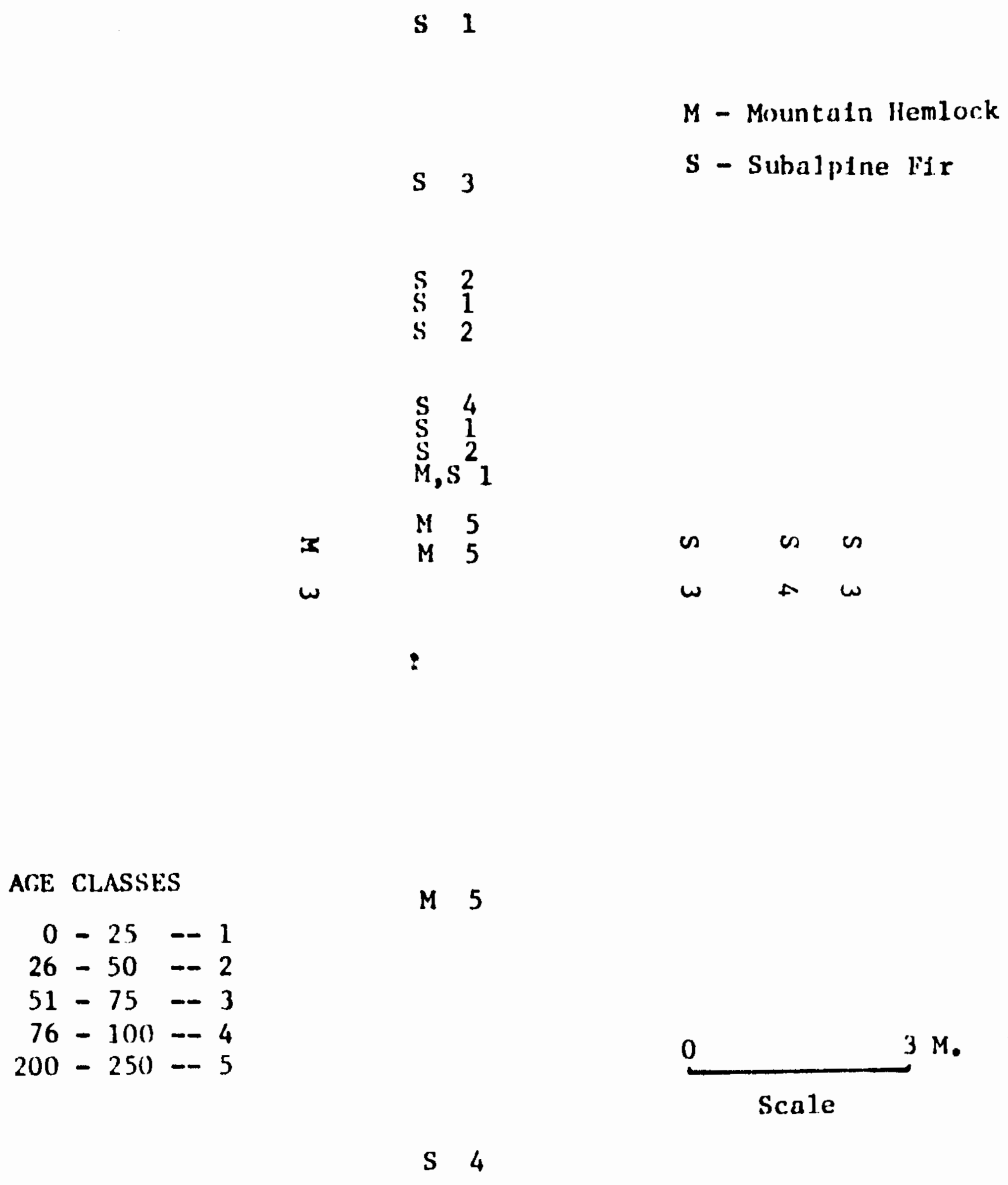
M - Mountain Hemlock

AGE CLASSES
0 - 10 -- 1
11 - 20 -- 2
21 - 30 -- 3
31 - 40 -- 4
41 - 50 -- 5

Table 4.9 - Regeneration characteristics of selected forest islands

Island No.	Oldest Tree Age	Seedling Growth	Expansion Evidence	Infilling Evidence	Elevation
1	331	poor	yes	no	1518 m.
11	42	good	yes	yes	1511
15	94	poor	yes	no	1718
22	115	good	yes	yes	1563
25	289	poor	no	no	1816
28	228	poor	no	yes	1836
42	277	poor	yes	no	1875
46	253	good	no	yes	1564
62	27	good	yes	yes	1494
81	245	good	yes	yes	1514
83	671	good	yes	yes	1513
85	383	good	no	yes	1521
86	69	good	yes	yes	1538
91	133	good	yes	yes	1670
96	669	good	yes	yes	1526
97	45	good	yes	yes	1513

FIG. 4.12 - TREE AGE DISTRIBUTION - FOREST ISLAND 81



studied there appears to be a mixture of tree ages throughout the forest island. This could mean that there has been an infilling with younger trees or a regeneration of the forests. It is possible that the forest islands were not initially established from a core of trees. Possibly there could be either a massive invasion of seedlings into a meadow area or a number of individual trees could become established followed by an infilling to form a larger forest island. The initial possibility is supported by the number of young forest islands with trees of the same approximate age. Support for the second suggestion comes from those forest islands which have widely scattered older trees with younger trees in between. Both types of forest islands were found in the area.

The scattering of young trees among old would seem to indicate that the forest islands are regenerating themselves. Similarly the presence of forest islands composed solely of young trees, usually less than fifty years of age, indicates the possibility of new forest islands becoming established.

One of the objectives in conducting the intensive tree coring was to detect a possible change in the area of the forest islands. A concentration of young trees or seedlings at the perimeters of forest islands would indicate a growth of the forest islands. In many of the forest islands examined there were a few younger trees present at the edges. This may indicate a very slow expansion of the forest islands.

The other possibility, a reduction in area, was not evident as there was no evidence of dead trees at the perimeters. The vast majority of dead or dying trees appeared to be very old.

To summarise the age analysis of the forest islands, it would appear that there is an ongoing regeneration in the present forest islands, the establishment of new forest islands and the possible expansion of both. The establishment of new trees does not appear to be evenly spaced over time but concentrated in a few years scattered over the age history. There was evidence for the regeneration and establishment of both mountain hemlock and subalpine fir.

The slow growth of the trees, by producing continual changes in the forest floor environment, and the sudden but major changes following the death of one of the larger trees, may never allow the species number in the forest islands to stabilize. The failure of variables such as island area, isolation, elevation and habitat to adequately explain variations in species diversity appears to suggest that the forest islands are in a nonequilibrium situation. This is further supported by the analysis of tree ages. The stronger correlation of species number to area for younger islands compared to older islands and the possible environmental changes that would accompany tree replacement in the forest indicate that there may be a number of equilibrium stages for the forest islands depending on the degree of development of the tree canopy. By looking at forest islands with a wide range in ages a general nonequilibrium situation could be produced.

Abbott and Grant (1976) think that nonequilibrium situations should occur in areas with strong climatic fluctuations. There is the possibility that small scale climatic changes have subtle effects on dispersal patterns and habitats which produce fluctuations in species number. Abbott and Grant's study was based on passerine birds on high latitude islands but the theory of climatic fluctuations should be transferable to high altitude conditions. In the subalpine, climatic conditions probably fluctuate as much or more than at high latitudes. These climatic changes in the harsh subalpine environment may prevent habitat saturation and equilibrium from occurring. The additional microclimatic and edaphic effects of a gradually changing tree canopy may re-inforce the nonequilibrium species number of the subalpine forest island flora which was induced by the climatic fluctuations. In this situation the equilibrium model would not be appropriate.

V. Conclusions

The equilibrium model of MacArthur and Wilson was found to have a number of shortcomings in its application to the forest islands of the study area. The central tenet of the model is that for an island of given area there is a temporally constant number of species of a given taxon that can occupy the island. This equilibrium number is determined by dynamic interactions between immigration of colonists and extinction of residents. The size of the equilibrium species pool is thus closely correlated with island area and its isolation from the mainland and other islands.

The weak correlation between species diversity and island size, in the study area, would seem to make the model inapplicable in this context. I suggest there are three reasons for this failure:

1. The effects of variable habitat utilization, compounded with the effects of habitat diversity
2. The effects of a fluctuating environment
3. The effects of incomplete biological isolation

The species-area relationship which was found to exist, appears to be the result of variable habitat utilization by the subalpine plant species. The relationship between habitat diversity and species diversity coupled with the colinearity of habitat diversity and island area produces the apparent species-area relationship. However, a relationship produced by habitat utilization rather than population dynamics is inconsistent with equilibrium theory. In addition, there are unpredictable increases in habitat diversity, which cannot be explained by area increases alone and this compounds the effects of variable habitat utilization. These increases in habitat diversity are related to the placing of topographic irregularities. Such features as streams, pondings, snow patches and avalanche slopes may have great influence over habitat diversity but they are not controlled by the area of the forest islands and help to explain the higher correlation of species diversity with habitat diversity than with area. The ordination analysis of the vegetation composition of the forest islands supports this conclusion. While no distinct clusters of forest islands are recognizable in the ordination, islands containing habitats produced by special topographic features were separated from islands that did not.

A second reason for the failure of the MacArthur and Wilson model may be due to the effects of a fluctuating subalpine environment, in terms of both local climatic trends and the microclimate of the island communities. Such a fluctuating environment could result in the forest islands not being in equilibrium. If a nonequilibrium state exists, then obviously a model based on a central tenet of equilibrium cannot be expected to mirror reality. A nonequilibrium situation could either result from the effects of the harsh physical environment in the subalpine regions, or from the continual microclimatic changes that accompany the aging of the forest islands. The climate of high-altitude areas is often unstable, fluctuating with year-to-year variations and also undergoing longer term warming and cooling trends. These instabilities accompanied by the relatively long life-spans and hardiness of the established subalpine flora may not allow the plant species to respond to climatic changes in time for equilibrium to be reached. This is a situation of no fixed equilibria, a hypothesis which Abbott and Grant (1976) made for high latitude islands. In both high altitude and high latitude areas climatic conditions fluctuate irregularly and so, correspondingly, do equilibrium sizes.

Changes which accompany the aging and development of the trees in the forest islands may also prevent an equilibrium species number being obtained. Such changes would be due to the development of the tree canopy, which would induce microclimatic variations on the forest floor and therefore create a continually changing understory habitat. Similarly, the manner in which the forest islands develop would have effects on equilibrium and species diversity. If a forest island gradually develops from a single or a small number of trees a progressively changing understory microclimate may be expected as the forest island expands. However, if the forest island develops from a group of seedlings all of the same age, the habitat changes may be of either a minor or a dramatic nature, depending on the age of the trees. Although nonequilibrium situations would be expected in both cases the species diversities may be substantially different. As there was evidence for both types of development in the study area this would suggest that there would be problems in applying the equilibrium model, particularly in attempting to fit a species-area relationship.

Finally, there may be effects of incomplete biological isolation. The meadows which isolate the forest islands are easily crossed by seed dispersal of many of the subalpine plants. As well, many of the understory species are able to inhabit both the forest floor and the meadows, thereby eliminating any isolation. The effect of the lack of isolation would be to increase colonization and possibly to inflate the species numbers present.

The study of the subalpine forest islands within an island biogeographic framework reaffirms some of the arguments which have been made against the blind application of the equilibrium theory to all situations. The species-area relationship, which forms the basis of equilibrium theory, has been frequently overemphasized and incorrectly accepted as proof of the model. A statistically significant species-area relationship may also be associated with a low degree of correlation between the other variables. In such a situation, it would be better to ignore the statistical significance and to search for a more realistic model. It would appear though that many researchers are continuing to apply the traditional model (eg. Holland and Jain, 1981) Furthermore the equilibrium theory may not be suitable for many habitat island situations as it tends to ignore important habitat characteristics such as the ability to support differing species diversities, which override many of the population interactions.

Any predictive model for the species diversity of the subalpine forest islands would have to include:

1. a measure of the influence and changes produced by the developing tree canopy over time
2. a method of assessing the importance of unique habitats to the total species composition of the forest island
3. a consideration of the importance of climatic fluctuations

Information on the climatic influence of the tree canopy could be obtained by taking climatic measurements beneath the canopies of forest islands of different ages. If the intervals separating the islands are short enough in terms of the island age, the climatic information should allow an assessment to be made of the changes that have occurred simultaneously with canopy development. The contributions from unique habitats might best be obtained by enumerating the species composition of the different types of habitats along with their physical conditions and properties. This type of information would generate a highly complicated model, but it appears that this is necessary as the previously used simpler models have been inappropriate.

Appendix A - Habitat Characteristic of Forest Islands

Column Headings

A - Forest Island Number
B - Species Number
C - Area (Square Meters)
D - Aspect (From True North)
E - Elevation (Meters)
F - Slope (Degrees)
G - Isolating Distance #1 (Meters)
H - Isolating Distance #2 (Meters)
I - Moisture Index
J - Habitat Diversity
K - Age of Oldest Tree (Years)
L - Maximum Tree Height (Meters)

A	B	C	D	E	F	G	H	I	J	K	L
1	5	144.4	144	1518	10	8.2	14.0	2	1	373	N/A
2	8	8.8	139	1521	4	4.9	17.4	2	1	207	9.1
3	11	16.4	139	1517	6	3.7	4.9	2	1	107	5.5
4	7	154.4	126	1532	18	4.0	11.0	2	1	254	10.7
5	20	600.6	156	1503	15	3.0	28.0	3	5	101	4.6
6	8	47.0	157	1540	24	3.0	6.1	2	2	384	15.2
7	8	512.4	183	1550	23	1.2	14.6	2	2	315	15.2
8	16	196.6	246	1553	36	7.3	11.0	3	4	77	3.7
9	12	12.6	251	1573	26	18.3	23.5	3	2	49	3.7
10	6	181.3	283	1563	10	9.8	18.3	2	2	441	15.5
11	12	52.8	273	1511	18	13.7	27.7	3	2	49	3.5
12	5	1.2	233	1562	13	1.8	109.7	1	1	46	1.2
13	27	466.6	271	1583	19	30.5	73.2	3	7	349	N/A
14	21	445.2	284	1641	27	6.1	9.1	3	3	194	10.7
15	10	29.2	205	1718	13	7.6	34.7	1	2	112	3.3
16	5	21.8	252	1714	25	3.0	7.6	1	1	67	3.8
17	5	7.3	158	1658	15	45.7	200.0	1	1	95	1.8
18	3	26.3	220	1691	17	2.7	4.6	2	2	150	7.6
19	6	26.3	248	1697	15	4.6	7.0	1	1	130	6.1
20	13	582.1	240	1530	35	3.7	6.1	2	4	497	16.7

21	9	26.3	283	1737	35	3.7	7.0	2	2	173	4.7
22	17	60.8	173	1563	23	8.5	15.5	2	3	116	4.2
23	9	14.3	188	1541	53	4.0	5.8	2	1	45	3.1
24	11	140.1	238	1827	9	1.8	3.4	2	2	N/A	N/A
25	13	14.2	203	1816	15	4.0	5.2	2	2	313	3.4
26	7	3.6	203	1816	20	2.1	3.0	2	1	38	1.0
27	8	14.3	202	1823	26	1.8	3.4	2	2	105	1.7
28	17	110.3	249	1836	24	4.3	10.7	2	3	414	3.1
29	8	280.5	256	1850	28	2.1	2.7	2	1	297	4.9
30	6	2.6	194	1862	8	2.4	3.4	2	1	93	3.3
31	15	180.6	195	1866	29	3.0	5.5	2	2	448	N/A
32	7	4.4	179	1863	33	3.0	4.6	2	1	32	1.2
33	5	3.6	208	1865	31	0.6	1.5	2	1	73	2.3
34	5	16.4	208	1866	31	1.5	3.0	2	1	81	2.1
35	6	3.6	225	1903	13	2.1	3.4	2	1	72	1.7
36	8	7.0	183	1976	23	2.1	4.6	3	2	107	2.9
37	6	1.2	257	1974	14	2.7	3.4	3	1	55	1.0
38	11	212.5	231	1948	12	2.4	7.3	3	3	275	3.4
39	7	21.4	276	1947	13	2.4	5.5	3	1	70	1.9
40	10	65.7	192	1920	37	9.1	13.4	3	2	N/A	2.9
41	8	25.2	225	1903	25	2.1	2.4	2	1	101	1.8
42	18	105.1	215	1875	26	2.7	6.7	2	2	308	3.3
43	4	0.7	213	1876	18	2.7	4.0	2	1	62	1.0
44	11	13.9	131	1885	43	4.6	7.6	2	2	95	3.9
45	29	433.4	148	1836	25	22.9	30.5	4	6	121	3.0
46	23	165.5	228	1504	40	3.7	4.3	3	2	239	10.1
47	8	32.2	218	1510	35	8.8	9.4	2	1	382	20.8
48	11	18.0	216	1496	35	8.8	10.7	2	1	718	N/A
49	19	128.7	216	1486	31	4.3	5.5	3	3	385	13.2
50	7	14.9	216	1489	30	5.5	19.7	2	1	N/A	2.0
51	8	59.6	232	1536	33	12.8	24.1	3	1	404	17.0
52	10	176.2	219	1638	21	10.1	12.8	3	2	77	3.1
53	19	59.4	261	1530	25	5.2	15.2	3	1	432	14.0
54	8	136.0	216	1531	21	11.5	21.3	3	1	601	N/A
55	9	26.6	224	1523	20	9.1	9.5	3	1	263	8.2
56	25	494.0	336	1501	30	2.7	6.7	2	5	112	7.7
57	10	56.2	203	1526	39	2.4	5.8	2	1	126	7.3
58	16	46.0	137	1530	29	2.1	6.7	2	2	81	4.9
59	12	2.6	164	1516	39	2.1	5.5	1	2	81	1.5
60	8	102.4	144	1501	10	2.4	6.7	1	1	223	10.0
61	10	0.8	289	1493	16	32.3	55.8	1	1	27	0.9
62	12	3.6	180	1494	6	23.5	32.3	1	1	27	4.0
63	11	0.7	0	1491	0	0.8	2.7	1	1	25	0.9
64	9	15.8	279	1565	26	10.1	10.4	2	1	450	10.7
65	11	85.3	146	1560	25	0.9	9.1	2	2	452	12.7
66	7	21.1	136	1573	23	2.4	16.2	2	1	152	10.0
67	10	41.6	136	1568	25	2.4	4.6	2	1	76	4.4
68	10	93.0	254	1572	41	3.7	10.4	2	1	659	15.8
69	9	322.1	230	1566	40	3.4	3.7	2	2	736	15.4

70	8	2.6	350	1563	49	3.4	13.1	1	2	68	1.1
71	8	38.5	185	1556	29	5.5	14.3	2	1	667	16.7
72	8	26.3	184	1558	31	5.5	7.9	2	2	50	3.0
73	11	125.3	275	1566	16	17.7	19.5	3	1	741	15.3
74	12	1.5	231	1539	27	8.8	11.3	3	1	41	5.8
75	15	6.4	241	1590	45	2.1	2.4	3	1	104	3.7
76	17	9.1	241	1582	45	2.1	2.7	3	1	80	4.3
77	16	12.3	213	1584	50	4.0	36.6	3	1	64	4.0
78	9	6.4	213	1579	39	9.4	13.1	3	1	50	2.7
79	11	88.1	0	1532	0	2.1	6.7	3	1	83	4.3
80	14	3.6	0	1530	0	2.7	7.6	3	1	65	2.5
81	18	168.5	127	1514	26	2.7	12.2	2	2	259	14.2
82	18	31.5	131	1481	25	12.8	15.8	2	1	245	7.8
83	12	291.1	132	1513	22	3.0	14.0	2	2	94	4.4
84	12	18.7	133	1512	22	3.0	12.8	2	1	114	13.3
85	10	70.2	130	1521	25	12.5	16.5	2	1	504	10.3
86	9	165.8	140	1538	15	1.5	6.1	2	2	74	1.8
87	9	96.7	131	1522	29	9.4	11.3	2	2	322	15.5
88	10	131.3	191	1522	19	6.1	9.4	2	1	210	15.9
89	14	12.8	234	1598	41	4.0	5.2	3	2	N/A	N/A
90	10	1.2	234	1598	5	5.2	5.5	3	2	38	1.5
91	19	87.5	226	1670	26	4.6	7.3	3	1	193	6.4
92	12	28.0	218	1670	32	2.1	11.6	2	1	297	26.6
93	22	1.8	0	1482	0	4.9	5.2	3	1	39	0.9
94	12	0.5	254	1487	17	0.6	2.1	1	1	22	0.5
95	14	0.9	328	1486	21	2.4	8.5	1	1	24	0.8
96	8	36.8	147	1526	25	8.8	11.0	2	1	742	18.0
97	12	17.7	100	1513	10	1.8	2.4	3	1	48	6.0
98	9	7.0	98	1515	11	1.5	4.9	3	1	59	3.7
99	14	40.7	144	1517	9	1.2	2.4	3	1	58	4.3
100	10	1.8	163	1517	10	2.4	3.7	3	1	65	2.7
101	10	7.0	163	1519	10	0.9	2.1	3	1	61	2.6

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