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PATTERNS IN THE DISTRIBUTION OF PLANTS AND ANIMALS ON LAVA FLOWS AND KIPUKAS IN SOUTHEASTERN IDAHO

by

Steven H. Lovejoy

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Date 4 June 1980

To the Graduate Faculty:

The members of the committee appointed to examine the thesis of Steven H. Lovejoy find it satisfactory and recommend that it be accepted.

Jay E. Anderson
Major Advisor

Graduate Faculty Representative

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ABSTRACT

Within the Craters of the Moon and the Wapi lava flows in southeastern Idaho are kipukas, islands of Snake River Plain habitat isolated by relatively barren lava. Physically the lava-kipuka ecosystem is strikingly patterned; in this research I examined biological patterns, seeking to elucidate patterns in the distributions of plants, small mammals, and reptiles.

Plant species composition and importance data were used to establish relationships among stands of vegetation through ordination. Aspect and soil texture were found to be significant variables influencing plant distributions on kipukas. Plots with relatively sandy soil were dominated by Stipa spp. and by Chrysothamnus nauseosus or C. viscidiflorus. In less sandy soil these species gave way to Agropyron spicatum, and to Artemisia tridentata under xeric conditions and to A. tripartita under relatively mesic conditions. As stands became increasingly mesic the amount of grass cover increased. On lava the cracks and crevices to which plants are restricted may have such favorable microenvironments that some other environmental variable may supplant moisture as the most important factor affecting distributions.

Correlation analysis revealed many pairs of associated species within study plots, apparently resulting from similar responses to environ ental gradients. For some associated pairs microdistributional factors may be important as well. No patterns relating the distribution of animals to the distribution of plants could be discerned.

The data were used to test predictions from the MacArthur-Wilson equilibrium model of island biogeography. The predicted decrease in number of species with increasing kipuka isolation was not confirmed;

lava does not serve as a significant barrier to dispersal for plants or for the most common small mammals. More isolated kipukas did have a greater density of animals, possibly because of limited or sporadic predation pressure. The predicted increase in number of species with increasing kipuka size was noted. The establishment of populations of less common small mammal species for which lava seemed to pose a barrier appeared to require a minimum size of suitable habitat that was close to the size of the largest kipukas that were trapped.

Although this research has identified some factors that are important in dictating patterns of species distributions, it has also successfully identified patterns for which the responsible environmental factors have not yet been discerned.

INTRODUCTION

The extensive lava flows of the Great Rift Wilderness Area of Southeastern Idaho form a broad and unique range of habitats, with correspondingly interesting plant and animal distributions. Notable in an examination of distributional patterns in this area are the numerous kipukas, isolated patches of undisturbed habitat surrounded by relatively barren lava.

A major objective of this study was to examine the applicability of the equilibrium theory of island biogeography to kipuka islands. Much theoretical and empirical work in community ecology has focused on explaining patterns in community structure and composition on the basis of insular effects. From extensive study of floral and faunal distributions on oceanic islands, a broadly accepted general theory of island biogeography has emerged (MacArthur & Wilson 1963, 1967; Simberloff 1974). According to this theory, the number of species that is maintained on an island is determined by a dynamic equilibrium established between immigration rate, dictated largely by the degree of isolation of the island, and extinction rate, which correlates with the area of the island. The applicability of equilibrial island biogeography has been extended to habitat islands, favorable patches of resources within a matrix of less favorable habitat; examples include caves (Culver 1970), mountaintops (Brown 1971), lakes (Lassen 1975) and host plants (Janzen 1968).

A second objective of this study was to ascertain if there is a

minimal area or minimal quality of any habitat characteristics that is required for the maintenance of populations of species found in the study area. One offshoot from the critical and empirical evaluation and extension of island biogeography theory has been recent interest in the function of an island's size as a determinant of the size and structure of its associated communities (Simberloff 1976; Forman, Galli, and Leck 1976). This subject has major practical applicability to conservation efforts (Simberloff & Abele 1976; Terborgh 1974; Diamond & May 1976).

A third objective of this research was to use ordination to reveal and to describe patterns in community structure and composition on the Great Rift lava flows and kipukas. Ordination is an alternative, non-insular approach to the study of distributions of species in communities (Gauch et al. 1977; Whittaker 1978). There are a number of techniques available for ordinating community samples, but basically all of the techniques work with species composition and importance data to establish relationships among stands. These relationships can then be analyzed in reference to the environmental variables that are likely to be influencing the distributions of species within the samples.

What little ecological work has been performed in the Great Rift area has occurred in the Craters of the Moon National Monument (Eggler 1941; Tisdale et al. 1965; Horning 1966; Ritchie 1968; Fuller 1969; Urban 1968, 1971; Urban & Bullard 1971); these studies have been largely descriptive. Yet, kipukas represent some of the last vestiges of the prehistoric sagebrush ecosytem, and offer opportunity to study

relationships among organisms in a system little influenced by man. The potential utility of Idaho kipukas for research has been recognized (Passey & Hugie 1962a, b; Tisdale et al. 1965), but not especially exploited. A detailed ecological purview of the Great Rift ecosystem was beyond the scope of this research; but a fourth objective was to gain first-approximation knowledge of the ecological relationships among plants and animals of the area.

These four objectives mesh nicely into what is perhaps the major reason that I undertook this project: to become more familiar and intimate with a magic and marvelous world.

THE STUDY SYSTEM

Area

The Snake River Plain extends across southern Idaho in a 650 km arc from the Yellowstone Plateau and the Teton Mountains to the east to the Oregon border to the west, where it merges with the Columbia Plateau (Fig. 1). The maximum width of the Plain is about 200 km in southeastern Idaho (Greeley & King 1975). Geologically, the Plain is an accumulation of Quaternary lava flows sandwiched with extensive loess deposition; this relatively flat structure is strikingly disrupted by scattered eruptive centers (Gibbs 1976).

There are five areas of recent volcanism, characterized by very fresh basalts, on the eastern Snake River Plain (Greeley & King 1975). Three of these areas - the Craters of the Moon lava field, the Wapi lava field, and the King's Bowl lava field - are associated with the Great Rift System. The Great Rift is a series of fissures that trend about 100 km southeasterly from the southern end of the Pioneer Mountains toward the Snake River (Prinz 1970); along the Rift are found some of the most spectacular volcanic formations in the continental United States. Some of the lava and surrounding desert lands along the northern portion of the Rift are incorporated into the Craters of the Moon National Monument. Outside the Monument most of the remaining land is federal land administered by the Bureau of Land Management.

Study Sites

The study sites were located on 16 kipukas on the Craters of the Moon and Wapi lava flows (Table 1): K1, K2, K4-K10 and K13-K16 are kipukas located in the northern study area, which was on the northeastern portion of the Craters of the Moon flow 4-16 km south of Arco and 5-20 km east of the Craters of the Moon National Monument (Fig. 2-4). K18 is about 21 km south of Arco (Fig. 2), and K20 is about 75 km south of Arco (Fig. 5); both are on the Craters flow. K25 is about 90 km south of Arco on the Wapi lava flow (Fig. 5).

Thirty-one study plots were established, from one to four on every study kipuka. Each plot was named with the number of the kipuka it was on and a number from one to four identifying which plot on the kipuka it was. Twenty-seven plots were established in the northern study area; plots 18.2, 20.1, 20.2 and 25.1 were located on kipukas south of this area. Four of the plots in the northern study area were established on lava sites: K3L, K21L, K22L and K23L (Fig. 3).

Research was concentrated in an area of limited extent to minimize the potential effect that differences in local climate might have on plant and animal distributions. The ease of access from Arco to a variety of kipukas of different sizes and degrees of isolation was an additional factor in this choice. There are larger and more isolated kipukas than the ones chosen; but sampling even one of these kipukas at the intensity demanded by the objectives of this study would have taken a team of field workers several weeks.

Lava

The best estimate currently available places the time of the opening of the Rift at King's Bowl at 2130 ± 130 years B.P. (Prinz 1970). Although the flows of lava probably did not occur concurrently along the rift, it is likely that the Craters of the Moon and Wapi flow events took place within a few hundred years of this date. The approximately 2000 years that have elapsed since the most recent flows have been insufficient to allow substantial vegetative recolonization. The recent flows stand out strikingly in satellite images of the Snake River Plain (Greely & King 1975) and in aerial photos. The flows are also distinctive from the ground. Rugged terrain and lack of economic values have discouraged human use and development sufficiently that the Bureau of Land Management has recommended that the majority of the land in the Wapi and Craters of the Moon lava flows be included in the National Wilderness Preservation System (Collins 1980).

There are two major forms of recent lava flows, a broken, jagged, fragmental type called aa and a smoother ropy or billowy type, generally known as pahoehoe (Eggler 1941). The two types of flows differ radically in regard to potential for travel or dispersal over them, at least for humans; to eliminate this complicating factor, all work was performed within pahoehoe flows.

Kipukas

A kipuka (from the Hawaiian word for window) is an area of older land surrounded by, but not buried by more recent lava flows. As lava flows, it loses heat and gas and becomes increasingly viscous. When a

section of a flowing front of lava no longer has the potential energy necessary to surmount a topographic obstacle, portions of the front may move around the obstacle. A kipuka is formed if the separated portions of flow rejoin on the other side of the obstacle.

The kipukas examined in this study fall into two broad categories, hill kipukas and hole kipukas. Hill kipukas were formed when the lava flowed around topographic high areas in the original landscape. These kipukas, often rising up prominently out of the lava, are visible from a distance. Examples include K8, K9, K10 and K18. (Appendix I is a verbal description of each kipuka.) K9 and K10 are particularly interesting because they represent the rims of craters built up during an earlier eruptive period. The recent lava washed up just high enough to breach the crater walls and inundate the craters without completely burying the rims.

If the topographic irregularity that caused the formation of a kipuka was not as high as the height of the viscous lava, then a hole kipuka resulted. These kipukas are one to four meters lower than the surface of the surrounding lava; at a distance they are generally not visible from the lava surface. Examples include K1, K2 and K4-K7. Hole kipukas are commonly found near the edges of lava flows, whereas more isolated kipukas are likely to be hill kipukas.

The kipukas of Area 4 appear to be intermediate forms between hill and hole types of kipukas; they are higher than the lava surface to the northeast but have high lava walls that climb up to the lava surface southwest. It is likely that lava flowing from the southwest encountered a ridge in the vicinity of Area 4. Lava moved around the area to the southeast and the northwest, and in addition, some lava

spilled over the top of the ridge at a few points, resulting in the distinct lava walls isolating kipukas within Area 4 from one another.

Vegetation and Substrate

Eggler (1941) examined the process of primary succession on lava of the Craters of the Moon flow. Organic breakdown of the lava proceeds at a very slow rate in the cold arid climate of the Snake River Plain. Soil accumulation depends primarily on the deposition of loess, but biotic input to the process of soil accumulation can be locally important, for example by pioneer plants acting to break the sediment-bearing wind and dropping organic material as litter. Soil accumulation occurs most rapidly in crevices and cracks. Microclimates, especially in terms of moisture relations, are generally most favorable for plant development in cracks and crevices as well. Dominant plants on the lava included *Potentilla glandulosa* Lindl. (gland cinquefoil)[1] and *Haplopappus resinosus* (Nutt.) Gray (Columbia goldenweed) in smaller crevices, and shrubs *Philadelphus lewisii* Pursh (Lewis' mockorange) and *Chamaebatiaria millifolium* (Torr.) Maxim. (fern-bush) in larger cracks. The vegetational patterns on kipukas are complex and heterogeneous, reflecting complex underlying edaphic patterns. The substrate on study kipukas varied from cinders on K8, to sandy loam on K1 and K20, to well-drained loam on K5, K6 and K7, to clay loam on K2 and K6. These substrate differences were reflected by vegetation.

The kipukas that I studied fell with the sagebrush-steppe vegetation zone (Kuchler 1975). The dominant shrubs were *Artemisia*

[1]Plant names follow Hitchcock and Cronquist (1973).

tripartita Rydb. (threetip sagebrush) and *Artemisia tridentata* Nutt. (big sagebrush), and the dominant grasses were *Agropyron spicatum* (Pursh) Schribn. & Smith (bluebunch wheatgrass) and *Stipa* spp. (needle-and-thread);[2] but the importances of these and of other plant species varied broadly from kipuka to kipuka and even within kipukas.

At the interface between recent lava and older, soiled areas was a zone of vegetational development I have termed edge. This zone varied widely in width, ranging from nonexistent to 100 m or more. The substrate was recent lava, but vegetational development has been accelerated; possible causes include increased contribution of the nearby biota to soil development and seed source, and increased available moisture due to runoff from the lava surface. The vegetation was often strikingly and thickly shrub-dominated, especially by *Artemisia tridentata, Chrysothamnus nauseosus* (Pall.) Britt. (rubber rabbitbrush), and *Chamaebatiaria millifolium;* also characteristic were *Cirsium utahense* Petr. (Utah thistle) and *Penstemon deustus* Dougl. (hot-rock penstemon).

Climate

The climate of the eastern Snake River Plain is characterized by hot summers and cold winters, with low total precipitation. The weather station nearest to the study areas is in Arco. The mean annual temperature at this station is 5.3°C. In the period 1969-1978 the minimum temperature in winter ranged from -24 to -38°C; the maximum summer temperature ranged from 33 to 36°C. Freezing temperatures can occur in any month. The mean annual precipitation is 25.3 cm; annual precipitation varies greatly, though, ranging from 16.0 to 33.0 cm during the past ten years. Precipitation also varies seasonally, with

[2]Most *Stipa* in the study area was *Stipa comata* Trin. & Rupr.; but, because early in the study *S. thurberiana* Piper (Thurber's needlegrass) and *S. occidentalis* Thurb. (western needlegrass) were misidentified as *S. comata,* the three species were treated as one taxon.

a peak in precipitation occurring during the winter months and a second peak occurring during May and June. The winter precipitation falls largely as snow. Although the amount of precipitation during the three years preceding 1979 was below average levels, precipitation during the first half of 1979 was near normal. (National Oceanic and Atmospheric Administration 1958-1979).

The kipukas of the northern Craters of the Moon flow study area are only 4-18 km from the Arco weather station, and are only 10-150 feet higher in elevation, so that the weather station and the northern kipukas should have very similar climates. K18, K20 and K25 are more distant, however; though the climatic patterns remain similar, values for mean climatic variables--especially precipitation--may differ considerably. The risk of interpolating climatic data for even short distances is attested by data from the Craters of the Moon National Monument headquarters, which is 550 feet higher in elevation than the Arco weather station but less than 25 km from Arco or any of the northern kipukas. Mean annual temperatures at the two stations are almost the same (5.6^{o}C at the Monument vs. 5.3^{o}C at Arco), but mean annual precipitation at the Monument is greater than that at Arco by a factor of 1.5 (39.8 vs. 26.6 cm). (National Oceanic and Atmospheric Administration 1958-1979).

METHODS

Plot Layout

Most small mammal, reptile, vegetation, and soil sampling took place within the organizational framework of study plots. Thirty-one study plots were established across 16 kipukas and four lava and edge sites, with from one to four plots on each kipuka (See Appendix I). The plots were chosen to represent a diversity of substrates, vegetative types, aspects, slopes, and kipuka sizes and isolations. On K20, and on each kipuka in the northern study area, I strove to establish enough plots to represent adequately the environmental diversity of the kipuka. The single plots established on K18 and K25, however, do not represent the range of diversities of these kipukas.

Each plot was established in an area subjectively judged to be vegetally homogeneous for an area of at least 20 by 50 m, the size of the plot. Each plot consisted of three 50 m lines 10 m apart, laid out with a compass and a 50 m tape; the orientation of the plot conformed with the perceived shape of the area of homogeneous vegetation.

For each kipuka plot, percent slope from each corner to the others was determined with an inclinometer; from these data and from the compass orientation of the plot the average slope and aspect of the plot were determined.

Three of the lava plots were located in edge-type vegetation. These areas are inherently quite heterogeneous; sharp changes from bare lava rock to well-soiled pockets took place within the distance of a meter. There was no uniformity of aspect or slope so these measures were not

taken. The fourth lava plot was located on a moderately flat and quite exposed lava surface.

Vegetation

Vegetation was sampled with a canopy-cover estimation technique (Daubenmire 1959). The percent cover of all perennial plants in a 0.2 by 0.5 m frame was estimated within six cover classes, with the midpoints of each class -- 2.5, 15, 37.5, 62.5, 85, 97.5 -- used to compute the mean; according to Daubenmire (1959), use of these classes greatly reduces the probability of a researcher making an error in assigning a value to an observed coverage, yet yields rather fine differences when the results from a number of frames are averaged (Hanley 1978). In all plots on kipukas, 30 frames were read: 10 were spaced five meters apart on each of the three lines of the plot. A taut steel tape was used to locate the sampling points. Although I tried to increase the sample size on the heterogeneous lava plots, the size and configuration of the areas to be sampled were limiting. Fifty frames were read on plot 23.1, the open lava plot, and 40 frames were read on plot 3.1, but only 33 frame placements were made on plot 21.1, and 29 were made on plot 22.1.

On each kipuka I recorded the presence of any plant species observed that was not noted during the schematic sampling; a walking survey of each kipuka was made in an attempt to develop comprehensive species lists that would be comparable among kipukas. The total species pool of the study area is not large; we encountered fewer than 80 species on lava or kipukas during the field study, and only 54 species were found in the plots, so I am reasonably certain that few plant species were overlooked on any kipuka.

Animals

A standardized snap-trapping regime was used to sample small mammal populations on the plots of all of the kipukas studied north of K18, as well as on lava plot 3.1. This system consisted of 18 trapping stations located 10 m apart, six on each of the three lines of each plot. Three Museum Special break-back snap traps and one McGill rat trap were placed at each station. Traps were baited with a mixture of rolled oats and peanut butter and left, unset, for three nights; on the fourth day the traps were rebaited and set. For the next three or four days the traps were checked for animals every morning and rebaited and reset as necessary. All captured animals were identified and weighed.

Two sizes of snap traps were used in order to increase the range of mammal sizes that could be sampled effectively. The use of four traps was inefficient in terms of the number of catches per trapping effort, because the probability of all of the traps being sprung on any one night is extremely low (Johnson 1977). I chose to use three Museum Specials, however, to see if I could discern differential use of microhabitats by rodents. At each station one Museum Special was placed directly under a shrub or in the greatest amount of cover available within 1.5 m of the flagged station center. A second trap was placed as far from cover as possible within the three meter in diameter area of the trapping station. The third Museum Special trap was placed at a location judged intermediate to the sheltered and open positions. I recorded the identity of the plant species closest to the cover and edge traps, and the distance from the nearest cover for the open traps. The type and location of trap was noted for each capture.

Because it seemed likely that kipukas might harbor small mammal species that were not encountered in the standardized trapping regimes, I used other traps on some kipukas in an attempt to increase the number of species captured. These traps included Museum Special and McGill traps placed on K2; additional Museum Specials located on lava near K8 and K10; and one Longworth and three Sherman small mammal livetraps placed on K8.

Reptile populations were assessed with unbaited pitfall traps. Fifty-eight pitfall traps consisting of buried no. 10 tin cans were placed on six kipukas. Three pitfalls 28 m apart were established diagonally across each plot on K1, K2, K6, K7, K8 and K9. Additional pitfalls were placed on K1, K3L, K8, and K9; the 12 additional pitfalls on K8 were conjoined with hardware cloth drift fences, each one meter in length and 0.2 m high. The pitfall traps were checked at irregular intervals not exceeding 10 days. Lizards captured were marked and released, but no lizard was ever recaptured.

During the field study I was able to observe and identify, independent of the trapping systems, individuals of a number of small mammal and reptile species. These sightings were recorded.

All mammal species names follows Hall & Kelson (1959); reptile species names follow Stebbins (1966).

Soil

Soil samples were taken from each of the 27 kipuka plots and in plot 3.1L. Generally two grab samples were made at representative locations in each plot. The locations chosen were devoid of vegetation and never directly under a shrub. Obvious organic material, stones, and gravel on the ground surface were brushed away; then a soil sampler was pressed

into the ground to a depth of 30 cm and a 30-40 g portion of soil was removed and placed in a plastic bag. These 30-40 g samples were pooled for each plot prior to analysis.

Plots 9.1 and 10.1 were heterogeneous and thus had no representative locations. Grab samples were taken at the vegetation-poor tops of the plots and at the vegetation-rich lower portions of the plots. To aggregate enough soil for the analyses, two top samples were pooled and three bottom samples were pooled.

The pooled samples for each plot were sieved with a 2 mm screen and dried at 80°C. Texture was analyzed by the Bouyoucos method (Bouyoucos 1939), following procedures outlined by McCreary et al. (1977). Percent organic material was estimated by baking 18-25 g portions of each sample at 450°C for 2.5 hours; the amount of the sample that was consumed represented organic material.

Other Sources of Data

Kipuka areas were determined by planimetry from United States Geological Survey 7½' series topographic maps. Comparison of the topographic maps with the aerial photos showed that representations of kipukas on the maps are accurate. Measures of kipuka isolation were also taken from topographic maps. These measures include shortest straight-line distance to mainland (off-lava) and minimum width of lava a colonist would have to cross, taking advantage of "stepping stone" kipukas. Huddle's Hole (Fig. 2), though a kipuka, probably functions like a mainland as a source of colonists to the much smaller study kipukas; I have treated it as a mainland in the calculation of kipuka isolations.

Analytic Techniques

Ordiflex, computer program CEP-25B in the Cornell Ecology Program Series (Gauch 1977), is a package of ordination techniques including Reciprocal Averaging (RA) and Principal Components Analysis (PCA). Ordiflex was used to examine patterns of distribution of plant species among stands. The major data set for all ordinations consisted of the cover values for each plant species, averaged for each plot and held in a 31 stand by 54 species matrix. Ordiflex was executed with Idaho State University's IBM 370/125 computer. Other manipulations of this data set and of other data were made on the University's HP 3000 Series III.

Stand environmental, vegetal, and small mammal variables (Table 9) were compared to each other and to stand position on PCA derived axes of variation with correlation coefficients computed with a program (LISA) available on the Idaho State University HP 3000. Axes of variation were compared to each other with Kendall's coefficient. Multiple regression analyses for kipuka diversity vs. kipuka size and isolation variables were also performed using LISA.

The diversity measures used were species richness; the Shannon-Wiener equitability index,

$$\text{Antilog } (H' = -\sum_{i=1}^{S} p_i \log p_i);$$

and the Simpson index,

$$C = \sum_{i=1}^{S} p_i^2;$$

p_i = relative cover value for plant species i, or p_i = relative abundance for small mammal species i (Whittaker 1975).

DISCUSSION OF METHODS

Homogeneity and Sample Size

The purpose of sampling the vegetation of an area is to describe the area quantitatively in terms of its vegetation. The conclusions that can be made as a result of sampling are highly dependent on the size of the area, the way that the area is defined, and the choice of a sampling scheme (Mueller-Dombois & Ellenberg 1974). It is generally accepted that the sampled stand must be homogeneous (Daubenmire 1968; Mueller-Dombois & Ellenberg 1974; Gauch 1977); this notion of homogeneity of vegetation needs to be examined in reference to the scale of perspective. A homogeneous monoculture becomes heterogeneous as soon as a second species is added to the system; yet the diverse vegetation of the Snake River Plain can be seen as homogeneous, in terms of its regular and recurring responses to edaphic variation, when viewed from the perspective of continental formations.

How one defines homogeneity, whether subjectively or objectively, depends on the purposes of the sampling. I approached the definition of homogeneity with two not totally compatible purposes, and the result is that the plots I chose are not comparably homogeneous. I wanted to characterize kipukas, not just arbitrarily defined plots. On K13, which showed no apparent environmental variation of significance to the vegetation, the kipuka and the plant community could be described with the same plot. (See Appendix I for descriptions of kipukas). K6 exhibited contrasts in environmental conditions, reflected in the observed vegetation patterns, but the four plots I established each described the vegetative response

to a distinct environmental situation and at the same time collectively characterized K6 successfully. On K14, however, I sampled across a topographic break with associated changes in both aspect and substrate: the majority of the plot was in the relatively flat, deep-soiled southern portion of the kipuka, but at the northern end of the plot the kipuka sloped down sharply, the soil was rocky, and the species composition was different. The species composition and cover that I used to describe this plot were an average of samples representing two different assemblages of species. From the perspective of small mammals, which probably ranged over the whole kipuka, this average is probably a representative characterization of the community. But in terms of the environmental factors dictating the distribution of plant species the average characterization is not quite like either of the real communities, and possibly the average hides some real distinction between the two.

The most heterogeneous plots in this study were 9.1 and 10.1, on two small and isolated kipukas in Area 3. On each of these kipukas well developed vegetation surrounded a rocky, sparsely vegetated central ridge that, particularly on K9, divided the kipuka into two prominent aspects. Significant environmental variables followed such sharp gradients that no combination remained constant over a large enough area to site a homogeneous plot, but I deemed characterization of the kipukas important enough to warrant establishing plots.

There is no satisfactory objective method to quantify homogeneity (Mueller-Dombois & Ellenberg 1974; Gauch 1977). Curtis (1959) used a chi square homogeneity test for each of his sample stands, comparing the density of dominant trees in four equal quarters of the stand. I

used a chi square analysis to compare the cover of dominant species in the three sampling lines of each plot, but in no plot for no species did the test show homogeneity. In an on-site inspection of the kipuka plots, however, an observer familiar with the Snake River Plain vegetation would conclude that at least some of them are homogeneous. Daubenmire (1959) considered this to be a sufficient criterion: "Objectivity....has no place....(in) selecting a unit of maximum homogeneity." (p.47).

A sufficient sample size is also difficult to ascertain objectively. The most commonly used procedures involve examination of "running means" (Mueller-Dombois & Ellenberg 1974), i.e., cumulative averages with increasing number of samples for species number, total cover (or frequency), and cover of dominant species (Mueller-Dombois & Ellenberg 1974; Daubenmire 1968). The most efficient and desirable sample size or minimal area for characterizing a plot is that at which the running mean approaches to within some arbitrarily fixed limit of variation from the mean that is established with the maximum number of samples.

Several workers have discussed efficient sample sizes for characterizing plant communities similar to the communities of this study (Daubenmire 1959, 1968; Hanley 1978; Wilkosz 1980). With these studies as guides, and desirous of maximizing the number of plots I could sample, I established, a *priori*, a sampling intensity of 30 placements per plot. For most plots sampled in this study, examination of running means of species number, total cover, and cover of dominant species appears to show reasonable stabilization of these statistics within 30 frames (Fig. 6-7). I have no data to extend the running means for any plot, however, so this conclusion is tentative.

The minimum number of samples necessary varies according to the

characteristics of the community being described. For instance, Hanley (1978) noted that the minimum number of samples necessary increased as overall cover decreased. Dahl (1960) developed a measure he called an index of uniformity. This index was derived from a Fisher et al. (1943) model relating species number to area or number of samples; the index is represented by S1/alpha, which is the ratio between mean number of species per sample and the Fisher index of diversity. Dahl (1960) published a chart that allows ready determination of S1/alpha when total number of samples, total number of species, and mean number of species per sample are known.

Dahl called his index of uniformity a measure of homogeneity, and found a close relationship between his index and Curtis' (1959) index of homogeneity among stands within a community. For each plot in my study, the index of uniformity value is closely correlated with total cover (Table 2). This agrees with the observation that in plots of low total cover, for example plots 1.1, 2.1 and 20.1, shrubs tended to be spaced several meters apart, with bare ground in between. Because the sampling area, 0.1 m^2, was small relative to the space between shrubs, within individual samples one usually found "all or none" vegetative cover.

Dahl's index of uniformity is useful because it reflects the distribution of vegetation from the perspective of the size of the sample area. Plot 2.1 is a virtual monoculture of *Artemisia tridentata*, homogeneous to the eye, yet its index of uniformity value is very low. The discrepancy suggests that the sample frame size is too small for the plots of low cover value. The same conclusion can be reached by following the guidelines for sample area size established by Daubenmire (1968), who suggested that a sampling area is too small if there are no

species in a stand being sampled that show a near-100% frequency of presence in samples. In only one of the 31 plots in this study was any species found in all of the samples (*Poa* in plot 25.1), and in ten plots - including all lava plots - no species were represented in more than 50% of the samples. The size of the sampling frame does not affect estimates of cover, but it does bear importantly on frequency data (Mueller-Dombois & Ellenberg 1974; Daubenmire 1968). Dahl's index of uniformity, which is a function of frequency, thus is also a function of sampling frame area. Analyses and interpretations based on the cover data -- including all ordinations -- are not affected by the small sample area size; but analyses of association among species must be interpreted carefully.

I remain with a less than satisfying grasp on the homogeneity of the plots I studied. The obviously heterogeneous plots 9.1 and 10.1 have been omitted from some of the analyses, so that the effectiveness of the samples as descriptors of the plots can be looked at; but the extent and direction of biases resulting from the possible non-homogeneity of some of the other plots are unknown.

Small Mammal Trapping

With the exception of exploratory trapping on K18 on July 17-18, all trapping took place between May 30th and July 9th. This interval corresponds to the period of peak overall rodent densities on the Snake River Plain (Johnson 1977). The probabilities of capture of different species vary with season (Johnson 1977), but I assume for comparison purposes that these probabilities did not change during the short time span over which I trapped. This is probably not exactly correct. The size of trappable populations of *Reithrodontomys megalotis*, *Perognathus parvus*, and *Spermophilus townsendii* show general reductions after May (Pitcher & Keller 1979; O'Farrell et al. 1975; B.L. Keller, pers. comm.);

relatively high densities of these three species remain trappable throughout June, however (Johnson 1977).

In all decisions regarding methodology I tried to ensure that the snaptrapping results from plot to plot be as comparable as possible. Prebaiting increases the rate of capture of rodents and decreases the variance in trappability (Smith et al. 1975), although it can also cause an influx of individuals from outside of the area. The area of effect of the trapping system is unknown and theoretically indeterminate, but the fact that most of the plots were virtually trapped out by the third or fourth day (Table 3) suggests that the traps were encountered by animals from within a fairly discrete area. Social interactions among small mammals can result in some species not being found in traps until the numbers of individuals of more aggressive species have been reduced (Smith et al. 1975). The low numbers of small mammals of any species caught beyond day two encouraged me to trap for only three days during the latter part of the trapping season. On only two occasions was a new species first captured beyond the second day: *Eutamias minimus* (least chipmunk) in Plot 1.2 and *Microtus montanus* (montane vole) in plot 7.1 were first caught on the third day.

Ordination

Ordination by compositional data, also termed indirect gradient analysis, is a useful technique for exploring patterns in phytosociological data (Peet and Loucks 1977; Whittaker 1978). Ordination is the process of arranging stands or species in relation to environmental gradients in order to develop a better understanding of relationships among stands and among species. Interpretation plays a critical role in ordination analysis (Gauch 1977). Ordination is simply a means of expressing variation; only

when this variation is interpreted relative to environmental variables does an ordination become ecologically meaningful (Peet & Loucks 1977). I used two ordination techniques: principal components analysis (PCA) and reciprocal averaging (RA). A description of how these techniques work is in Appendix V.

Choice of an appropriate ordination technique depends on the beta diversity of the system of which the plots are samples (Gauch et al. 1977). Beta diversity is the compositional difference among the samples of a set (Whittaker & Gauch 1978). PCA using community sets of more than moderate beta diversity - about three half-changes (HC) - can cause serious distortion in the resulting ordinations (Gauch et al. 1977; Peet & Loucks 1977; Whittaker & Gauch 1978). RA, on the other hand, remains reliable in ordering stands along a first axis of variation even at high beta diversities of 10 HC.

The beta diversity of a set of stands can be calculated from the degree of species turnover along the major axis of variation (Whittaker et al. 1979). The calculation uses the first RA eigenvalue (EV);

$$HC = 2.568\ EV/(1-EV).$$

The beta diversity of the lava-kipuka ecosystem is about 3.5 HC. This diversity is substantially lowered, however, by removing the four lava plots from consideration: the beta diversity of the kipuka plots is about 2.7 HC.

These beta diversities indicate that use of PCA to ordinate the lava and kipuka stands is inappropriate, and that use of PCA to ordinate the kipuka stands is only marginally appropriate. Therefore, interpretations that I make about patterns within the entire kipuka-lava system are based on RA ordinations. Most analyses of pattern deal with the subsets that exclude the four lava stands, however, because I only have measures for

environmental variables on kipukas.

I chose to use PCA for the kipuka ordinations because RA, unlike PCA, often does not provide ecologically interpretable axes of variation beyond the first axis it extracts (Gauch et al. 1977, Whittaker & Gauch 1978). Furthermore, PCA worked, according to the criteria that I established for judging successful ordinations. These criteria include 1) good dispersion of species and especially of stands along the extracted axes of variation, because, with nonlinearity of relationships presumed (Gauch 1977; Gauch et al. 1977), it is important to avoid the blurring of relative positions that may result when species or stands are closely clumped; 2) reasonable fit to the subjective impressions of ecological relationships that resulted from a summer of extensive fieldwork; and 3) a significant correlation with at least one measured environmental variable. As a further check on the PCA ordinations, I compared the first PCA ordination with the first RA ordination for each subset of the data that I studied. In all subsets that did not include the lava stands there was an extremely close correspondence between the two ordinations.

The true test of an ordination is its interpretability. Because my use of PCA on the data set leads to ecologically reasonable conclusions, I judge the techniques I used successful.

RESULTS AND DISCUSSION

Sixteen kipukas were studied, ranging in size from 0.16-68 ha and in isolation from 0.07-3.5 km from the nearest mainland (Table 4). A verbal description of these kipukas is in Appendix I. A tally of the number of plant species was made for all 16 kipukas; these totals ranged from 25-49 species (Table 4). There were from 3-7 small mammal species trapped on each of 13 kipukas, and the number of reptile species encountered on each of seven kipukas ranged from 0-3 (Tables 4-5). The total number of species encountered on lava or on kipukas during the course of the fieldwork included about 80 plants, 14 mammals, and five reptiles. Annotated lists of these species are in Appendices II-IV.

Average slope, average aspect, and texture and organic content of the soil were physical characteristics measured in the 27 kipuka study plots (Table 6). Fifty-four plant species were sampled in the 31 lava and kipuka plots; the number of species in individual plots ranged from 4-20 (Table 2). Of the four lava plots, three supported edge communities dominated by *Chamaebatiaria millifolium* and *Chrysothamnus nauseosus;* the fourth was dominated by bare lava rock and *Potentilla glandulosa; C. millifolium* and *C. nauseousus* dominated in plots 9.1 and 10.1 as well, along with *Leptodactylon pungens* (Torr.) Nutt. (prickly phlox) and *Agropyron spicatum.* Ten of the 25 homogeneous kipuka plots were dominated by *Artemisia tripartita* and *Agropyron spicatum;* four were dominated by *Artemisia tridentata;* three were dominated by *Chrysothamnus*

nauseosus, *C. viscidiflorus* (Hook.) Nutt. (green rabbitbrush), and *Stipa* spp.; five were dominated by mixtures of *C viscidiflorus*, *A. tridentata*, and *A. tripartita*; two were dominated by *Elymus cinereus*, Scribn. & Merr. (giant wild rye), *Stipa* spp., and *A. tripartita*; and the plot on the Wapi was dominated by *Balsamorrhiza sagittata* (Pursh) Nutt. (arrowleaf balsamroot) and *Poa* L. spp. (bluegrass). A list of the species found in each plot, ranked by cover, can be found in Appendix VI. The same data are presented differently in Appendix VII where, for each species, plots are ranked according to the importance of the species in the plot.

Eight small mammal species were captured in plots on 13 kipukas and one lava site (Table 7). Most abundant was *Peromyscus maniculatus* (white-footed deer mouse), which inhabited all kipuka and lava habitats explored. Plots on seven kipukas and one lava site were trapped for reptiles (Table 7). Two lizard species were captured, with most captures consisting of *Sceloporus graciosus* (sagebrush lizard).

ORDINATION

I examined ordinations of a number of subsets of the 31 stand data set. Following a detailed description of the interpretation of one such subset, I will discuss insights gained by comparing this interpretation to interpretations made for other subsets.

25 Stand Subset

The data subset for this analysis consisted of 25 stands--all but the four lava plots and plots 9.1 and 10.1, two obviously heterogeneous stands--characterized by the cover of the 28 plant species that occurred in at least five of the 25 stands. The first axis of variation extracted by PCA accounted for 49.8% of the total variation. Examination of the

species ordination (Table 8) shows *Artemisia tridentata* at one end and *A. tripartita* at the other, with all other plant species clustered between 44 and 64% of the distance between *A. tridentata* and *A. tripartita*. The stand ordination reflects the same relationships, of course (Table 9): three *A. tridentata* dominated stands fall within the first 9% of the ordination and, as one passes along the ordination, stands show decreasing cover values for *A. tridentata* and increasing values for *A. tripartita*.

The rather large first eigenvalue indicates that the factor or factors dictating the described arrangement of stands and species is of major importance to the community. Of the environmental variables measured, only aspect shows a significant correlation with the ordination (Table 10). The single most important factor influencing plant species distributions in the arid semi-desert of the Snake River Plain is probably moisture, and aspect is one indication of moisture availability. Aspect is a prime determinant of how much solar radiation impinges on an area. Changes in solar radiation are tightly associated with changes in evaporation from the soil, plant evapotranspiration, rate of snowmelt, and other factors relating to moisture relations of plants. The two species highlighted by the species ordination, *Artemisia tridentata* and *A. tripartita*, play similar ecological roles, except that *A. tripartita* replaces *A. tridentata* as the environment becomes less dry. It appears, then, that moisture is the environmental variable dictating the relationship of species and samples along the first axis of variation.

A note of caution about this interpretation is in order. Aspect is the only important feature relating to moisture relations recorded; yet it is not an entirely satisfactory measure. The three strongly *A. tridentata*-dominated stands represent the xeric extreme according to my interpretation of the ordination, but the three stands rank on the mesic end of the aspect scale. At least two possible explanations for this discrepancy exist: the ordination does not represent the relation of stands and species to water; or aspect is but one variable influencing plant water relations and other variables that were not measured, such as soil water capacity, are also operating to determine the expressed relationships. I prefer the latter explanation. It is hard to conceive that water might not be the environmental factor of prime importance when evidence of its importance is so clearly visible on the Snake River Plain.

Several other variables are significantly correlated with the ordination and thus are presumably moisture-dependent (Table 10). These include percent organic material in the soil, total canopy cover of plants, and diversity as expressed by the Shannon-Wiener and the Simpson indices. Cover and organic material are correlated with each other as well as with the ordination. They are indirect measures of productivity (Daubenmire 1968; Odum 1971); and productivity generally increases, in arid climates, with increasing available moisture (Whittaker 1975). Soil organic material may be a causal as well as a relational variable on this ordination, because

organic material can increase the moisture holding capabilities of a soil (Brady 1974). Plant species diversity increases as moisture becomes increasingly available (Whittaker 1975).

The second axis extracted by PCA, explaining a further 17.1% of the variation, groups *Artemisia tridentata* and *A. tripartita* together at one end of the species ordination and places all of the other species on the opposite 50% of the arrangement (Table 8). The species farthest from the *Artemisia* spp. are *Stipa* spp., *Chrysothamnus viscidiflorus, C. nauseosus, Balsamorrhiza sagittata,* and *Elymus cinereus.* The corresponding stand ordination (Table 9) places the three *A. tridentata* stands together with the most heavily *A. tripartita* dominated stand. Toward the opposite end of the arrangement stands have increasingly less *Artemisia* and increasingly more *Chrysothamnus.*

Soil texture appears to play a role in this ordination. Soil texture is a variable that influences plant moisture and nutrient relations. Coarser soils, with greater percent sand, are generally better drained, often droughtier, and are often nutrient-poor as a result of leaching (Brady 1974). Both percent sand and percent silt in the soil are significantly correlated to the ordination (Table 10) although inversely to each other: greater percent sand in soil is associated with increased cover of *Stipa* spp. and *Chrysothamnus;* increased silt is associated with increasing cover of *Artemisia.* Both the Shannon-Wiener and the Simpson indices of plant diversity are correlated with this axis as well as with the first

axis: sandier-soiled stands show greater vegetal diversity.

The third axis of variation has an eigenvalue representing 12.0% of the total variation among the stands and species. This ordination strikingly separates stands according to their grass cover, with *Agropyron spicatum* at one pole and *Stipa* spp. at the other. It is likely that some environmental gradient is responsible for a shift in dominance between the two grasses; unfortunately, I did not measure any variables that correlate with this axis. According to the criteria set up to assess ordinations, this arrangement is not successful.

It is interesting to note, however, that the polarity between *Stipa* spp. and *A. spicatum* evidenced in the third ordination can also be seen in the second axis (Table 8). Soil texture thus appears to be an important determinant of the distribution of the grasses. Yet, soil texture appears to be more important to the distribution of the major shrubs than of the grasses: when the stands are ordinated, in axis 3, along with what appears to be solely a grass gradient, then the correlation with soil texture classes disappears. Perhaps *A. spicatum* and *Stipa* spp. polarize in axis 2 as a result of their "associations" with *Artemisia* and *Chrysothamnus*, respectively. *Stipa* spp. and *C. viscidiflorus* seem to be similarly distributed within the area of this study, for instance, because of similar affinities for positions along some set of environmental gradients. But even so, the environmental variable that primarily accounts for the differences in distribution

of *C. viscidiflorus* and other shrubs need not be the same variable as the one that primarily accounts for the differences in distribution of *Stipa* spp. and other grasses. More data are obviously needed.

Juxtaposition of the first two stand axes gives a two-dimensional representation of patterns of distribution that accounts for 66.9% of the variation among stands and species (Fig. 8). A triangular arrangement of stands results, with *A. tripartita* the strongly dominant shrub in stands at the mesic, high silt/low sand vertex; *A. tridentata* strongly dominating in stands at the xeric, high silt/low sand vertex; and *Chrysothamnus* dominating stands at the high sand vertex. *A. spicatum* is the dominant grass at the high silt side of the graph, in both mesic and xeric stands where either *Artemisia* sp. dominates; *Stipa* spp. dominate in sandier-soiled stands. A similar juxtaposition can be made with the two species ordinations, resulting in a two-dimensional representation of relationships among species (Fig 9).

It is often useful to recognize a group of stands as some sort of community unit, and the two-dimensional arrangement of stands created by PCA can be used to classify stands of vegetation, but classification must be approached with caution, because species are distributed independently, and stands will intergrade continuously along environmental gradients rather than separating into quantifiably distinct groupings. Stands close to each other in the two-dimensional stand arrangement have many similarities, but they differ in important ways as well. Some of these differences are illustrated by comparing dominance-diversity curves. A dominance-diversity curve is an arrangement of the species in a community in

a sequence from the most important to the least important; it represents the way that the resources of a community are divided up by the species. The various shapes that the curves take express different patterns of competition and niche differentiation in communities (Whittaker 1965). The dominance-diversity curves for plots of three of the most prominent groupings (Fig. 10-12) show marked differences in importance relations. For instance, community resources are more equitably distributed among the species of intermediate importance in plot 16.2 than in plot 13.1, even though the two stands cluster very closely together and the amount of resource claimed by the dominant species in both plots (*A. tripartita*) is virtually identical. Differences in the dominance-diversity curves of *A. tridentata*-dominated stands (Fig. 11) and of *Chrysothamnus*-dominated stands (Fig. 12) are even more important.

Isolines that delineate areas of stands with similar values for given species can be drawn across the two-dimensional arrangement of stands. When this is done for the *Artemisia* species (Fig. 13), a distinct pattern is found, representing the responses of these two species to the environmental gradients represented by the axes of the graph. Although *A. tridentata* appears to respond almost entirely to the presumed moisture gradient along the horizontal axis, *A. tripartita* apparently responds to the sandier soils as dryer soils, with the result that the isolines slant diagonally.

Two stands fall off the triangle on the mesic side, stands 16.3 and 15.1 (Fig. 8). These stands support the greatest cover of *Stipa* spp. noted in any stand. *Stipa* spp. is associated with sandy soils,

which may be a result of its ability to germinate and emerge from deeper depths than other grasses, permitting its roots to remain in a moist environment below the rapidly drying soil surface (Hironaka & Fosberg 1979). But, although this explanation is supported by the soil textures of most stands in which *Stipa* spp. is more or less successful, the soils of stands 15.1 and 16.3 are less sandy than expected. The positions of these stands on the two-dimensional graph may reflect the association of *Stipa* spp. with *Elymus cinereus*, which also achieves its greatest cover in these plots; it appears that some unmeasured environmental variable affects the distribution of *E. cinereus* and *Stipa* spp. Only further data can reveal the nature of the association of *E. cinereus* with *Stipa* spp., and of both of these species with environmental gradients; but the anomaly noted here supports the earlier proposition that a soil texture gradient is not the only important gradient to which *Stipa* spp. responds.

Other Ordinations

Not all of the 31 study stands could be treated equivalently to the ordination analysis. The four lava plots were outliers, very unlike the other stands and thus likely to disrupt ordinations in which they are included (Gauch 1977; Whittaker 1978). Twenty-three of the 27 remaining stands were geographically clustered within a 16 by 6 km area, so that differences among these stands in macroclimate or in species source were minimized. Two obviously heterogeneous plots, 9.1 and 10.1, might complicate the interpretation of an ordination that included them if the sampled vegetation reflected responses to a conflicting combination of environmental variables.

By comparing ordinations resulting from the use of various subsets of the total data set, I hoped to assess how interpretations of patterns of species responses can be affected. The most conservative set of ordinations I examined used only 21 of the 31 stands. These ordinations did not differ significantly from corresponding axes derived from any other subset of stands except those including lava stands. Interpretations of patterns in species distributions, then, remain the same no matter which stands are involved.

The geographically distinct plots are 18.2, 20.1, 20.2, and 25.1. Plots 20.1 and 20.2 occupy reasonable positions in the two-dimensional arrangement of stands (Fig. 8) based on their aspects and soil textures and also based on their vegetative compositions. Although 20.1 is the only stand that is strongly dominated by *Chrysothamnus nauseosus*, this species ordinates closely with its congener *C. viscidiflorus*, and the values of environmental variables in stands supporting good populations of these congeners are comparable. Plot 20.2, located less than 100 m from 20.1, has strikingly different vegetation presumably related to edaphic differences. The soil of plot 20.2, although a sandy loam like that of plot 20.1, contained considerably less sand; enough less that apparently the soil was able to consolidate and to develop some structure and stability. Instead of the clumped pattern evident in plot 20.1, where most plants congregated beneath shrubs and only *Bromus tectorum* L. (cheat grass) was found between clumps, in plot 20.2 understory plants--and almost no *B. tectorum*--were scattered between *Artemisia tridentata* plants.

Here and there within this matrix of *A. tridentata* and apparently stable soil were pockets of loose, unconsolidated soil two to three meters in diameter; *C. nauseosus* and *B. tectorum* generally grew in these pockets.

When stand 18.2 is included among the stands being ordinated it assumes the mesic endpoint of the first axis of variation, supplanting 13.1. The vegetation reflects presumed mesic conditions--high canopy cover, large percent cover of *Artemisia tripartita*--yet the stand had a fairly xeric southeast facing aspect. Aspect can serve effectively as a relative measure of a stand's moisture conditions only when other important moisture variables like annual precipitation are assumed to be constant among stands. In this case it appears likely that a greater amount of precipitation falls on K18 than on the kipukas to the north. This hypothesis is reasonable with respect to the very localized differences in weather observed on the Snake River Plain (J. E. Anderson, pers. comm.). Furthermore, evidence supporting increased rainfall in the vicinity of K18 is offered by the plant species list. *Symphoricarpos oreophilus* Gray (mountain snowberry) is scattered across the kipuka and is occasionally found even on a south facing aspect, but this species is not found on any other kipuka I studied. The thickets of *Amelanchier alnifolia* Nutt. (western serviceberry) on the north facing slope of K18 are also unique within the study system. Both of these relatively mesic species are at the dry ends of their ranges.

The position of plot 25.1 in the stand arrangement graph, when considered with respect to the correlations of the axes with environmental variables, indicates that the stand is an anomaly. It is situated at

the sand end of the sand-silt soil texture gradient; yet its soil had a lower sand and a higher silt content than the soil of any other study plot (Table 6). This was the only plot that had noticeable cover of cryptogams on the soil. Floristically, the stand appears unique. Although there was no unique species, the combination of importances was very different than was observed elsewhere: *Balsamorrhiza sagittata*, *Poa* spp, and *Agropyron spicatum* shared dominance. As the only study plot located on the Wapi flow, plot 25.1 was geographically distinct from the other plots. Weather patterns were probably different, and other factors that affect patterns of species distributions were likely to differ as well.

The axes extracted by PCA using a data subset that included plots 9.1 and 10.1 were virtually identical to the corresponding ordinations that did not include these heterogeneous plots (Fig. 14-15). The two additional plots fitted into the middle of the first ordination. On the second axis, they established a new endpoint supplanting the sandy-soiled plots. Nevertheless, a plot of the stands against the two axes shows the same triangular arrangement. Visual inspection of the kipukas revealed two contrasting vegetational regimes: a rocky, sparsely vegetated zone and a zone of edge-type vegetation (Appendix I). The soil of the rocky zone was high in silt and clay and low in organic material (Table 6); the soil of the edge-type zone was very sandy and very high in organic material; but the plots ordinate as if they were completely sandy. The rocky zone, with vegetation of low cover value, was overwhelmed by the much higher values of the edge zone

vegetation in the creation of average stand values.

The first two axes produced by RA correlated tightly with those produced by PCA for all data subsets that did not include lava plots, although the percentage of the total variation explained by the PCA axes was generally about twice that explained by the RA axes. But RA and PCA ordinations that included lava plots differ greatly. In the two-dimensional stand arrangements resulting from PCA the lava plots cluster near the heterogeneous and sandy-soiled plots. Such an arrangement is an obvious distortion, because the lava plots are strikingly distinct from the kipuka plots, not only vegetally but probably in terms of the environmental factors of importance as well.

A two-dimensional stand arrangement based on RA shows the stand relationships more accurately (Fig. 16-17). The fact that the four lava plots are as unlike each other as they are unlike the kipuka plots compresses the kipuka plots onto one end of the first ordination. Despite the compression the directions of stand variation among kipukas, discovered in earlier analyses, can still be discerned: from xeric *A. tridentata* stands to mesic *A. tripartita* stands along one axis, and toward increasing sand content in the stand soils along the other axis. Whether lava stands bear the same relationships as kipuka stands to these two environmental gradients is unknown, because I have no measures for environmental variables in lava plots. But, if we assume that the same relationships do hold, two interesting observations can be made. First, the soil texture and moisture gradients are transposed; moisture appears to be of secondary importance to plant distributions on lava. Seconds, lava stands take extreme positions on both axes, lava stands are more mesic and are characterized by sandier soils.

Most plant species commonly found on lava are normally found at higher elevations where moisture is a less cricital factor than on the Snake River Plain. The success of these mesophytes on lava is due to the favorable microenvironment of crevices, where evaporation from the soil and transpiration are considerably reduced and precipitation is concentrated (Eggler 1941). Given the widespread existence of these conditions on lava, and noting the virtual impossibility of plant growth on lava other than in crevices, it appears possible that the most critical factor affecting distributions on lava is not moisture. Perhaps soil texture, or some other soil characteristic, is more important.

Analysis of relations among stands by ordination has successfully identified two likely sources of stand variability, water availability and soil texture. Water availability is correlated with plant diversity, plant coverage, and soil organic content. Soil texture -- which may relate to plant moisture relations or plant nutrient relations -- is correlated with plant diversity and cover, but not as strongly as is water availability. Certain key plants define stand positions along the ordinations. *Artemisia tridentata, A. tripartita,* and *Chrysothamnus nauseosus/C. viscidiflorus* define three vertices of a triangular arrangement of stands; a linear shift in importance from *A. spicatum* to *Stipa* spp. is superimposed on the triangular pattern.

The species in plots south of the northern study area appear to respond to the same environmental factors as do northern plants. Inclusion of plots that have been sampled in violation of strictures

against sampling heterogeneous plots, served in this case to strengthen rather than weaken the ordinations, although it is unclear what significance the position of the stands in the ordinations has relative to the true character of the plots. Inclusion of the disjunct lava plots seriously distorted the PCA axes, but the effect on RA ordinations was to compress kipuka plots away from the lava plots without disrupting their order. The ordinations are much more interpretable, though, without the lava plots. The major limitation to this analysis is the low number of environmental variables measured.

SPECIES RELATIONSHIPS

Plant Associations by Plot

Two species may be positively associated because one is dependent on the other or because both are responding similarly to a third factor in the environment. A negative association may be a result of spatial exclusion, some other form of competition, or allelopathy; or the two species may have differing environmental requirements (Goodall 1978). Any generalizations made about the relationship between two species, though, must include the area covered by the conclusions (Goodall 1978); all species on the Snake River Plain are positively associated if we consider all North American plants. Further consideration must be given to the size of the samples in which the species are located.

The vegetation sampling scheme of this study affords an opportunity to examine plant species associations from two perspectives. One approach looks at the association of species within the 20 by 50 m plots, which can be considered 1000 m^2 samples taken from the kipuka-

lava ecosystem. A second approach looks at the association of species within 0.1 m^2 sampling frames placed in the 1000 m^2 plots.

Associations of species within plots have been determined using correlation coefficients calculated from the species cover values within plots (Table 11).

The data set used for calculation of correlation coefficients was made up of the 31 species that were found in at least six different plots. There are 465 correlations possible. Twenty-four correlations would be expected to be significant at the .05 level on a chance basis; 50 significant correlations were observed (Table 11). The number of positive associations observed, 44, greatly exceeds the expected number, 12; but there are fewer negative associations than would be expected by chance alone, six versus twelve. The explanation for the paucity of negative correlations is that the low total number of occurrences of many species precludes any negative association between them (Agnew 1961). The actual expected number of negative associations, then, is somewhat less than 12.

The negative associations are readily explained on the basis of different distributions of species along environmental gradients. *Artemisia tridentata* and *A. tripartita* replace each other along a moisture gradient. *Penstemon deustus* is found in the cracks and crevices of lava while *Agropyron spicatum* requires deeper soils for success. Two of the four negative associations involve *Sitanion hystrix* (Nutt.) Smith (bottlebrush squirreltail). *S. hystrix* was not common in any stand; but it was most common in the sandier, *Chrysothamnus*-dominated plots, and on lava, where it was the most common grass. These preferred

habitats contrast with the stable, deep soils where *Agropyron spicatum* and *Artemisia tripartita* are in the greatest abundance.

All of the positive correlations are probably a result of species pairs responding similarly to some factor in the environment; there are no data to indicate otherwise. To aid in the interpretation of the positive correlations, I constructed a diagram of species relationships (Fig. 18) using the positive correlations between species to arrange the species (Agnew 1961). The purpose of this arrangement is similar to that of the PCA species ordinations: to look for evidence of patterns in the distribution of species by examining the relationships among species. This approach has both an advantage and drawbacks relative to the ordination by RA or PCA. Some sort of relationship among all of the species can be noted in the species relationships diagram, whereas both PCA and RA ten to push most species into the center of the ordiantion (e.g., Fig. 15) (Gauch et al. 1977). On the other hand, RA and PCA ordinations are more readily related to environmental variables; and distances between species in a species relationships diagram are not interpretable except perhaps when measured through correlated species.

Examination of the species relationships diagram (Fig. 18) reveals several centers of association. Edge species like *Penstemon deustus* and *Chamaebatiaria millifolium* are located to the left of the diagram; *Sitanion hystrix* is independently associated with *Chrysothamnus nauseosus*, reflecting *C. nauseosus'* dual roles as an edge species and as a member of sandy soiled stands. To the right of the edge species are taxa such as *Arabis* L. spp. (rockcress), **Phlox hoodii Rich.** (Hood's phlox), and *Calochortus macrocarpus* Dougl. (sagebrush mariposa), which are primarily

associated with the drier, not readily classified stands located below the central vertex of the two-dimensional patterns graph (Fig. 9). At the bottom of the diagram are the species that dominate the anomalous stands 15.1 and 16.3 -- *Elymus cinereus, Penstemon cyaneus* Pennell, (darkblue penstemon), and *Stipa* spp. Above them on the right is the largest cluster of related species, the species found in the stands dominated by *Artemisia tripartita* and *Agropyron spicatum.*

Three of the 31 species used for this correlation analysis are not shown in the diagram. The only significant correlation with *Artemisia tridentata* is negative. *Oryzopsis hymenoides* (R. & S. Ricker (Indian ricegrass) and *Chrysothamnus viscidiflorus* have no significant associations at all. *O. hymenoides* is a rare throughout the plots, whereas *C. viscidiflorus* is fairly uniformly distributed throughout the plots.

Other species have varying numbers of significant positive correlations. Most of the species that are significantly correlated to the largest number of other species are within the *A. tripartita* - *A. spicatum* cluster of species.

The diagram shows many chains of association. For instance, *Calochortus macrocarpus* is related to *Poa* spp., which is related to *Balsamorrhiza sagittata,* which is related to *Opuntia polyacantha* Haw. (prickly pear), which is related to *Crepis accuminata* Nutt. (longleaved hawksbeard); yet none of these species is directly associated with any other of the five species except through the linear chain of associations. The linear nature of these species associations suggests the importance of the independent response of species to changing values along environmental gradients: species will show some overlap, but generally

one species will be increasing in importance as another species decreases in importance when one moves along an environmental gradient.

Almost all of these chains of association close, so that the species relationships diagram is really an interlocking set of circles of species associations. The closures reflect the fact that a variety of environmental gradients are simultaneously affecting species distributions. A species may show an affinity for the end of one particular environmental gradient yet show an optimum response at the center of some other gradient. Detailed measures of a variety of environmental variables, in conjunction with a species relationships diagram, may be very useful in determining what these environmental gradients are.

Plant Associations by Frame

Most if not all significant associations within plots can be explained on the basis of macroenvironmental variables--such factors as precipitation or incoming solar radiation, for which average values can successfully characterize a plot. Analysis of species associations within 0.1 m^2 sampling areas is more likely to reveal micro-distributional similarities and differences between species. Interactions between species are much more likely to be shown by an analysis of associations within the smaller area as well. The analytical tool I used was a chi-square test of association: presence or absence of pairs of species within 0.1 m^2 areas were used to build 2 x 2 contingency tables. Significant associations were found for eight species (Table 12).

Artemisia tridentata is negatively associated with four species: *Agropyron spicatum, Artemisia tripartita, Chrysothamnus viscidiflorus,* and *Stipa* spp. This is interesting considering that *A. spicatum* is the

major grass species found in *A. tridentata* stands. The negative association with the shrubs is not surprising; spatial exclusion of one shrub by another is expected in so small an area. Other possible reasons for negative association include competition for light and for moisture, and allelopathy. *A. tridentata* leaves have a strongly inhibitory effect on the germination of grass seeds, although the importance of this inhibition has not been demonstrated in the field (Groves 1980; Hoffman & Hazlett 1977; Weaver & Klarich 1977). *A. tridentata* is also noted as a fierce competitor for water (Sturges 1977). The mechanisms that result in the negative associations of *A. tridentata* with the two grasses are certainly worthy of further study.

Artemisia tripartita and *Chrysothamnus viscidiflorus* also exhibit significant negative associations with other shrubs, as is expected. But, in contrast to its congener, *A. tripartita* is positively associated with *Agropyron spicatum* and negatively associated with *Poa* spp. *C. viscidiflorus* is negatively associated with *A. spicatum*. Many of the ways that a shrub can affect a grass or forb growing beneath it can be interpreted as being either positive or negative; which interpretation holds probably varies from one species to another. Shrubs supply shade, reducing sunlight available for photosynthesis but also reducing water loss. Shrubs may catch windblown seeds. The attraction of shrubs as cover for animals may lead to heavy grazing pressure on grass or forb individuals underneath the shrub canopy, but shrubs may protect the herbaceous plants from large herbivores. Shrubs drop much litter on the ground directly below the canopy, with concomitant effects on the soil. As a result, the moisture and nutrient holding capacity

of the soil may be increased, or allelopathic effects may be intensified.

Agropyron spicatum is significantly associated not only with the three shrubs but also positively with *Leptodactylon pungens* and negatively with *Elymus cinereus* and *Stipa* spp. *Stipa* spp. is significantly associated with *A. tridentata* and *A. spicatum;* these associations are negative. The lack of significant positive association with *E. cinereus* is a surprise, considering the close relationship seen between the two species in the PCA-derived species ordinations, but the number of stands in which *E. cinereus* was found is low enough that the limits of discrimination by a chi-square test may have been reached.

A comparison of associations determined from 1000 m^2 quadrat data with associations determined from 0.1 m^2 quadrat data shows (Table 12) that, although there are no reversals in association, some species pairs show shifts from non-association within plots to positive or negative association within 0.1 m^2 frames. Some of these shifts are trivial, for instance the negative associations of shrubs seen only within 0.1 m^2 quadrats, and demonstrate the importance of careful interpretation of association data. Examination of patterns of association at more than one level of analysis is useful to discriminate between trivial and non-trivial associations. But other shifts appear to be meaningful; they demonstrate the importance of micro-environmental factors to the distribution of plant species.

Artemisia

Three types of *Artemisia* were noted within the study area: *Artemisia tridentata* ssp. *wyomingensis*, *A. tridentata* ssp. *tridentata*, and *A. tripartita*. The subspecies of *A. tridentata* found in all but one

kipuka plot was *wyomingensis*. *A. tridentata* ssp. *tridentata* was found in only one kipuka stand, plot 8.4; but it was present on most kipukas as a component--sometimes a major component--of the edge community. The three sagebrushes take successive but overlapping positions on a moisture gradient (Hironaka & Fosberg 1979). Their response to a moisture gradient was illustrated on K8, where *A.t.* ssp. *wyomingensis* grew on the xeric south and west facing slopes, *A.t.* ssp. *tridentata* grew on the east slope, and *A. tripartita* grew on the most mesic north facing slope.

The two subspecies of *A. tridentata* were not treated as separate taxa when the ordinations were calculated. This results in a misleading cluster of stands in the two-dimensional arrangement of the 25 stand data set. Plots 8.2, 8.3 and 8.4 were ordinated together largely on the basis of similar cover of *A. tridentata*. These plots were fairly dissimilar in terms of aspect and vegetation, however; the *A. tridentata* ssp. *tridentata* of plot 8.4 was not the same taxon as the *A. tridentata* ssp. *wyomingensis* of plots 8.2 and 8.3

Although the three *Artemisia* types were often growing in close proximity, only rarely were they growing together; generally, edaphic conditions dictated discrete areas of dominance for each type. The distinct manner in which all three taxa segregated themselves out on K4 suggests a topic for future research. K4 was small, and almost round. Near the center of the kipuka was a rock outcrop; the soil was shallow near the outcrop, and appeared to get deeper further out toward the kipuka perimeter. *A. t.* ssp. *wyomingensis* was dominant in the center of the kipuka. Along the inside perimeter was a belt dominated

by *A. tripartita*. *A.t.* ssp. *tridentata* dominated the edge community. All three of these zones had remarkably discrete boundaries. One hypothesis for the segregation of *A.t.* ssp. *wyomingensis* and *A. tripartita* asserts that bedrock or a strongly developed clay horizon shallowly underlying the soil can cause the creation of a perched water table in the spring, with resultant poor root aeration conditions. The distribution of *A. tridentata* (ssp. *tridentata* or *wyomingensis*) and *A. arbuscula* is known to be controlled by the ability of *A. arbuscula* to tolerate poor root aeration conditions better than *A. tridentata* (Fosberg & Hironaka 1964). Perhaps *A. tripartita* requires deep, well drained soils, and only in the absence of such soils can *A. tridentata* ssp. *wyomingensis* prosper. The soils of the three stands most dominated by *A. tridentata* ssp. *wyomingensis* appeared to be poorly drained, although hard data are needed to support this contention. Both *A. tridentata* ssp. *tridentata* and *A. tripartita* are generally found on deeper soils than *A. tridentata* ssp. *wyomingensis* (Hironaka & Fosberg 1979), but the mechanisms for and the strength of these relationships have not yet been ascertained.

If *A. tridentata* ssp. *tridentata* had been treated as a separate taxon and positioned according to an RA ordination with all 31 plots, it would be with other edge species, perhaps somewhere between *Chrysothamnus nauseosus* and *Chamaebatiaria millifolium* (Fig. 17). In this position *A. tridentata* ssp. *tridentata* would be on the opposite end of the soil texture gradient from *A. tripartita*--if the gradient exists for edge species. The question of which of these two taxa is more mesic is hard to answer the basis of present data; but the ecological status of *A. tripartita* is considered a puzzle by others as well (Hironaka 1979). Clarification of the factors that segregate *A. tripartita* and *A. tridentata* ssp. *tridentata* in the

lava-kipuka ecosystem is yet to be achieved.

Small Mammals

This study has not shed very much light on the subject of species interactions involving small mammals. Small mammal diversity in plots was not significantly correlated with any of the PCA ordinations. There were no meaningful correlations of small mammal species with any plant species. Regressions of small mammal diversity on kipukas versus plant species diversity were not significant.

Heteromyids in desert ecosystems have been noted to forage within different microhabitats, presumably to reduce competitive interactions (Brown 1975). By setting equal numbers of traps in shrub, edge, and open microhabitats I attempted to ascertain where species are most likely to be encountered. The results suggest that partitioning of microhabitats may not occur in this ecosystem. Of course, the numbers of individuals captured for all species except *Peromyscus maniculatus* and *Eutamias minimus* are too limited for statistical treatment; but the ratio of captures of these two species in the three classes of traps is not significantly different from a 1:1:1 relationship.

P. maniculatus is a generalist (Baker 1968). It has not responded evolutionarily to competitive pressures by specializing, as most heteromyid species have done. It is not surprising, then, to see that it does not restrict its foraging to particular microhabitats, particularly in an ecosystem such as the lava-kipuka system where it has "the run of the house".

ISLAND BIOGEOGRAPHY

Theory

The theory of island biogeography (MacArthur & Wilson 1967) postulates that the number of species on an island is the result of an equilibrium between two counterbalancing forces, extinction and immigration (Fig. 21). Extinction has historically been considered an important process only on an evolutionary basis, until MacArthur and Wilson (1963, 1967) and others (Janzen 1968; Levins & Culver 1971; Horn & MacArthur 1972) hypothesized that extinction in localized situations is important in the development and maintenance of community structure. The basis for the community wide importance of extinction lies in population dynamics: populations fluctuate in size. Below a certain population level the population--and therefore that species in some localized area--will become extinct. Reestablishment of the species depends on immigration of enough new individuals (propagules) into the localized area. According to the equilibrium model, then, the number of species in an area depends on the factors that directly affect the probabilities of either extinction or immigration.

Extinction and immigration are time-dependent functions. It is not easy to demonstrate directly that these processes are recurrent on a short-term basis (although see Cairns et al. 1969, Schoener 1974, Simberloff 1976, Simberloff & Wilson 1969). Most support for the MacArthur-Wilson theory has therefore come from indirect evidence. This study has looked at a system of island-like patches at almost an instant in time, and thus direct demonstration of extinction or colonization has been impossible; but the data collected in this study can be used to test two predictions made by the equilibrium model.

Species-isolation Effect

The first major prediction made by the MacArthur-Wilson model concerns rates of colonization. Kipukas that are more isolated from a source of potential colonists will have lower rates of immigration than kipukas that are less isolated. According to the MacArthur-Wilson model, since populations periodically become extinct on kipukas, higher rates of immigration will lead to faster recolonization. The model predicts, then, that for a set of kipukas of similar size, the more isolated kipukas will have lower numbers of species. This prediction is not true for either plant species or animal species on kipukas (Table 13).

Application of the MacArthur-Wilson species-isolation model has rarely been made to plants (Simberloff 1974; but see Crowe 1979). This is probably because the persistence of individuals of perennial species is long relative to immigration rates. Only in systems with very broad barriers to plant dispersal or with short-lived plants dominant would the isolation effect be important. Certainly Snake River Plain vegetation and the system of lava barriers do not fit these models. Immigration of plant propagules into kipukas probably differs little from the cross-seeding that occurs among the heterogeneous habitats of the Snake River Plain.

One is most likely to observe an isolation effect with small mammals. Since this effect does not appear, it is of interest to examine the question of just how great a barrier to small mammal dispersal the lava is.

Based on where animals were captured (Tables 5, 7; Appendix III) I can make a rough evaluation of the degree to which the dispersal of each species is limited by the presence of lava. *Peromyscus maniculatus* (deer mouse) was by far the most common species trapped in any habitat, including on-lava sites; it comprised of 83% of all captures. *Neotoma cinerea* (bushy tailed woodrat) is ubiquitous; its distinctive urine markings were seen on lava at the perimeter of every kipuka. That it was captured only a few times reflects its restriction on or very near lava. *Sylvilagus nuttalli* (mountain cottontail) ranges widely over lava, for we saw cottontails and rabbit scat on lava far from any kipuka. Here, too, capture data are misleading: *S. nuttalli* was too large to be caught reliably by the snap traps. *Eutamias minimus* (least chipmunk) was observed a number of times on lava and was trapped more often than any species except *P. maniculatus*. *N. cinerea* nests and breeds on lava: the other three species listed above range freely over the lava and possibly nest and breed on lava as well. Although the low amount of vegetation on the lava may limit population sizes of these animals on lava, it apparently does not restrict their presence or their ability to disperse.

It seems reasonable to expect that these four species have a very low probability of extinction on kipukas, because there is a permanently ready pool of potential colonists in the lava habitat nearby ready to move into vacancies in the favorable kipuka habitats. Individuals of these four species made up over 96% of all small mammal captures. Obviously there will be no isolation effect if lava is not a barrier to the animals.

It is much less likely that the other species I trapped--*Perognathus parvus* (Great Basin pocket mouse), *Spermophilus townsendii* (Townsend's ground squirrel), *Microtus montanus* (montane vole), and *Reithrodontomys megalotis* (western harvest mouse)--actually reside on lava. A vole was sighed one night on lava less than 50 m from both a kipuka and the mainland; in no other instance were any of these species sighted or captured on lava. On the other hand, they were not very common on kipukas either: only 24 individuals of these four species were captured. On most kipukas only one individual of a species was caught. Given the high trapping intensity on kipukas, it is fair to assume that these single individuals are immigrants to the kipukas rather than representatives of established populations. There were 11 encounters of these four species during the study; only in four cases were we sampling a population (Table 14). The other seven encounters involved a single individual, despite exhaustive trapping of the habitats in which these individuals were found.

One would expect to see an isolation effect for the encounters of these immigrants. Seven individuals are not enough for a very firm conclusion, of course. It is suggestive, however, that four of the immigrants were captured in Area 4, sandwiched between two major species sources; one immigrant was captured on K1, less than 100 m from the mainland; and both of the immigrants caught on isolated kipukas were ground squirrels, which appear to disperse better than the other three rare species.

Isolation seemed to play no role in the number of reptile species present on a kipuka, either. But, in light of the observed abundance of the desert short-horned lizard, *Phrynosmoa douglassi*, on mainland

close to the lava's edge, its total absence on kipukas suggests that lava is more of a barrier to the dispersal of this slow-moving reptile than it is to the dispersal of its quicker relatives.

Density-isolation Effect

One interesting and unexpected isolation effect does exist: the density of animals is significantly and positively correlated with isolation (Fig. 22).

Increased density relative to mainland has been noted on some oceanic islands (MacArthur 1972). This may be related to the inability of members of island populations to emigrate; some species rely on emigration to maintain populations within stable limits (Krebs et al. 1969). But the density measure, individuals per 100 trap nights, reflects changes in the density of the common species, not the rare species, and the common species are not restricted by lava. Another explanation of increased density of oceanic islands involves release from the competitive pressure of absent species (MacArthur & Wilson 1967; Diamond 1973), but common species do not appear to face any different competitors on near kipukas than on more isolated kipukas.

Another possible explanation for the density-isolation effect assumes that space, not food, is a limiting resource. Perhaps animals nest in lava but forage communally on a vegetatively more rich nearby kipuka. Trapping the kipuka but not the lava would produce the impression of a high density, when, in reality, animals that resided elsewhere would be captured when they came onto the kipuka to feed. This hypothesis is supported by the fact that the very isolated kipukas K9 and K10 show

almost no trapping-out effect (Table 3): generally, when trapping small mammals, the number of individuals captured declines steeply from the first to succeeding days of trapping; but if animals being trapped were coming from outside of the trapping area this decline would not occur.

One other possible mechanism for increased density on isolated kipukas involves predation. Animal densities are higher on kipukas than they are on nearby lava, because of the relative abundance of vegetation on kipukas. As a result of this concentration of prey, predators in the area are likely to focus their attention on kipukas, and densities might be substantially reduced by predation. On the other hand, predation pressure is likely to be intermittent, particularly on small kipukas like K9 and K10. These kipukas are probably not large enough to support a snake population. We rarely observed birds of prey over the northern study area, perhaps because of the lack of roosts. Although coyotes appear to be periodic visitors on all study kipukas, none of the kipukas are large enough to support a resident coyote. So, between periods of possibly intense predation, kipukas may enjoy periods of total release from predation pressure. During these lulls, small mammal populations may be able to build up to densities that greatly exceed densities on less isolated kipukas, where predators may forage more frequently.

None of these explanations accounting for the density-isolation effect is completely acceptable on the basis of present data; certainly this phenomenon deserves further study.

Species-area Effect

The second major prediction of the MacArthur-Wilson model deals with rates of extinction. For most species, the larger a kipuka the larger the average number of individuals of any species that can live on the kipuka. If the MacArthur-Wilson model is correct, larger population sizes will result in noticeably lower rates of extinction. The prediction is that larger kipukas will have larger numbers of species. This prediction is true for both plant and animal species on kipukas (Fig. 23-24). The data can be transformed in several ways and still maintain the significant regression of species area on kipuka size. The power function model, linearly approximated by $\log S = \log k + z \log A$, shows the best fit for plants, while the untransformed model, $S = k + zA$, shows the best fit for small mammals.

Many workers have ascribed biological significance to the parameters associated with the power function model of the species-area relationship, $S = kA^z$, or with its linear approximation (Conner & McCoy 1979). The particularly examined parameter is z, the slope of the linear relation. The value of the slope for the small mammal species-area relation observed in this study, $z = 0.31$, falls within the 0.20-0.35 range commonly observed for island systems, and is much higher than the 0.12-0.17 range generally observed for the slope of the species-area relation among non-insular areas (MacArthur & Wilson 1967). The slope thus affirms the obvious; kipukas serve as islands of habitat for small mammals, with reduced rates of immigration relative to mainland habitat. In contrast, the value of the slope for the plant species-area relation is $z = 0.08$, which falls a bit below the range generally observed for continental areas. Kipukas do not represent island of habitat to plants.

This conclusion certainly corresponds well with the failure to observe an isolation effect for plants. The intrinsic significance of species-area slopes is currently in doubt (Crow 1979), but it still has importance as a means of comparing the species-area relation of kipuka islands to the species-area relation of other island and continental systems (Connor & McCoy 1979).

Although the MacArthur-Wilson theory predicts that the number of species on an island increases as the size of the island increases, this prediction is not unique to the MacArthur-Wilson model. Increase in species diversity with the increase in island area has been much noted historically (Simberloff 1974); furthermore, in non-insular situations as well the number of species increases with an increase in the area sampled (Oosting 1956; Mueller-Dombois & Ellenberg 1974). Three hypotheses have been proposed to explain the species/area relationship (Connor & McCoy 1979). The historical view is that as an area increases in size the variety of habitats increases; and since each habitat has its own set of species, larger areas have more species. The MacArthur-Wilson model shows that larger islands support larger population sizes, which in turn result in a lower rate of extinction and a higher number of species. Connor and McCoy (1979) suggest a null hypothesis: if species number in an area is controlled by passive sampling from the total species pool, then larger areas may receive larger samples and as a result contain more species.

Determining which of these hypotheses operates in the real world is a difficult task; probably all do, with one or another being more

important depending on circumstances (Connor & McCoy 1979). Data from this study can be used to support all three hypotheses. Certainly environmental heterogeneity increases with increasing kipuka size, simply because larger kipukas have more topographic variation. Support for the null hypothesis can be observed by looking strictly at the numbers of immigrants on kipukas of different sizes (Table 14). These immigrants have presumably reached the kipuka on which they were found by chance; nevertheless they show a species-area effect, indicating the kipukas are passively sampling small mammal dispersers.

The MacArthur-Wilson model is also relevant in accounting for the number of small mammal species on kipukas. This relevance is noted in an analysis of minimum area requirements necessary for maintenance of populations. Of the small mammal species observed on kipukas for which lava poses an impediment to dispersal, three species appeared to have had established populations: *P. parvus*, *S. townsendii*, and *M. montanus*. None of these populations was on a kipuka less than three hectares in size (Table 14). The species involved did not appear to be restricted to a particular type of habitat that was unavailable on smaller kipukas, nor did the increase in environmental heterogeneity on kipukas of larger size appear to be important to the individual species. Instead it is possible that these species need an area of at least three hectares in this ecosystem to support a large enough number of individuals to maintain a population. Perhaps those species that did not have populations on any of the study kipukas have minimum area requirements larger than three hectares.

The minimum size requirements of many species relate to energetics

and the available food resource. Species vary in the amount of food required for living and reproducing: larger animals require more food, as do metabolically more active animals. This might account for the absence of *Lepus californicus* (blacktail jackrabbit) and *Dipodomys ordii* (Ord's kangaroo rat) from all study kipukas. Energy transfer along a food chain involves the loss of some of the energy at every step; animals at higher positions in community trophic structures thus require more cumulative biomass to stay alive, and populations of such animals will require larger areas in which individuals can forge for food. The absence of the carnivorous *Onychomys leucogaster* (grasshopper mouse) might be explained by this reasoning. Snakes, too, were found only on those kipukas or kipuka clusters that are greater than three hectares in size (K8, K18, and in the vicinity of K13, K14, and K15).

Social behavior is another factor that plays a role in the determination of minimum area requirements; social behavior is to a large degree an evolutionary response to energetic considerations, of course. The home range of an animal is an expression of both the social and energetic factors, so that home range sizes, when known, are a rough indication of minimum size requirements for small mammals. Literature values for the home range sizes of two species not found on kipukas (1.3-1.4 ha for *O. leucogaster*, 2.7-4.6 ha for *D. ordii* (French et al. 1975)) are considerably larger than those for kipuka-dwelling *P. parvus* (0.05-0.4 ha (O'Farrell et al. 1975)).

Of course, alternative explanations exist for the absence of the small mammal species that were not found. There might be a lack of suitable habitat on kipukas for some species; for instance, *D. ordii* is generally associated with sandy soils for digging, and only one trapped kipuka met

this criterion. If the absent species was absent from the mainland immediately adjacent to the lava flow, there would be no source of immigrants to colonize kipukas. Lava might be a very effective, perhaps impenetrable barrier to some species. Probably the observed distribution of small mammal species is the result of a number of mechanisms such as these operating together.

SUMMARY AND CONCLUSIONS

1) Kipukas are islands of habitat, isolated by barren lava, within the Craters of the Moon and Wapi lava flows on the eastern Snake River Plain in Idaho.
2) During the summer of 1979, 31 study plots were established on 16 kipukas and four lava sites. Vegetation was sampled by a quadrat cover estimation technique. Small mammal populations were assessed with Museum Special and McGill snap traps. Reptiles were captured with pitfall traps. Environmental variables measured on each plot included slope, aspect, and soil texture.
3) About 80 species of perennial plants were encountered, 54 in the study plots. The dominant shrubs were *Artemisia tripartita* and *A. tridentata*. The dominant grasses were *Agropyron spicatum* and *Stipa* spp. Nine small mammal species and five reptile species were captured; 83% of the small mammals taken were *Peromyscus maniculatus*, and *Sceloporus graciosus* constituted over 65% of the reptiles caught.
4) Through ordination analysis, plant species composition and importance data were used to establish relationships among stands of vegetation. Aspect and soil texture were found to be significant variables influencing the distributions of species throughout the study plots.
5) The ordination-derived arrangement of kipuka stands, omitting lava stands, was presented in a two dimensional graph. One axis represented a presumed moisture gradient, the other a soil texture gradient. Based on this graph, four categories of stands could be identified;

the remaining stands were intermediate in character. The largest category had mesic stands with silty soils, dominated by *Artemisia tripartita* and *Agropyron spicatum;* these stands were characterized by high total cover of vegetation and high diversity. Three xeric stands, with soils with little sand, were dominated by *Artemisia tridentata;* total cover of vegetation was low. Three stands characterized by sandy soils were dominated by *Chrysothamnus* spp., *Stipa* spp., and *Balsamorrhiza sagittatta;* diversity and total cover were low. Two stands with sandy soils and very mesic aspects were dominated by grasses, particularly *Stipa* spp. and *Elymus cinereus;* diversity and total cover were high.

6) Ordinations that include the lava plots reflect the difference between lava plots and kipuka plots. Life for plants on a lava flow is so rigorous that it can take place only within cracks and crevices; but these microenvironments may be so favorable that some other environmental gradient may supplant moisture as the most important factor affecting distributions.

7) Three types of sagebrush were encountered: *Artemisia tripartita; A. tridentata* ssp. *wyomingensis,* the *A. tridenta* ssp. generally found in kipuka plots; and *A. tridentata* ssp. *tridentata,* which was rooted in lava cracks, particularly within kipuka edge communities. Factors controlling the distribution of these types, other than moisture, are unknown. One possible factor is differential tolerance of roots to conditions of poor aeration during the spring.

8) Correlation analysis showed that a number of plant species were more likely than not to be found in study plots with associated

species. These associations appeared to be a result of the similar responses of associated species to environmental gradients.

9) Chi-square tests of association identified species pairs that were associated as a result of microdistributional factors. *Artemisia tridentata* and *Chrysothamnus viscidiflorus* were negatively associated with *Agropyron spicatum*, whereas *Artemisia tripartita* and *A. spicatum* were positively associated.

10) No correlations of small mammal species with plant species were found. Small mammal diversity was not related to plant diversity. Systematic placement of snap traps revealed no patterns of microhabitat use.

11) The data were used to test four predictions derived from the MacArthur-Wilson equilibrium model of island biogeography. According to this model, the number of species on an island is the deterministic result of a dynamic equilibrium between two counteracting rates: immigration, which is a function of island isolation, and extinction, which is a function of island size.

12) The number of plant species on a kipuka did not depend on how isolated the kipuka was; this result is contrary to a prediction based on the MacArthur-Wilson model. The probable reason for this result is that lava poses scant barrier to plant dispersal, so that the persistence of individuals of perennial species is long relative to immigration rates.

13) Contrary to prediction, the number of small mammal species on a kipuka did not depend on how isolated the kipuka was. Data indicate that, although the dispersal of some species was restricted by lava, other species were not, and these species made up over 96% of all small mammal captures. Considering only the 24 captures of individuals of species that were restricted by lava, there was an isolation effect.

14) The number of plant species on a kipuka depended on the size of the kipuka. This result is as predicted by the MacArthur-Wilson model. Other models can also account for this relationship; notably, the increased plant diversity of a larger kipuka may have resulted from an increased environmental diversity, which was observed in the study areas.

15) The number of small mammal species on a kipuka depended on the size of the kipuka, as predicted by the MacArthur-Wilson model. Other models can also account for this relationship. The species-area affect was heightened when only those small mammal species restricted by lava were considered.

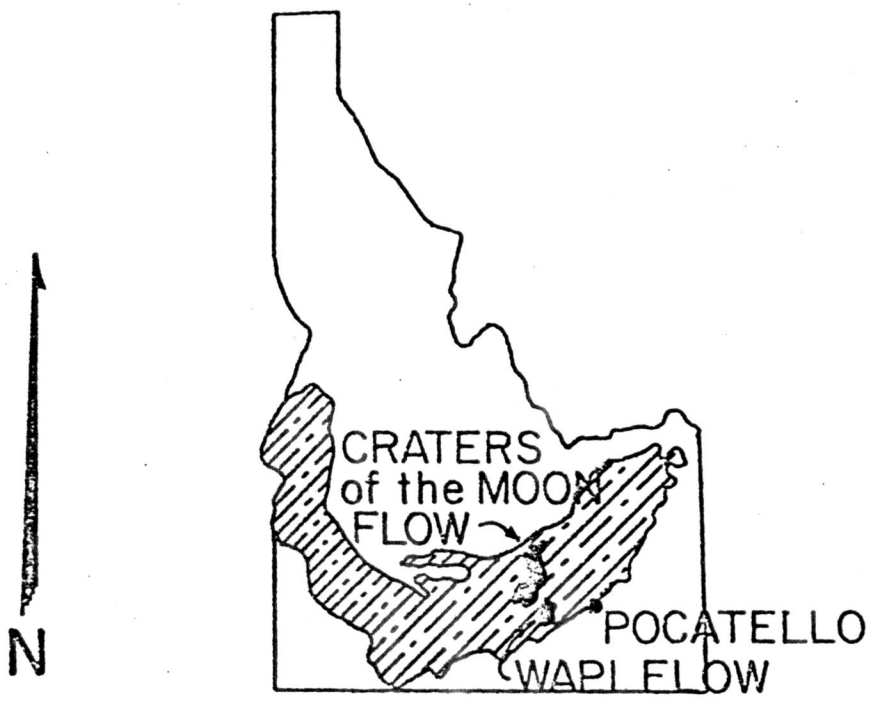
16) More isolated kipukas had larger densities of small mammals than less isolated kipukas. Two possible explanations for this result are that faunas of small, more isolated kipukas may have had longer periods of release from predation pressure, or, that small mammals on isolated kipukas may have nested in the lava and foraged on kipukas, so that trapping just the kipuka would have revealed an artifically high density.

17) There appeared to be a minimum size required for the establishment of a population for many small mammal species. Of the species that were restricted by lava, three appeared to be established in populations on kipukas, but no populations existed on kipukas less than three hectures in size. The absence from kipukas of other species often encountered in mainland habitats may have been a result of specific minimum area requirements greater than the size of the largest study kipukas.

18) Limitations of this study include the following: The arbitrary choice of study area introduces possible bias into the results; the area of the study was small, considering the total area of the flows and the range in patterns observed outside of the northern study area. The study itself was limited to a relatively small range of kipuka sizes and isolations. The number of environmental measures made was small, and some measures were possibly artificial: for example, soil texture may not be as meaningful a factor as the source and derivation of the soil.

19) This study has only scratched the surface of the useful biological research that can be performed within the kipuka-lava ecosystem. The unaltered nature of the kipukas, the freedom from human interference, and the unique and fascinating character of the environment make the Great Rift Wilderness Area a compelling location for research.

Figure 1. Maps of the Craters of the Moon lava flow and the Wapi lava flow in Idaho. The top map depicts the two flows in relation to the Snake River Plain (indicated by hatching) in Idaho. The bottom map shows the two flows in relation to nearby towns and highways.


N
CRATERS
of the MOON
FLOW
POCATELLO
WAPI FLOW

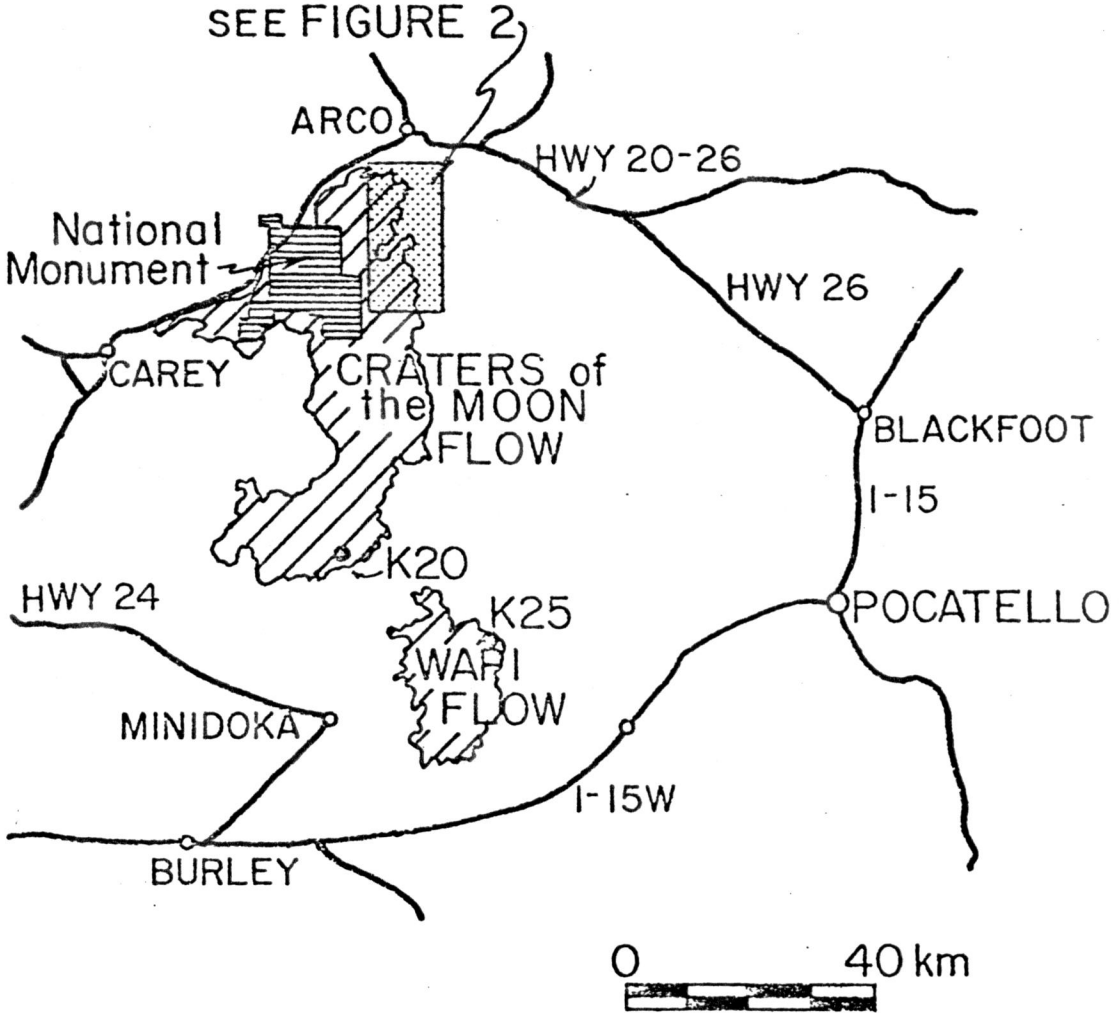

SEE FIGURE 2
ARCO
HWY 20-26
National
Monument
HWY 26
CAREY
CRATERS of
the MOON
FLOW
BLACKFOOT
I-15
K20
HWY 24
K25
POCATELLO
WAPI
FLOW
MINIDOKA
I-15W
BURLEY
0
40 km

Figure 2. Map of the northern study area on the Craters of the Moon lava flow.

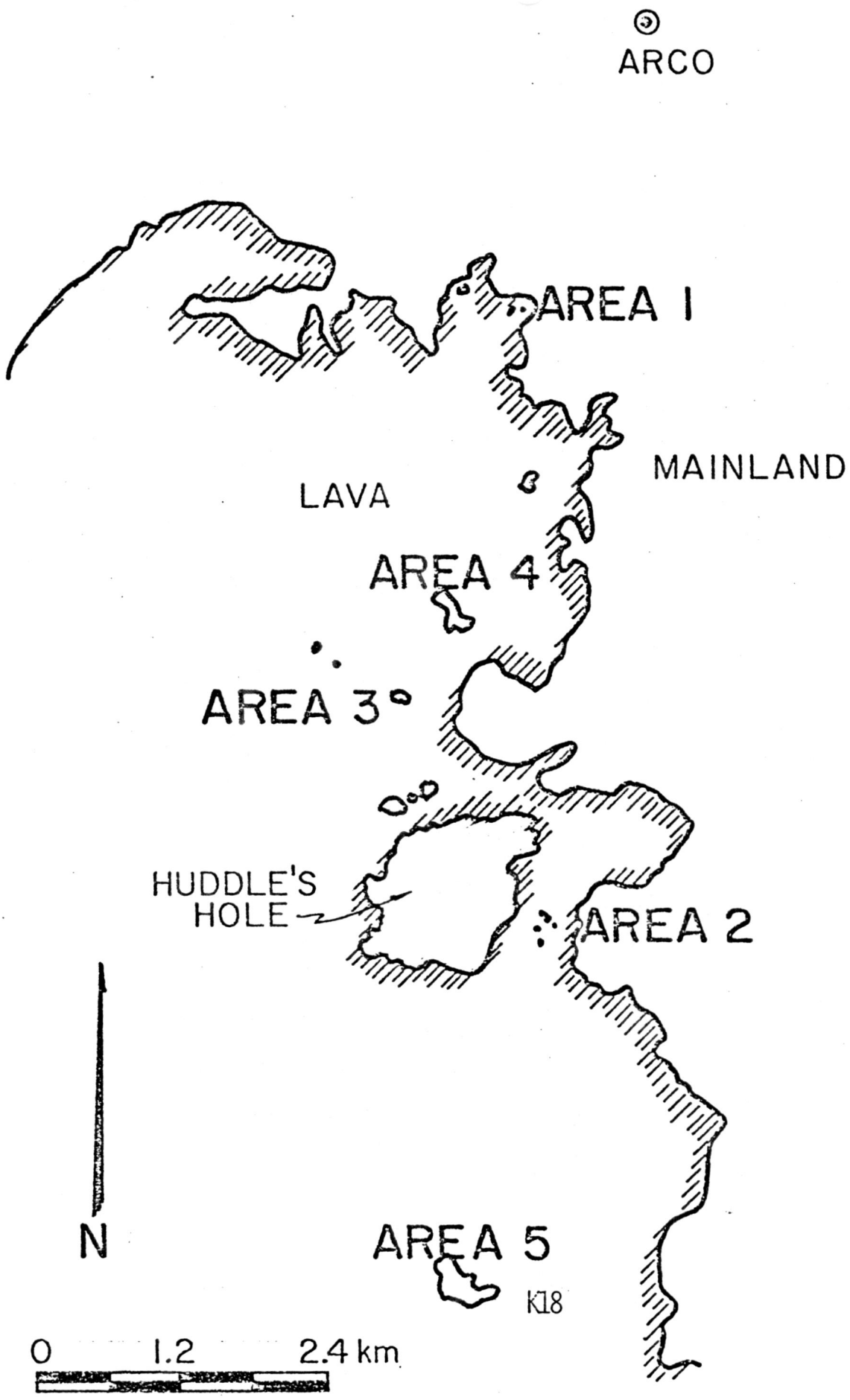

ARCO
AREA 1
MAINLAND
LAVA
AREA 4
AREA 3
HUDDLE'S
HOLE
AREA 2
N
AREA 5
K18
0
1.2
2.4 km

Figure 3. Maps of study area 1 and study area 2 in the northern study area of the Craters of the Moon lava flow. Kipukas are shown in relation to other kipukas and to the mainland.

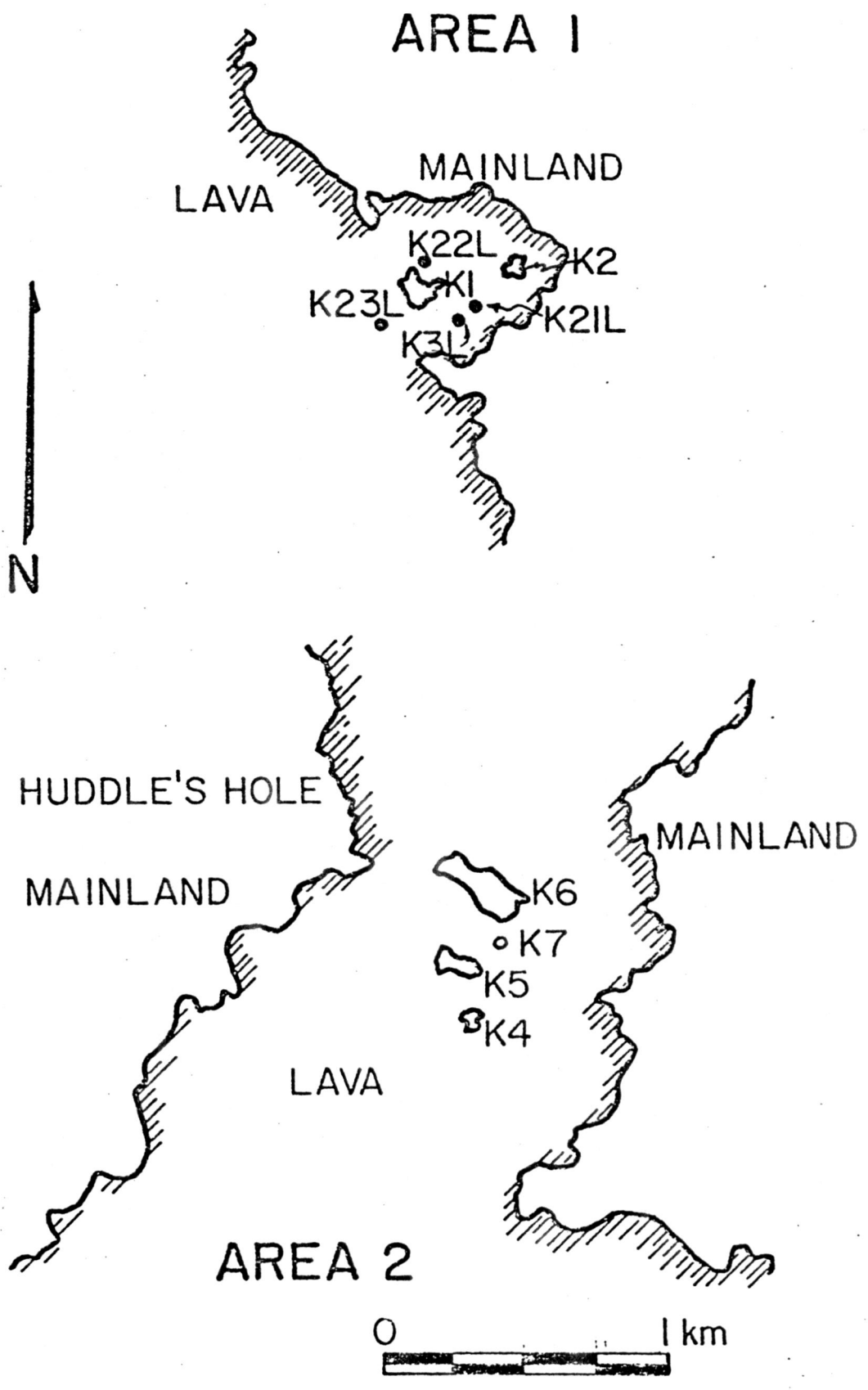

AREA 1
MAINLAND
LAVA
K22L
K2
K1
K23L
K21L
K3L
N
HUDDLE'S HOLE
MAINLAND
MAINLAND
K6
K7
K5
K4
LAVA
AREA 2
0
1 km

Figure 4. Maps of study area 4 and study area 3 in the northern study area of the Craters of the Moon lava flow. Kipukas are shown in relation to other kipukas and to the mainland.

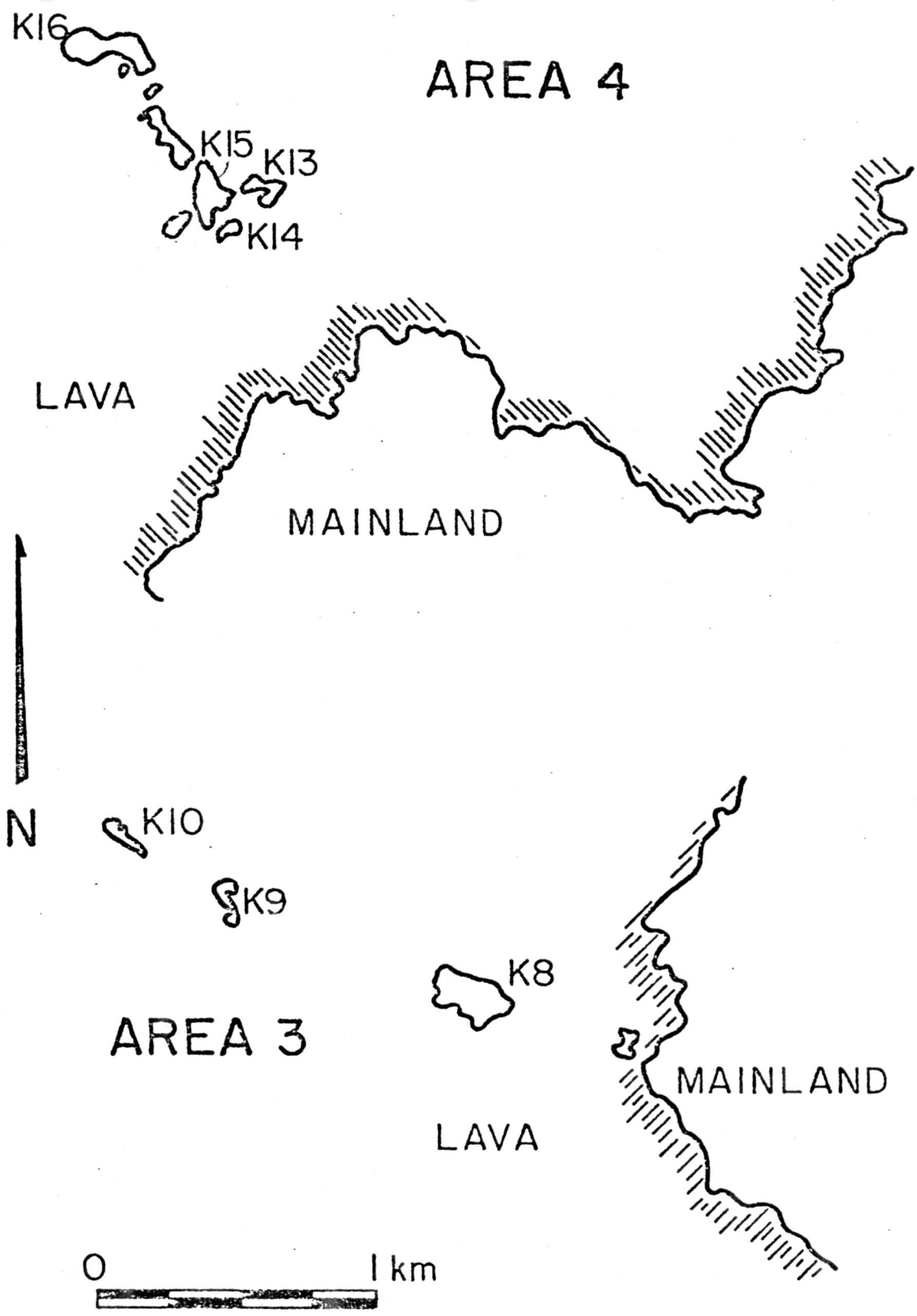

K16
AREA 4
K15
K13
K14
LAVA
MAINLAND
N
K10
K9
K8
AREA 3
MAINLAND
LAVA
0
1 km

Figure 5. Maps of K20 on the southern portion of the Craters of the Moon lava flow and K25 on the Wapi flow in relation to other kipukas and to the mainland.

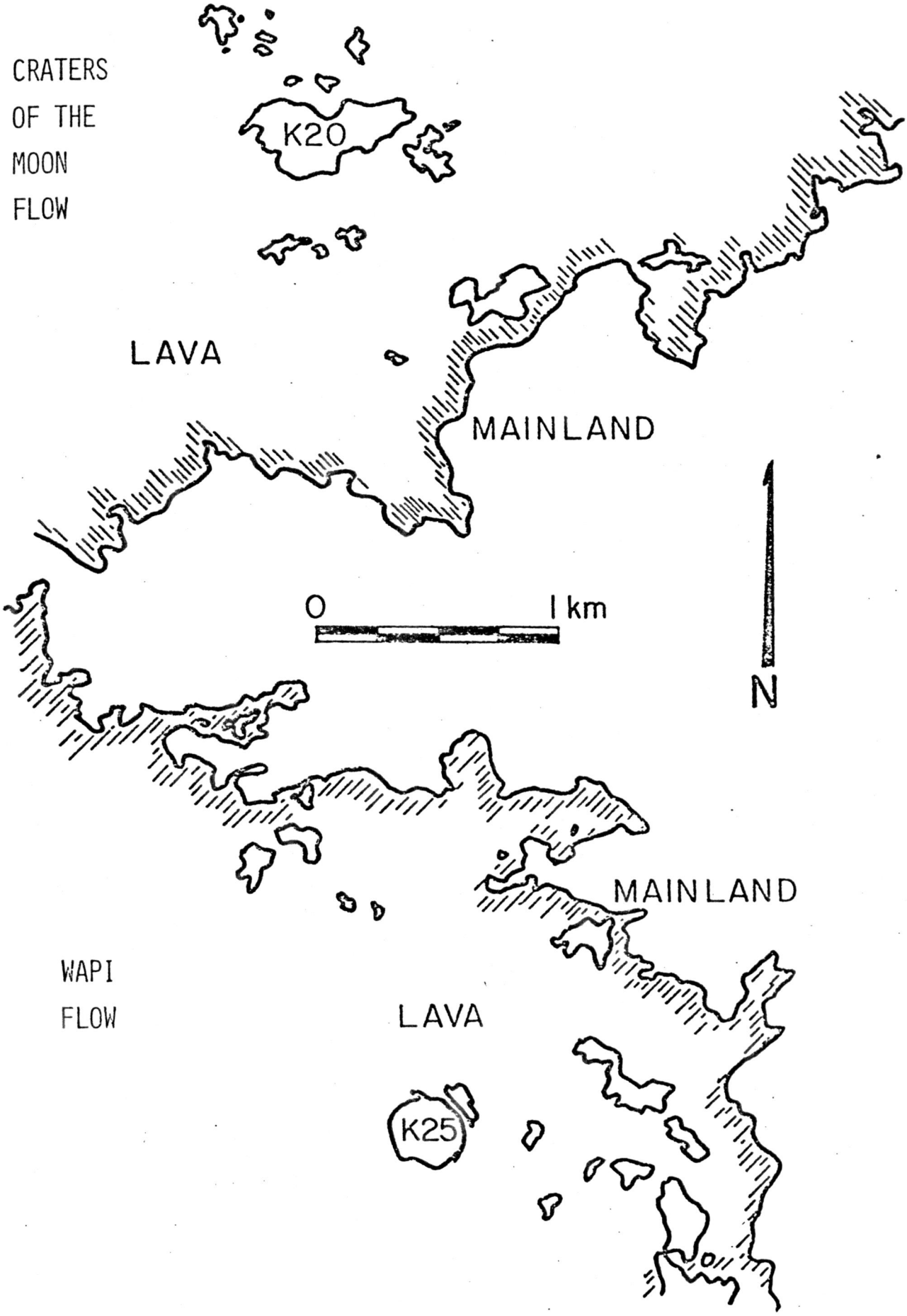

CRATERS
OF THE
MOON
FLOW
K20
LAVA
MAINLAND
0
1 km
N
MAINLAND
WAPI
FLOW
LAVA
K25

Figure 6. Cumulative means for total cover, for cover of Chrysothamnus viscidiflorus, and cumulative number of plant species for from 1 to 30 frames in plot 1.1.

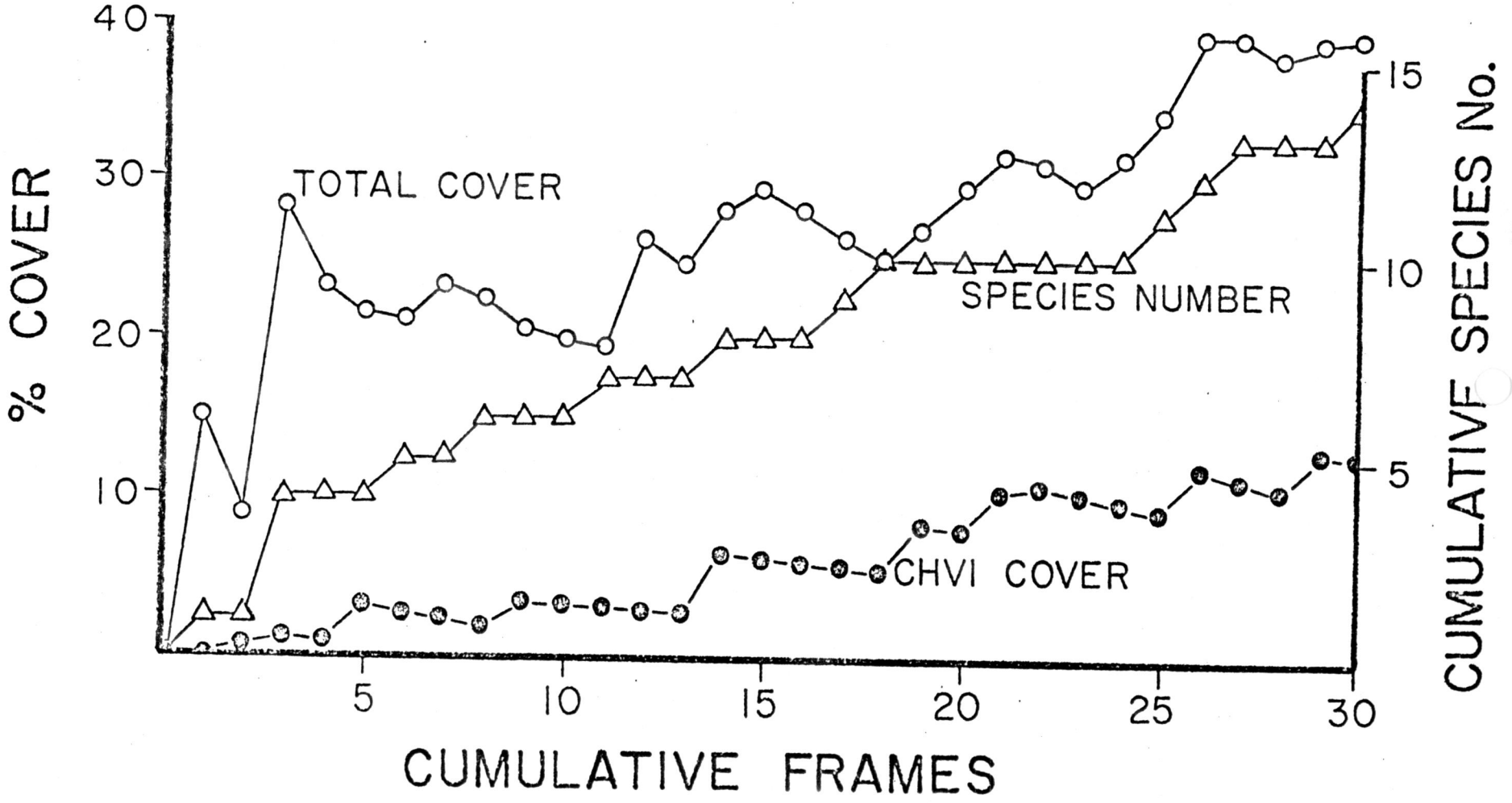
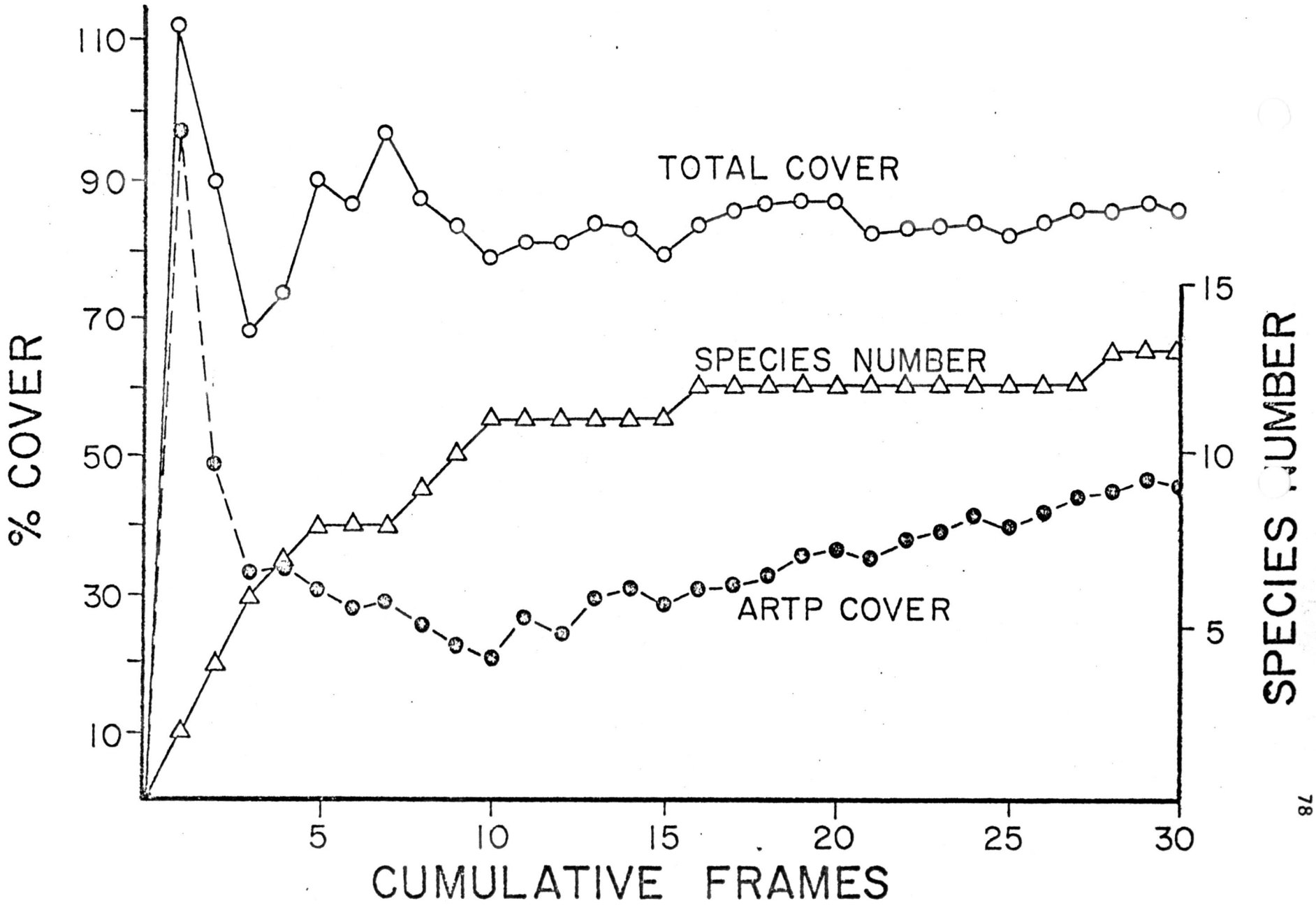

40
30
20
10
% COVER
TOTAL COVER
SPECIES NUMBER
CHVI COVER
15
10
5
CUMULATIVF SPECIES No.
5
10
15
20
25
30
CUMULATIVE FRAMES

Figure 6. Cumulative means for total cover, for cover of *Artemisia tripartita*, and cumulative number of plant species for from 1 to 30 frames in plot 18.2.


110
90
70
50
30
10
% COVER
TOTAL COVER
SPECIES NUMBER
ARTP COVER
15
10
5
SPECIES NUMBER
5
10
15
20
25
30
CUMULATIVE FRAMES

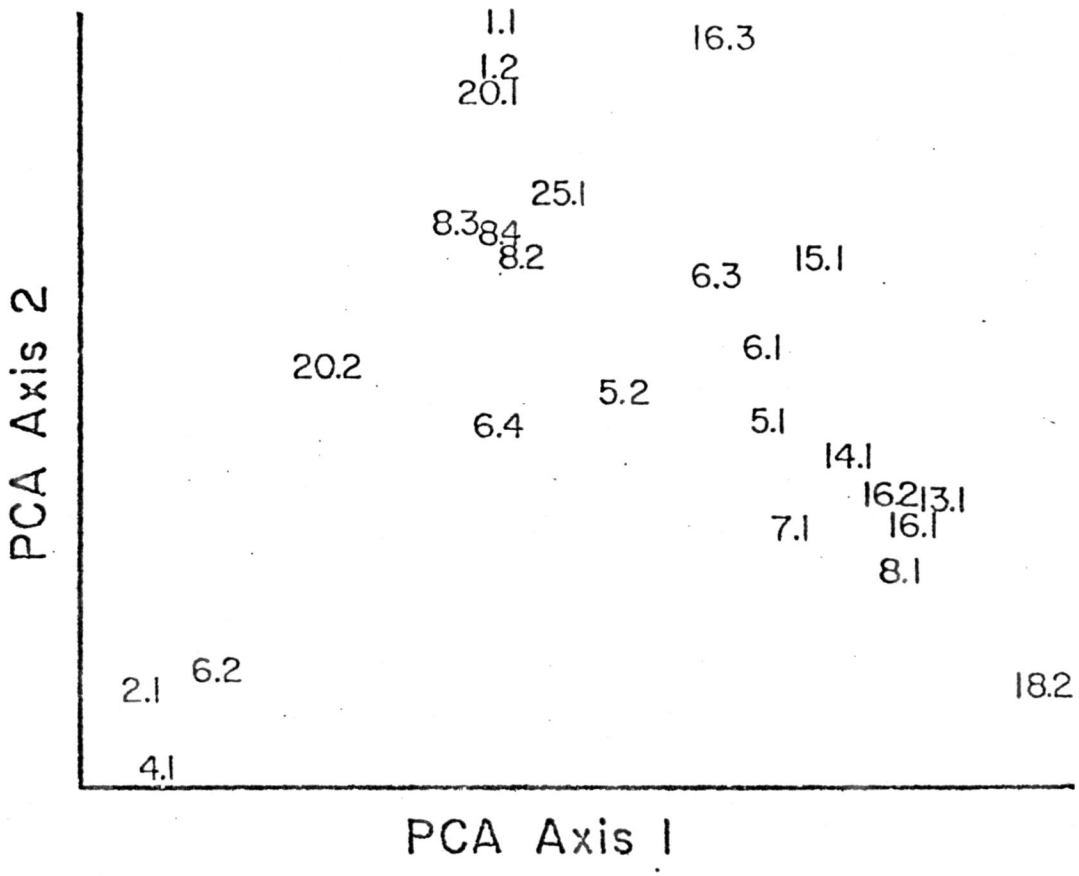


Figure 8. A two-dimensional arrangement of 25 kipuka plots, ordered by PCA. The numbers in the graph are the names of the plots. Axis 1 represents a moisture gradient, with dryer stands on the left and wetter stands on the right. Axis 2 represents a soil texture gradient: as one moves from the bottom of the graph to the top, the soils of plots have increasingly less silt and increasingly more sand. Plots close together are more similar than plots that are far apart.

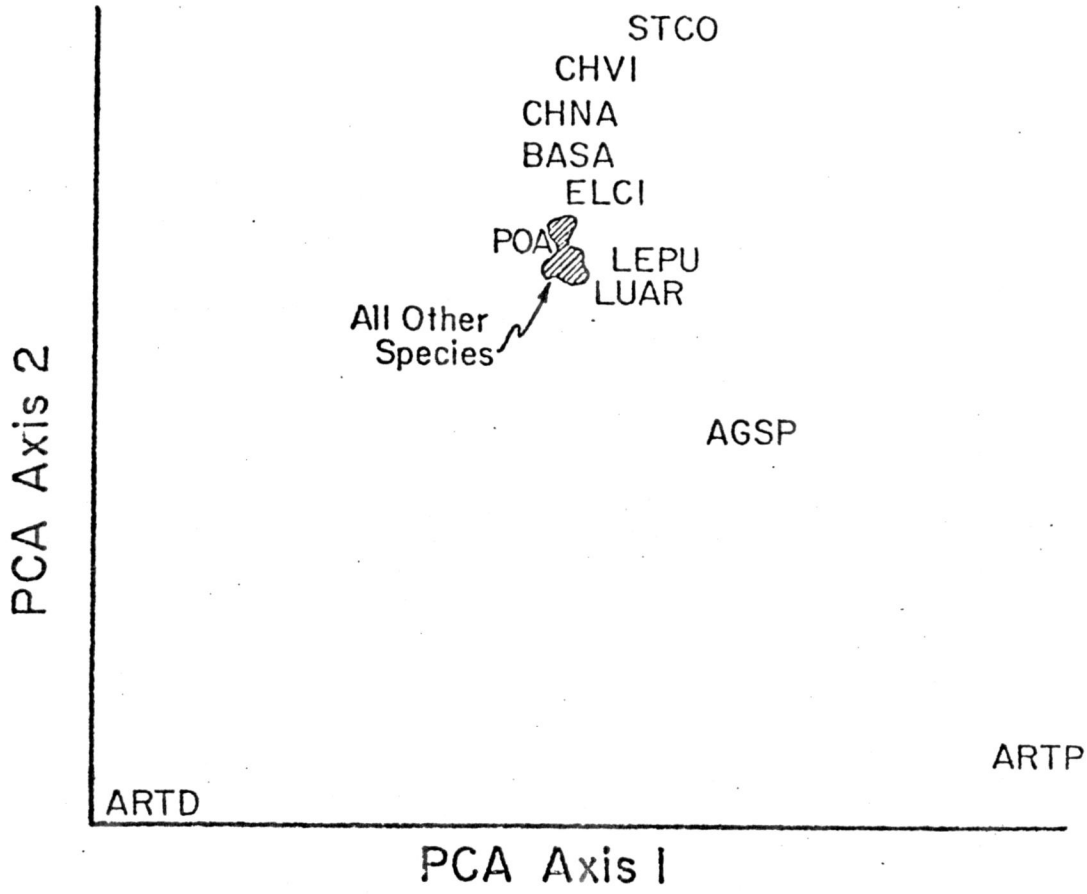


Figure 9. A two-dimensional arrangement of species from 25 kipuka stands, ordered by PCA. Letter combinations in the graph are species abbreviations (Appendix II). Only species that occur in five or more of the 25 plots are ordinated; the cluster near the center of the graph includes 11 species. Axis 1 represents a moisture gradient, with more mesic species to the right. Axis 2 represents a soil texture gradient; species near the top of the graph have an affinity for sandier soils, species near the bottom of the graph have an affinity for siltier soils.

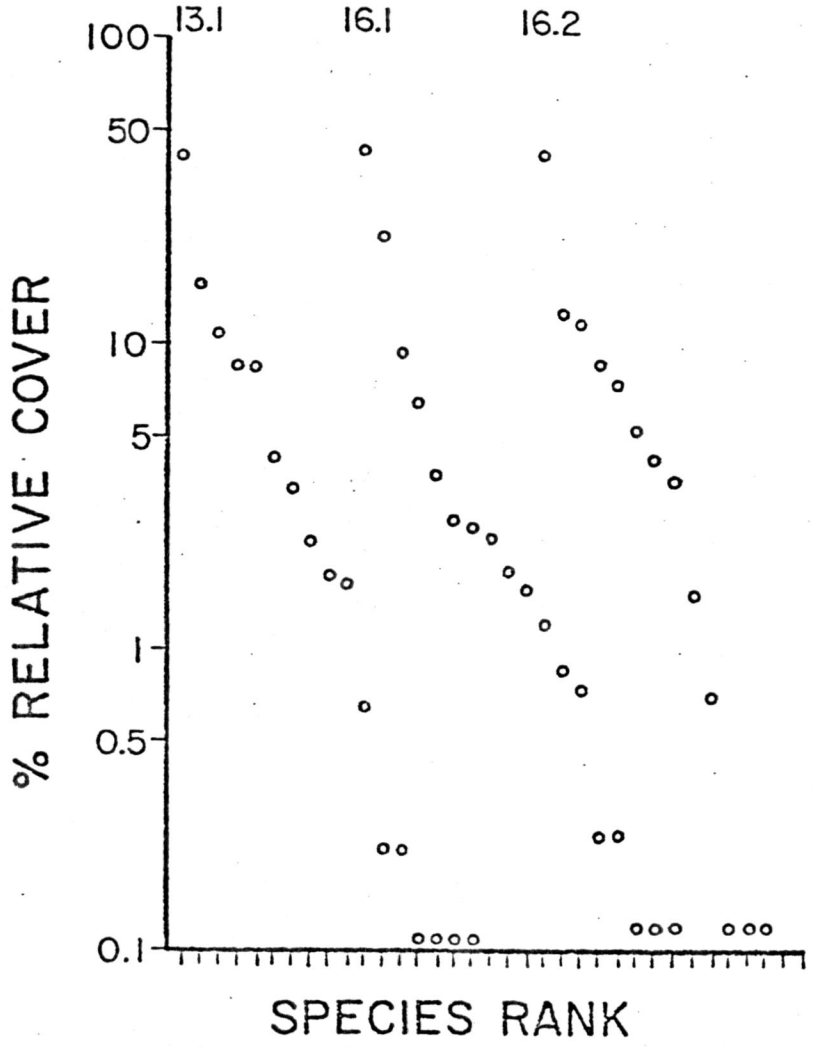


Figure 10. Dominance-diversity curves for stands 13.1, 16.1, and 16.2. For each plot, each species is represented by a point located by that species' relative importance (the percentage that that species represents of the total cover of all species in the stand, on a logarithmic scale) on the vertical axis, and its position in the sequence of species from highest to lowest importance values on the horizontal axis. The names of the species represented by each point can be ascertained from Appendix VI.

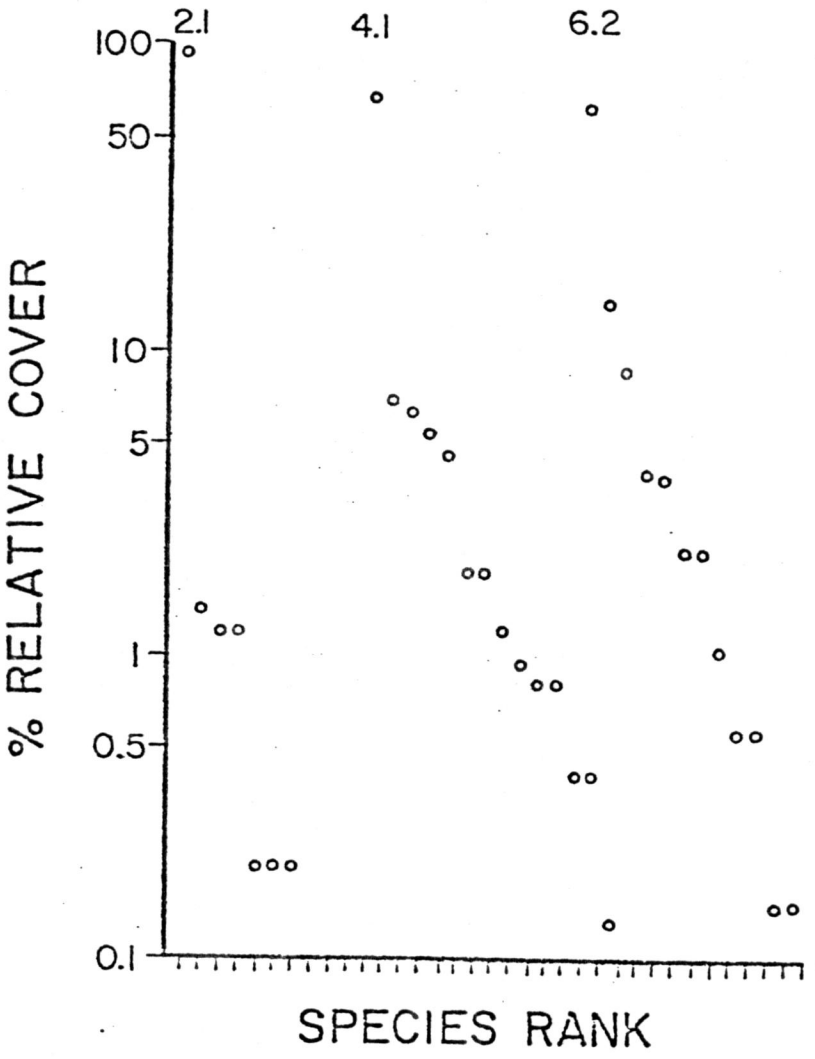


Figure 11. Dominance-diversity curves for stands 2.1, 4.1, and 6.2. For each plot, each species is represented by a point located by that species' relative importance (the percentage that that species represents of the total cover of all species in the stand, on a logarithmic scale) on the vertical axis, and its position in the sequence of species from highest to lowest importance values on the horizontal axis. The names of the species represented by each point can be ascertained from Appendix VI.

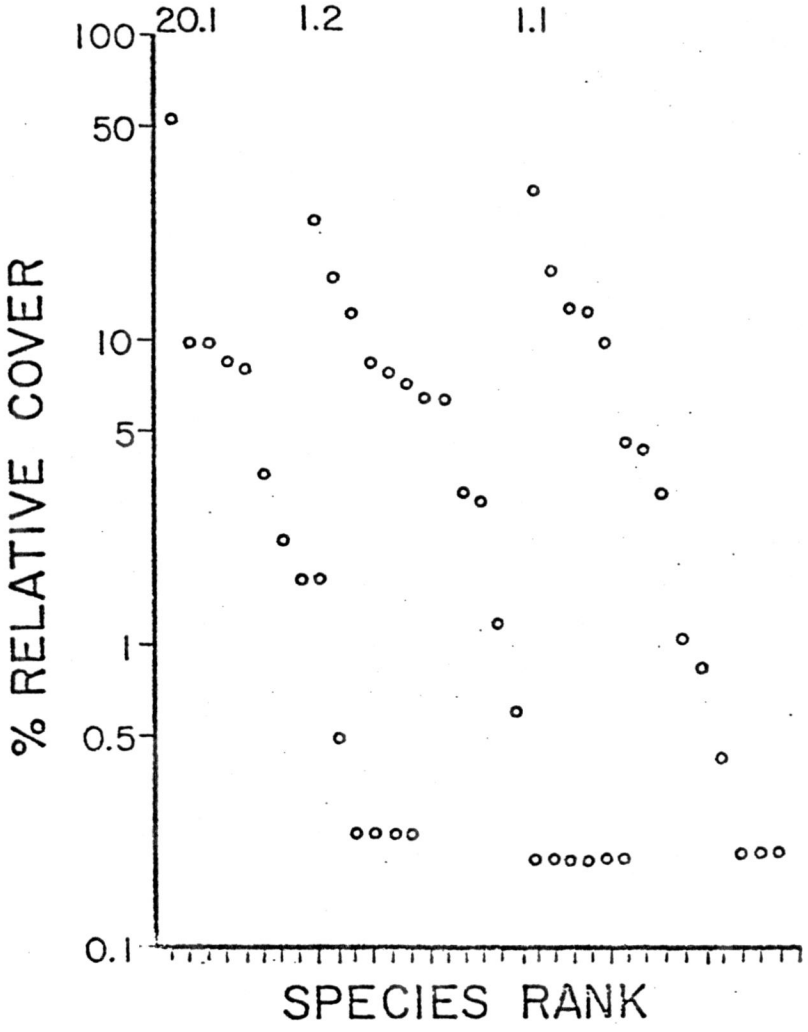
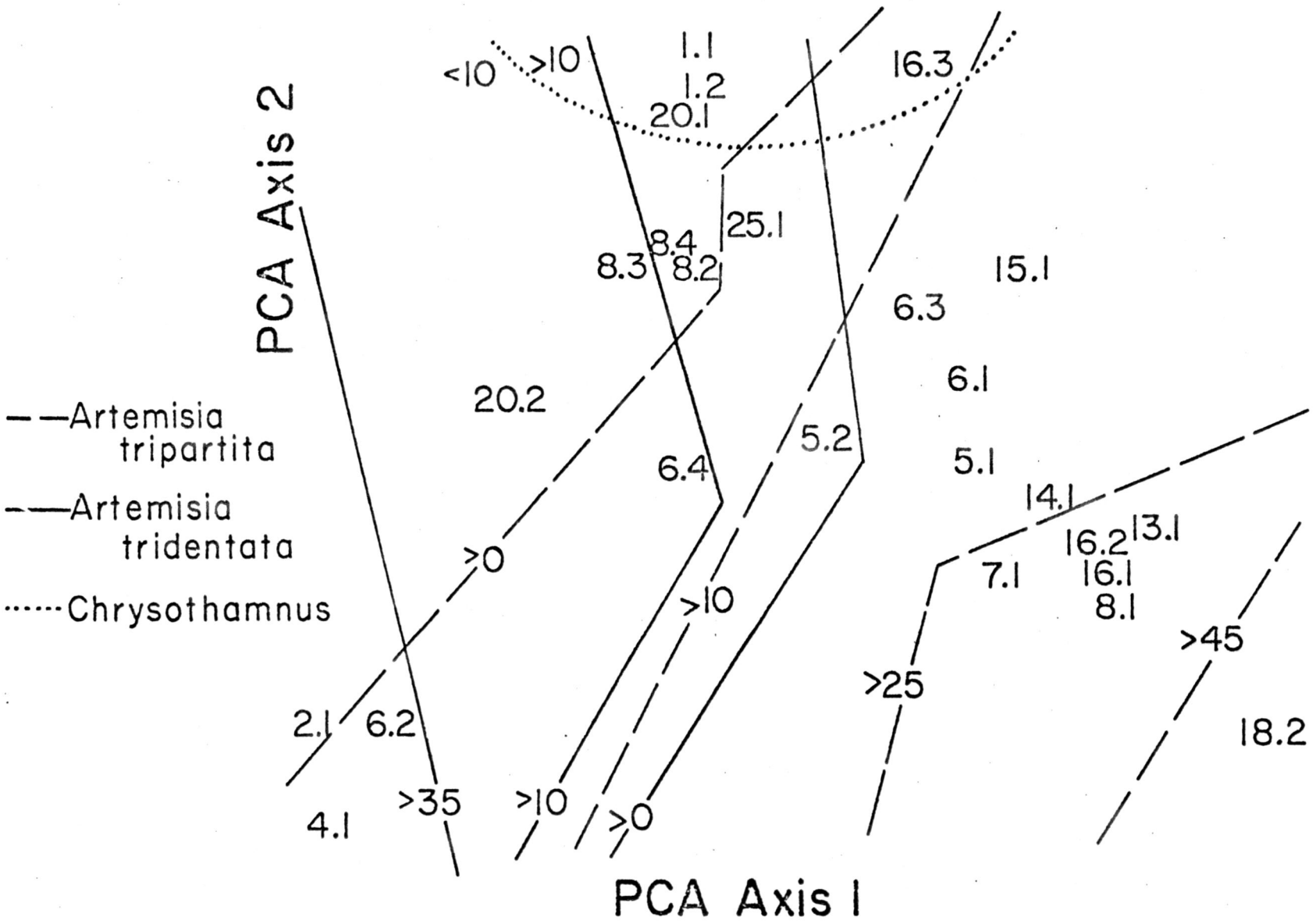


Figure 12. Dominance-diversity curves for stands 20.1, 1.2, and 1.1. For each plot, each species is represented by a point located by that species' relative importance (the percentage that that species represents of the total cover of all species in the stand, on a logarithmic scale) on the vertical axis. The names of the species represented by each point can be ascertained from Appendix VI.

Figure 13. An isograph showing the relationship between the first two PCA ordinations and variations in the importance of dominant shrubs. Isolines representing gradients in the cover of Artemisia tripartita, A. tridentata, and Chrysothamnus nauseosus and C. viscidiflorus (treated together) are superimposed on the arrangement of 25 stands depicted in Figure 8. Non-decimal numbers by the isolines refer to percent relative cover. A. tridentata decreases from left to right; Chrysothamnus decreases from top to bottom; and A. tripartita decreases both from left to right and from bottom to top.


PCA Axis 2
PCA Axis 1
Artemisia tripartita
Artemisia tridentata
Chrysothamnus
<10
>10
1.1
1.2
20.1
16.3
25.1
8.4
8.3
8.2
15.1
6.3
6.1
20.2
5.2
6.4
5.1
14.1
16.2
13.1
7.1
16.1
8.1
>45
>25
18.2
>0
>10
2.1
6.2
>35
4.1
>10
>0

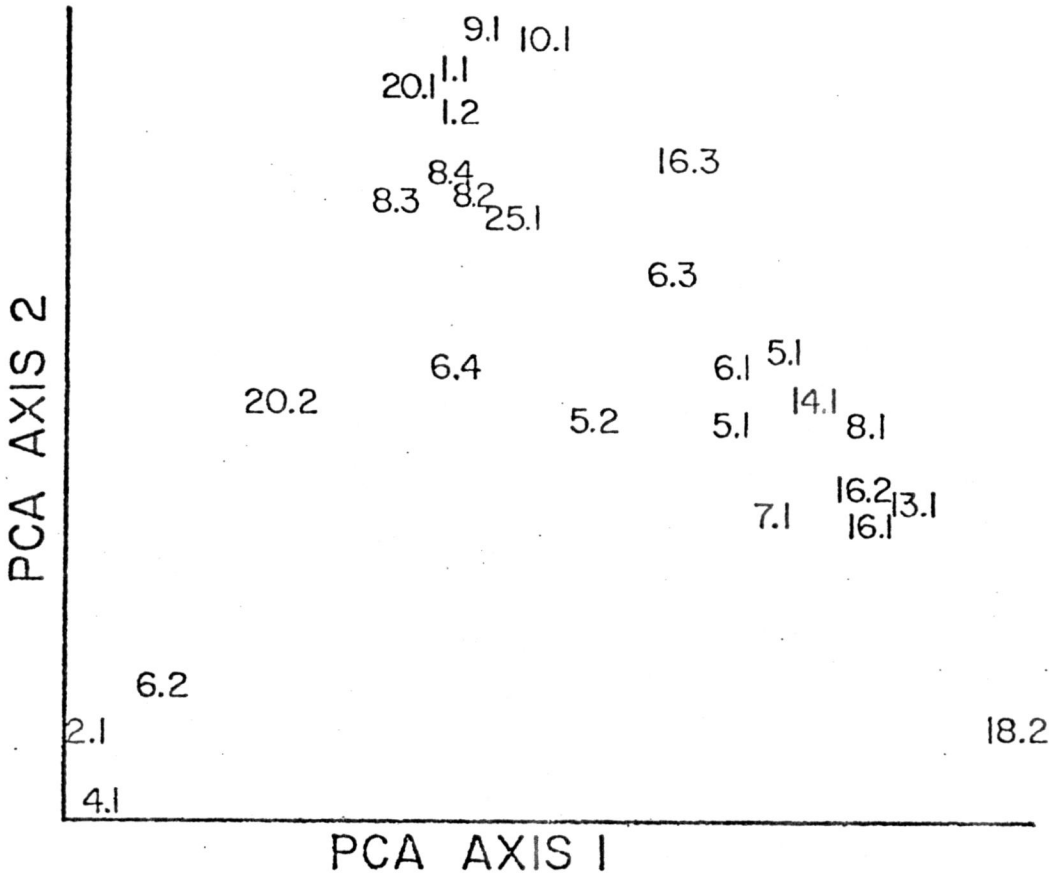


Figure 14. A two-dimensional arrangement of plots, ordered by PCA, that includes the 25 kipuka plots and plots 9.1 and 10.1. The numbers in the graph are the names of the plots. Axis 1 represents a moisture gradient, with dryer stands on the left and wetter stands on the right. Axis 2 represents a soil texture gradient: as one moves from the bottom of the graph to the top, the soils of plots have increasingly more sand. Plots close together are more similar than plots that are far apart.

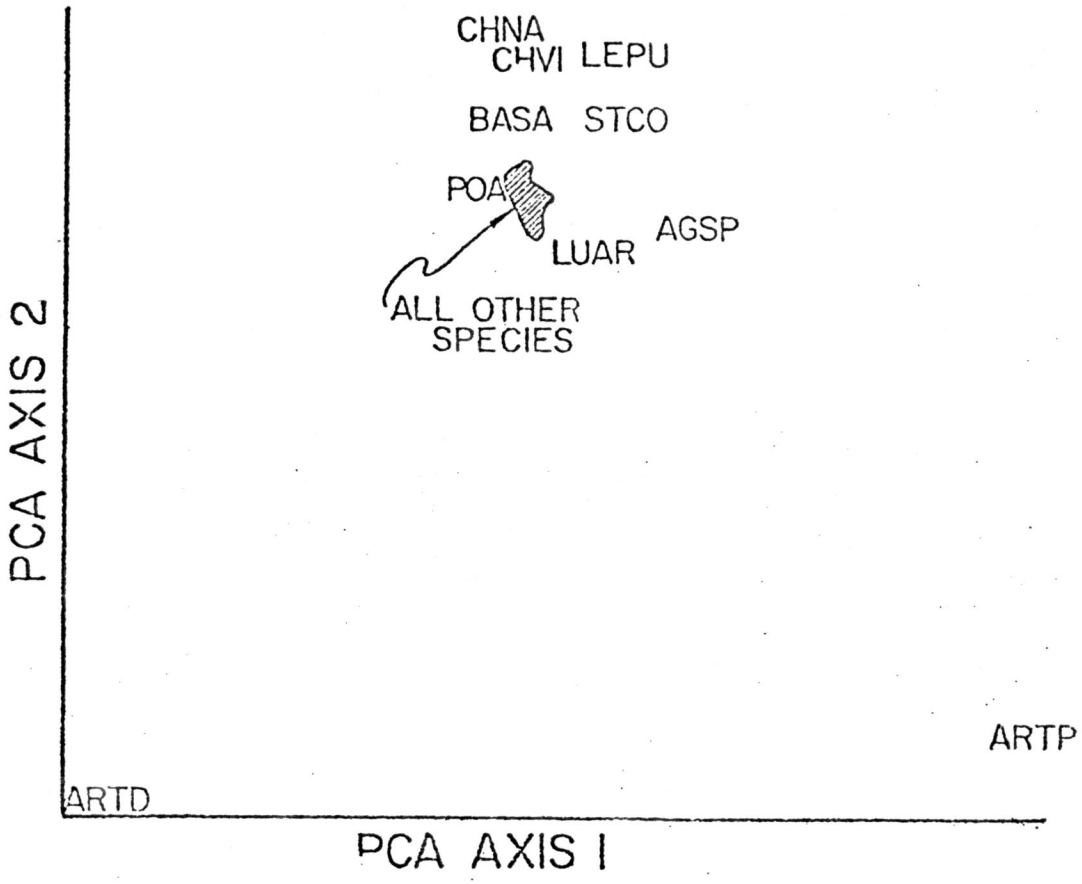


Figure 15. A two-dimensional arrangement of species from 25 kipuka plots and plots 9.1 and 10.1, ordered by PCA. Letter combinations in the graph are species abbreviations (Appendix II). Only species that occur in five or more of the 27 plots are ordinated. Axis 1 represents a moisture gradient, with more mesic species to the right. Axis 2 represents a soil texture gradient; species near the top of the graph have an affinity for sandier soils, species near the bottom of the graph have an affinity for siltier soils.

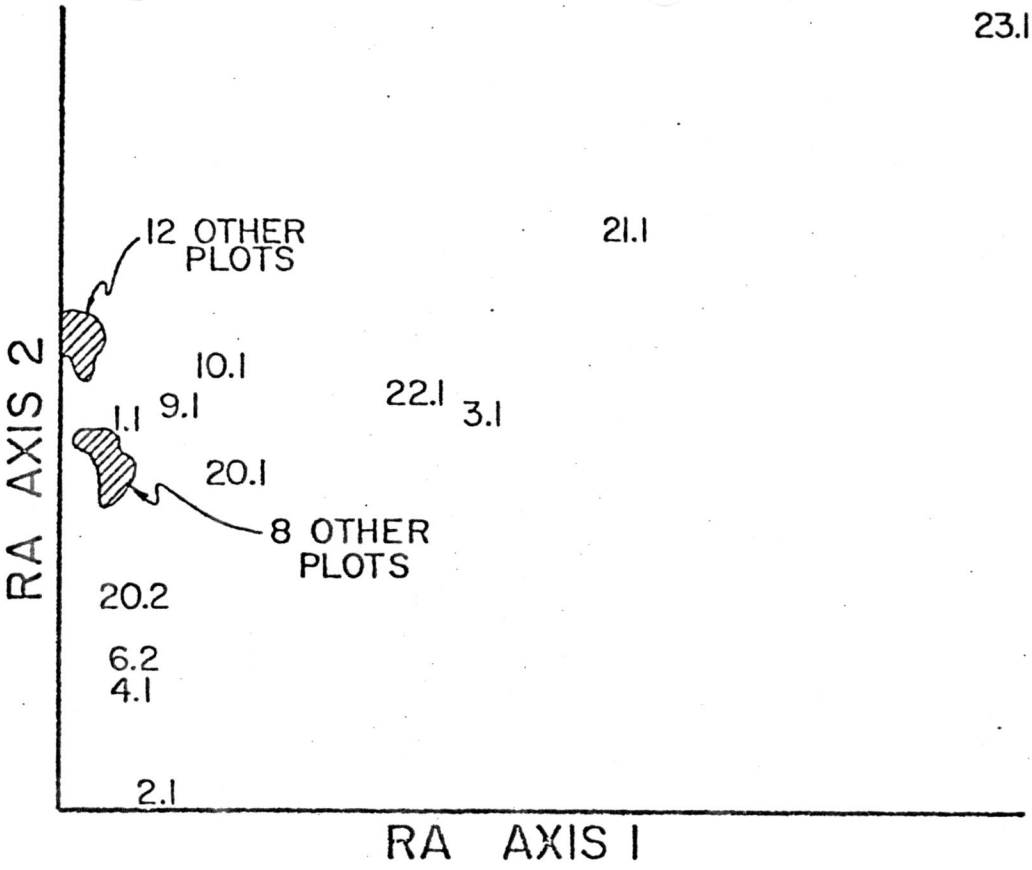


Figure 16. A two-dimensional arrangement of 31 plots, ordered by RA. The numbers in the graph are the names of the plots; plots close together are more similar than plots that are far apart. The environmental gradients corresponding to the axes are unknown, but the primary (horizontal) axis clearly seperates lava and edge plots from kipuka plots.

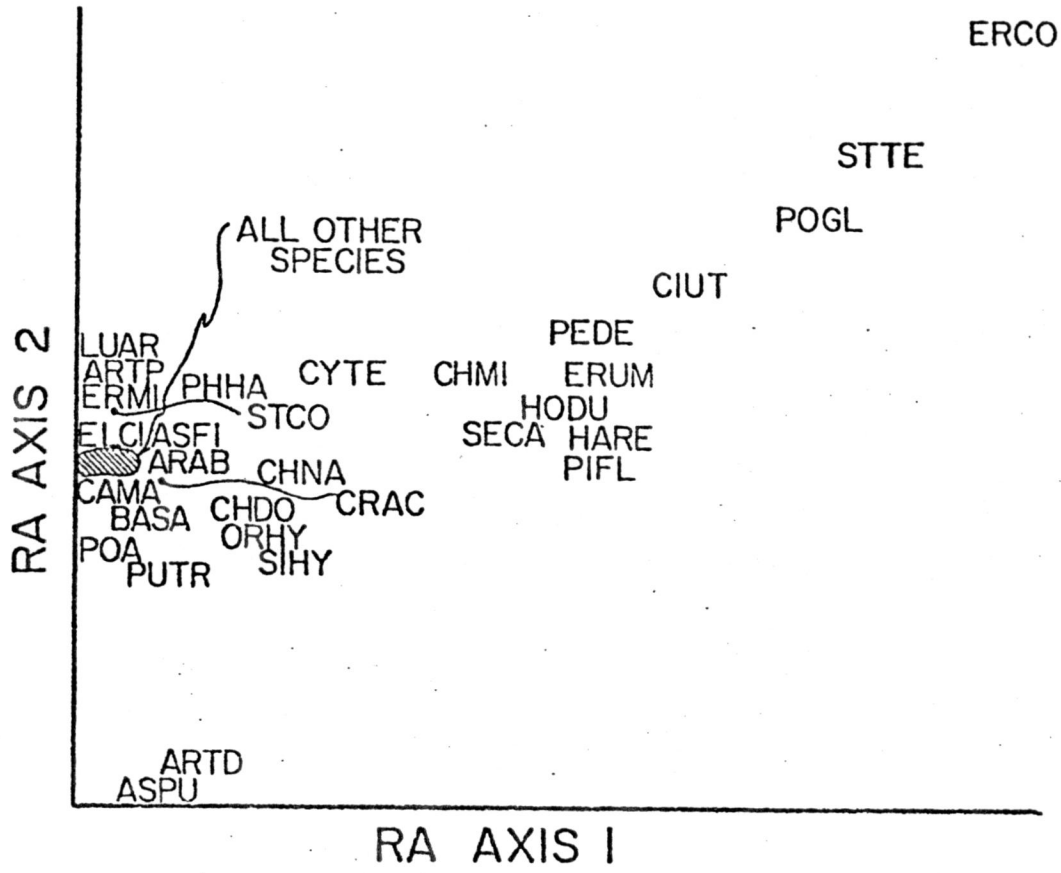


Figure 17. A two-dimensional arrangement of species from 31 stands, orderd by RA. Letter combinations in the graph are species abbreviations (Appendix II). All plant species were ordinated, but only species that occur in the lava plots or that occur in five or more of the kipuka plots are depicted on the graph. The environmental gradients corresponding to the axes are unknown, but the primary (horizontal) axis clearly seperates lava and edge species from kipuka species.

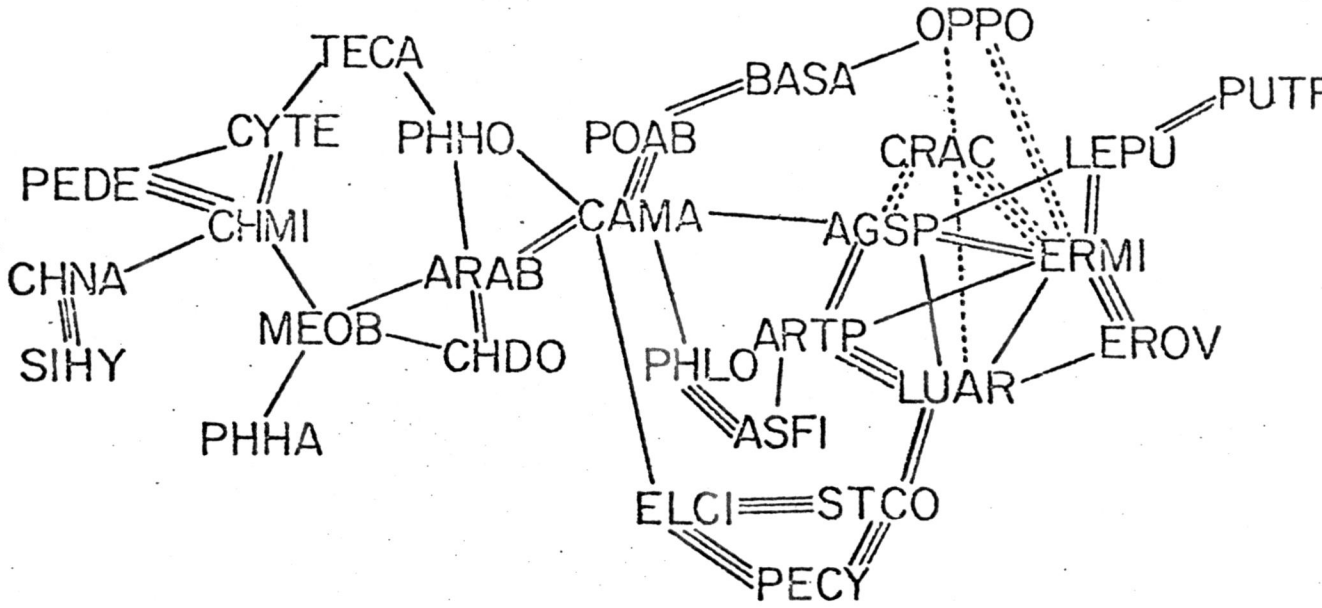
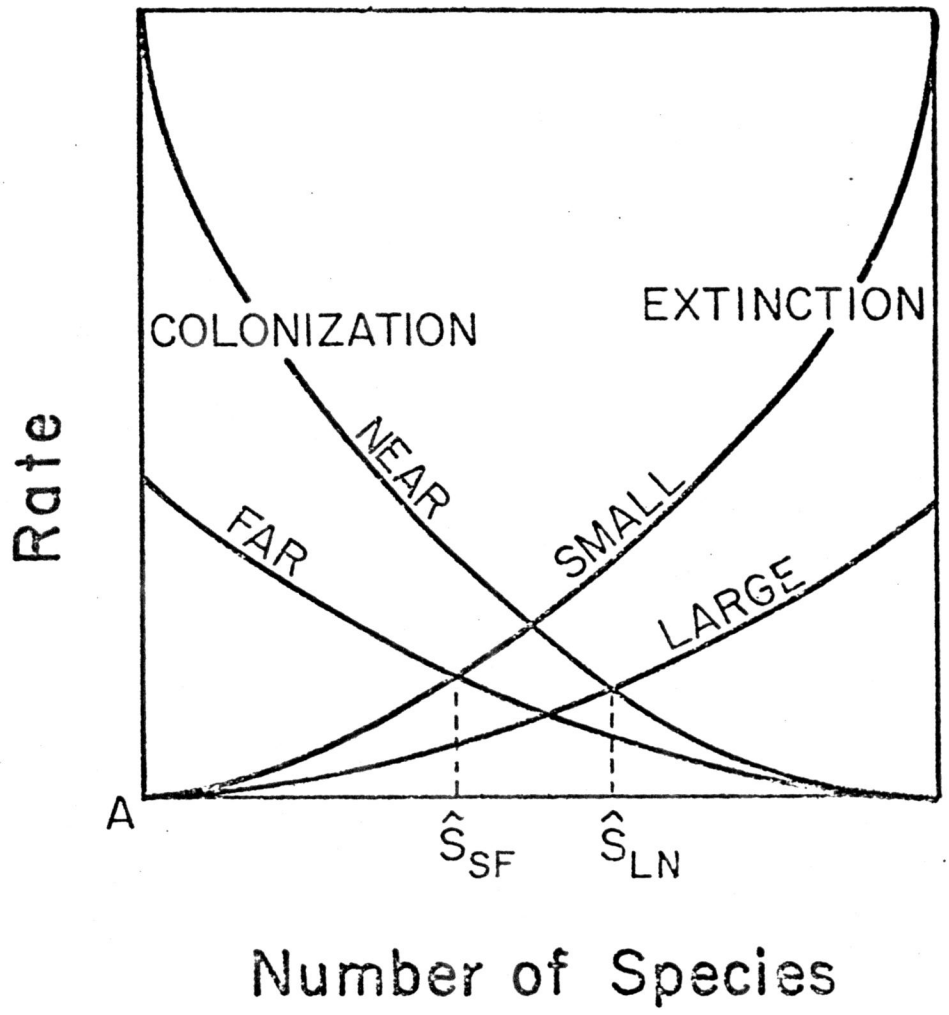


Figure 18. A species relationships diagram for the 31 plant species that occur in six or more plots. Linkages are significant positive correlations between the linked species. Single links indicate significance at p 0.05, double links indicate significance at p 0.001. Species represented by the abbreviations can be found in Appendix II.

Figure 19. The MacArthur-Wilson equilibruim model of island biogeography. The horizontal axis represents the number of species on islands, the vertical axis represents relative rates of colonization or extinction on islands. Colonization rates decline with increasing species number, because, as more species become established, fewer immigrants will belong to new species. Extinction rates increase with species number, since the more species present the more that can become extinct. The rate of colonization is a function of the degree of isolation of an island. The intersection of the colonization and extinction curves can be extrapolated to the horizontal axis to give the equilibrial species numbers for islands of various sizes and isolations. (MacArthur & Wilson 1967.)


COLONIZATION
EXTINCTION
NEAR
FAR
SMALL
LARGE
Rate
A
$\hat{S}_{SF}$
$\hat{S}_{LN}$
Number of Species

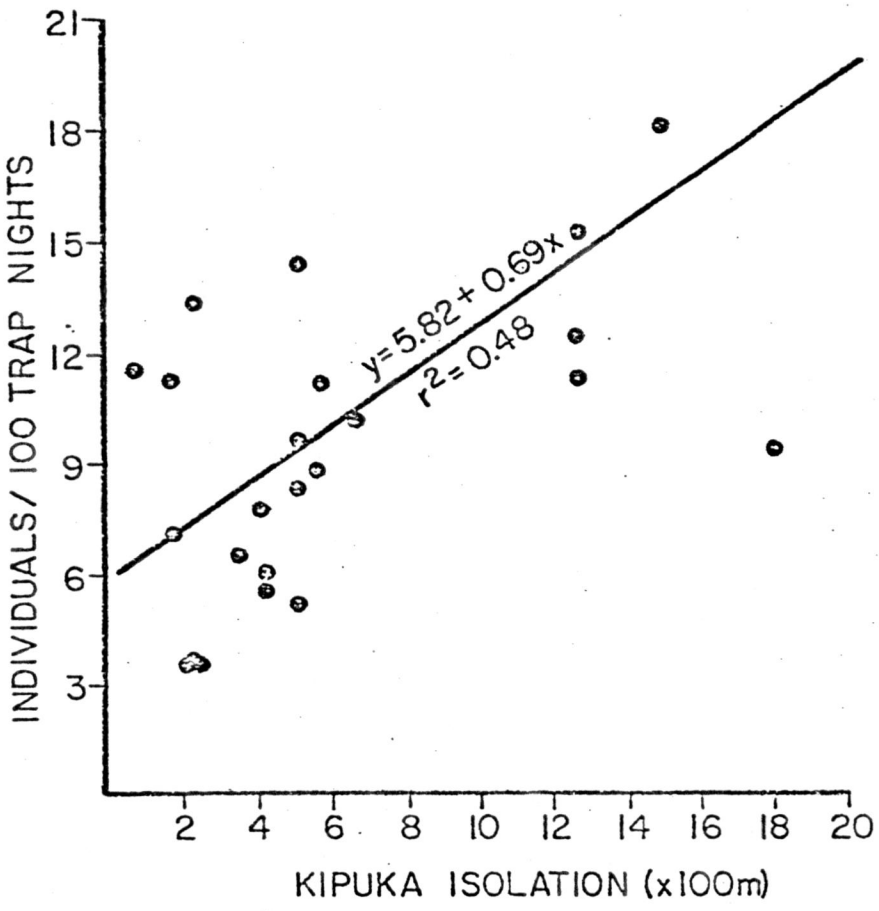


Figure 20. The density-isolation effect: small mammal density (number of individuals captured for every 100 nights of trapping) as a function of kipuka isolation (straight line distance to the nearest mainland). $P<0.05$.

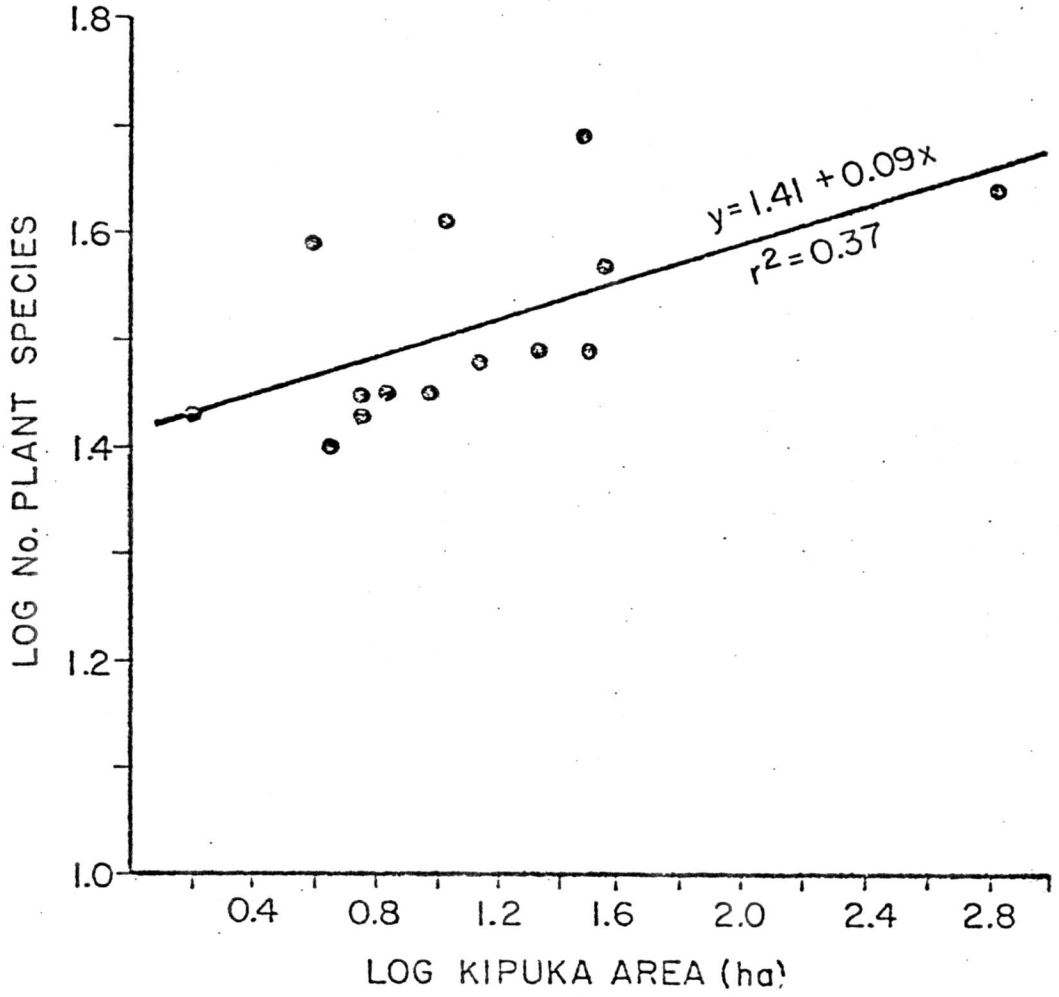


Figure 21. Species-area effect: number of plant species on a kipuka as a function of the size of the kipuka. Both variables are transformed to show a linear relationship. $P<0.05$.

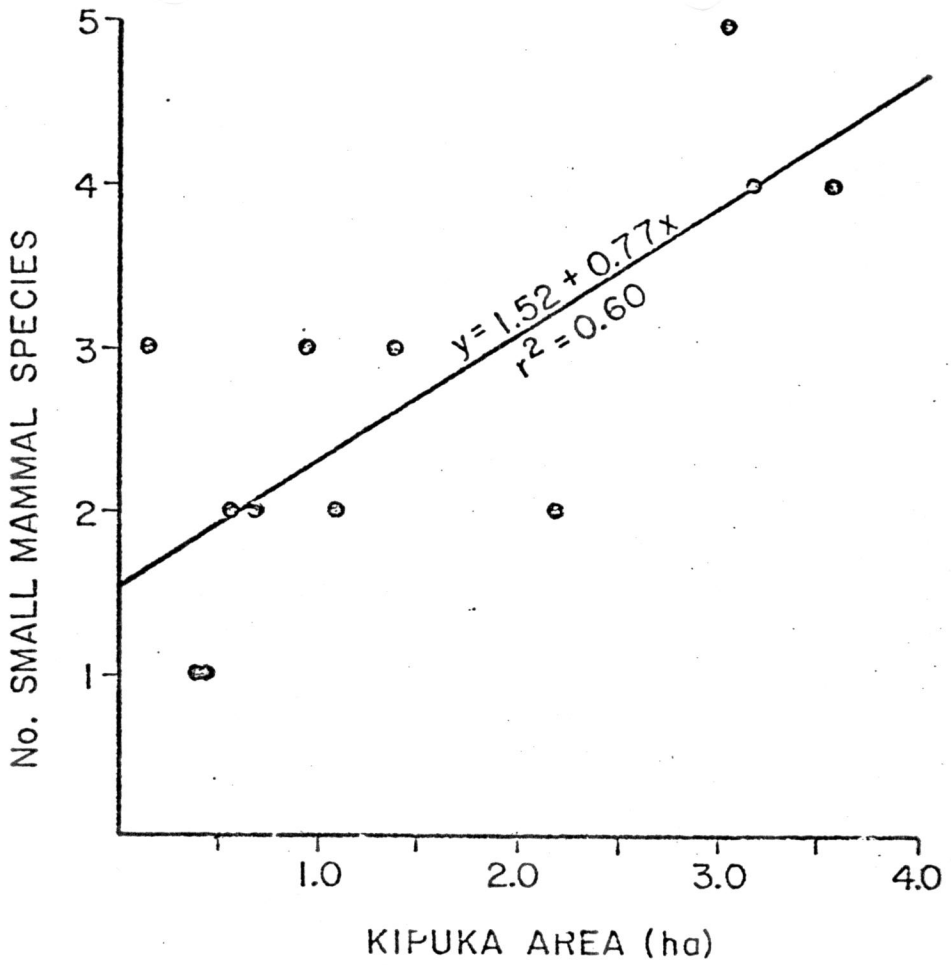


Figure 22. Species-area effect: number of small mammal species on a kipuka as a function of the size of the kipuka. $P<0.01$.

Table 1. The location and elevation of kipukas studied. Plots 3.1L, 21.1L, 22.1L, and 23.1L were situated on lava in Area 1.

AREA	KIPUKA	USGS 7½' QUADRANGLE	LOCATION	ELEVATION (to nearest 20')
1	1,2	Arco South	SW¼ Sec. 27, T3N,R26E	5340
2	4	Fingers Butte	NE¼ Sec. 7, T1N,R27E	5360
	5,6,7		SE¼ Sec. 6, T1N,R27E	
3	8	Fingers Butte/ The Watchman	SW¼ Sec. 21, SE¼ Sec. 20, T2N,R26D	5480-5520
3	9	The Watchman	W½ Sec. 20 T2N,R26E	5460-5480
	10		NW¼ Sec. 20, T2N,R26E	
4	13-16	Arco South/ Fingers Butte	SE¼ Sec. 16, T2N,R26E	5380-5400
5	18	Fingers Butte/ Pratt Butte	Sec. 36, T1N,R26E	5340-5410
6	20	Bear Park	NE¼ Sec. 11, T5S,R25E	4680
WAPI FLOW	25	Pillar Butte	SW¼ Sec. 24, T6S,R28E	4740-4780

Table 2. Total cover of all vegetation, number of species, values for the Shannon-Wiener (S-W) and the Simpson diversity indices, and index of uniformity for 31 sampled plots.

PLOT	TOTAL COVER(%)	SPECIES NUMBER	S-W INDEX	SIMPSON INDEX	UNIF. INDEX
1.1	39.08	14	.1394	.8218	.375
1.2	41.91	18	.1067	.8659	.325
2.1	41.33	7	.0862	.7805	.4
4.1	62.08	14	.2745	.5166	.425
5.1	78.25	16	.1023	.8615	.7
5.2	64.83	20	.1000	.8767	.45
6.1	68.42	15	.1267	.8393	.55
6.2	56.50	13	.2671	.5777	.5
6.3	61.75	17	.1261	.8359	.65
6.4	60.17	18	.1423	.7879	.45
7.1	52.83	16	.2158	.6794	.35
8.1	103.17	16	.1408	.8179	1.0
8.2	33.92	14	.1494	.7834	.475
8.3	59.00	13	.1104	.8702	.5
8.4	53.33	15	.1218	.8316	.625
9.1	46.25	12	.1460	.8317	.675
10.1	55.25	16	.1530	.8131	.4
13.1	76.83	17	.1534	.7707	.5
14.1	78.58	14	.1373	.8234	.7
15.1	75.33	15	.1510	.8000	.625
16.1	68.92	18	.1617	.7462	.575
16.2	71.75	13	.1607	.7665	.8
16.3	79.58	10	.1562	.7949	1.25
18.2	85.33	13	.1960	.6831	.95
20.1	34.17	14	.1957	.6820	.15
20.2	52.75	17	.1619	.7709	.525
25.1	58.92	13	.1560	.8092	1.0
3.1L	20.94	16	.1065	.5777	.1
21.1L	17.50	14	.1887	.5166	.1
22.1L	38.11	17	.1301	.8182	.175
23.1L	3.90	4	.4274	.0862	2.75

Table 3. Trapping out effect: the change on successive trapping days in the number of animals trapped in each plot.

	NUMBER OF ANIMALS CAPTURED			
PLOT	DAY 1	DAY 2	DAY 3	DAY 4
1.1	11	3	1	1
1.2	16	5	3	2
2.1	14	8	3	-
3.1	8	0	3	-
4.1	12	4	1	0
5.1	9	2	2	0
5.2	9	3	0	2
6.1	24	4	1	4
6.2	8	0	0	-
6.3	5	2	1	-
6.4	4	3	1	-
7.1	10	2	2	-
8.1	16	10	5	1
8.2	15	1	2	1
8.3	8	3	0	1
8.4	15	2	4	2
9.1	13	14	12	-
10.1	8	4	8	-
13.1	9	7	3	2
14.1	15	7	3	2
15.1	17	3	2	0
16.1	21	3	0	1
16.2	21	5	1	0
16.3	22	11	0	0

Table 4. Kipukas as islands: Size, degree of isolation, species numbers, and relative densities of animals.

KIPUKA	1	2	4	5	6	7	8	9	10	13	14	15	16	18	20	25
SIZE (HA)	1.4	.45	.40	1.1	3.1	.16	3.6	.57	.97	.69	.57	2.2	3.2	68	14	7.6
DISTANCE TO M.L. (x100m)[a]	1.6	0.7	4.0	4.1	2.2	3.5	5.0	14.9	18.0	5.5	5.6	6.7	12.7	35	6.5	8.9
WIDTH OF BARRIER (x100m)[b]	1.6	0.7	4.0	3.9	2.2	2.8	4.1	11.7	14.4	5.5	5.6	5.8	6.5	35	5.5	6.5
DISTANCE TO >K (x100m)[c]	1.6	0.7	1.2	1.7	2.2	0.7	5.0	7.6	11.5	0.3	0.2	6.7	12.7	35	6.5	8.9
# PLANT SPECIES	30	25	39	41	49	27	37	27	28	28	31	31	31	44	33	29
# MAMMAL SPECIES[d]	5	3	3	4	7	5	6	4	5	4	4	4	6	-	-	-
MAMMALS/ 100 TN[e]	7.38	12.3	5.90	4.69	6.20	6.51	7.79	18.2	13.6	7.29	9.09	7.63	10.0	-	-	-
# REPTILE SPECIES[f]	2	1	1	-	1	0	3	2	-	-	-	-	-	-	-	-
REPTILES/ 100 TN[e]	0.74	2.50	5.56	-	0.32	0	2.38	9.26	-	-	-	-	-	-	-	-

[a]Distance to mainland: shortest directline distance across lava.

[b]Width of barrier: utilizing kipukas as "stepping stones" if possible, minimum distance across lava necessary to reach mainland.

[c]Distance to >K: distance to nearest kipuka, if any, that is larger.

[d]# Mammal species: numbers include Neotoma cinerea and Sylvilagus nuttalli, presumed present on every kipuka.

[e]Animals/100 TN: number of individuals of all species captured for every 100 trap nights.

[f]# Reptile species: numbers include any snakes sighted, but only for those kipukas that were pitfall-trapped.

Table 5. Number of animals of each species captured on each kipuka.

KIPUKA	1	2	3L	4	5	6	7	8	9	10	13	14	15	16	18	TOTAL
P. maniculatus	39	30	6	17	25	48	9	77	34	42	17	25	19	69	15	472
E. minimis	1	0	0	0	2	4	2	10	1	15	4	1	3	11	0	54
S. nuttalli	1	1	0	0	0	3	2	3	2	0	0	0	0	0	0	12
P. parvus	0	0	0	0	0	1	0	10	0	0	0	0	0	0	0	11
N. cinerea	0	1	5	0	0	0	0	0	2	0	0	0	0	0	0	8
S. townsendii	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	6
M. montanus	1	0	0	0	0	0	1	2	0	0	0	0	0	2	0	6
R. megalotis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
# mammal spp.	4	3	2	1	2	6	4	5	4	3	2	2	2	4	1	8
Total # mammals	42	32	11	17	27	58	14	102	39	58	21	26	22	86	15	570
mammals/ 100 trap-nights	7.38	5.09	12.3	4.69	5.90	6.51	6.20	18.2	7.79	7.29	13.6	7.63	9.09	14.4	10.0	8.34
S. graciosus	1	2	3	-	-	0	0	16	3	-	-	-	-	-	-	25
E. skiltonianus	1	0	0	-	-	1	0	0	7	-	-	-	-	-	-	9
Total # reptiles	2	2	3	-	-	1	0	16	10	-	-	-	-	-	-	34
reptiles/ 100 trap-days	0.74	5.56	2.50	-	-	0.32	0	2.38	9.26	-	-	-	-	-	-	2.16

Table 6. Slope, aspect, soil texture, and soil organic material for 27 non-lava plots.

PLOT	SLOPE CLASS	ASPECT CLASS	% SAND	% SLIT	% CLAY	% ORGANIC	SOIL CLASS
1.1	1	4	62	21	17	3.1	sandy loam
1.2	1	3	65	16	19	2.1	sandy loam
2.1	1	3	32	39	29	2.9	clay loam
4.1	1	4	29	47	24	6.5	loam
5.1	3	0	37	41	22	7.3	loam
5.2	3	5	30	49	21	3.7	loam
6.1	2	0	25	43	32	5.5	clay loam
6.2	0	1	31	51	18	3.8	silt loam
6.3	2	0	34	36	30	5.7	clay loam
6.4	1	3	48	36	16	5.8	loam
7.1	0	1	24	45	31	4.7	clay loam
8.1	4	0	34	47	19	10.2	loam
8.2	4	5	51	32	17	4.6	loam
8.3	3	4	50	32	18	4.4	loam
8.4	4	3	47	32	21	4.7	loam
9/10bot*	-	-	55	30	15	9.2	sandy loam
9/10top*	-	-	18	57	25	3.0	slit loam
13.1	1	0	41	41	18	4.5	loam
14.1	2	0	39	39	22	5.0	loam
15.1	4	2	45	37	18	6.0	loam
16.1	3	0	45	40	15	7.8	loam
16.2	0	1	45	37	18	5.1	loam
16.3	3	0	45	41	14	8.4	loam
18.2	2	4	28	29	43	7.2	loam
20.1	1	3	75	10	15	1.5	sandy loam
20.2	2	3	54	29	17	1.8	sandy loam
25.1	4	2	12	58	30	3.1	silty clay loam

key to slope classes:

CLASS	AVG.% SLOPE
0	FLAT
1	0-2
2	2-5
3	5-12
4	> 12

key to aspect classes:

CLASS	AVG. ASPECT (° from true N)
0	N (300-60)
1	FLAT
2	E (60-120)
3	W (240-300)
4	SE (120-180)
5	SW (180-240)

*Soil samples for K9 and K10 were pooled. 9/10bot values are for samples from the lower, edge-like portions of the kipukas. 9/10-top values are for samples from the ridges.

Table 7. Number of small mammals caught in each plot, along with Shannon-Wiener (S-W) and Simpson diversity indices and individuals per 100 trap nights. Individuals per 100 trap nights uses capture data for the first three days of trapping only.

PLOT	PERO MAN	EUTA MIN	SYLV NUT	PERO PAR	NECT CIN	SPER TOW	MICR MON	REIT MEG	S-W INDEX	SIMPSON INDEX	INDS/ 100TN
1.1	14	1	1						.6291	.2266	7.04
1.2	25						1		.8496	.0740	11.37
2.1	24		1						.8454	.0768	11.57
3.1L	6				5				.5021	.4959	5.09
4.1	17								1.0	0.0	7.87
5.1	13								1.0	0.0	6.02
5.2	12	2							.6636	.2449	5.56
6.1	32	1							.8730	.0588	13.43
6.2	5	3							.5160	.4688	3.72
6.3	5		2					1	.4065	.5312	3.70
6.4	5		1	1		1			.3418	.5625	3.70
7.1	9	2	2				1		.3575	.5408	6.51
8.1	25	2		3			2		.4670	.3730	14.35
8.2	16			3					.6465	.2659	8.33
8.3	10			2					.6373	.2778	5.09
8.4	15	7	1						.4597	.4802	9.77
9.1	34	1	2		2				.5956	.2341	18.22
10.1	17	3							.6553	.2550	9.26
13.1	17	4							.6145	.3084	8.80
14.1	25	1							.8496	.0740	11.16
15.1	19	3							.6715	.2355	10.19
16.1	16	6				1	2		.3833	.5248	11.32
16.2	24	1				2			.6573	.2030	12.50
16.3	28	4				1			.6058	.2645	15.28

Species names:

Peromyscus maniculatus
Eutamias minimus
Sylvilagus nuttalli
Perognathus parvus
Neotoma cinerea
Spermophilus townsendii
Microtus montanus
Reithrodontomys megalotis

Table 8. First two species ordinations derived by PCA from a 25 stand subset of the vegetative data. Only the species that appear in at least five plots are used. Letter combinations are species abbreviations (abbreviations are explained in Appendix II). Numbers represent the relative positions of species along the ordination, with the length of the axis fixed at 100.

AXIS 1		AXIS 2	
ARTD	0.00	ARTD	0.00
POAB	44.5290	ARTP	8.3849
BASA	45.5971	AGSP	49.9475
CHNA	46.1208	LUAR	66.1736
SIHY	46.6350	ERMI	68.8000
PUTR	46.7838	ASFI	68.8683
ORHY	47.4978	PHHO	68.9716
CHDO	47.6578	CYTE	69.1610
CAMA	47.7546	PUTR	69.2174
PHLO	47.7867	LEPU	70.1784
OPPO	47.8574	ARAB	70.6378
PECY	47.8737	PHHA	70.7345
EROV	47.8916	EROV	70.8343
PHHA	47.9111	PHLO	70.8934
ARAB	47.9287	CRAC	70.9037
CHVI	48.3141	CAMA	71.0112
PHHO	48.5219	CHDO	71.1170
TECA	48.6042	PECY	71.1608
CYTE	48.9368	OPPO	71.6872
CRAC	49.1512	ORHY	72.0543
ERMI	49.4713	POAB	72.8359
ASFI	49.7646	SIHY	73.7033
ELCI	50.2480	TECA	74.5659
LUAR	53.7424	ELCI	79.6464
LEPU	54.1253	BASA	85.7880
STCO	57.9863	CHNA	87.2654
AGSP	63.8704	CHVI	92.4185
ARTP	100.0000	STCO	100.0000

Table 9. First two stand ordinations derived by PCA from a 25 stand subset of the vegetative data. The numbers in the first and third columns are plot names. The numbers in the second and fourth columns represent the relative positions of plots along the ordination, or axis of variation, with the length of the axis fixed at 100.

AXIS 1		AXIS 2	
2.1	0.00	4.1	0.00
4.1	2.2484	2.1	12.1764
6.2	8.6544	18.2	13.9575
20.2	20.8240	6.2	15.7767
8.3	34.9657	8.1	29.8634
20.1	37.0076	7.1	32.6261
8.4	39.5184	16.1	35.7797
6.4	39.8380	13.1	36.1632
1.1	40.4363	16.2	37.1858
1.2	40.6057	14.1	43.5419
8.2	41.2298	5.1	47.3307
25.1	45.3286	6.4	47.4022
5.2	53.8976	5.2	50.9786
6.3	62.1904	20.2	55.2680
16.3	63.8399	6.1	56.5886
6.1	68.8374	6.3	65.4602
5.1	69.4001	15.1	69.5595
7.1	72.9968	8.2	70.5475
15.1	73.9296	8.4	71.2805
14.1	77.3227	8.3	72.0753
8.1	82.7740	25.1	76.1786
16.2	83.4013	20.1	91.9252
16.1	83.5120	1.2	93.8745
13.1	85.3941	16.3	97.2050
18.2	100.0000	1.1	100.0000

Table 10. Variables tested by correlation analysis against ordinations.

CAUSAL[a]		RELATIONAL[b]	
kipuka size			
slope			
aspect	*		
topography index			
% sand in soil	*		
% silt in soil	*		
% clay in soil			
% stones in soil			
% organic in soil	*	% organic in soil	*
		# of plant species	*
		Shannon-Wiener index for plants	*
		Simpson index for plants	*
		% cover of vegetation	*
		# of mammal species	
		Shannon-Wiener index for mammals	
		Simpson index for mammals	
		individuals/100 trap-nights	
		# of P. maniculatus captured	

* significant at p .05

[a]Variables that might be responsible for the observed relationships among stands.

[b]Variables whose values might result from the observed relationships among stands.

Table 11. Species correlations within plots.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1.AGSP X				+2			+1					+2			+2	+1	+1	+1					-1						-1	
2.ARAB X							+2	+2											+1						+1						
3.ARTD X	-1																														
4.ARTP X	+1														+1			+3											-1		
5.ASFI X																											+3				
6.BASA X																				+1								+2			
7.CAMA X													+1												+1		+1	+3			
8.CHDO X																			+2												
9.CHMI X	+1												+2						+1				+3								
10.CHNA X																													+3		
11.CHVI X																															
12.CRAC X															+3	+1	+1	+1		+2											
13.CYTE X																							+1								+1
14.ELCI X																						+3								+3	
15.ERMI X	+3	+2	+1																	+2											
16.EROV X			+1																												
17.LEPU X																												+2			
18.LUAR X																														+2	
19.MEOB X																									+1						
20.OPPO X																															
21.ORHY X																															
22.PECY X																														+3	
23.PEDE X																															
24.PHHA X																															
25.PHHO X																															+1
26.PHLO X																															
27.POAB X																															
28.PUTR X																															
29.SIHY X																															
30.STCO X																															
31.TECA X																															

The numbers at the top of the columns correspond to the numbered species abbreviations along the left side of the matrix rows; abbreviations are explained in Appendix II. A number within the matrix indicates a significant correlation between the row and column species that correspond to the position of the number. The sign of the number indicates whether the correlation is positive or negative. The value of the number indicates the strength of the relationship: for 1, $p<.05$; 2, $p<.01$; 3, $p<.001$.

Table 12. Comparison of correlation coefficients between species on a plot level of analysis with chi square values testing association between species on a sample frame level of analysis. Numbers 0-3 refer respectively to no significant association, significance at $p<.05$, significance at $p<.01$, and significance at $p<.001$. Signs refer to positive or negative associations.

SPECIES	ASSOCIATED SPECIES	SIGNIFICANT ASSOCIATION WITH r	SIGNIFICANT ASSOCIATION WITH X^2
AGSP	ARTD	0	-2
	ARTP	+2	+1
	CHVI	0	-1
	ELCI	0	-1
	LEPU	+1	+3
	STCO	0	-3
ARTD	AGSP	0	-3
	ARTP	-1	-3
	CHVI	0	-2
	STCO	0	-3
ARTP	AGSP	+2	+3
	ARTD	-1	-3
	CHNA	0	-1
	CHVI	0	-2
	POAB	0	-3
LEPU	PUTR	+2	0
	AGSP	+1	0
CHVI	AGSP	0	-3
	ARTD	0	-2

Table 13. Plant and small mammal species numbers for kipukas that are grouped into size-classes and arranged according to degree of isolation.

KIPUKA	SIZE (ha)	DISTANCE TO M.L.[a] (m)	# MAMMALS SPECIES[b]	# PLANT SPECIES
2	.45	70	3	25
7	.16	350	5	27
4	.40	400	3	39
13	.69	550	4	28
14	.57	560	4	31
9	.57	1490	4	27
1	1.4	160	5	30
5	1.1	410	4	41
15[c]	2.2	670	4	31
10	.97	1800	5	28
6	3.1	220	7	49
8	3.6	500	6	37
15[c]	2.2	670	4	31
16	3.2	1270	6	31

The use of the other isolation measures (see Table 4) caused no change of order of isolations within any of the size classes, with this exception:

KIPUKA	SIZE	DISTANCE TO >K[d]	# MAMMAL SPECIES[b]	# PLANT SPECIES
14	.57	20	4	31
13	.69	30	4	28
2	.45	70	3	25
7	.16	70	5	27
4	.40	120	3	39
9	.57	760	4	27

[a] Distance to mainland: shortest direct-line distance across lava.

[b] # mammal species: numbers include Neotoma cinerea and Sylvilagus nuttalli, presumed present on every kipuka.

[c] K15 is placed in two size classes because of its intermediate size.

[d] Distance to >K: distance to nearest kipuka, if any, that is larger.

Table 14. Relationship between kipuka size and encounters of rare small mammal species. (Rare species are considered to be Perognathus parvus, Spermophilus townsendii, Microtus montanus, and Reithrodontomys megalotis.)

KIPUKA	SIZE (HA)	# RARE SPECIES
8	3.6	3(2)
16	3.2	2(2)
6	3.1	3
15	2.2	0
1	1.4	1
5	1.1	0
10	.97	1
13	.69	0
14	.57	0
9	.57	0
2	.45	0
4	.40	0
7*	.16	1

* K7 is only 70 m from 3.1 ha K6.

() indicates likely populations.

APPENDIX I

Kipuka Descriptions

K1 was a deep-soiled kipuka of low relief, dominated by *Chrysothamnus viscidiflorus* and *Balsamorrhiza sagittata*. The soil was loose and largely bare between clumps of vegetation. Plot 1.1 was located with a southwest facing aspect; plot 1.2 was on the southeast.

K2 was a small, flat and high-walled hole kipuka. Plant diversity was low--vegetation away from the edge consisted almost solely of *Artemisia tridentata*, although there was a substantial edge community on the south and the west sides. The soil was hard-baked and fine-textured, mostly bare. In addition to the trapping done in plot 2.1, some traps were placed in the edge area.

3.1L was an area of relatively well-vegetated lava. From the high and fairly barren northern end the plot sloped down toward a pocket of accumulated soil and organic matter which was heavily vegetated with *A. tridentata, Chrysothamnus nauseosus,* and *Chamaebatiaria millifolium*. The one pitfall trap established in this plot was located in this pocket.

K4, like K2, was small, high-walled, and dominated by *A. tridentata,* but there was a substantial cover of grasses and forbs. Near the center, bedrock emerged from the soil and *Purshia tridentata* was an important species. *Artemisia tripartita* replaced *A. tridentata* at the perimeter of the kipuka, particularly on the west side furthest from the central

outcrop; *A. tridentata* again dominated in the edge. Plot 4.1 was situated almost entirely within the central *A. tridentata/P. tridentata* vegetation.

K5, a low-walled kipuka of moderate relief, offered three contrasting communities: a mesic-appearing grass-dominated community in the loose soil of the north and east side; a xeric-appearing but very diverse *A. tripartita* community in the stoney, rocky soil of the exposed southwestern slope; and a *A. tridentata* community in the clay soil of the center and southeastern portion of K5. Plots 5.1 and 5.2 were established in the first two of these communities.

K6 was a fairly large kipuka of low relief. On the east was a belt of largely bare soil, dominated by *A. tridentata*. Further west ran a belt of diverse low shrubs and grasses that swung along the north side toward the west. At the south-center of the kipuka stretching west was a stoney, rocky "spine" characterized by *A. tridentata* and *P. tridentata*. Plot 6.1 was established in the *A. tridentata* zone, plots 6.2 and 6.3 were in the grassy zone, and plot 6.4 was situated on the "spine" at the west end of the kipuka.

K7 was so small that the endpoints of the plot were on the lava edge. The kipukas was flat, with clay soil, and the vegetation was dominated by *A. tripartita* with *A. tridentata* scattered throughout.

K8 was a kipuka of strong relief, rising well up out of the surrounding lava and offering strong contrasts in aspect. Plots 8.1-8.4 were established on four different aspects. The heavily vegetated north

facing slope, dominated by *A. tripartita, A. spicatum,* and *Leptodactylon pungens,* had deep but stoney soil. The west facing slope had stoney shallow soil and was dominated by *C. viscidiflorus, A. tridentata,* and *P. tridentata.* The east facing slope was characterized by *A. tridentata* ssp. *tridentata,* with a diversity of undercover.

K9 and K10 were remnants of old crater walls so that, except for at the bottoms, where organic matter has collected, there was much rock and little soil. Neither kipuka had a site 20 x 50 m homogeneous vegetatively. There was strong influence by edge species such as *Chrysothamnus nauseosus* and *Chamaebataria millifolium.*

K13, K14, K15 and K16 were all located along what was apparently a relict ridge almost entirely inudated by lava. The lava formed a high wall to the southwest of Area 4 but was almost flat to the kipukas on the northeast side, so that all of the kipukas were more or less north facing. K13, K14 and K15 were within 50 m of each other; all had fairly stoney soil.

K13 was flat and dominated by low vegetation: *A. tripartita, C. viscidiflorus,* and *L. pungens.* Plot 13.1 was on the northwestern portion separated from the rest of the kipuka by a narrow isthmus.

K14 was divided topographically into two parts: a shallowly sloping southern section dominated by *L. pungens, A. tripartita,* and *A. spicatum,* and a strongly sloping northern part more diverse vegetatively due to the rock cropping out at the break in the slope. Placement of plot 14.1 included both of these areas.

K15 too had many rock outcrops and was consequently a diverse mix of *A. tripartita* and *A. spicatum* interspersed with *A. tridenta* and *P. tridentata*. Plot 15.1 was situated in the more steeply sloping north central zone.

The large K16 was located at the western end of Area 4. Plots were placed in each of three distinct vegetational communities. Plot 16.1 was on the east side: separated from the rest of the kipuka by a rocky ridge was a fairly heterogeneous community consisting of *A. tripartita, A. spicatum* and scattered *Chrysothamnus* and *Elymus cinereus*. To west of the ridge on the higher, flatter southern portion of the kipukas was a low *A. tripartita* community broken up by scattered clumps of *A. tridentata* corresponding to rock outcrops; here was plot 16.2. On the lower northern portion, where plot 16.3 was located, soil was fairly loose and the vegetation was dominated by *Stipa* and *E. cinereus*.

K18 was a very large kipuka with strong relief and a variety of communities including mesic *Amelanchier alnifolia/Symphoricarpos oreophilus* thickets. One plot was sampled, in an *A. tripartita* community, and some traps were laid out. We did not have an opportunity to prebait the traps and only *Peromyscus maniculatus* came to the traps in one night.

K20 was a large kipuka with fairly low relief. The higher east end had loose sandy soil; it was dominated by *C. nauseosus* and *Bromus tectorum*; here plot 20.1 was placed. The lower west, where plot 20.2 was located, had about the same aspect, but the soil was hard-baked, with more clay, and the vegetation differed correspondingly: *A. tridentata*

dominated, and *C. nauseosus* and *B. tectorum* were by and large restricted to pockets of sand within the clay.

21.1L, 22.1L, and 23.1L were all in Area 1.

21.1L was located just north of 3.1L, in an area of vegetation similar to that of 3.1L, although the pocket of vegetation was less well developed and the lava above the pocket was more barren. Edge species dominated.

22.1L was adjacent to the north side of K1; it was part of the edge of K1, not much higher than K1 and one to three meters lower than the surrounding lava. *A. tridentata* dominated but there was much bare lava.

23.1L was the only truly barren lava we sampled. It was located south and well above K1; the surface was fairly smooth, with no major irregularities. Only four species were sampled in 50 frame placements.

K25 was a crater remnant. The dominant vegetation on this kipuka was grass, *A. spicatum* and *Poa* and *Stipa*, along with *A. tridentata* and *A. tripartita*, and occasionally *P. tridentata*. The soil surface was stoney but the soil beneath the surface was deep and not stoney. The central crater appeared to have been burned in the past; there was little shrub, mostly *B. tectorum* and annual mustards. Plot 25.1 was situated on the northeastern outer slope of the kipuka.

APPENDIX II

Vascular plants identified during field research, Summer 1979

(The numbers following the common name of a plant refer to the kipukas on or near which the plant was identified. For those species that were sampled in plots, the four letter combination preceding the name is the abbreviation used in figures in the text.)

AGDA Agropyron dasytachum (Hook.) Scribn., thickspike wheatgrass; 20
Encountered on only one kipuka.

AGSP Agropyron spicatum (Pursh) Scribn. & Smith, bluebunch wheatgrass; all but lava plots
The most common grass; found on every kipuka.

Alium geyeri Wats., Geyer's onion; 4
This generally inconspicuous lily may have been overlooked on other kipukas.

Amelanchier alnifolia Nutt., western serviceberry; 18
Found only on the kipuka with the greatest relief, reflecting its greater moisture requirement. It also occurred at several locations along the lava's edge, rooted in deep moisture-retaining cracks.

Antennaria microphylla Rydb., rosy pussy-toes
Found on the eastern side of Huddle's Hole near the lava's edge.

Arenaria franklinii Dougl., Franklin's sandwort; 2
Possibly confused occasionally with Leptodactylon pungens when not in flower.

ARAB Arabis L. spp., rockcress; all but 3L,7,9,13,14,21L,23L
The most common species were A. holboelli Hornem. and A. sparsiflora Nutt., but at least two other species were found. Especially common in stonier soils.

Arnica sororia Greene, twin arnica; 6
Found also on Huddle's Hole.

ARTD Artemisia tridentata Nutt., big sagebrush; all but 10,13,14,15,23L

ARTP Artemisia tripartita Rydb., threetip sagebrush; all but 1,2, and lava plots
One of these two Artemisia species was a dominant shrub in almost every kipuka community. A. tripartita prevailed more often in deeper soils, steeper slopes, and moister aspects; A. tridentata often was present within a stand of A. tripartita, associated with rock outcrops and patches of shallower soil. We found two subspecies of A. tridentata coexisting on most kipukas where big sagebrush was found: ssp. wyomingensis,

Wyoming big sagebrush, and ssp. tridentata , basin big sagebrush.

ASFI Astragalus filipes Torr., basalt milkvetch; 1,4,5,6,7,13,16,18
Quite abundant in some communities.

ASPU Astragalus purshii Dougl., wooly-pod milkvetch; 4,5,6
One other Astragalus species was found on K15.

ATSP Atriplex spinosa (Hook.) Collotzi, spiny hopsage; 8
A dominant shrub on the cindery soil atop K8. Also found on an unnamed kipuka in Area 4.

BASA Balsamorrhiza sagittata (Pursh) Nutt., arrowleaf balsamroot; 1,2,5,6,18,20,25
Where found it was generally quite abundant.

Bromus tectorum L., cheat grass; 6,8,20,25
Also found on Huddle's Hole. Cheat grass was not common on the northern kipukas of the Craters of the Moon flow except on Huddle's Hole, which was subject to livestock grazing; but it was very common on the southern portion of the Craters flow.

CAMA Calochortus macrocarpus Dougl., sagebrush mariposa; 4,5,6,8,9, 13,14,15,18,20,25
A widely-occurring lily.

CAFI Carex filifolia Nutt., threadleaved sedge; 4,5,6,16
Growing in deep-soiled low areas of these kipukas, generally near the kipuka edge. One other species of Carex was found in a deep crack on the lava north of K1.

CAAN Castilleja angustifolia (Nutt.) G. Don, northwest paintbrush; 6,8
Also found on Huddle's Hole.

Castillega chromosa A. Nels., desert paintbrush
A widely occurring lava species.

Castillega inverta (Nels. & Macbr.) Pennell & Ownbey
Found only on Huddle's Hole.

CHDO Chaenactis douglasii (Hook.) H. & A., hoary false-yarrow; all but 3L,7,13,23L,25
A common and widespread edge species, growing in stony or cindery soils on kipukas and occasionally rooted in the shallow soil of cracks or crevices on lava.

CHMI Chamaebatiaria millifolium (Torr.) Maxim., fern-bush; all but 23L
A very common shrub of edge and lava.

CHNA Chrysothamnus nauseosus (Pall.) Britt., rubber rabbitbrush; all but 23L
Common on kipukas especially associated with rocky or sandy soil. Also common on the lava edge surrounding kipukas, but rarely found very far away from a kipuka.

CHVI Chrysothamnus viscidiflorus (Hook.) Nutt., green rabbitbrush; all but 21L,22L,23L
Required better developed soils than its congener, although it was equally common. Almost never found growing on lava.

CIUT Cirsium utahense Petr., Utah thistle; all but 2,14,22L,23L
A common edge species, sometimes found on lava far from the nearest kipuka.

Clematis ligusticifolia Nutt., western virgin's-bower; 20
Growing in the edge.

CRAC Crepis accuminata Nutt., longleaved hawksbeard; 1,2,4,5,6,8,18,20,25
Usually abundant where present.

CRIN Cryptantha interrupta (Greene) Pays., bristly cryptantha; 1,3,10
An inconspicuous but not uncommon edge and lava species.

CYTE Cymopterus terebinthus (Hook.) T. & G., turpentine cymopterus; 4,6,8,20,23L,25
A common, widespread edge and lava species, also found near the center of some kipukas associated with rock outcrops.

Cystopteris fragilis (L.) Bernh., brittle bladder-fern
Found exclusively in deep lava cracks.

Delphinium andersonii Gray, desert larkspur; 4,6
Associated with rock outcrops and P. tridentata. An early bloomer, possibly overlooked on some other kipukas.

Descurainia Webb & Berth. sp., tansymustard; 20,25
Weedy annuals like this and B. tectorum were significant components of the plant communities on the Wapi flow and on the south portion of the Craters flow. Descurainia was also found on Huddle's Hole.

ELCI Elymus cinereus Scribn. & Merr., giant wild rye; all but 3L,22L,23L
Widely but patchily distributed; occasionally dominant, as on K15 and K16.

ERCO Erigeron compositus Pursh, cut-leaved daisy; 6,21L,22L,23L
A very common lava plant.

ERPU Erigeron pumilis Nutt., shaggy fleabane; 6
Not found on the lava.

ERMI Eriogonum microthecum Nutt., slenderbrush buckwheat; 1,6,8,14,15,16,18,20,25
A common subshrub on stony soils.

EROV Eriogonum ovalifolium Nutt., cushion buckwheat; all but 1,2,7,25, and lava plots
A widespread kipuka plant.

ERUM Eriogonum umbellatum Torr., sulfur buckwheat; all but 2,6,7,20,22L,23L,25
A widespread edge plant.

Eurotia lanata (Pursh) Moq., winterfat; 6

Festuca idahoensis Elmer, Idaho fescue
Growing on Huddle's Hole.

Fritillaria atropurpea Nutt., checker lily; 8
An early bloomer; possibly unnoticed elsewhere.

HARE Haplopappus resinosus (Nutt.) Gray, Columbia goldenweed; 2,3L,6, 9,10,13,14,15,18,21L,22L
A dominant lava plant, generally growing in tiny cracks.

HODU Holodiscus dumosus (Hook.) Heller, gland oceanspray; 2,3L,4,5,6, 9,10,13,14,18,21L,22L
A widespread inhabitant of deep lava cracks.

Juniperus osteosperma (Torr.) Little, Utah juniper; 24,25
This tree was very common rooted in deep lava cracks on the Wapi flow and on the southern portion of the Craters flow.

Juniperus scopulorum Sarg., Rocky Mountain juniper
The only species of juniper found in the northern part of the Craters of the Moon flow, located at the very northern edge of the lava to the north of Area 1, rooted in deep lava cracks.

KOCR Koeleria cristata Pers., prairie Junegrass; 4,5,6,18
Found in deep soil.

Lactuca serriola L., prickly lettuce
Found on lava on the southern portion of the Craters flow.

LEPU Leptodactylon pungens (Torr.) Nutt., prickly phlox; all but lava plots
A common subshrub on kipukas; it was often found growing on lava as well.

LIRU Lithospermum ruderale Dougl., western gromwell; 4,6,7,14,15,16,18
A fairly widespread plant on deep-soiled areas of kipukas.

LODI Lomatium dissectum (Nutt.) Math. & Const., fern-leaved desert parsley; 1,4,5,6,7,18
A locally significant forb.

LUAR Lupinus argenteus Pursh, silvery lupine; all but 8,10,25, and lava plots
A widespread kipuka and edge plant.

MACA Machaeranthera canescens (Pursh) Gray, hoary aster; 20
Frequently noted on the Wapi flow and on the southern portion of the Craters flow.

MEOB Mertensia oblongifolia (Nutt.) G. Don, leafy bluebells; 1,5,6,7, 18,20,22L
When not in flower this was occasionally confused with P. cyaneus

Oenothera caespitosa Nutt., desert evening primrose; 20
Also found on old lava west of Area 2.

OPPO Opuntia polyacantha Haw., prickly pear; all but 9 and lava plots
A widespread kipuka plant.

ORHY Oryzopsis hymenoides (R. & S.) Ricker, Indian ricegrass; all but 9,14,21L,23L,25
A widespread but not major grass.

PECY Penstemon cyaneus Pennell, dark blue penstemon; all but 25 and lava plots
A widespread kipuka plant occasionally confused with M. oblongifolia.

PEDE Penstemon deustus Doubl., hot-rock penstemon; all but 23L
A ubiquitous lava and edge species.

PHHA Phacelia hastata Dougl., silverleaf phacelia; all but 3L,9,10,21L, 23L,25
This plant grew near the edge, but not usually in the edge.

Philadelphus lewisii Pursh, Lewis' mockorange; all but 2,4,15,16, 21L,23L
A widely occurring inhabitant of deep lava cracks.

PHHO Phlox hoodii Rich., Hood's phlox; all but 10 and lava plots
A kipuka plant associated with stony and rocky soils.

PHLO Phlox longifolia Nutt., long-leaf phlox; 1,2,4,5,6,7,16
This inconspicuous plant may have occurred elsewhere as well.

PIFL Pinus flexilis James, limberpine; 1,3L
Found only on the northern portion of the Craters flow, rooted in deep lava cracks; further south it appears to be replaced ecologically by J. osteosperma. Particularly common between K18 and Huddle's Hole.

POAB Poa L. spp., bluegrass; all but 2,21L,23L
P. sandbergii Vasey, Sandberg's bluegrass, most common on shallow rocky soil, was often difficult to distinguish from P. nevadensis Vasey, Nevada bluegrass, which was found on better soils but also inhabited lava cracks and crevices; often they coexisted. Poa was rarely a dominant grass but was almost always present.

Polystichum scopulinum (D.C. Eat.) Maxon, rock sword-fern
Found exclusively in deep lava cracks.

POGL Potentilla glandulosa Lindl., gland cinquefoil; all but 2
The most common plant on the lava flows.

PUTR Purshia tridentata (Pursh) D.C., antelope bitterbrush; all but 1, 2,16, and lava plots
Especially associated with rock outcrops.

Ribes aureum Pursh, golden currant; 5,8,14,15,18,25

Ribes cereum Dougl., squaw currant; 8,14,15,18
Like R. aureum, an edge species that is occasionally found in association with rock outcrops.

SECA Senecio canus Hook., wooly groundsel; 3L,6,21L,22L
A lava plant.

SEIN Senecio integerrimus Nutt., western groundsel; 1,2,4,6,8,10,14
A kipuka plant.

SIHY Sitanion hystrix (Nutt.) Smith, bottlebrush squirreltail; all but 4,7,13,15,16,21L
Often present but usually rare on kipukas, this grass was the most common grass on lava.

STTE Stephanomeria tenuifolia (Torr.) Hall, narrow-leaved skeletonweed; 1,3L,4,5,8,9,18,21L,23L
A lava plant, widespread but not abundant.

STCO Stipa L. spp., needle-and-thread; all but lava plots
Frequently the dominant grass in well-soiled, especially sandy-soiled areas. S. occidentalis Thurb., western needlegrass; S. thurberiana Piper, Thurber's needlegrass; and S. comata Trin. & Rupr., needle-and-thread, were treated together.

Symphoricarpos oreophilus Gray, mountain snowberry; 18
An inhabitant of relatively moist situations, this plant was found only on K18, although at both south and north facing aspects.

TECA Tetradymia canescens D.C., gray horsebrush; all but 2,7, and lava plots
A widespread and common kipuka shrub. This shrub was found on the lava on the Wapi flow but not on lava on the northern Craters of the Moon flow.

Tragopogon dubius Scop., yellow salsify
Found on lava on the southern portion of the Craters flow.

VINU Viola nuttallii Pursh, valley yellow violet; 1,6
This early bloomer may have been overlooked on other kipukas.

ZIPA Zigadenus Michx. sp., death-camas; 8,25
Also found on Huddle's Hole. This lily was very common on the mainland north of Area 1, yet none were seen on the kipukas of Area 1.

APPENDIX III

Mammals identified during field research, Summer 1979

(Numbers following the common name of an animal refer to the kipukas on which the animal was captured.)

Canis latrans, coyote
We never saw a coyote, but scat was found on almost all kipukas and at many locations on open lava. They were also heard at various times in all portions of the study area.

Eutamias minimus, least chipmunk; 1,5,6,7,8,9,10,13,14,15,16
The second most common animal captured; often observed on kipukas and in the lava due to its abundance and its diurnal habits.

Lepus californicus, blacktail jackrabbit
Only one individual was sighted, on Huddle's Hole.

Marmota flaviventris, yellow-bellied marmot
Observed on K8, K9, and on a kipuka just north of Huddle's Hole. Based on scat found and on their habitat preferences it is likely that they were more widely distributed.

Microtus montanus, montane vole; 1,7,8,16
Only six specimens taken, at north facing locations. Another individual was spotted on the lava north of K1 one night.

Neotoma cinerea, bushy tailed woodrat
Caught only by traps set on or near the edge of the lava; often they were not killed by the traps. Although they apparently do not venture far from lava, we saw woodrat sign--their highly visible urine markings--near every kipuka we visited.

Ochotona princeps, pika
Spotted or heard in talus-like lava rock in or near Areas 1, 3, and 4 as well as far removed from any kipukas between Area 1 and Area 4. Generally inhabitants of higher elevations, they appear to be successful in the lava environment. Unlike woodrats, which associated with kipuka edges, pikas seemed to have no dependence at all on kipukas.

Odocoileus hemoinus, mule deer
Observed on K18 and in Area 4; these ungulates seemed comfortable moving over lava.

Perognathus parvus, Great Basin pocket mouse; 6,8
Only one was captured on K6, but they were as common as chipmunks on K8 where they were found in a variety of habitats.

Peromyscus maniculatus, deer mouse; all kipukas
By far the most abundant animal everywhere we trapped; it was obviously widely distributed over both kipukas and lava.

Reithrodontomys megalotis, western harvest mouse; 6
Only one specimen captured, although it is a fairly common animal on the nearby desert.

Sorex sp., shrew; 1
One specimen captured in a pitfall trap on K1. Its distribution is hard to assess because, being carnivorous, shrews are not attracted to peanut butter-baited snap traps.

Spermophilus townsendii, Townsend's ground squirrel; 6,10,16
Only six captured in all, and four of the six were captured on K16. K16 was the only kipuka where ground squirrel digging activity was noted. Another ground squirrel was seen on K8.

Sylvilagus nuttalli, Nuttall's cottontail; 1,2,6,7,8,9
Very common; observed on every kipuka and quite frequently seen on lava, occasionally far from any kipuka. Their distribution is poorly revealed by the trapping data, because they are too large to be captured reliably by the snap traps we used.

APPENDIX V

Reptiles identified during field research, Summer 1979

(Numbers following the common names of the lizards refer to the kipukas on which the lizards were captured.)

Coluber constrictor, racer

Two sightings were made, on consecutive days, one on each side of the narrow band of well-vegetated lava separating K14 and K15; probably we saw the same individual. A third sighting was made near the center of K8.

Crotalus viridis, Great Basin rattlesnake

Captured east of K18, in an area of lava characterized by talus-like lava rock and strong shrubbiness. Popular lore to the contrary, this was the only rattlesnake encountered on the flows.

Eumeces skiltonianus, western skink; 1,6,9

Trapped on only three strongly dissimilar kipukas; apparently quite abundant on K9. We did not sight any skinks except those in the pitfalls.

Pituophis melanoleucus, Great Basin gopher snake

Captured near the center of K8 by hand; another seen on K18.

Sceloporus graciosus, sagebrush lizard; 1,2,3,8,9

Common and visible animals, frequently observed during the course of our work. Often they were seen on lava near kipukas and occasionally sighted on lava at some distance from any kipuka. They were sighted on all kipukas in the northern Craters of the Moon flow except for K18 and for the kipukas in Area 4; this latter absence is somewhat surprising in light of their ubiquity elsewhere.

APPENDIX V

A description of the functions of principal components analysis and reciprocal averaging as ordination techniques.

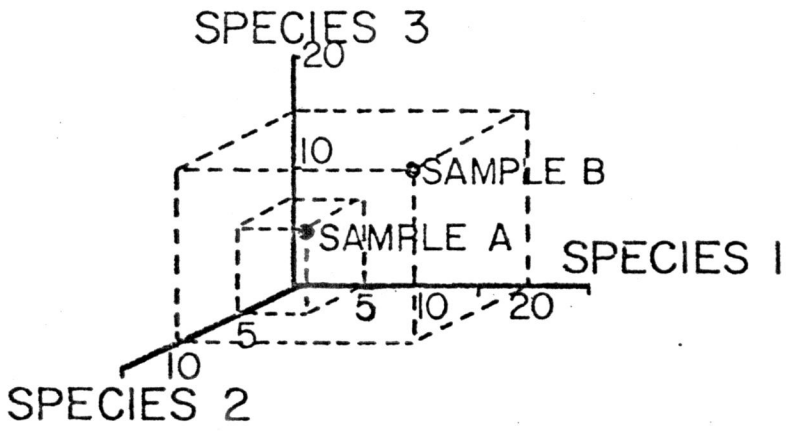
The function of principal components analysis (PCA) is most readily described geometrically. This description follows closely that of Gauch (1977). The structure of a data matrix of I stands and J species may be conceived as points in multidimensional space. Two such spaces exist: in species space, J axes are defined by the J species, and each stand is represented by points within this space, positioned in reference to each axis according to the score (cover) of that species within that stand (Fig. VA). Correspondingly, plot space is an I-dimensional space defined by the stands, with J species positioned as points within. Stand points located in species space have two important properties. 1) Stands with similar abundances of many species will be near to each other and dissimilar stands will be far apart. 2) The overall distribution of stands is not random, but concentrated in certain places or directions, reflecting the fact that some combinations of species abundances are more frequent than others. Given these two properties, the distribution of stand points within the species space should be informative.

A difficulty lies in trying to visualize a multidimensional space. By projecting the original J dimensional species space onto two or three dimensions, it is possible to inspect the distribution of stand points. When this is done, all structure except that along the chosen two or three dimensions will be lost. But if the structure of stand points is concentrated within two or three dimensions because other

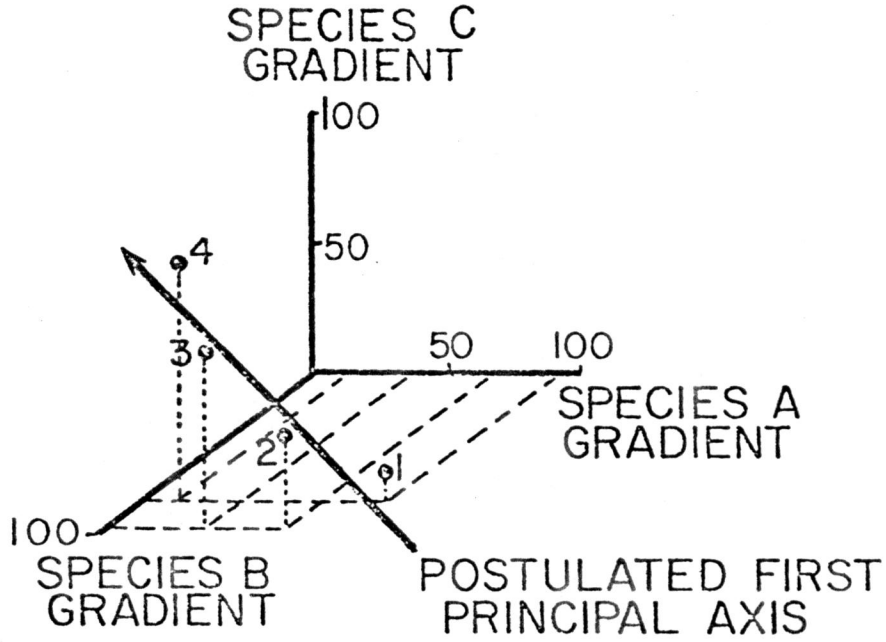
Figure V. A. Representation of two stands in three-dimensional species space. The importance value of a species in a stand fixes the position of the stand along the particular axis represented by that species.

B. Representation of the derivation of a first axis of variation among four stands in a three-dimensional species space.

A)


SPECIES 3
20
10
SAMPLE B
SAMPLE A
SPECIES 1
5
10
20
5
10
SPECIES 2

B)


SPECIES C
GRADIENT
100
50
4
3
50
100
SPECIES A
GRADIENT
2
1
100
SPECIES B
GRADIENT
POSTULATED FIRST
PRINCIPAL AXIS

dimensions are correlated with these, then it is possible to examine just a few dimensions and get a fairly accurate look at the structure of the points in their original space.

The function of PCA is simply to determine which axes through multidimensional space can be utilized with the least loss of original structure and information. The first PCA axis is situated, then, such that the variance of scores on the axis is maximized (Fig. VB); each succeeding axis extracts as much of the remaining variance on the axis as possible. The measure of variance on the axis is termed the eigenvalue. Any eigenvalue or sum of eigenvalues for axes 1 to N can be compared with the total variance to see what percentage of the total variance is accounted for by an axis or by the first N axes. If the structure of the stand positions in multidimensional species space is non-random, the bulk of the variance will be extracted in the early eigenvalues.

When an axis is specified in species space, the points representing stands are projected orthogonally onto the axis and are given scores representing their positions on the axis.

In this discussion of PCA I have for simplicity only talked of stand points in species space. The stand by species matrix has an analogous multidimensional stand space as well, and in PCA both species and stands are ordinated at the same time.

Reciprocal averaging (RA) (Hill 1973; Gauch 1977; Gauch et al. 1977) is another eigenanalysis, but a description of the technique is best made (Gauch 1977) with reference to a third ordination technique, weighted averages ordination (Whittaker 1960, 1967, 1978; Gauch 1977). In weighted averages ordination, ecological preferences of species for

positions along some environmental gradient are known; the species can be grouped by relative positions along the gradient and weighted values can be assigned to each species. These weights can be used to compute a weighted average of species composition within a stand. Since the species have been grouped according to an environmental gradient, values of the weighted averages for stands can be used to establish a relationship among the stands according to the same environmental gradient. It is possible as well to produce weighted average scores for species based on their occurrence in stands of known position along an environmental gradient. In other words, stand scores can be derived from species scores or species scores can be derived from stand scores.

Reciprocal averaging in effect derives both stand scores from species scores and species scores from stand scores, iteratively. Starting with arbitrarily assigned species scores, RA uses weighted averages to produce new species scores. With sufficient iteration, species and stand scores converge to a unique solution that is not affected by the initial choice of species scores. This convergent solution represents the axis of maximum variation; further axes can be extracted by correcting for the preceeding axes, each successive axis explaining a smaller share of the total variation. Like PCA, RA ordinates species and stands simultaneously. Unlike PCA, extracted axes beyond the first are frequently not interpretable in terms of additional environmental gradients (Gauch 1977; Gauch et al. 1977; Peet & Loucks 1977; Whittaker et al. 1978).

APPENDIX VI

For each plot, species ranked by importance value (absolute and relative cover in %).

TOTAL COVER IN PLOT 1.1 IS 39.0833

SPECIES	ABS COVER	REL COVER
CHVI	12.3333	31.5564
BASA	6.75	17.2708
CHNA	5.08333	13.0064
STCO	5	12.7932
TECA	3.91667	10.0213
ARTR	1.83333	4.69084
ASFI	1.75	4.47762
OPPO	1.25	3.1983
CRAC	.416667	1.0661
SIHY	.333333	.852879
ORHY	.166667	.42644
AGSP	8.33333E-02	.21322
ERMI	8.33333E-02	.21322
LEPU	8.33333E-02	.21322

TOTAL COVER IN PLOT 1.2 IS 41.9167

SPECIES	ABS COVER	REL COVER
CHVI	10.4167	24.851
STCO	6.83333	16.3022
BASA	5.25	12.5248
CRAC	3.66667	8.74751
ARTR	3.33333	7.95227
TECA	3.08333	7.35586
AGSP	2.75	6.56063
ASFI	2.75	6.56063
CHNA	1.33333	3.1809
ELCI	1.25	2.9821
ORHY	.5	1.19284
SIHY	.25	.596421
ARAB	8.33333E-02	.198807
CHDO	8.33333E-02	.198807
LEPU	8.33333E-02	.198807
LUAR	8.33333E-02	.198807
PHLO	8.33333E-02	.198807
VINU	8.33333E-02	.198807

TOTAL COVER IN PLOT 2.1 IS 41.3333

SPECIES	ABS COVER	REL COVER
ARTR	39.5	95.5645
AGSP	.583333	1.41129
CYTE	.5	1.20968
PHHO	.5	1.20968
BASA	8.33333E-02	.201613
CHVI	8.33333E-02	.201613
SIHY	8.33333E-02	.201613

TOTAL COVER IN PLOT 4.1 IS 62.0833

SPECIES	ABS COVER	REL COVER
ARTD	42.5	68.4564
AGSP	4.25	6.84564
ELCI	3.91667	6.30872
ARTR	3.33333	5.36913
PUTR	2.83333	4.56376
ASFI	1.16667	1.87919
POAB	1.16667	1.87919
CRAC	.75	1.20805
PECY	.583333	.939597
ASPU	.5	.805369
STCO	.5	.805369
PHHO	.25	.402685
PHLO	.25	.402685
CHVI	8.33333E-02	.134228

TOTAL COVER IN PLOT 5.1 IS 78.25

SPECIES	ABS COVER	REL COVER
ARTR	19.8333	25.3461
AGSP	15.3333	19.5953
LODI	9.5	12.1406
ELCI	6.5	8.30671
CRAC	5.33333	6.81576
KOCR	3.91667	5.00532
STCO	3.75	4.79233
ASFI	3.08333	3.94036
CAFI	2.58333	3.30138
LUAR	1.91667	2.44941
ARTD	1.83333	2.34292
POAB	1.75	2.23642
CHVI	1.25	1.59744
CHNA	1	1.27796
PHHA	.5	.638978
PHLO	.166667	.212992

TOTAL COVER IN PLOT 5.2 IS 64.8333

SPECIES	ABS COVER	REL COVER
ARTP	13.75	21.2082
AGSP	9.5	14.653
ARTD	8.16667	12.5964
ELCI	7.5	11.5681
POAB	6.58333	10.1542
STCO	6.58333	10.1542
PHHO	4.16667	6.42674
LEPU	2.58333	3.98458
ARAB	1.33333	2.05656
BASA	1.16667	1.79949
CRAC	1.16667	1.79949
ASFI	.5833	.899692
CHDO	.5	.771209
ORHY	.5	.771209
CAMA	.25	.385604
MEOB	.166667	.25707
ASPU	8.33333E-02	.128535
KOCR	8.33333E-02	.128535
LODI	8.33333E-02	.128535
SIHY	8.33333E-02	.128535

TOTAL COVER IN PLOT 6.1 IS 68.4167

SPECIES	ABS COVER	REL COVER
ARTP	19	27.771
KOCR	11.5	16.8088
AGSP	11.25	16.4434
ASFI	6.91667	10.1096
STCO	6.58333	9.62241
BASA	5.41667	7.91718
LIRU	2.58333	3.77588
POAB	1.5	2.19245
TECA	1.33333	1.94884
PHLO	.583333	.852619
CHVI	.5	.730816
LEPU	.5	.730816
PHHO	.5	.730816
MEOB	.166667	.243605
CAMA	8.33333E-02	.121803

TOTAL COVER IN PLOT 6.2 IS 56.5

SPECIES	ABS COVER	REL COVER
ARTI	35.25	62.3894
AGSP	8.25	14.6018
POAB	4.91667	8.70206
ASFI	2.25	3.9823
BASA	2.16667	3.83481
ARTR	1.25	2.21239
STCO	1.25	2.21239
LEPU	.583333	1.03245
CRAC	.166667	.294985
VINU	.166667	.294985
ASPU	8.33333E-02	.147493
CHDO	8.33333E-02	.147493
CHVI	8.33333E-02	.147493

TOTAL COVER IN PLOT 6.3 IS 61.75

SPECIES	ABS COVER	REL COVER
AGSP	17.0833	27.6653
ARTR	11.9167	19.2983
POAB	9	14.5749
ELCI	8.16667	13.2254
STCO	4.41667	7.1525
ASFI	3.66667	5.93793
CHVI	2.83333	4.5884
BASA	1.08333	1.75439
SEIN	.916667	1.48448
CRAC	.583333	.94467
PECY	.583333	.94467
PHLO	.583333	.94467
CAMA	.25	.404859
CAFI	.166667	.269906
PHHO	.166667	.269906
TECA	.166667	.269906
VINU	.166667	.269906

TOTAL COVER IN PLOT 6.4 IS 60.1667

SPECIES	ABS COVER	REL COVER
AGSP	22.75	37.8116
ARTD	12.6667	21.0526
POAB	6.83333	11.3573
ARTP	3.33333	5.54016
PUTR	3	4.98615
BASA	2.91667	4.84764
TECA	2.83333	4.70914
PHHO	1.75	2.90859
LEPU	1.25	2.07756
STCO	1.16667	1.93906
ASFI	.583333	.969529
SIHY	.5	.831025
ARAB	.166667	.277008
ASPU	8.33333E-02	.138504
CAMA	8.33333E-02	.138504
CRAC	8.33333E-02	.138504
ERPU	8.33333E-02	.138504
CHDO	8.33333E-02	.138504

TOTAL COVER IN PLOT 7.1 IS 52.8334

SPECIES	ABS COVER	REL COVER
ARTP	25.1667	47.6341
AGSP	15.3333	29.0221
POAB	3.83333	7.25552
ARTD	2.58333	4.88959
CHNA	1.25	2.36593
ASFI	1.08333	2.05047
ELCI	1.08333	2.05047
CHMI	.5	.946372
LODI	.5	.946372
LUAR	.5	.946372
PHHA	.5	.946372
PHLO	.166667	.315457
CYTE	8.33333E-02	.157729
MEOB	8.33333E-02	.157729
OPPO	8.33333E-02	.157729
PHHO	8.33333E-02	.157729

TOTAL COVER IN PLOT 8.1 IS 103.167

SPECIES	ABS COVER	REL COVER
AGSP	29.4167	28.5137
ARTP	23.8333	23.1018
LEPU	16.1667	15.6704
CRAC	12.75	12.3586
LUAR	6.5	6.30048
ERMI	3.91667	3.79645
POAB	3.75	3.63489
TECA	2.08333	2.01939
PUTR	1.75	1.69628
OPPO	1.25	1.21163
ARAB	.5	.484653
CAAN	.5	.484653
EROV	.5	.484653
ATSP	8.33333E-02	8.07754E-02
CAMA	8.33333E-02	8.07754E-02
ERUM	8.33333E-02	8.07754E-02

TOTAL COVER IN PLOT 8.2 IS 33.9167

SPECIES	ABS COVER	REL COVER
AGSP	12.75	37.5921
LEPU	6.75	19.9017
ARTD	5.33333	15.7248
POAB	2.58333	7.61671
ATSP	1.75	5.15971
CRAC	.833333	2.457
CHDO	.583333	1.7199
ERMI	.583333	1.7199
EROV	.583333	1.7199
STCO	.583333	1.7199
CAAN	.5	1.4742
ORHY	.5	1.4742
SIHY	.5	1.4742
PHHO	8.33333E-02	.2457

TOTAL COVER IN PLOT 8.3 IS 59

SPECIES	ABS COVER	REL COVER
CHVI	11.6667	19.774
ARTD	10.5833	17.9379
AGSP	8.75	14.8305
CRAC	6.41667	10.8757
LEPU	6.08333	10.3107
PUTR	5.41667	9.18079
STCO	2.5	4.23729
ELCI	2.25	3.81356
CHNA	2.08333	3.53107
POAB	1.41667	2.40113
PHHO	1.25	2.11864
SIHY	.5	.847458
PECY	8.33333E-02	.141243

TOTAL COVER IN PLOT 8.4 IS 53.3333

SPECIES	ABS COVER	REL COVER
LEPU	17.0833	32.0312
AGSP	8.41667	15.7812
ARTI	7.33333	13.75
POAB	5	9.375
CRAC	3.41667	6.40625
PUTR	3.25	6.09375
STCO	3.16667	5.9375
TECA	1.41667	2.65625
ORHY	1.25	2.34375
CAAN	.75	1.40625
PECY	.583333	1.09375
SIHY	.583333	1.09375
CHNA	.5	.9375
LUAR	.5	.9375
ERMI	8.33333E-02	.15625

TOTAL COVER IN PLOT 9.1 IS 46.25

SPECIES	ABS COVER	REL COVER
LEPU	10.6667	23.0631
CHNA	10.0833	21.8017
AGSP	8.41667	18.1982
CHVI	6.83333	14.7748
PUTR	3.33333	7.20721
POAB	2.83333	6.12613
CHMI	2.5	5.40541
STCO	1.25	2.7027
ARTI	8.33333E-02	.18018
ELCI	8.33333E-02	.18018
ERUM	8.33333E-02	.18018
PEDE	8.33333E-02	.18018

TOTAL COVER IN PLOT 10.1 IS 55.25

SPECIES	ABS COVER	REL COVER
AGSP	15.1667	27.451
LEPU	13.3333	24.1327
CHMI	8.58333	15.5354
CHNA	7.66667	13.8763
CHVI	4.33333	7.84313
STCO	2.58333	4.67571
POAB	2.08333	3.77074
SIHY	.5	.904977
CRAC	.333333	.603318
PECY	.166667	.301659
ARAB	8.33333E-02	.150829
ARTP	8.33333E-02	.150829
CRIN	8.33333E-02	.150829
CYTE	8.33333E-02	.150829
PEDE	8.33333E-02	.150829
PUTR	8.33333E-02	.150829

TOTAL COVER IN PLOT 13.1 IS 76.8334

SPECIES	ABS COVER	REL COVER
ARTP	32.0833	41.757
AGSP	12.0833	15.7267
LEPU	8.41667	10.9544
CHVI	6.5	8.45987
STCO	6.41667	8.35141
PUTR	3.25	4.22993
CYTE	2.58333	3.36225
ELCI	1.75	2.27766
CHNA	1.33333	1.73536
POAB	1.25	1.6269
PHHO	.5	.650759
LUAR	.166667	.21692
PHHA	.166667	.21692
ASFI	8.33333E-02	.10846
CAMA	8.33333E-02	.10846
EROV	8.33333E-02	.10846
PECY	8.33333E-02	.10846

TOTAL COVER IN PLOT 14.1 IS 78.5833

SPECIES	ABS COVER	REL COVER
ARTP	23.5833	30.0106
AGSP	14.9167	19.982
LEPU	13.5833	17.2853
TECA	7.41667	9.43797
CYTE	4.91667	6.25663
PHHO	4.66667	5.93849
STCO	4.58333	5.83245
LUAR	1.33333	1.69671
CHVI	1.25	1.59067
PUTR	1.25	1.59067
POAB	.583333	.742312
ERMI	.25	.318134
PECY	.166667	.212089
SIHY	8.33333E-02	.106045

TOTAL COVER IN PLOT 15.1 IS 75.3333

SPECIES	ABS COVER	REL COVER
STCO	22	29.2035
ARTP	21.25	28.208
ELCI	9.75	12.9425
LIRU	7.25	9.62389
AGSP	6.16667	8.18584
CHNA	2.08333	2.76549
CHVI	2.08333	2.76549
LUAR	1.91667	2.54425
PECY	.75	.995575
LEPU	.666667	.884956
TECA	.583333	.774336
ERMI	.5	.663717
OPPO	.166667	.221239
EROV	8.33333E-02	.110619
PHHA	8.33333E-02	.110619

TOTAL COVER IN PLOT 16.1 IS 68.9167

SPECIES	ABS COVER	REL COVER
ARTP	29.5833	42.9262
AGSP	15.75	22.8537
STCO	6.5	9.43168
LUAR	4.5	6.52963
CHVI	2.58333	3.74849
ASFI	1.83333	2.66022
CHNA	1.75	2.5393
ERMI	1.58333	2.29746
LEPU	1.25	1.81379
ELCI	1.08333	1.57195
PECY	.833333	1.20919
ARAB	.583333	.846433
EROV	.5	.725514
LIRU	.166667	.241838
POAB	.166667	.241838
CYTE	8.33333E-02	.120919
PHHA	8.33333E-02	.120919
PHHO	8.33333E-02	.120919

TOTAL COVER IN PLOT 16.2 IS 71.75

SPECIES	ABS COVER	REL COVER
ARTP	31.3333	43.6701
LEPU	9.25	12.892
AGSP	8.5	11.8467
CHVI	6.16667	8.59466
STCO	5.33333	7.43322
ASFI	3.75	5.22648
ERMI	3	4.18119
PHHO	2.58333	3.60047
POAB	1.08333	1.50987
CRAC	.5	.696864
CHDO	8.33333E-02	.116144
LUAR	8.33333E-02	.116144
PHLO	8.33333E-02	.116144

TOTAL COVER IN PLOT 16.3 IS 79.5833

SPECIES	ABS COVER	REL COVER
STCO	30.0833	37.801
ELCI	11.5	14.4503
ARTP	9.66667	12.1466
CHVI	7.91667	9.94764
AGSP	6.58333	8.27225
LUAR	5.58333	7.01571
LEPU	4.83333	6.0733
LIRU	2.66667	3.35078
PECY	.666667	.837696
ERMI	8.33333E-02	.104712

TOTAL COVER IN PLOT 18.2 IS 85.3333

SPECIES	ABS COVER	REL COVER
ARTP	45.0833	52.832
AGSP	10.25	12.0117
LUAR	8.33333	9.76563
STCO	8.33333	9.76563
CHVI	3.33333	3.90625
ASFI	3	3.51563
POAB	2.58333	3.02734
BASA	1.25	1.46484
CRAC	1.08333	1.26953
PHHO	1	1.17188
KOCR	.833333	.976563
ELCI	.166667	.195313
PECY	8.33333E-02	9.76563E-02

TOTAL COVER IN PLOT 20.1 IS 34.1667

SPECIES	ABS COVER	REL COVER
CHNA	18.1667	53.1707
ARTD	3.33333	9.7561
BASA	3.33333	9.7561
SIHY	2.91667	8.53659
POAB	2.75	8.04878
CHVI	1.25	3.65854
STCO	.75	2.19512
AGDA	.583333	1.70732
CRAC	.583333	1.70732
ORHY	.166667	.487805
LEPU	8.33333E-02	.243902
MACA	8.33333E-02	.243902
PEDE	8.33333E-02	.243902
PHHO	8.33333E-02	.243902

TOTAL COVER IN PLOT 20.2 IS 52.75

SPECIES	ABS COVER	REL COVER
ARTD	20.5833	39.0205
POAB	11.5	21.8009
CHVI	6.83333	12.9542
STCO	4.33333	8.21485
SIHY	2.33333	4.42338
AGSP	1.75	3.31753
PHHO	1.75	3.31753
LEPU	1.6667	3.15962
CRAC	1.25	2.36967
MEOB	.166667	.315956
AGDA	8.33333E-02	.157978
BASA	8.33333E-02	.157978
CAMA	8.33333E-02	.157978
EROV	8.33333E-02	.157978
OPPO	8.33333E-02	.157978
PECY	8.33333E-02	.157978
ERMI	8.33333E-02	.157978

TOTAL COVER IN PLOT 25.1 IS 58.9167

SPECIES	ABS COVER	REL COVER
BASA	15.75	26.7327
POAB	13.4167	22.7723
AGSP	13	22.065
STCO	5.25	8.91088
ARTD	4.5	7.6379
ARTP	3.91667	6.6478
PHHO	1.08333	1.83875
CRAC	.583333	.990098
CHVI	.5	.848656
OPPO	.5	.848656
ERMI	.166667	.282885
ZIPA	.166667	.282885
CAMA	8.33333E-02	.141443

TOTAL COVER IN PLOT 3.1 IS 20.9375

SPECIES	ABS COVER	REL COVER
CHNA	4.3125	20.597
ARTD	3.75	17.9104
CHMI	3.0625	14.6269
POGL	2.9375	14.0299
SIHY	1.8125	8.65672
HARE	1.1875	5.67164
ERUM	1	4.77612
ORHY	.9375	4.47761
HODU	.4375	2.08955
STTE	.4375	2.08955
CYTE	.375	1.79104
CIUT	.3125	1.49254
PEDE	.1875	.895522
PIFL	.0625	.298507
POAB	.0625	.298507
SECA	.0625	.298507

TOTAL COVER IN PLOT 21.1 IS 17.5

SPECIES	ABS COVER	REL COVER
CHMI	8.9167	50.9525
CYTE	2.66667	15.2381
POGL	2.08333	11.9047
STTE	1	5.71428
CIUT	.583333	3.33333
PEDE	.583333	3.33333
ERUM	.5	2.85714
HODU	.5	2.85714
ERCO	.166667	.952379
HARE	.166667	.952379
CHDO	8.33333E-02	.47619
CHNA	8.33333E-02	.47619
SECA	8.33333E-02	.47619
SIHY	8.33333E-02	.47619

TOTAL COVER IN PLOT 22.1 IS 38.106

SPECIES	ABS COVER	REL COVER
CHNA	10.6818	28.0318
CHMI	10.2273	26.839
ARTD	4.4697	11.7296
CYTE	3.48485	9.14513
HODU	2.57576	6.75945
SECA	1.74242	4.57257
SIHY	1.13636	2.98211
POGL	1.06061	2.7833
HARE	.530303	1.39165
ARAB	.454545	1.19284
CHDO	.454545	1.19284
PHHA	.454545	1.19284
MEOB	.378788	.994036
ORHY	.151515	.397614
PEDE	.151515	.397614
ERCO	7.57576E-02	.198807
POAB	7.57576E-02	.198807

TOTAL COVER IN PLOT 23.1 IS 3.9

SPECIES	ABS COVER	REL COVER
POGL	2.75	70.5128
STTE	.65	16.6667
ERCO	.45	11.5385
SIHY	.05	1.28205

APPENDIX VII

For each species, plots ranked by the absolute cover (%) of the species in the plot.

FOR AGDA

20.1	.583333
20.2	8.33333E-02

FOR AGSP

8.1	29.4167
6.4	22.75
6.3	17.0833
16.1	15.75
7.1	15.3333
5.1	15.3333
10.1	15.1667
14.1	14.9167
25.1	13
8.2	12.75
13.1	12.0833
6.1	11.25
18.2	10.25
5.2	9.5
8.3	8.75
16.2	8.5
8.4	8.41667
9.1	8.41667
6.2	8.25
16.3	6.58333
15.1	6.16667
4.1	4.25
1.2	2.75
20.2	1.75
2.1	.583333
1.1	8.33333E-02

FOR ARAB

5.2	1.33333
16.1	.583333
8.1	.5
22.1	.454545
6.4	.166667
1.2	8.33333E-02
10.1	8.33333E-02

FOR ARTD

4.1	42.5
2.1	39.5
6.2	35.25
20.2	20.5833
6.4	12.6667
8.3	10.5833
5.2	8.16667
8.4	7.33333
8.2	5.33333
25.1	4.5
22.1	4.4697
3.1	3.75
20.1	3.33333
1.2	3.33333
7.1	2.58333
1.1	1.83333
5.1	1.83333
9.1	8.33333E-02

FOR ARTP

18.2	45.0833
13.1	32.0833
16.2	31.3333
16.1	29.5833
7.1	25.1667
8.1	23.8333
14.1	23.5833
15.1	21.25
5.1	19.8333
6.1	19
5.2	13.75
6.3	11.9167
16.3	9.66667
25.1	3.91667
6.4	3.33333
4.1	3.33333
6.2	1.25
10.1	8.33333E-02

FOR ASFI

6.1	6.91667
16.2	3.75
6.3	3.66667
5.1	3.08333
18.2	3
1.2	2.75
6.2	2.25
16.1	1.83333
1.1	1.75
4.1	1.16667
7.1	1.08333
6.4	.583333
5.2	.5833
13.1	8.33333E-02

FOR ASPU

4.1	.5
6.2	8.33333E-02
6.4	8.33333E-02
5.2	8.33333E-02

FOR ATSP

8.2	1.75
8.1	8.33333E-02

FOR BASA

25.1	15.75
1.1	6.75
6.1	5.41667
1.2	5.25
20.1	3.33333
6.4	2.91667
6.2	2.16667
18.2	1.25
5.2	1.16667
6.3	1.08333
2.1	8.33333E-02
20.2	8.33333E-02

FOR CAAN

8.4	.75
8.1	.5
8.2	.5

FOR CAFI

5.1	2.58333
6.3	.166667

FOR CAMA

6.3	.25
5.2	.25
6.1	8.33333E-02
6.4	8.33333E-02
8.1	8.33333E-02
13.1	8.33333E-02
20.2	8.33333E-02
25.1	8.33333E-02

FOR CHDO

8.2	.583333
5.2	.5
22.1	.454545
1.2	8.33333E-02
6.2	8.33333E-02
16.2	8.33333E-02
21.1	8.33333E-02
6.4	8.33333E-02

FOR CHMI

22.1	10.2273
21.1	8.9167
10.1	8.58333
3.1	3.0625
9.1	2.5
7.1	.5

FOR CHNA

20.1	18.1667
22.1	10.6818
9.1	10.0833
10.1	7.66667
1.1	5.08333
3.1	4.3125
8.3	2.08333
15.1	2.08333
16.1	1.75
13.1	1.33333
1.2	1.33333
7.1	1.25
5.1	1
8.4	.5
21.1	8.33333E-02

FOR CHVI

1.1	12.3333
8.3	11.6667
1.2	10.4167
16.3	7.91667
9.1	6.83333
20.2	6.83333
13.1	6.5
16.2	6.16667
10.1	4.33333
18.2	3.33333
6.3	2.83333
16.1	2.58333
15.1	2.08333
14.1	1.25
5.1	1.25
20.1	1.25
6.1	.5
25.1	.5
2.1	8.33333E-02
6.2	8.33333E-02
4.1	8.33333E-02

FOR CIUT

21.1	.583333
3.1	.3125

FOR CRAC

8.1	12.75
8.3	6.41667
5.1	5.33333
1.2	3.66667
8.4	3.41667
20.2	1.25
5.2	1.16667
18.2	1.08333
8.2	.833333
4.1	.75
6.3	.583333
20.1	.583333
25.1	.583333
16.2	.5
1.1	.416667
10.1	.333333
6.2	.166667
6.4	8.33333E-02

FOR CRIN

10.1	8.33333E-02

FOR CYTE

14.1	4.91667
22.1	3.48485
21.1	2.66667
13.1	2.58333
2.1	.5
3.1	.375
7.1	8.33333E-02
10.1	8.33333E-02
16.1	8.33333E-02

FOR ELCI

16.3	11.5
15.1	9.75
6.3	8.16667
5.2	7.5
5.1	6.5
4.1	3.91667
8.3	2.25
13.1	1.75
1.2	1.25
7.1	1.08333
16.1	1.08333
18.2	.166667
9.1	8.33333E-02

FOR ERCO

23.1	.45
21.1	.166667
22.1	7.57576E-02

FOR ERPU

6.4	8.33333E-02

FOR ERMI

8.1	3.91667
16.2	3
16.1	1.58333
8.2	.583333
15.1	.5
14.1	.25
25.1	.166667
1.1	8.33333E-02
8.4	8.33333E-02
16.3	8.33333E-02
20.2	8.33333E-02

FOR EROV

8.2	.583333
8.1	.5
16.1	.5
13.1	8.33333E-02
15.1	8.33333E-02
20.2	8.33333E-02

FOR ERUM

3.1	1
21.1	.5
8.1	8.33333E-02
9.1	8.33333E-02

FOR HARE

3.1	1.1875
22.1	.530303
21.1	.166667

FOR HODU

22.1	2.57576
21.1	.5
3.1	.4375

FOR KOCR

6.1	11.5
5.1	3.91667
18.2	.833333
5.2	8.33333E-02

FOR LEPU

8.4	17.0833
8.1	16.1667
14.1	13.5833
10.1	13.3333
9.1	10.6667
16.2	9.25
13.1	8.41667
8.2	6.75
8.3	6.08333
16.3	4.83333
5.2	2.58333
20.2	1.6667
6.4	1.25
16.1	1.25
15.1	.666667
6.2	.583333
6.1	.5
1.1	8.33333E-02
1.2	8.33333E-02
20.1	8.33333E-02

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     FOR LIRU
15.1            7.25
16.3            2.66667
6.1             2.58333
16.1            .166667

     FOR LODI
5.1             9.5
7.1             .5
5.2             8.33333E-02

     FOR LUAR
18.2            8.33333
8.1             6.5
16.3            5.58333
16.1            4.5
15.1            1.91667
5.1             1.91667
14.1            1.33333
7.1             .5
8.4             .5
13.1            .166667
1.2             8.33333E-02
16.2            8.33333E-02

     FOR MACA
20.1            8.33333E-02

     FOR MEOB
22.1            .378788
6.1             .166667
5.2             .166667
20.2            .166667
7.1             8.33333E-02

     FOR OPPO
1.1             1.25
8.1             1.25
25.1            .5
15.1            .166667
7.1             8.33333E-02
20.2            8.33333E-02

     FOR ORHY
8.4             1.25
3.1             .9375
1.2             .5
8.2             .5
5.2             .5
1.1             .166667
20.1            .166667
22.1            .151515
```

FOR PECY

16.1	.833333
15.1	.75
16.3	.666667
6.3	.583333
8.4	.583333
4.1	.583333
10.1	.166667
14.1	.166667
8.3	8.33333E-02
13.1	8.33333E-02
18.2	8.33333E-02
20.2	8.33333E-02

FOR PEDE

21.1	.583333
3.1	.1875
22.1	.151515
9.1	8.33333E-02
10.1	8.33333E-02
20.1	8.33333E-02

FOR PHHA

7.1	.5
5.1	.5
22.1	.454545
13.1	.166667
16.1	8.33333E-02
15.1	8.33333E-02

FOR PHHO

14.1	4.66667
5.2	4.16667
16.2	2.58333
6.4	1.75
20.2	1.75
8.3	1.25
25.1	1.08333
18.2	1
2.1	.5
6.1	.5
13.1	.5
4.1	.25
6.3	.166667
7.1	8.33333E-02
8.2	8.33333E-02
16.1	8.33333E-02
20.1	8.33333E-02

FOR PHLO

6.1	.583333
6.3	.583333
4.1	.25
7.1	.166667
5.1	.166667
1.2	8.33333E-02
16.2	8.33333E-02

FOR PIFL

3.1	.0625

FOR POAB

25.1	13.4167
20.2	11.5
6.3	9
6.4	6.83333
5.2	6.58333
8.4	5
6.2	4.91667
7.1	3.83333
8.1	3.75
9.1	2.83333
20.1	2.75
8.2	2.58333
18.2	2.58333
10.1	2.08333
5.1	1.75
6.1	1.5
8.3	1.41667
13.1	1.25
4.1	1.16667
16.2	1.08333
14.1	.583333
16.1	.166667
22.1	7.57576E-02
3.1	.0625

FOR POGL

3.1	2.9375
23.1	2.75
21.1	2.08333
22.1	1.06061

```
    FOR PUTR
8.3             5.41667
9.1             3.33333
8.4             3.25
13.1            3.25
6.4             3
4.1             2.83333
8.1             1.75
14.1            1.25
10.1            8.33333E-02

    FOR SECA
22.1            1.74242
21.1            8.33333E-02
3.1             .0625

    FOR SEIN
6.3             .916667

    FOR SIHY
20.1            2.91667
20.2            2.33333
3.1             1.8125
22.1            1.13636
8.4             .583333
6.4             .5
8.2             .5
8.3             .5
10.1            .5
1.1             .333333
1.2             .25
2.1             8.33333E-02
14.1            8.33333E-02
5.2             8.33333E-02
21.1            8.33333E-02
23.1            .05

    FOR STTE
21.1            1
23.1            .65
3.1             .4375
```

FOR STCO

16.3	30.0833
15.1	22
18.2	8.33333
1.2	6.83333
6.1	6.58333
5.2	6.58333
16.1	6.5
13.1	6.41667
16.2	5.33333
25.1	5.25
1.1	5
14.1	4.58333
6.3	4.41667
20.2	4.33333
5.1	3.75
8.4	3.16667
10.1	2.58333
8.3	2.5
6.2	1.25
9.1	1.25
6.4	1.16667
20.1	.75
8.2	.583333
4.1	.5

FOR TECA

14.1	7.41667
1.1	3.91667
1.2	3.08333
6.4	2.83333
8.1	2.08333
8.4	1.41667
6.1	1.33333
15.1	.583333
6.3	.166667

FOR VINU

6.2	.166667
6.3	.166667
1.2	8.33333E-02

FOR ZIPA

25.1	.166667

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