PHYTOGEOGRAPHICAL VARIATION WITHIN JUNIPER-PINYON WOODLANDS OF THE GREAT BASIN

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ABSTRACT.—About 22 percent of the pigmy conifer woodlands of the United States occur within the Great Basin. Only a very few reports of these woodlands exist in the literature. Available reports are either of general descriptive nature or specific analysis of vegetation-environmental relationships on one mountain range. In order to better understand basin-wide synecological patterns, a cooperative study was carried out by personnel at Utah State University and the University of Nevada-Reno between 1972 and 1975. Vegetation, landform, geology, and soils data obtained from 463 systematically placed stands on a randomly chosen set of 66 mountain ranges have been used to derive patterns of latitudinal, longitudinal, and altitudinal variation in the floristic diversity in juniper-pinyon dominated woodlands across the Great Basin.

The latitudinal-longitudinal patterns show greatest environmental and floristic diversity on the higher mountain ranges on the southern end of the Central Plateau portion of the study area where the Great Basin-Mojave Desert transition occurs. This is also where the elevational breadth of the woodland belt is greatest. Juniper-pinyon woodlands are largely lacking from northwestern Nevada. The lowest elevations for the type are found in the Dixie Corridor centered in southwestern Utah. The general elevation of these woodlands is highest in the west-central part of the Great Basin and declines both toward the Sierra Nevada on the west and the Wasatch Front-High Plateaus on the east.

Use of the equilibrium theory of island biogeography gave incomplete explanations of the diversity patterns observed. Certain conceptual and methodical problems forced by this overly simplistic theory are discussed. The best correlations obtained were between species richness and an index of ecotopic diversity.

Correlation of Basin-wide patterns of woodland floristics with surficial geology, landforms, and soils is non-discriminatory. However, broad-scale, phytogeographical variations in these woodlands are closely associated with climatic differences. Although much direct climatic data are lacking, it seems likely that the relative contributions of the transitory frontal systems moving inland from the Pacific, continental cyclones developing over the Great Basin, and convectional storms associated with the moist air from the Gulf of Mexico to induce precipitation at different seasons are regionally important in the causation of vegetation distribution and composition.

The instability of temperature inversions is a likely determinant of the position of woodlands along the northern boundary of the type. The Pacific frontal systems break the inversions most readily and are thought to be the major cause for the lack of this vegetation in northwestern Nevada and on exposed mountain ranges along the northern boundary of the type. Such observations provide leads for relevant ecophysiological research to support or reject these notions.

The juniper-pinyon woodlands are a major vegetation type of the Intermountain West. West, Rea, and Tausch (1975) have indicated that about 325,000 km^2 (125,000 mi^2) are involved. About 7.1 million ha, or 22 percent of this total, occur in the Great Basin. It is the phytogeography of this portion of the type that we wish to consider here.

Brief descriptions of the Great Basin pinyon-juniper woodlands, along with considerations of other Great Basin vegetation types and their distributions have been made by Billings (1951), Cronquist et al. (1972), Tueller (1975), and Young, Evans, and Tueller (1976). They all characterized these woodlands as generally covering low hills or as forming a belt of vegetation at lower elevations on the higher mountains with sagebrush-dominated belts both above and below.

Beeson (1974) mapped the typed and de-

scribed the general longitudinal and latitudinal variations from a large set of vegetational data collected on approximately one-third of the mountain ranges found in the Great Basin. In this paper we wish to examine further aspects of this and additional data, expanding the discussion of longitudinal, latitudinal, and elevational floristic diversity (beta diversity, according to Whittaker 1975) and propose possible explanations for some peculiarities of latitudinal limits and variations in elevational extent of the type.

METHODS

Data set collection and prior analysis: The data set available involves quantitative data on landform, geology, soils, and vegetation collected between 1972 and 1975 for 463 stands systematically placed on a randomly chosen set of 66 Great Basin mountain ranges (Nabi 1978).

We defined woodlands as having at least 25 pinyon and/or juniper trees per hectare (10/acre). At least one tree had to be in our mature size-age-form class. These criteria kept the samples from extending too far into ecotones, yet allowed a good coverage of the main juniper-pinyon woodland type.

Stands were sampled at regular elevational intervals on all of the four major exposures where the juniper-pinyon belt existed on each mountain range. We are therefore able to discuss the Basin-wide distribution of these woodlands from fairly objective bases. The full details of the sampling design, data collection, and prior analysis are given elsewhere (Nabi 1978).

Supplementary sampling of the Shoshone Mountains added stands in broad canyon bottoms and on secondary slopes of faces along major ridges. These additions were made to sample for one area a greater range of ecotopic heterogeneity than was provided by the regularly placed upland sites on exposures in cardinal directions.

In addition to presentation of broad, longitudinal-latitudinal patterns of woodland distribution via a map derived from field-checked space photography, Beeson (1974) grouped the sampled mountain ranges into three first-order divisions, based on floristic composition. The stress was on the major species found on at least 25 percent of the mountain ranges sampled. These major species were commonly found in most of the stands on the mountain range where they occurred.

This approach yielded one group of ranges with moderate floristic diversity in the Central Plateau region that had considerable similarities to the foothills and ranges directly adjacent to the Sierra Nevada on the west and the Wasatch Front-High Plateaus of central Utah on the eastern boundary of the basin. Another grouping with low floristic richness was designated for all lower elevation ranges occurring in the generally lower, drier portions of the Great Basin. The third grouping consisted of ranges with the highest floristic diversity. These all occurred along the southern end of the Central Plateau where the Great Basin-Mojave desert transition occurs.

These floristic units were related to patterns of surficial geology, landform, soils, and climate. Weak correspondences were found at this scale with all environmental factors except climate. The widescale longitudinal-latitudinal differences observed were therefore thought to be largely related to current patterns of precipitation and temperature.

Current analysis methods: Mueller-Dumbois and Ellenberg (1974), in their recent textbook on the *Aims and Methods of Vegetation Ecology,* emphasize that a complete understanding of the distribution of plant communities involves a consideration of flora, accessibility, ecological properties of the plants, habitat, and time. Our further analysis here involves an in-depth examination of the total floristic diversity in our samples of Great Basin pigmy conifer woodlands in an attempt to relate these floristic diversity patterns to likely paleocological influences and to present environmental

heterogeneity with emphasis on the present climatic patterns through space and time.

We also examined the appropriateness of applications of island biogeographical theory (Simberhoff 1974). These analyses followed a strategy similar to that used by Brown (1971) and Johnson (1975). Data from the 18 mountain ranges sampled at 200 m elevation intervals were used (Nabi 1978). The variables accounted for were total woodland species per mountain range, total mountain area, total mountain area occupied by woodland (taken from our previously published map), mountain height, width of barrier, and an index of ecotopic diversity.

The width of the barrier was calculated similarly to Johnson's (1975) approach except that we considered distance to the nearest of three "continental" areas: The Sierra Nevada, Wasatch Front-High Plateaus of central Utah, and the northern boundary of the Snake River Plains, all defined as in Cronquist et al. (1972).

The ecotopic diversity where woodlands occurred on each mountain was indexed by the use of an arbitrary, numerical scale (Table 1) taking into account those variables on which we had direct data. The higher the variety of factor conditions, the greater the presumable ecotopic diversity. Untransformed data for the variables assessed are presented in Table 2. Correlation coefficients (r) between the variables were then calculated for both the raw and logarithmically transformed data.

Additional tabular and graphical organizations of the data were employed in order to clarify our broad-scale phytogeographical view of latitudinal, longitudinal, and altitudinal variation in these woodlands. A series of range-by-range comparisons were made on the basis of total species richness for each range, average stand species richness, and altitudinal distribution of the woodland. Each type of analysis was mapped and compared with each other and the broad-scale climatic patterns for the region.

RESULTS AND DISCUSSION

Overall species richness: A total of 367 vascular plant species were found within

TABLE 1. Point system for ecotopic diversity score.

		Range of Values Possible	Range of Values Observed
Exposure	Cardinal slopes having woodlands 1 = north only 2 = north and east, etc.	1–4	2–4
Slope	Number of slope classes (10% increments) 0–10% = 1, 0–10% plus 11–20 = 2, etc.	1–5	2–5
Elevation	Elevations at which woodlands were sampled (200 m intervals) 1800–2000 m = 1: 1800–2000 m plus 2001–2200 m = 2, etc.	1–4	2–4
Landform	Five major landforms encountered (valley, foothill, bajada, terrace, mountain) (defined in Nabi 1978)	1–5	1–5
Geology	classified to clan (Nabi 1978)	1–19	1–8
Soils	Classified to subgroup according to Soil Survey Staff, USDA, Soil Conservation Service (1951, 1960, 1967)	1–24	1–16
Total possible score		61	(10–40)

the juniper-pinyon woodlands sampled. The number of species in the woodlands on individual mountain ranges varied from 164 species on the Shoshone Mountains of west-central Nevada to under 30 species on small isolated ranges of western Utah. Figure 1 shows that most of the mountain ranges had fewer than 50 species in their woodlands. Furthermore, the ranking of species numbers per mountain range frequencies (Fig. 2) shows an expected log-normal distribution over the sampled ranges (May 1975). Many species were found at only one stand on a given mountain range. If the species frequency sequence is plotted against the number of stands in which they occur (Fig. 3) the right hand portion of the curve also follows a log-normal form. The frequency values for the rare species (those occurring in one to four stands) are in excess of the expected value (Fig. 4). These high frequencies of rarer species are indicative of an over-saturation of relictual species probably remaining from the vegetation migrations resulting from the more favorable climate of the recent geologic past. This is a situation similar to that found by Brown (1971)

for small mammals and Johnson (1975) for permanent resident birds in the same area. Our estimates of such oversaturation are conservative since sampling was restricted to upland areas on all ranges except the Shoshone Mountains, which included some broad drainage bottoms and major ridge faces. Judging from the high species density of the Shoshone Range, inclusion of more pronounced topographic situations such as narrow drainage channels and searches of atypical geological outcrops and unusual landforms on the other ranges, in addition to our predetermined sampling scheme, would have yielded more plant taxa within the woodland belt.

If the average number of species per stand within a given mountain range is plotted against the total number of species found in the woodlands of that range (Fig. 5) the envelope including the data points illustrates that there is a very general increase in stand diversity with increasing floristic diversity of the ranges sampled. The variation, however, is high. Except for the ranges with greatest and least diversity, there are few mountain ranges fitting with-

TABLE 2. Untransformed data used to test appropriateness of equilibrium theory of island biogeography.

Mountain Range	Pigmy Conifer Woodland Species Encountered	Total Area of Mountain[1] (km²)	Total Area of Woodland (km²)	Mountain Height (m)	Width of Smallest Barrier (km)	Ecotopic Diversity Score (See Table 1)
Burbank Hills	19	43	43	2384	36	10
Confusion	32	145	145	2461	39	13
Pine Valley	37	143	143	1989	10	18
Black Pine	38	458	113	2853	20	16
Toana	38	286	263	2117	31	19
White	40	1691	1305	3091	10	19
Goose Creek	42	1691	1305	2295	28	14
Tushar	46	1412	706	3713	10	18
Pilot	48	321	293	3265	20	24
Excelsior	48	187	187	2532	10	13
East Humboldt	49	592	54	2456	42	18
Schell Creek	54	1523	1076	3353	12	22
Mineral	65	298	187	2921	10	20
Monitor	69	1908	1564	2845	35	22
Toiyabe	76	2069	974	3292	42	24
Needle	93	1213	1083	2699	10	40
Highland	94	286	263	2865	15	27
Shoshone	164	519	450	3145	42	32
Mean	58.4	821.4	564.1	2793.1	24.0	20.5
S.D.	33.2	708.9	512.1	466.0	13.2	7.3

[1]Area above 1800 m.

in a similar range of limited average stand diversity. The majority of the mountain ranges within any total diversity class have a wide variation of average stand diversity. For example, in the interval of 80 to 95 species on a range, the average stand diversity varies from 9 to over 25 species.

Latitudinal and longitudinal diversity patterns: A currently fashionable way of explaining geographical patterns of diversity would be by application of island biogeography theory. The results of the correlations of total species richness with total mountain area, total area of woodland on the mountain, width of barrier, mountain

Fig. 3. Relationships of stand frequency to species richness. (366 stands of woodland on 66 mountain ranges.)

Fig. 1. Total number of plant species in the woodland belts on each mountain range ordered from the richest to the most depauperate.

Fig. 4. Number of species ordered by number of stands in which they occurred (frequency octaves). Line represents log-normal interpolation.

Fig. 2. Range frequency of total number of plant species in the woodland belts organized by frequency octaves. Line represents log-normal interpolation.
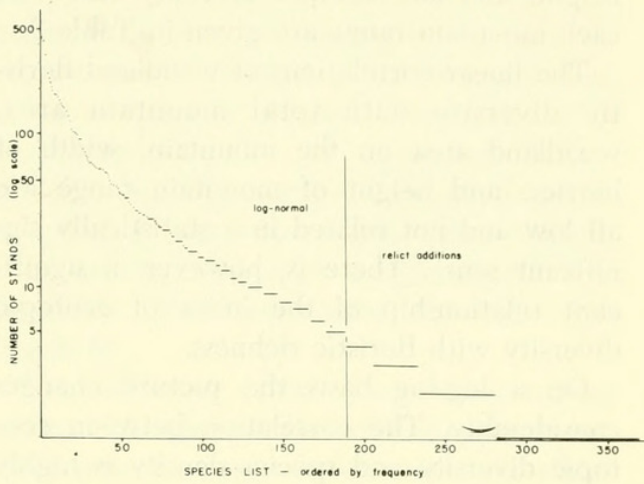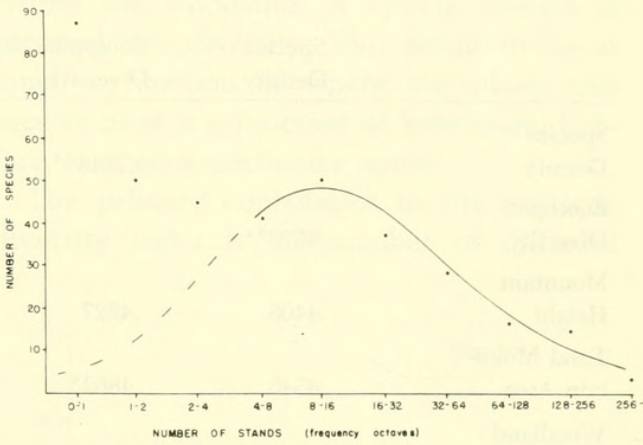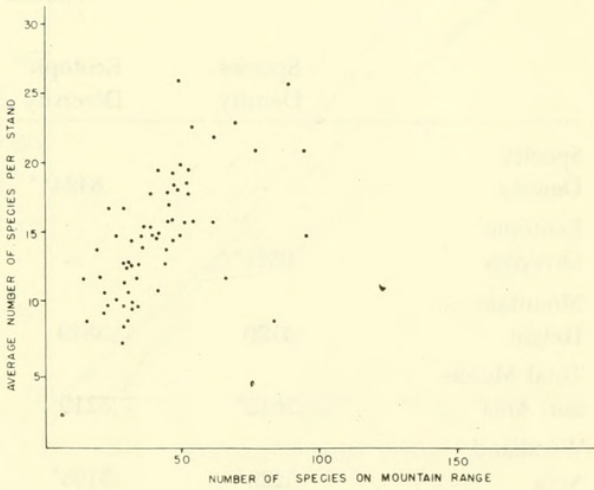

Fig. 5. Relationship of average number of species per stand with total number of species in the woodlands sampled on each of 66 mountain ranges.

height, and an ecotopic diversity score for each mountain range are given in Table 3.

The linear correlations of woodland floristic diversity with total mountain area, woodland area on the mountain, width of barrier, and height of mountain range are all low and not related in a statistically significant sense. There is, however, a significant relationship of the index of ecotopic diversity with floristic richness.

On a log-log basis the picture changes considerably. The correlation between ecotopic diversity and species density is highly

significant with little change in value, with or without data from the Shoshone Mountains. Species density is significantly correlated with total area and woodland area at the 0.05 level without the Shoshone Mountains and barely insignificant with them included.

The relationships between other factors shows scattered significance. Ecotopic diversity is significantly correlated with total mountain area and woodland area for both analyses. Mountain height and total mountain area, but not woodland area, are signif-

TABLE 3. Correlation coefficients (r) between variables. Lower triangular matrix for log-transformed data, upper for untransformed data.

	Species Density	Ecotopic Diversity	Mountain Height (m)	Total Mountain Area (km²)	Woodland Area (km²)	Width of Barrier (km²)
With Shoshone Mountains						
Species Density	—	.7846°°	.3470	.1182	.1669	.1392
Ecotopic Diversity	.8570°°	—	.3446	.2349	.3133	−.1355
Mountain Height	.4408	.4227	—	.4676	.3390	−.1743
Total Mountain Area	.4545	.4862°	.5326°	—	.9265°°	.0068
Woodland Area	.4572	.5049°	.4620	.8510°°	—	−.1108
Width of Barrier	−.3806	−.1691	−.1688	−.0743	−.2325	—
Without Shoshone Mountains						
Species Density	—	.8424°°	.3303	.3354	.3479	−.2279
Ecotopic Diversity	.8521°°	—	.2993	.3035	.3658	−.3125
Mountain Height	.4120	.3849	—	.4995°	.3565	−.2580
Total Mountain Area	.5612°	.5219°	.5422°	—	.9272°°	.0459
Woodland Area	.5229°	.5198°	.4596	.8524°°	—	−.0978
Width of Barrier	−.2763	−.3135	−.2413	−.0790	−.2629	—

° = p ≤ 0.05 = ≥ 0.4820   °° = p ≤ 0.01 = ≥ 0.6060

icantly correlated. Total mountain area and woodland area are significantly correlated; however, all these variables are so inter-related that significant correlations are to be automatically expected. The discrepancy between the actual and perfect correlation is probably due to historical accidents such as fire eliminating some woodland from where it has potential on those portions of mountains where climatic unfavorableness exists, as will be explained later.

We interpret this failure of width of barrier to account for any of the variation observed to be at least partially due to a variety of methodical problems created by some simplistic decisions forced by the current development of the theory. First of all, it is impossible to choose one continent contributing flora to the woodlands. Any one mountain range has floristic affinities with all surrounding areas. The mixture could be better described by the degree of affinities to all possible continents. The Mojave desert also contributes to the understory composition. However, because some of the mountain ranges are imbedded in the Mojave Desert, we knew of no way to calculate barrier width in such circumstances.

The overall height of the mountain range probably yields a poor correlation because these woodlands have both boreal-derived and lowland-derived components. Thus, height of connecting ridges or valleys would have a variable effect on what species could have migrated across the Great Basin and have had a route of escape as environments changed. As Johnson and Raven (1970) have previously pointed out, height has inevitable covariation with total environmental diversity. Therefore, it is not surprising that the index of ecotopic diversity, which reflects combined physical variables, gives a much better correlation coefficient.

The linear relationship of the index of ecotopic diversity with species richness changes if the Shoshone Mountains, with their expanded sampling scheme, are excluded ($R^2 = .6156$ to $R^2 = .7096$). As can be seen from Figure 6, the increased sam-

pling on the Shoshone Mountains did not result in an obvious increase in ecotopic diversity, but it did give an obvious increase in the number of species encountered. This is possibly due to an increased micro-climatic heterogeneity resulting from the sampling scheme used. Some minor changes also occurred for other relationships when Shoshone Mountain data was excluded (Table 3).

The influence of the increased sampling scheme on the results with the Shoshone Mountains has been minor with less effect on the log-transformed data than on the linear data. What this appears to show is that, within a reasonably uniform sampling scheme, the floristic diversity encountered within the woodlands is closely related to physical site diversity. This seems to be as much a function of where the plants can survive as it is a function of how many habitats exist on a particular range.

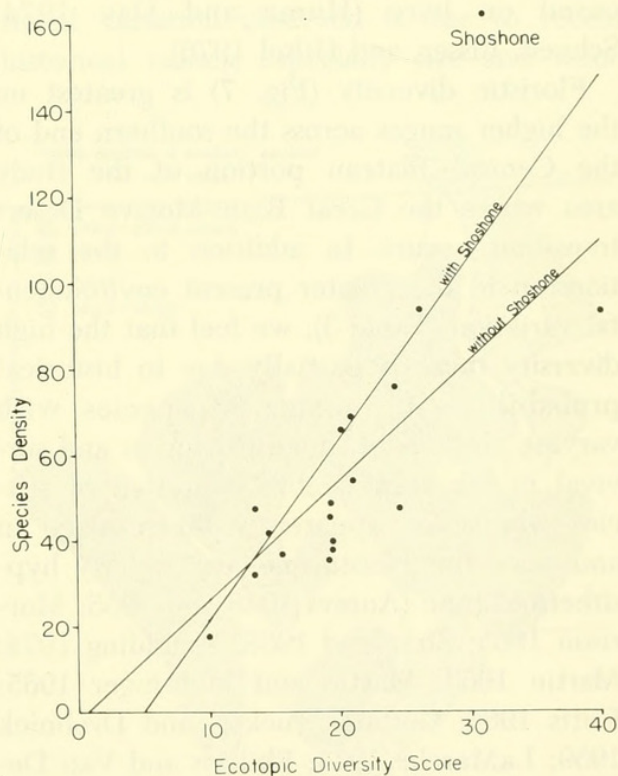The primary contributor to the ecotopic diversity index is the number of different

Fig. 6. Regression between ecotopic diversity index and species density in juniper-pinyon woodlands on 17 and 18 mountain ranges in the Great Basin (with and without the Shoshone Mountains included).

soil types encountered (Table 2). Analyses thus far completed have shown no relationship between any specific soil type and any specific vegetation composition on a Basin-wide basis. The diversity of soil and topographic conditions appears to indicate the potential for diversity of vegetation composition but not necessarily which taxa may be involved. This further complicates any attempt at an island biogeographical approach.

Attempts to map latitudinal and longitudinal differences in the equitability components of diversity were found to be of little value since juniper-pinyon woodlands are almost uniformly dominated by one or two trees plus one or two shrubs. One stand had only three species altogether. Most stands had only trace amounts of plants other than the most common five or six species. What equitability gradients that occurred are mostly elevational and successional, as will be demonstrated later. The species presence-absence approach is deemed more useful at the scale being focused on here (Hume and Day 1974, Schnell, Risser, and Hilsel 1976).

Floristic diversity (Fig. 7) is greatest on the higher ranges across the southern end of the Central Plateau portion of the study area where the Great Basin-Mojave Desert transition occurs. In addition to the relationship to the greater present environmental variation (Table 3), we feel that the high diversity there is partially due to historical probabilities of mixing of species with varying abilities of range expansion and survival in the considerable migration of species which has apparently taken place in and since the Pleistocene, particularly hypsithermal time (Antevs 1948 and 1955; Morrison 1965; Birkeland 1969; Spaulding 1974; Martin 1963; Martin and Mehringer 1965; Fritts 1965; Cottam, Tucker, and Drobnick 1959; LaMarche 1974; Phillips and Van Devender 1974; Van Devender 1974; Wells and Jorgenson 1964; Wells and Berger 1967; Elston 1976).

These previous papers and analysis of our

data favor the view that the pigmy conifer woodlands were once continuous across the Great Basin and northern Mojave Desert regions. Subsequent aridity and consequent plant migrations have fragmented these woodlands into the patterns of distribution seen today. The differences in floristic richness are probably more related to rates of extinction (Stebbins 1974 and 1975) than to long-distance dispersal from source biotas on the several possible continents. The richness of the present woodland flora is thus understandably related to the overall environmental favorability of the various mountain ranges at present and in the recent past.

Elevational variability: Billings (1951) and Hollermann (1973a and b) have previously commented on the puzzling variation in the elevational extent of Great Basin juniper-pinyon woodlands. We also noted wide variation in the Basin-wide elevational limits of this vegetation type. This variation, however, shows a close relationship to the general topography of the area, with climatic modification being important in the northern portions.
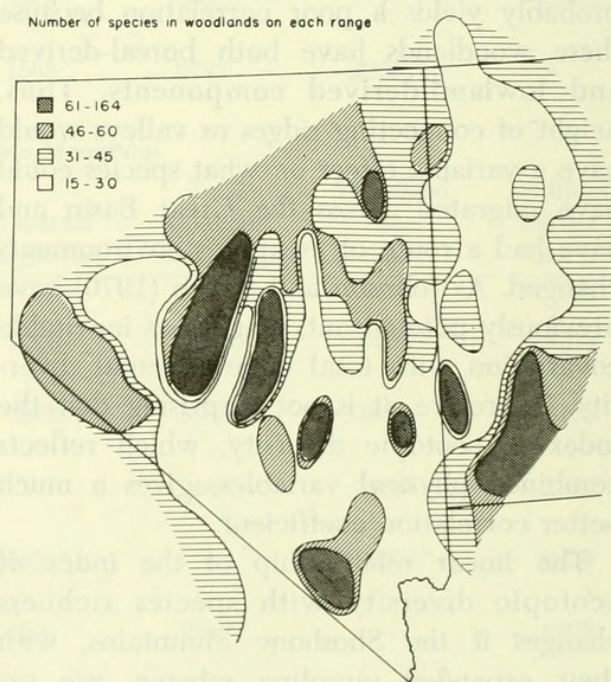
Our lowest sample in the juniper-pinyon

Fig. 7. Isolines of species richness in the woodlands between the 66 mountain ranges.

woodland was a stand at 1200 m on the south slope of the Beaver Dam Mountains of extreme southwestern Utah. This area is also the topographic low point of the area studied. The highest lower boundaries are found in the White, Excelsior, and Silver Peak ranges in the southwestern portion of the study area, and the Toquima and Monitor ranges of the central plateau, some of the highest parts of the topography of the whole study area. The regional distribution of the lowest woodland boundaries are definitely along the eastern and southern boundaries of the study area (Fig. 8).

The highest boundary of the woodland belt is much less definite (Fig. 9), largely due to great differences in mountain heights. The upper extreme of these woodlands in our data set was a 2800 m elevation stand on the west slope of the White Mountains of California. The geographical distribution of upper boundaries is partially correlated to those of lower boundaries.

The difference between the actual elevation of the lower limit and upper limit varies greatly from aspect to aspect on a mountain range and from range to range

over the Great Basin. An average woodland belt width of about 350 m elevational extent occurred on the mountain ranges we sampled. Further analysis of the data shows extremes of belt width ranging from over 700 m in elevation in the White Mountains of California, Highland Peak of Nevada, and the Needle Range of Utah to essentially zero at the northern boundaries of the type. The band of woodland is also extremely narrow in western Utah.

These elevational extremes and band widths are graphically portrayed in Figures 10 through 13, which depict transects across the Great Basin. These transects could be combined to make a response envelope. The breadth of these woodlands is generally greatest in the areas where the extremes of elevational extent occur. (Exceptions to this will be explained later). This greater breadth also approximately coincides with and contributes to the higher floristic diversity in the Great Basin-Mojave transition discussed earlier.

Although undoubtedly some of the elevational variation observed is due to recent historical causes, especially fire and wood
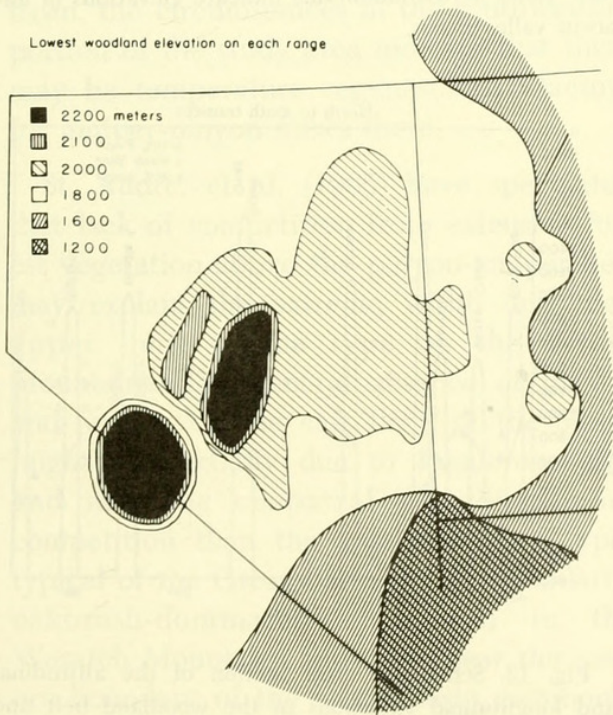

Fig. 8. Isolines of lowest woodland elevation sampled. Interpolation between 66 mountain ranges.
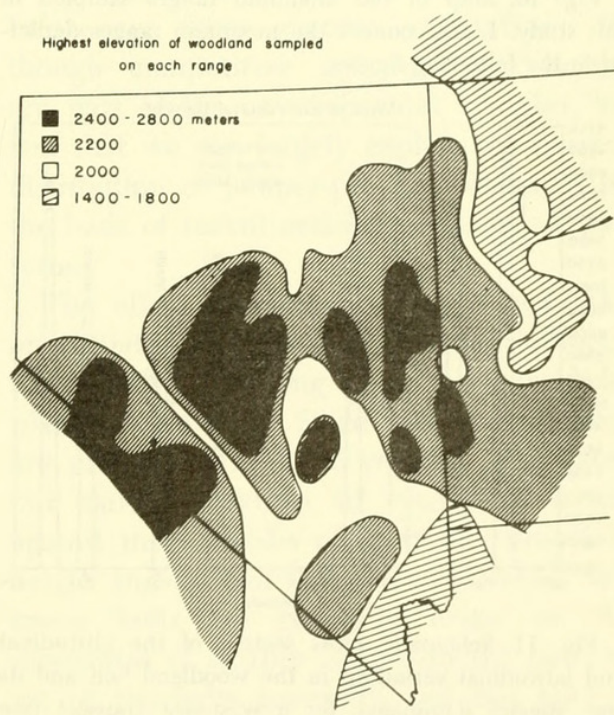
Fig. 9. Isolines of highest woodland elevation sampled.

cutting (Lanner 1976), there are consistent patterns of elevational extent related to topography and climate. The west and east relationships show this most clearly. Woodlands in the eastern Great Basin are generally lower than those to the west. The woodland belt also narrows considerably at the Wasatch Front. The average elevation increases, and then decreases, while the width of the woodland type generally decreases from south to north.

The relative composition of the dominant trees and associated understory varies considerably within the belt (Fig. 11–13). The usual case is for pinyon to increase with altitude and juniper to dominate the lower half of the belt. On many of the higher mountain ranges in the Great Basin, the up-
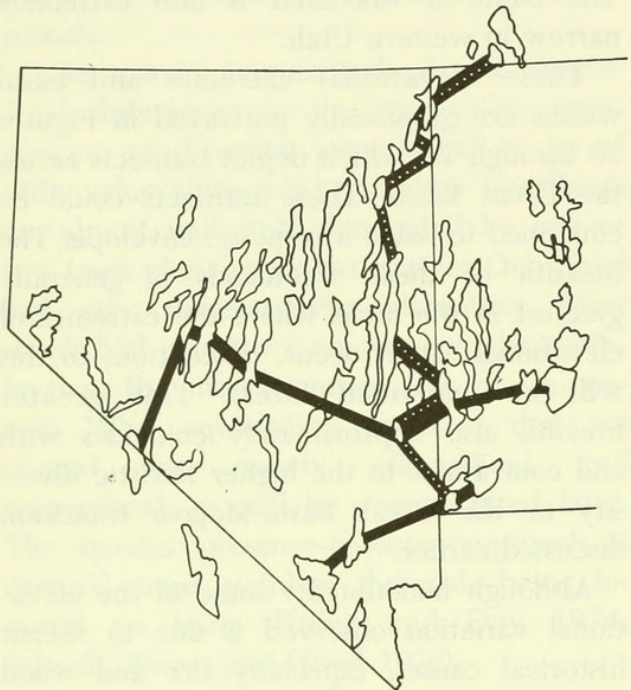
Fig. 10. Map of the mountain ranges sampled in this study. Lines connect the mountain ranges depicted in the following figures.
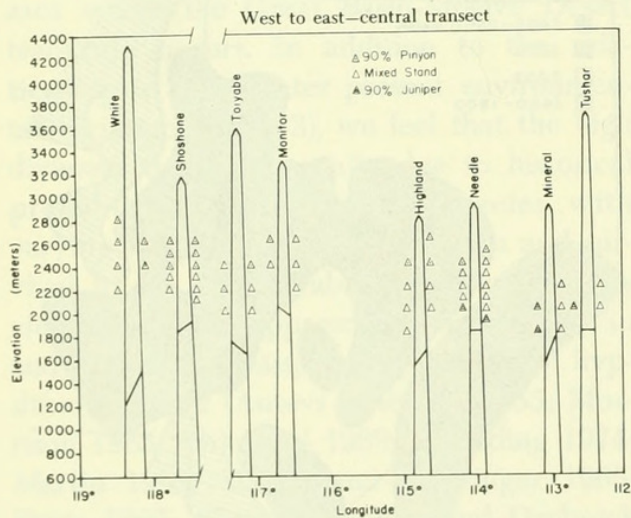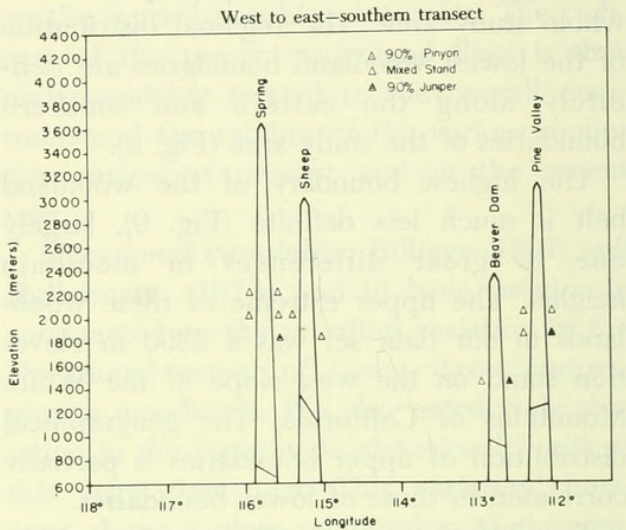

Fig. 12. Schematic cross section of the altitudinal and latitudinal variations in the woodland belt and its tree species dominants for a west-east transect (see Figure 10) of some of the southernmost ranges sampled. Lines across mountains indicate elevations of adjacent valley floors.

Fig. 11. Schematic cross section of the altitudinal and latitudinal variations in the woodland belt and its tree species dominance for a west-east transect (see Figure 10) of some of the southcentral ranges sampled. Lines across mountain indicate elevations of adjacent valley floors.
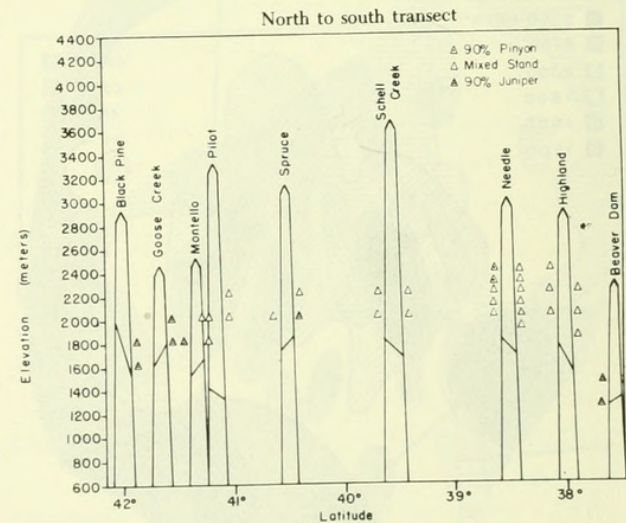

Fig. 13. Schematic cross section of the altitudinal and longitudinal variations in the woodland belt and its tree species dominants for a north-south transect (see Figure 10) in the Great Basin. Lines across mountains indicate elevations of adjacent valley floors.

per part of the woodland belt is a pure pi-
nyon overstory. Juniper is more widespread,
dominating areas in the north and at lower
elevations that do not have pinyon. The
quantity of juniper appears to increase with
increasing soil moisture stress over most of
the Great Basin.

The greater proportions of pinyon don't
always appear to be purely due to increas-
ing precipitation, usual at higher altitudes.
Single leaf pinyon appears to have a wider
range of moisture tolerance than does juni-
per at the higher moisture levels. The in-
cidence of pinyon pine with double needles
and amounts of juniper increases as the pro-
portion of summer rainfall increases from
west to east across the Great Basin. The
summer dry, extreme western boundary of
the basin is the only place where some
mountain ranges have single-leaf pinyon but
lack juniper. On the west side of the White
Mountains there are belts of pure pinyon
both above and below juniper (St. Andre,
Mooney, and Wright 1965). These two cir-
cumstances suggest that although summer
soil moisture stress may largely explain the
lower elevational limits over most of the
basin, the circumstances in the southwestern
portion of the study area indicate that there
may be temperature regimes unsatisfactory
for juniper-pinyon mixes there.

St. Andre, et al. (1965) have speculated
that lack of competition from extensive for-
est vegetation above the pinyon-juniper belt
may explain the extreme width and high
upper limit of the type on the White
Mountains. The general absence of pinyon
and juniper on the east flank of the Sierra
might be partially due to Ponderosa pine
and montane chaparral providing more
competition than the sagebrush-grass types
typical of the Great Basin Ranges. Similarly,
oakbrush-dominated vegetation in the
Wasatch Mountains and those near the east-
ern boundary of the Great Basin commonly
occur above or replace juniper-pinyon
woodland vegetation. Could oakbrush pro-
vide competition limiting the extent of the

pigmy conifer woodlands there? Could the
likely upward migrations of juniper-pinyon
woodlands and the other conifer belts (La-
Marche and Mooney 1972) during the hyp-
sithermal have resulted in the elimination of
conifer forests at higher elevations of the
smaller mountain ranges of the Great Basin?
When temperature cooled and precipitation
increased in more recent times (LaMarche
1974), pinyon and juniper could have ex-
panded with less competition from other
tree forms. Are current precipitation-
temperature relationships suitable for more
competitive species? Unfortunately, little di-
rect data exists to answer these questions.

Ponderosa pine exists in a few scattered
locations on the ranges of southwestern
Utah and southeastern Nevada without
dominance occurring. In those areas ponde-
rosa pine seems to be limited to the most
favorable sites, e.g., moist sites along
streams or northeastern slopes. Pinyon and
juniper compete largely with shrubs at both
their upper and lower boundaries within the
Great Basin.

Until more definitive evidence is in from
palynological, dendroclimatological, and
woodrat midden studies, we can only go on
inferences from current vegetation. Al-
though competitive and historical factors
are part of the environmental complex, we
feel that we can largely explain the current
distribution of juniper-pinyon woodlands on
the basis of recent and current climatic pat-
terns.

The effect of mountain height and mass
on climatic patterns (the "Merriam Effect,"
Lowe 1964) has long been recognized by
plant geographers. Since its manifestations
are greatest in semiarid regions, we related
our data on width of woodland bands
against the variables of maximum mountain
height and area of the mountain mass. Nar-
rower belts are generally found on the
mountains of smaller area with the narrow-
est of the belts generally, but not always,
found on those ranges with less than 700
km^2 area (Fig. 14). Mountain area above
this size has little relation to the width of

belts. The widest belts are found on the highest peaks and are relatively independent of mountain area (Fig. 15). A high peak will not, however, necessarily have a wide belt of woodland (e.g., Wheeler Peak, Ruby Mountains, etc.). In circumstances where the belt is wide, the height of the peak dominates, but the location of the peak in the Great Basin is of much more importance. Figure 16 makes a separation of the Great Basin on the basis of where woodland belt widths are either greater or less than 400 meters. There are many peaks in the area of narrow belt width that are as high or higher than those found in the area of the wide belt width, but they are all in the region of greater orographic impact from Pacific Frontal storm systems (Houghton 1969). Because of their elevation, the very high ranges of east central Nevada have a climate similar to the ranges more north and west. These climatic controls will now be expanded on.

The lower woodland boundaries in the northern half of the study area appear to be related to valley bottom topography (Figs. 10-13). Wernstedt (1960) shows that little difference occurs in summer temperatures between the southern and northern Great Basin, but greatly lowered winter values are encountered as latitude increases. This trend applies best to valley bottom stations. Knowledge of temperature within the woodlands is minimal because few meteorological stations with long-term records exist. Most of the U.S. Weather Service meteorological data is from desert valley bottom stations where most of the scarce human habitation occurs. Billings (1954) has correlated the occurrence of juniper-pinyon woodlands in northwestern Nevada to thermal belts. This led us to suspect that the breadth of the woodland belt all across the northern portions of the Great Basin is at least partially related to the strength of development and persistence of thermal belts. Analysis of what temperature data that do exist (Fig. 17) shows a strong relationship of fewer degree-days below freezing indexes
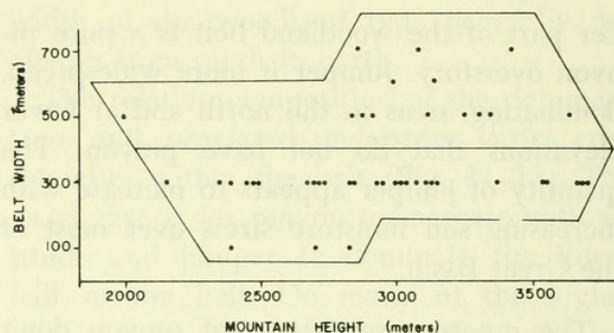

Fig. 14. Average woodland belt width (in nearest 100 m increments) in relation to maximum mountain height.
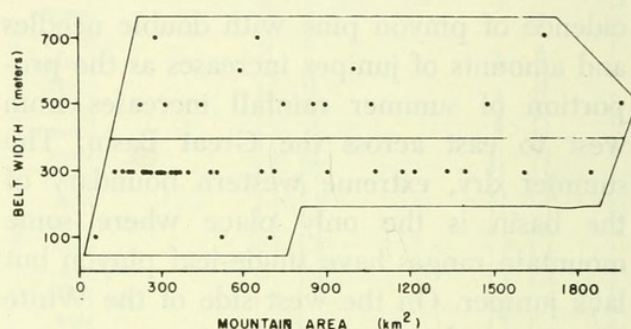

Fig. 15. Average woodland belt width (in nearest 100 m increments) in relation to mountain area above the lower boundary of woodland.

Average woodland elevational belt width

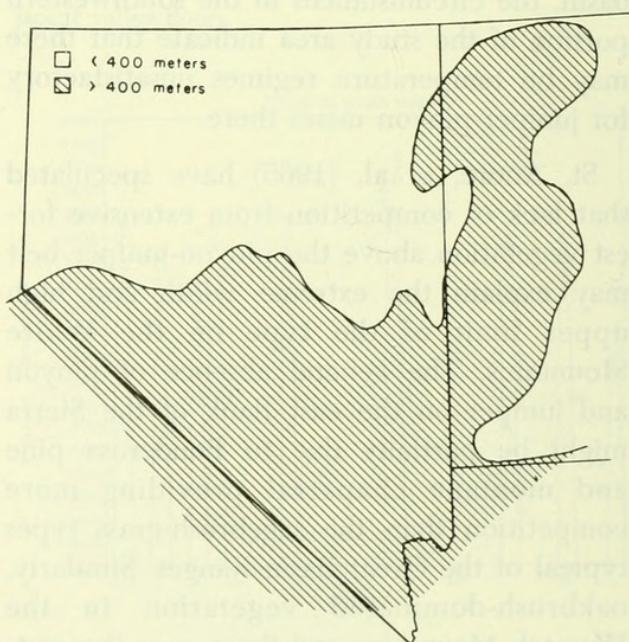☐ < 400 meters
☒ > 400 meters

Fig. 16. Division of the Great Basin on the basis of mountain ranges having an average woodland belt width of greater or less than 400 meters vertical extent.

for meteorological stations within the woodland belt, except in the southeastern Great Basin (Pioche and Ursine, Nevada). Degree days above freezing are much higher in most woodland areas than those in the valley bottoms where various cold-winter, semidesert shrub-dominated vegetation types occur.

Juniper-pinyon woodlands are nearly absent north of Interstate Highway U.S. 80 across northwestern Nevada. Critchfield and Allenbaugh (1969) noted the correspondence of the northwestern limits of *Pinus monophylla* with the southern boundary of pluvial Lake Lahontan and speculate as to the lake being a possible barrier to plant migration. The occurrence of pinyon pine on the Virginia and Stillwater Ranges and the frequent invasion of juniper in areas that were once under the pluvial lakes of the Great Basin makes this seem unlikely. The correspondence of lakes to the pools of cold air and/or lower precipitation now in these basins seems more of an etiological factor in present distribution patterns.

Arlo Richardson (personal communication) has mapped the progression of late winter and early spring chill-unit (Richardson, Seeley, and Walker 1974) accumulations across the Great Basin. The valleys of northwestern Nevada have the most rapid progression and resultant ending of winter plant dormancy of any area in the Great Basin. Warming periods are, however, more dramatically punctuated by cold periods brought by Pacific Frontal storms there than elsewhere. This knowledge, combined with existing knowledge of air circulation and storm patterns summarized by Houghton (1969), leads us to speculate that a primary reason for the narrowing and absence of the woodland belt in the north, in addition to the latitudinal decrease in solar input, is due to the increased frequency of Pacific frontal winds breaking thermal inversions. This pattern is thought to encourage earlier plant growth but greater subsequent susceptibility of plants to direct frost damage or frost drought in a manner

similar to that found for other conifers (Hocker 1956, Newnham 1968). Supporting evidence of the net effect on woodland trees can be seen on space photography where the most northerly and westerly of the mountain ranges in the Great Basin are devoid of pinyon and juniper. In the north central portion of Nevada, ranges such as the Santa Rosa's are almost devoid of conifers altogether (Critchfield and Allenbaugh 1969). Ranges to the south and east of the ranges devoid of the woodland contain one or both tree species, implying a lee protection effect, e.g., Spruce Mountain, the southern Ruby Mountains, and the southern most tip of the East Humboldt Range (Fig. 18).

In the southern Great Basin the westerly fronts have lost most of their energy; thus their disruptive effect on the development and maintenance of thermal belts is not as frequent. Furthermore, most of the precipitation in the southern Great Basin comes from the moist Gulf air masses with rainfall triggered by the lows aloft. As a consequence, there are weaker adiabatic lapse rates (decrease in temperature with elevation) and a corresponding smaller increase in precipitation with elevation because of reduced orographic effects. For example, on the west slope of the White Mountains, the
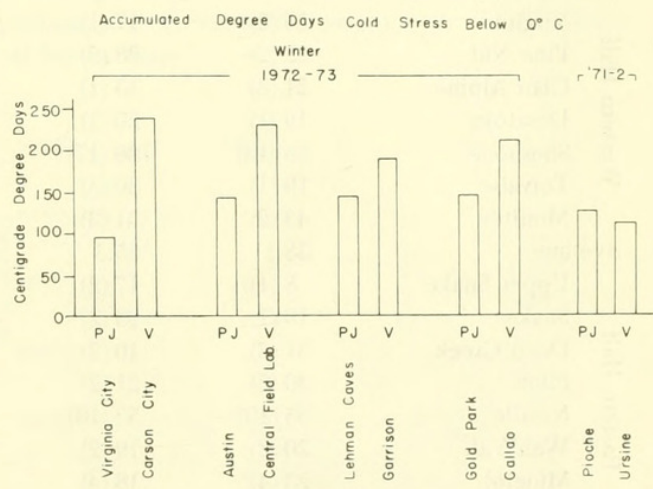

Fig. 17. Accumulated degree days cold stress below 0°C for selected woodland (PJ) and valley floor (V) climatic stations across the Great Basin (west on left, east on right). Data obtained from U.S. Weather Service climatic summaries for years indicated.

change in precipitation with elevation over the entire woodland belt is only 10 cm (4 inches) (St. Andre et al. 1965).

Although west slopes are usually the most mesic and diverse in the Basin, the woodlands on some of the mountain ranges in our study areas have higher floristic richness on the eastern and southern slopes (Table 4). This apparent reversal of the usual trend is believed to be due to the effects of nearby ranges creating rain shadows and other orographic effects. For example, in the Silver Peak Range most of the moisture must come from lows aloft positioned to the north and east. Johnson (1956) noted that the woodland belt on the south and eastern sides of the nearby Kawich Mountains had the most breadth, highest cover, and largest trees, providing corroborative evidence of this situation.

In the southern two-thirds of the study area, the lower boundary of woodlands appear to be more controlled by precipitation than temperature. Degree day values for Pioche and Ursine, Nevada (Fig. 17), are an example of how heat sums do not differ between foothill, woodland, and valley stations

in the southeast. In fact, the situation may be slightly reversed over that of the more northerly and westerly pairs of stations.

Further evidence of the interaction of temperature and moisture may be observed in the variation of the width of the woodland belt as related to mountain symmetry. Generally, the north-south axes of Great Basin mountain ranges are longer and the highest peaks are also usually in the center (Lustig 1969). When the range is protected to the west (e.g., Table Mountain in the Monitor Range) (Fig. 19), the widest belts are in the wider, higher, central east-west axis; and the belt-width decreases and average elevation increases toward the north and south ends. This is an apparent response to the Merriam effect of the greater mountain mass intercepting more moisture at a similar elevation. Extra high mountains such as Arc Dome in the Toiyabes (Fig. 19) appear to effect excessively cold, wet conditions for woodland development and the high, central axes have narrower, lower belts primarily on western slopes under such circumstances.

We have ignored here the short-term suc-

TABLE 4. Number of species (and number of stands) on each aspect of selected ranges in a west to east belt.

Mountain Range		N	E	S	W	Total	Average per stand
Western Half	Virginia	35 (2)	17 (1)	27 (2)	– (–)	50 (5)	19
	Pine Nut	32 (2)	28 (2)	23 (2)	32 (2)	57 (8)	18
	Clan Alpine	21 (2)	15 (1)	– (–)	– (–)	28 (3)	12
	Desatoya	19 (1)	20 (1)	15 (2)	28 (2)	47 (6)	15
	Shoshone	98 (13)	106 (17)	108 (22)	78 (7)	159 (59)	25
	Toiyabe	19 (1)	30 (3)	23 (2)	46 (3)	75 (9)	15
	Monitor	43 (2)	31 (3)	29 (3)	34 (2)	68 (10)	17
Average		38.1	35.3	37.5	43.6	69.1	17.1
Eastern Half	Upper Snake	8 (1)	17 (2)	10 (2)	9 (2)	27 (7)	7
	Snake	10 (1)	23 (2)	11 (1)	25 (2)	49 (6)	12
	Deep Creek	31 (2)	16 (2)	17 (2)	24 (2)	49 (8)	14
	Pilot	30 (2)	21 (2)	13 (2)	26 (3)	50 (9)	12
	Needle	55 (13)	53 (16)	33 (15)	43 (12)	92 (56)	9
	WahWah	20 (2)	19 (2)	17 (2)	16 (2)	45 (8)	10
	Mineral	23 (4)	18 (4)	31 (5)	32 (4)	62 (17)	9
	Stansbury	13 (1)	23 (2)	12 (1)	– (–)	37 (4)	12
	Tushar	32 (2)	17 (2)	18 (2)	9 (1)	48 (7)	10
Average		26.3	22.9	18.7	23.3	52.0	10.1

cessional changes that are known to be operating in these woodlands. If we plot by aspect, relative tree cover, richness, and relative equitability against elevation for an example mountain range (Fig. 20), we see that richness is minimal in the closed woodlands in the middle of the belt where understory has been largely excluded by high relative tree cover. Equitability patterns are more complicated.

The approach to equitability used measures how evenly the existing total cover is divided among the species present. For each different total cover and species number a different maximum equitability is possible. To make an equitability comparison between areas of different cover and density, it is necessary to convert the figure to a relative one; in this case the percent of the maximum possible for each site. During succession (West et al. 1975) invasion by juniper and pinyon shifts in relative cover toward more trees. However, before a significant drop in total species number oc-

curs, equitability drops. As tree suppression substantially reduces the number of understory species, equitability rises. Equitability is thus highest at either end of the sere and lowest in the intermediate seral stages. This is contrary to the linear model for xericforests proposed by Auclair and Goff (1971).

Fig. 19. Interactions of exposure to westerly storm tracks, mountain height, and mountain mass on the variation in woodland belt width and elevation in west-central Nevada. Stippled area is juniper-pinyon woodland. Outer (lower) line is 2134 m (7000 ft.) contour. Inner (higher) line is 2743 m (9000 ft.) contour. Dots are major mountain peaks: A = Arc Dome in the Toiyabe Range, T = Table Mountain in the Monitor Range. (Vegetation map derived from LANDSAT-1 photography. Elevational contours from U.S. Geological Survey maps.)
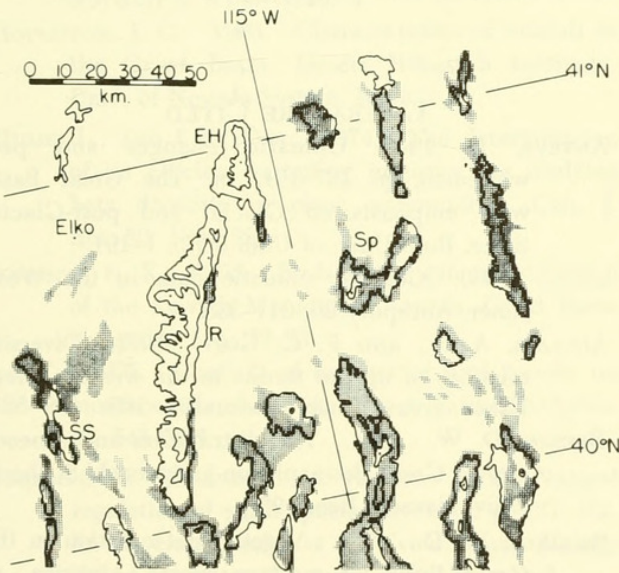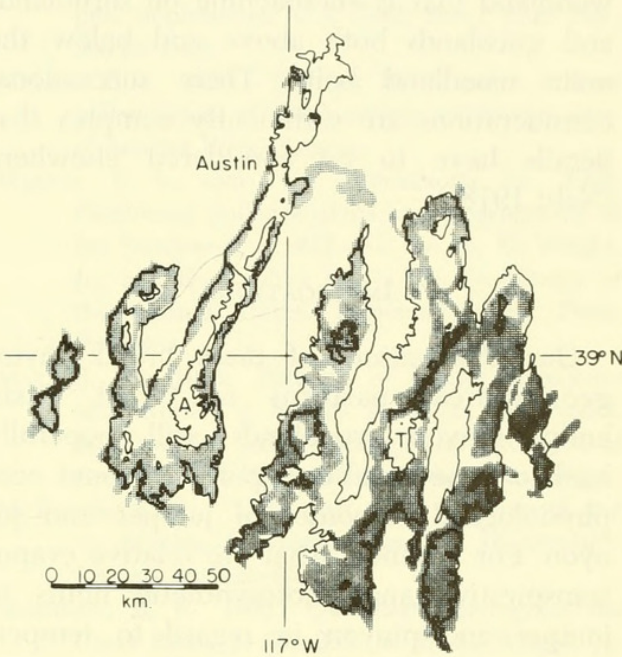

Fig. 18. Effects of exposure to westerly winds and storm tracks on occurrence of the woodland belt at the northern boundary of the type in northeastern Nevada. Stippled area is juniper-pinyon woodland, outer (lower) line is 2134 m (7000 ft.) contour, inner (higher) line is 2743 m (9000 ft.) contour. Dots are major mountain peaks: SS = Sulphur Springs Range, EH = East Humboldt Range, Sp = Spruce Mountain, R = Ruby Mountains. (Vegetation map derived from LANDSAT-1 photography. Elevational contours from U.S. Geological Survey maps.)
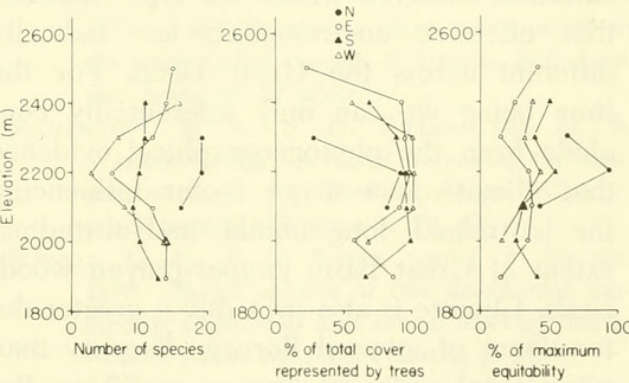

Fig. 20. Species density (floristic richness), relative percent of total cover contributed by trees, and percent of maximum equitability calculated by the McIntosh (1967) index plotted by elevation and aspect, Needle Range, Beaver-Iron Cos., Utah.

In general, the north slopes at any elevation have a larger number of species, a lower percent relative cover of trees, and a higher equitability value than the other three aspects.

Higher average diversity values were obtained in our data by including some of the woodland that is encroaching on shrublands and grasslands both above and below the main woodland belts. These successional considerations are sufficiently complex that details have to be considered elsewhere (Nabi 1978).

IMPLICATIONS

Our observations of these broad phytogeographical patterns in Great Basin juniper-pinyon woodlands will hopefully lead to some testable hypotheses about eco-physiological responses of juniper and pinyon. For instance, what are relative evapotranspirative and photosynthetic limits of juniper and pinyon in regard to temperature and moisture? Does needle number on pinyon relate to effective soil moisture? What are the tolerances of seedlings to temperature and moisture extremes compared to those of the mature trees? Are there late winter-early spring low temperature susceptibilities? Research to answer these questions provoked by our synecological results will be necessary to confirm our hunches.

The distributional and phytosociological variation observed within the type indicates that effective environments are radically different across the Great Basin. For the time being we can only inferentially conclude from the phytogeographical evidence that climate is a major factor influencing the latitudinal, longitudinal, and altitudinal extent of Great Basin juniper-pinyon woodlands. Climate is also probably a greater determinant of internal floristic diversity than migrational and evolutionary equilibria. Regarding the mountains and their woodlands as islands in a uniform "sea" of desert leads to dangerous basic conclusions and confounds management application, since climatic patterns are so different in the various portions of the Great Basin. These differences are striking even at the same elevation on different portions and aspects of the same mountain range. This is especially evident in data from the Shoshone Range. In general, such differences are most pronounced in the Mojave-Great Basin transition area. Stratification of landscapes into units of some homogeneity for management purposes must take these phytogeographical patterns into account, if confusion is to be avoided.

ACKNOWLEDGMENTS

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