Topographic Effect on Spatial Variation of Plant Diversity in California

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Abstract

Plant diversity of 94 subcounty regions in California was analyzed at species, genus, and family levels. The richness indices at the three taxonomic levels were related to the mean and standard deviation of the elevation of each region, and the statistical relationships are examined. Species-genus and species-family ratios, used as indicators of speciation capacity, are also related to the elevation mean and standard deviation. We found that all indices of richness and speciation capacity correlated positively with both variables of topography; an apparent distinction in the degree of correlation existed among taxonomic levels; the correlation coefficient decreased as the taxonomic level moves from species to genus to family. The speciation capacity correlated more closely with elevation mean and standard deviation than the richness indices did, suggesting that the topography affect species richness indirectly through influencing speciation capacity. In addition, the correlation coefficients for standard deviation of elevation were all greater than those of elevation mean, indicating that spatial variability of elevation was more directly related to plant diversity. The habitat heterogeneity hypothesis was modified to explain our result and discrepancies among results from various studies.

I. INTRODUCTION

A fundamental question that has puzzled Humboldt, Darwin and generations of naturalists and ecologists is why there are a certain number of species in a given environment and what factors contribute to the spatial variation in species richness (May 1986, Currie 1991). There have been a number of hypotheses proposed to explain species diversity and its relationships to environmental factors. The island biogeography theory explains the relationship between species richness and area (island size), but sheds little light on the mechanisms underlying spatial variation (Preston 1962, MacArthur and Wilson 1967). The species-energy theory attempts to base the species richness on a biophysical foundation. The difficulty of the species-energy theory lies in converting many different factors into a commonly agreed energy term. Habitat heterogeneity hypothesis stresses the importance of spatial and compositional heterogeneity of habitats in affecting species richness (Brown 1988). The underlying mechanisms of habitat heterogeneity effect on diversity are yet to uncover. We will examine in this study the applicability of the habitat heterogeneity hypothesis to explaining the effect of topography.

The effect of topography on species richness has long been noted. Hamilton et al. (1964) and Watson (1964) studied the effect of elevation and other factors on island bird faunas. Hamilton et al (1964) and Hamilton and Rubinoff (1967) found that island elevation generally accounted for 2-15% of the variation, while area accounted for 80-90%. In explaining the spatial patterns of tree species richness of North America, Currie and Paquin (1991) pointed out that topography was significantly related to the residual variation in addition to actual evapotranspiration. Richerson and Lum (1980) analyzed the effect of topographic heterogeneity on plant species richness in 94 subcounty regions (to be defined later in this paper) of California. They found significant correlation between the two variables when topographic heterogeneity was expressed as elevation range of each subcounty region. Birks (1996) found that elevation alone explained up to 38% of the variance in plant species richness of Norwegian mountain flora. These studies used elevation or elevation range or both to represent topography. A statistically significant effect of topography was detected in most cases.

Nevertheless, the specific relationships between species richness and elevation have not been well documented (Brown 1988). There have been scattered

studies on the patterns of species richness along elevation gradients. For example, variations in bird species diversity in elevation gradients in New Guinea and the Amazonian slope of the Peruvian Andes were reported by Kikkawa and Williams (1971) and Terborgh (1977), respectively. Both studies showed monotonic decreases in species richness with increasing elevation. Whittaker and Niering (1975) reported a unimodal function of the variation in plant species richness with elevation on a desert mountain in Arizona. They found the peak richness occurred at intermediate elevation (approximately 1300m a.s.l.). Grastein and Pocs (1989) documented a similar unimodal function in Bryophyte diversity on a mountainside in Columbia. They found the peak richness occurred at about 2100 m a.s.l.. In discussing the various forms of relationships between elevation and species richness, we must bear in mind that the discrepancies among these results may simply reflect the differences in locations, taxonomic groups, or sampling methods used in the studies. For instance, the latitudes of the study sites may change the diversity-elevation relationship.

The seemingly conflicting results highlight the need for further studies on the effect of topography on species diversity, and particularly on its underlying mechanisms. MacArthur and Wilson (1967) pointed out that elevation may not exert a direct effect on species richness. Elevation is related to other environmental factors such as climate and habitat diversity, and it exerts an indirect effect on species richness. It has been suggested that a theory on species diversity should be able to explain three fundamental processes: speciation, immigration, and extinction (MacArthur and Wilson 1967, Rosenzweig 1997). While it is difficult to link topography directly with immigration or extinction, there is evidence to support the effect of topography on speciation. Geography, polyploidy, and competition are three basic modes proposed to explain speciation. Geography theory emphasizes the effect of geographical isolation which incorporates topography. Some observations relate polyploidy directly to elevation. In the tropical regions, a greater proportion of polypoidy is often found at higher elevations in the mountains, while a lower proportion in the lowlands (Rosenzweig 1997). But this pattern becomes insignificant, or even reversed, in the high latitudes (Gustafson 1948). Proportion of polyploidy obviously parallels with overall species diversity.

It is helpful to make two distinctions to evaluate the effect of topography on biodiversity. The first is between elevation and its spatial variability. These two variables represent two fundamental but very different aspects of topography. The second is among indi-ces of plant diversity. In this study, we use genus and family numbers in addition to species richness to indicate plant diversity. In addition, we introduce species-genus and species-family ratios as indices of speciation capacity and evaluate their relationships with topography. Unlike speciation itself which is a process of species generation, speciation capacity measures the net outcome of the processes affecting the total number of species including speciation, immigration (colonization) and extinction. In this study, we first construct the statistical function of plant diversity with elevation and with its spatial variability. Then we explore the underlying mechanisms by which elevation and its variability affect plant diversity at species, genus and family levels. We also critically examine the applicability of existing hypotheses to explaining the results from this and other studies. Finally, we propose a hypothesis that can accommodate the seemingly conflicting results from various studies.

II. DATA AND METHODS

Plant diversity data were derived from a taxonomic inventory database of the state of California. Named Calflora, this database is constructed by the US Forest Services following Lum (1976) and Richerson and Lum (1980), and supplemented with other sources of data. The database divides the state of California into 94 subcounty regions. Each region is created by using a whole county or by partitioning a county so that all subregions have equivalent sizes. The division is somewhat arbitrary, although geomorphologic features are used whenever convenient. Each plant species, its associated genera and families, and its geographical distribution are listed. The species list data are converted to derive the numbers of species, genera, and families for each subcounty region. Mapping of these numbers of each region generates the spatial patterns and variation of plant diversity (Figure 1).

The elevation data used in this study were clipped from the 1km x 1km digital elevation model (DEM) developed by the USGS EROS Data Center in Sioux Falls, South Dakota. The original data are for the North American continent. We cut out the state of California using the Arc/Info grid clip module. The DEM was overlaid with the subcounty boundary map to calculate the mean and standard deviation (SD) of elevation for each subcounty region. The mean is used to represent the elevation, and the SD to represent the spatial variability of each region. The two resultant data layers for subcounty regional mean and SD of elevation are shown in Figures 2 and 3.

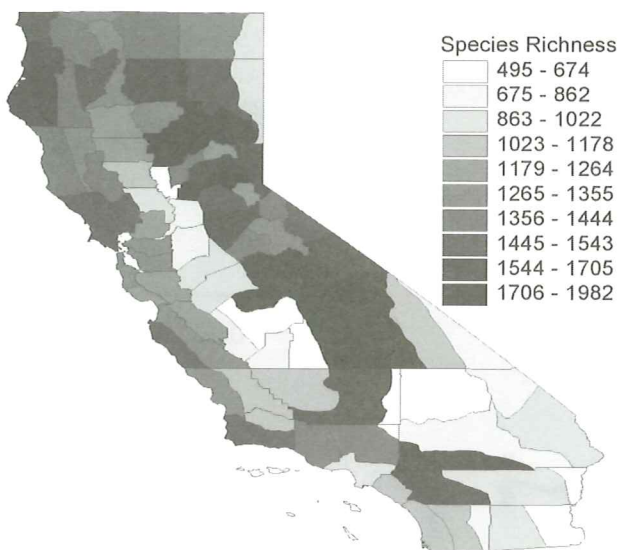We calculated the species-genus and species-family

Figure 1. Spatial variation of plant species richness in the 94 subcounty regions of California

ratios for each of the 94 subcounty regions through dividing the species number by the genus and family number, respectively. These ratios were used as indicators of average speciation capacity of each subcounty region. For example, a high species-family ratio in a region indicates a great capacity of speciation of the families. Speciation capacity as we use the term here is not the *process* of speciation, rather it is the *net outcome* of the processes that affect species richness, including speciation, immigration (or colonization) and extinction. Univariate regression was performed to relate the elevation mean and SD to different mea-

sures of plant diversity, including the species-genus and species-family ratios.

III. RESULTS AND ANALYSES

Species, genus and family numbers versus elevation mean and SD

We plotted the numbers of species, genera and families in each of the 94 subcounty regions against the mean and SD of elevation (Figure 4a-f). Figure 4a shows a positive correlation between species number and elevation. The correlation is confirmed using a linear regression analysis in which elevation is treated as an independent variable and species number as a dependent variable. Elevation alone explains 22% of the variation in species richness (Table 1, column 2). In contrast, neither genus nor family numbers exhibits an apparent correlation with elevation (Figure 4b and c), although a weak, but significant, positive correlation is indicated in the regression analysis (Table 1, column 3 and 4).

The standard deviation of elevation seems to correlate more closely than elevation mean with species, genus and family numbers (Figure 4d, e and f). The standard deviation explains 45.5% of the variation in species richness, doubling that for elevation (Table 1, column 7). The correlation of the standard deviation with genus and family numbers is also much higher as compared to that of elevation, with coefficients of determination of 25.7% and 11.4%, respectively. Striking distinctions exist between different
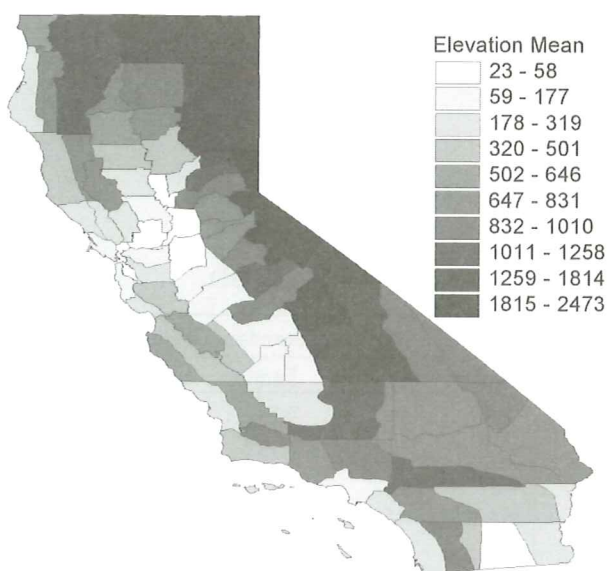

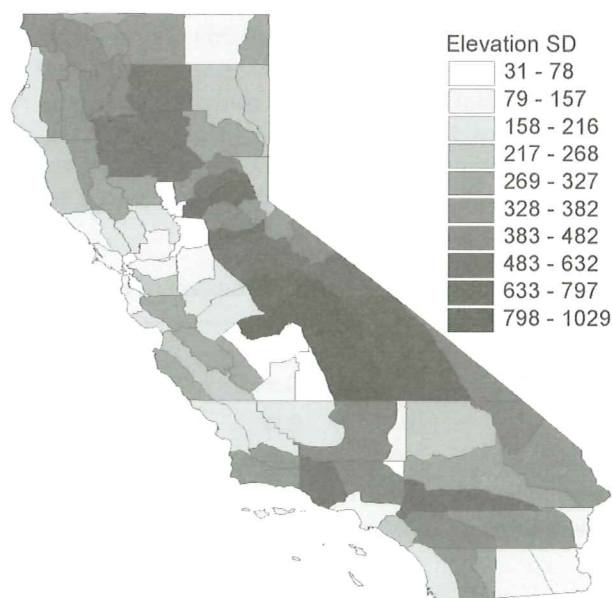**Figure 2.** Pattern of elevation means of the 94 subcounty regions

Figure 3. Pattern of standard deviation of elevation of the 94 subcounty regions
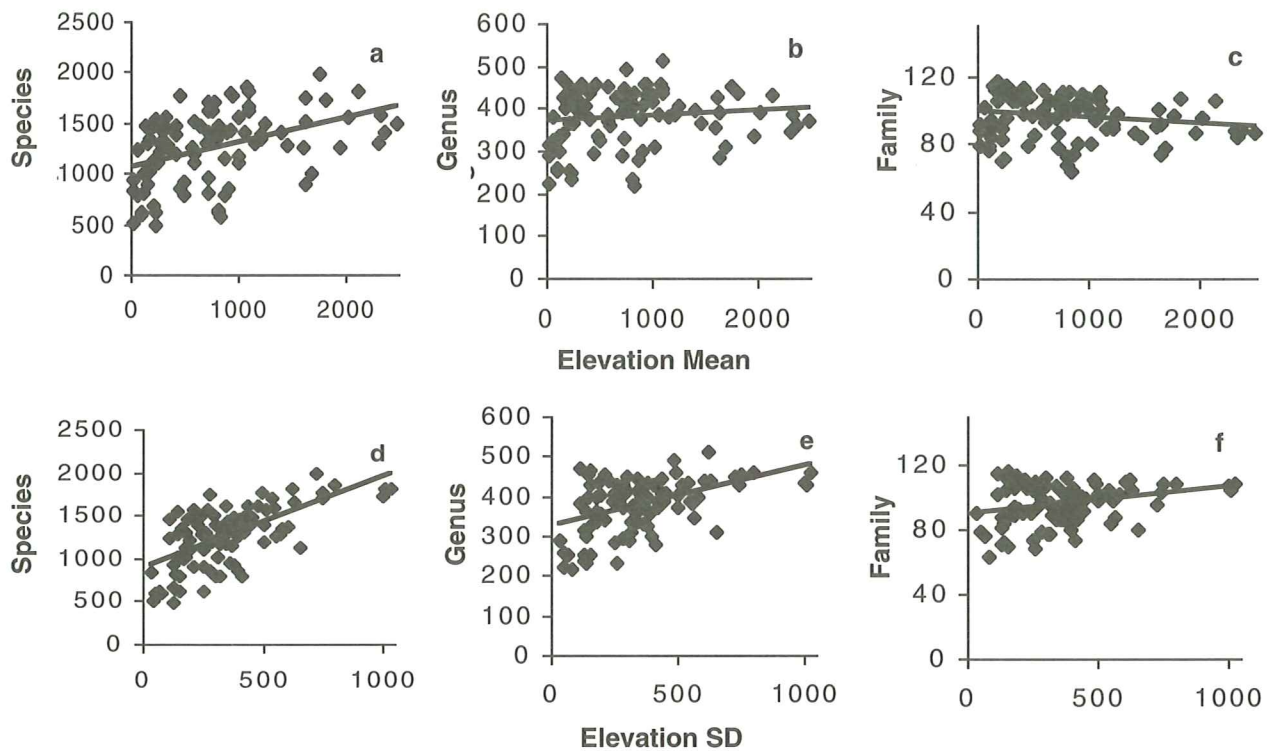
Figure 4. Richness of species, genus, and family versus elevation mean and SD

taxonomic levels in their correlation with the standard deviation of elevation, with the highest for species, lower for genus and lowest for family.

Species-genus and species-family ratios versus elevation mean and SD

The species-genus and species-family ratios were plotted against elevation mean and SD (Figure 5a - d). All four panels of Figure 5 show an apparent positive correlation. Both species-genus and species-family ratios are strongly correlated with elevation, with the coefficients of determination of 0.51 and 0.49, respectively (Table 1, columns 5 and 6). Compared to the

species richness correlation in Figure 4a, these ratios clearly correlate more closely with elevation.

The correlation of the ratios with the elevation SD has also improved. The coefficients of determination are 0.50 for species-genus and 0.47 for species-family, as compared to 0.46 for species richness. However, the increase for SD is not as significant as for the elevation mean.

IV. DISCUSSION

Table 1. Result of linear regression of diversity indices against elevation mean and SD

| Independent Variable	Elevation Mean					Elevation Standard Deviation				
Dependent Variable	Species	Genus	Family	Spe/Gen	Spe/Fam	Species	Genus	Family	Spe/Gen	Spe/Fam
Multiple R	0.47	0.19	0.08	0.76	0.70	0.68	0.51	0.34	0.71	0.68
R Square	0.22	0.04	0.01	0.51	0.49	0.46	0.26	0.12	0.50	0.47
Adjusted R Square	0.21	0.03	-0.00	0.51	0.48	0.45	0.25	0.11	0.49	0.46
Standard Error	322.47	69.74	13.38	0.36	2.09	269.57	61.19	12.62	0.37	2.13
F	26.56	3.40	0.63	98.24	88.99	78.52	32.53	12.11	93.64	82.15
Significance F	1.40E-06	6.85E-02	4.30E-01	2.84E-16	2.95E-15	4.85E-14	1.35E-07	7.63E-04	8.95E-16	1.80E-14
Intercept	1046.43	362.28	97.23	2.81	10.45	870.97	322.15	88.78	2.69	9.83
EleMean	0.28	0.02	-0.00	0.00	0.00	1.10	0.16	0.02	0.00	0.01
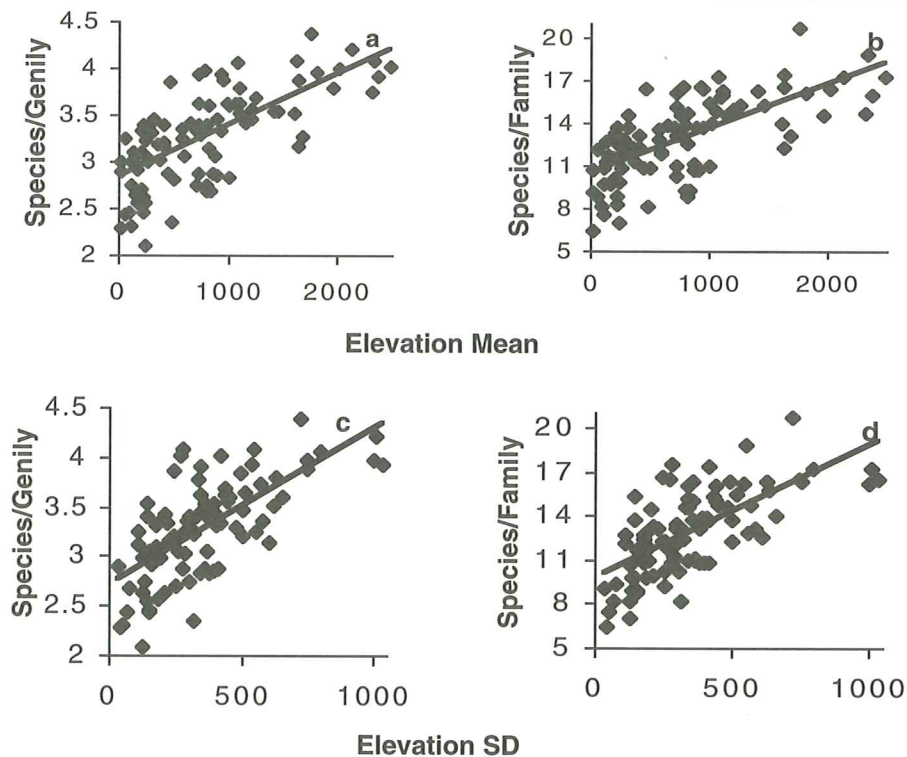
Figure 5. Species-genus and species family ratios versus elevation mean and SD

Differential Responses of Species, Genus and Family

This study demonstrates marked differences in how various taxonomic levels correlate with elevation or its spatial variation. The coefficient of determination is greatest for species richness, smaller for genus number, and smallest for family number. In other words, the correlation decreases as taxonomic level goes up. This result has important implications for understanding how elevation and its spatial variability affect plant diversity. Lower taxonomic level (species) is more responsive to the gradients of both elevation and its spatial variation. To the contrary, we see no apparent trend in family numbers along neither elevation mean nor standard deviation. It may be that the gradients are not large enough to make a difference in the number of families, but it may also be that topographic gradients do not affect family richness. A major role that topography plays in plant ecology is to affect the microenvironment, including soil condition and microclimate. Local plant communities respond with adaptation in composition, structure, and functions. Species composition and richness may change as a result. However, the localized modification of microenvironment may not be enough to family richness which is more likely to be determined by factors operating at macroscales in both space and time. These factors may include large-scale climate, size of the subcounty region, evolution history and the disturbance regimes. How these factors may affect the numbers of genus and family is yet to be determined. Nevertheless, we may speculate that the relative role of elevation or its spatial variability diminishes as the taxonomic level goes up. Our results suggest that the role of elevation and its spatial variability is played through affecting the environmental conditions, such as microclimate and soil properties, at relatively localized scales.

Most studies on the effect of elevation have focused on species richness and neglected other taxonomic levels such as genus and family (e.g. Kikkawa and Williams 1971, Whittaker and Niering 1975, and Terbourgh 1977). Knowledge on the relative effects on other taxonomic levels helps to better understand the mechanisms of the topographic effect in general. O'Brien et al. (1998) studied the relationship of climate with the numbers of species, genus and family in southern Africa. They found similar patterns and degrees of correlation for different taxonomic levels. To the contrary, our result suggests that significant differences exist in the responses of different taxonomic levels, and that the higher taxonomic levels tend to be less responsive. We note that O'Brien et al.

(1998) chose climate as the dependent variable, while we used elevation and its spatial variability. The discrepancy in the results of the two studies may derive from the choice of variables; but it may also be due to different sample sizes used. O'Brien et al. (1998) used a regular grid size of 25000 km², while our study used irregularly sized subcounty regions with an average of 4354 km².

Effect of topography: Species Richness vs. Speciation Capacity?

We found a significant linear correlation of species richness with both elevation mean ($r^2 = 0.22$) and standard deviation ($r^2 = 0.46$). This result concurs with those of Whittaker and Niering (1975) and Gradstein and Pocs (1989) in the range below 1500m and 2100m in elevation. However it does not concur with the patterns reported by Kikkawa and Williams (1971) and by Terbourgh (1977), in which a negative correlation was detected. These similarities and differences may be superficial. Before we try to explain their possible causes, it may be useful to look more closely at the fact that the speciation indices always have greater correlation with both elevation and its spatial variation. If the correlation reflects the causal effects of elevation or its spatial variation, the effects are greater on speciation capacity as measured by species-genus and species-family ratios than on species richness.

Species richness is quantitatively related to speciation capacity indices. It is simply the product of the speciation capacity index and the corresponding genus or family number. Because of this relationship and the high correlation in speciation capacity, we speculate that the correlation between species richness and elevation (or its spatial variation) is a result of the correlation between speciation capacity and elevation (or its spatial variation). In other words, elevation (or its spatial variation) indirectly affects the species richness of a region. It does so through affecting the speciation capacity.

Effect of Elevation Mean versus Spatial Variability?

Our results indicate that both elevation and its spatial variability have certain degrees of positive correlation with species richness and speciation indices. The standard deviation apparently has a much greater degree of correlation with all measures. The two forms of correlation (elevation mean versus SD) may be causally related themselves, although it is difficult to discern the cause and effect. For the 94 subcounty regions of California, an overall positive correlation exists between elevation mean and standard deviation (Figure 6). The outliers are in counties that are relatively flat but at high elevations, e.g. Mono, Alpine, and Tuolumne counties. This may suggest that the spatial variability as measured by standard deviation, rather than elevation mean, is more directly related to speciation capacity or species.

V. SYNTHESIS

A few conclusions can be drawn from this study. First, richness at different taxonomic levels has different degrees of correlation with elevation mean and SD. Variations in elevation mean and SD affect species richness more strongly than family richness. It is indicated that topographic effect is localized at smaller spatial scales. On the other hand, richness at higher taxonomic levels is more likely to be affected by environmental factors at greater spatial scales (see section IV.1). Second, compared to richness, speciation capacity, as measured by species-genus and species-family ratios, is perhaps more directly related to elevation mean or SD or both, since the former always has higher correlation coefficients with both elevation mean and SD. Correlation between species richness and elevation is likely the result of the correlation between elevation and speciation capacity. Third, spatial variability of elevation emerged as a possibly more direct cause for higher speciation capacity than elevation means. The three conclusions can be placed in an integrated framework (Figure 7). Together they support the habitat heterogeneity hypothesis of species richness. This hypothesis suggests that heterogeneity of habitats contributes to or determines species richness (e.g. Brown 1988, Cody 1975). It is used by some as an alternative to the island biogeography theory to explain the species-area relationship (Williams 1988). In explaining our results, we may consider that, on the one hand, spatial variability of el-
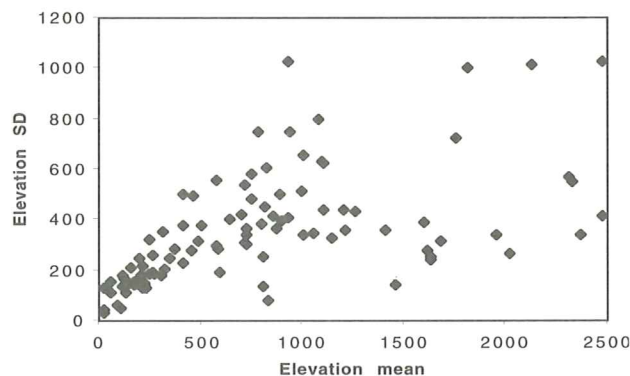

Figure 6. Scattered plot showing the correlation between elevation mean and SD of the 94 subcounty regions (correlation between elevation and its spatial variation)
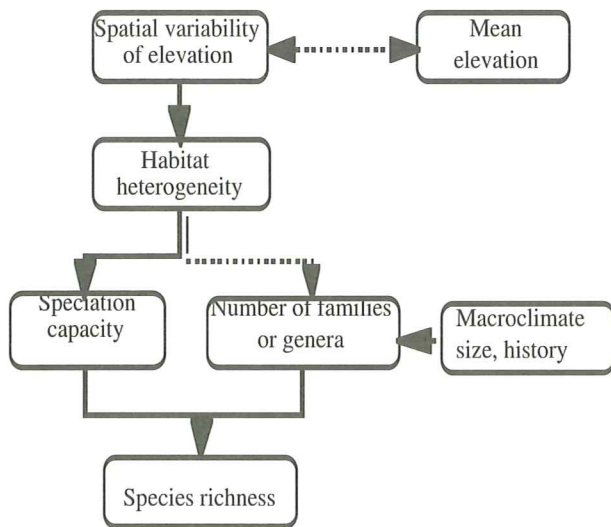
Figure 7. Diagram of topographic effect on plant diversity in California

evation contributes to and is closely correlated with the habitat heterogeneity. On the other hand, high habitat heterogeneity is a cause for high speciation capacity. Habitat heterogeneity may also enhance the richness at higher taxonomic levels, but the effect is limited when compared to its effect on speciation capacity (shown in Figure 7 with a dotted line). The species richness is the result of both speciation capacity and the richness in higher taxonomic levels. We speculate that the number of families is primarily determined by factors such as climate at large-spatial scales, the size of the sampling polygons, and the evolution history of the flora in the region. Elevation variability plays only a minor role in affecting family numbers.

Using this integrated framework, and considering that elevation mean is positively correlated with standard deviation, we can explain the positive, but much weaker, correlation of species richness with elevation mean. This framework also explains the conflicting results of the species-elevation relationship reported in previous studies and between this study and previous studies. If the effect of elevation is a consequence of more fundamental processes, such as the effect of habitat heterogeneity on speciation capacity, the shape of the species richness- elevation curve depends both on how elevation mean is related to habitat heterogeneity and on how speciation capacity is affected by habitat heterogeneity. This elevation curve can monotonically increase (this study), decrease (Kikkawa and Williams 1971, Terborgh 1977), or be modal (Whittaker and Niering 1975).

In summary, our results support the habitat heterogeneity hypothesis of species diversity in general. It allows us to go one step further to explore the mechanisms by which habitat heterogeneity affects species richness. The key elements in the mechanisms include the effect of habitat heterogeneity on speciation capacity, and the determination of richness of higher level taxonomy by factors that function and determine the spatial pattern at even larger spatial scales.

We used the numbers of species, genera and families in each region without correcting for the possible effect of the size differences among regions. The species-area relationship may still exist in our data, but the scattered plots of richness against area do not demonstrate such a relationship, or any other apparent pattern. This may be attributed to two factors. First, the richness-area relationship may be obscured by the effect of climate, topography, soil and other factors. Second, the size variation is insufficient to exhibit the relationship. The latter can be very significant considering that the average sizes of the subcounty regions are large as compared to the variation in size.

REFERENCES

[1] Birks, H.J.B. 1996. Staistical approaches to interpreting diversity patterns in the Norwegian mountain flora. *Ecography,* 19:332-340.

[2] Brown, J.H. 1988. Species diversity. In A.A. Myers and P.S. Giller (eds.) *Analytical Biogeography,* London: Chapman and Hall, pp.57-90.

[3] Cody, M.L. 1975. Towards a theory of continental species diversity. In M.L. Cody and J.M. Diamond (eds.) *Ecology and Evolution of Communities.* Cambridge: Harvard University Press, pp214-357.

[4] Currie, D. J. 1991. Energy and large-scale patterns of animal and plant-species richness. *The American Naturalist,* Vol.137(1):27-49.

[5] Gradstein, S.R. and Pocs, T. 1989. Bryophites. In Ecosystems of the World, Vol. 14B. *Tropical rain forest ecosystems; biogeographical and ecological studies,* ed. H. Lieth and M.J.A. Werger, pp311-325. Amsterdam: Elsevier Scientific.

[6] Gustafson, A. 1948. Polyploidy, life form and vegetative reproduction. *Hereditas,* 34:1-22.

[7] Hamilton, T.H., R.H. Barth, Jr., and I. Rubinoff 1964. The environmental control of insular variation in bird

species abundance. *Proceedings of the National Academy of Sciences of the United States.* 52:132-140.

[8] Hamilton, T.H. and I. Rubinoff 1967. Measurements of isolation for environmental predictions of insular variation in endemism or sympartry for the Darwin finches in the Galapagos Archipelago. *American Naturalist,* 100:419-424.

[9] Kikkawa, J. and E.E. Williams, (1971), Altitudinal distribution of land birds in New Guinea, *Search,* 2:64-69.

[10] Lum, K-L. 1975. *Gross patterns of vascular plant species diversity in California.* Thesis. University of California, Davis.

[11] MacArthur, R.H. and E.O. Wilson 1967. *The Theory of Island biogeography*. Princeton: Princeton University Press.

[12] May, R. M. 1986. The search for patterns in the balance of nature: advances and retreats. *Ecology.* Vol.67:1115-1126.

[13] O'Brien, E.M., R.J. Whittaker, and R. Field 1998. Climate and woody plant diversity in southern Africa: relationships at species, genus and family levels. *Ecography,* 21:495-509.

[14] Preston, F.W. 1962. The canonical distribution of commonness and rarity: Part I. *Ecology,* 43:185-215; Part II. Ibid 43:410-432.

[15] Richerson, P.J. and K-L. Lum 1980. Patterns of plant species diversity in California: Relation to weather and topography. *American Naturalist*, 116:504-536.

[16] Rosenzweig, M.L. 1997. Species Diversity in Space and Time. Cambridge, UK: Cambridge University Press.

[17] Terborgh, J. 1977. Bird species diversity on a Andean elevational gradient. *Ecology,* 58:1007-1019.

[18] Watson, G. 1964, *Ecology and evolution of passerine birds on the islands of the Aegean Sea*. Ph.D. Thesis, Department of Biology, Yale University.

[19] Whittaker, R.H. and W.A. Niering 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. *Ecology,* 56:771-790.

[20] Williams, M. 1988. Relationship of species number to area, distance and other variables. In AA.Myers and P.S. Giller (eds.) *Analytical Biogeography*, London: Chapman and Hall, pp.91-148.