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BULLETIN OF THE TORREY BOTANICAL CLUB
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Diversity patterns in forest vegetation of the Wenatchee Mountains, Washington[1]

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DEL MORAL, R. (Dept. Botany, Univ. Washington, Seattle, 98195). Diversity patterns in forest vegetation of the Wenatchee Mountains, Washington. Bull. Torrey Bot. Club 99: 57–64. 1972.—Patterns of species richness, dominance and Brillouin diversity are described for mature forests on serpentine and nonserpentine soils. Where continuous forest canopies can develop, increased dominance and reduced habitat heterogeneity result in lower diversity. Where conditions prevent a continuous canopy from developing, dominance is less pronounced and the habitat is more heterogeneous leading to increased diversity. Within either a continuous or an open forest, increased environmental rigor reduces diversity. A model is presented which details the interactions among rigor, competition, dominance, and habitat heterogeneity.

The subject of species diversity has spawned innumerable hypotheses, models, and conjectures concerning the causes of and factors influencing this aspect of community structure. There are few data with which to test or develop hypotheses concerning plant species diversity (cf. Monk 1967, Auclair and Goff 1971). How species diversity is regulated is a question that derives from a desire to understand community structure and process more clearly. In this paper I will report the results of my descriptions of vascular plant species diversity and use these data to develop a model regarding its regulation within land plant communities.

Species diversity may be controlled by any of several factors acting singly or in combination. Pianka (1966) discusses six hypotheses which might account for latitudinal diversity gradients, and several papers on the subject of diversity regulation appear in Woodwell and Smith (1969). Hypotheses based on habitat heterogeneity, environmental rigor, and competition may be most relevant to understanding patterns of diversity within a small region. Ecological or evolutionary time, predation, and productivity are thought to bear less directly on this problem in terrestrial communities. Time is probably an important variable in dealing with differences between regions but of no great significance in the current study. A major purpose of this paper is to investigate the effect on diversity of gradients of moisture and temperature, habitat heterogeneity, and competition in plant communities.

Auclair and Goff (1971) cite twelve common diversity indices ranging from simple richness to slope (equitability vs. dominance) measures such as the Shannon-Wiener and Simpson indices. I have chosen to investigate the behavior of richness and two equitability measures. The Brillouin (1956) equitability index (H) derives from information theory and is influenced both by the number of species and their relative abundance. It was chosen in preference to the Shannon-Wiener function (H') because, unlike the latter, it is interpreted as a property of the sample rather than as an estimate of a property of a population from which a random sample has been obtained (Pielou 1966). The Simpson index (C) was chosen as an additional equitability or "evenness" statistic. This index measures the concentration of dominance and is not strongly affected by richness.

The Wenatchee Mountains form a south-east trending spur of the Washington Cascades (latitude 47° 25′ N). Geologically complex, these rugged mountains are clothed with a distinctive pattern of vegetation intensified by the mosaic of different edaphic types. Kruckeberg (1969) described the general features of the vegetation, and a detailed gradient analysis of

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the vegetation upon which this study is based is in preparation (del Moral, unpubl.).

Methods. SAMPLING AND CLASSIFICATION. I sampled the vegetation of the Teanaway River drainage and some surrounding slopes during the summers of 1969 and 1970 by direct gradient analysis (Whittaker 1967). Parent materials in this region are diverse but fall into two major types. Peridotite and serpentinite are ultramafic soils of low fertility which support structurally depauperate vegetation. Vegetation samples from both of these parent materials have been pooled and are considered to come from *serpentine* (S) soils. Sandstone, quartz diorite, and greenstone produce predominantly acidic soils which are more fertile than those from ultramafic materials. Samples from acidic parent materials will be considered to be from nonserpentine (NS) soils.

I sampled over 75 0.1 ha plots on serpentine soils between 1190 and 1770 m above sea level and over 125 0.1 ha plots on nonserpentine soils between 850 and 1770 m such that each plot was vegetationally homogeneous and mature, with no evidence of recent disturbance. For each sample, density, basal area, and intercept cover were determined for trees and shrubs, and frequency and cover for herbs in 25 1-m^2 plots. The plots were placed in the landscape pattern to sample representative combinations of solar exposure and elevation.

Thirty stands, representing the range of vegetational variation in each 200-m elevation band, were grouped following procedures outlined by Whittaker (1960). Each stand was assigned a moisture index value on the basis of exposure and topography (cf. Whittaker, 1967) and the stands grouped according to this index. The modal index value for each species was determined from which a weighted moisture index was calculated for herbs and trees separately. Stands for which the two indices did not agree were discarded. This procedure resulted in an ordination of stands called a weighted moisture transect which was divided into five classes, designated A (mesic) to E (xeric) with five stands per class.

On NS soil there are five bands, designated band 1 (low elevation) to band 5 (high elevation), while on S soil there are three bands, designated bands 3 to band 5. A series of seven continuous-recording thermographs operating from May to October, 1971 confirmed that mean temperatures declined with elevation and that the time between spring thaw and fall snows declined regularly with elevation.

DIVERSITY CALCULATIONS. The clusters of five stands yield pooled diversity (H_p) values. These stands treated individually and then averaged yield mean diversity ($\bar{H}$) values.

Calculations are based on cover values obtained from a 50-m intercept for trees and arborescent shrubs and from the average cover in 25 1-m quadrats for small shrubs, forbs and graminoids. I calculated the Brillouin index,

$$H = \frac{1}{N} \log_2 \frac{N!}{n_1!\, n_2! \ldots n_s!},$$

with N the total leaf cover and n the cover of each of s species for each of the 200 stands. The table of Lloyd *et al.* (1968) was used for calculating H.

Whittaker (1965) distinguishes among several richness attributes. The number of species within a habitat is alpha (α), while beta (β) measures the rate at which species are replaced along some particular gradient. Whereas α expresses niche differentiation, and β expresses habitat differentiation, they tend to vary together (Whittaker 1960).

I calculated β as if it were a half-change value analogous to radioactive decay rates. The formula is:

$$\beta = \frac{\log_{10} a - \log_{10} z}{\log_{10} 2}$$

where a is the mean coefficient of community [$CC = Sab/(Sa + Sb - Sab)$ where Sa and Sb are the number of species in samples a and b, and Sab is the number of species common to both] between samples adjacent on a transect, and z is the similarity of samples from the extremes calculated as if the rate at which similarity declines were uniform for the transect (Whittaker 1960).

For each group of five samples, I also calculated $\bar{H}$ (mean diversity) and H_p (pooled diversity). These values give a better interpretation of the general patterns of diversity and form the basis of the discussion.

Simpson's index, $C = \sum_{i=1}^{s} (ni/N)^2$, where

C is the concentration of dominance, and other notations are as above, was calculated from cover data. This aspect of equitability aids in the interpretation of diversity patterns.

CANOPY DOMINANCE. The use of individual cover estimates makes it possible to estimate the degree of shading by trees and shrubs. This method counts overlaps twice, though usually only a single species was responsible for cover. I assume that the percent canopy determines light interception and thus below ground biomass, which approximates the intensity of soil resource utilization. By determining the effects of changing degrees of canopy dominance on diversity, the effects of competition on diversity may be suggested.

GROWTH-FORM SPECTRA. Shifts in the growth-form composition along various gradients were investigated to ascertain how one aspect of physical structure changed with diversity. I distinguished four growth-forms: trees, shrubs, forbs, and graminoids. Because they behave somewhat differently, the shrubs were subdivided into arborescent shrubs and low shrubs.

Results and discussion. DESCRIPTION OF VEGETATION BANDS. The vegetation on nonserpentine soils is divided into five elevation bands, the lowest occurring at the limits of undisturbed vegetation at around 1200 m and the highest having an upper boundary near timberline. Band 1 is dominated by *Abies grandis, Achlys triphylla,* and *Rubus parviflorus* in the mesic sites and *Pseudotsuga menziesii, Ceanothus velutinus,* and *Carex geyeri* in the xeric sites. (Nomenclature follows that of Hitchcock, et al. 1955, 1959, 1961, 1964, and 1969.) Band 2 dominants include *Abies grandis, Pachistima myrsinites,* and *Vaccinium membranaceum* in mesic sites and vegetation similar to band 1 in xeric sites. Band 3 dominants include *Abies lasiocarpa, V. membranaceum,* and *Clintonia uniflora* in the mesic sites and *A. grandis, Arctostaphylos nevadensis,* and *Pachistima* in the xeric sites. In band 4, dominants include *Abies amabilis, Rubus lasiococcus,* and *Rhododendron albiflorum* in mesic sites and *Pseudotsuga, Pteridium aquilinum,* and *Pachistima* in xeric sites. In band 5, dominants include *A. amabilis, Rhododendron,* and *V. membranaceum* in mesic sites and *A. lasiocarpa, Ceanothus,* and *Arctostaphylos* in the xeric sites.

Serpentine vegetation was divided into three bands with the lower boundary determined by the limits of serpentine in the study area and the upper boundary reflecting the local tree line. Band 3 is dominated by *A. lasiocarpa, Rhododendron,* and *V. membranaceum* in mesic sites and *Pseudotsuga, Agropyron spicatum,* and *Arctostaphylos* in the xeric sites. Dominants in Band 4 are similar to band 3. Band 5 dominants include *A. lasiocarpa, Rhododendron, Dodecatheon jeffreyi,* and *V. membranaceum* in mesic sites and *Pinus albicaulis, Agropyron, Anenome drummondii,* and *Arctostaphylos* in the xeric sites. A more complete description of this vegetation is in preparation.

GRADIENTS OF ALPHA DIVERSITY. Values of alpha diversity are summarized for pooled vegetation samples on the two soil types (Table 1). The mean number of species per stand (S_s), the total number of species in the group (S_g), the mean Brillouin index of the group ($\bar{H}$), and the pooled Brillouin index (H_p) are shown for each group.

The following general trends can be seen (Table 1). Maximum richness, S_s, on nonserpentine soils occurs on the wettest sites, except at low elevation where very rich meadow communities are absent. In the more mesic types, maximum S_s occurs at mid-elevation but shifts to low-elevation in the drier types. These trends suggest that decreasing available moisture limits richness. Reduced richness with increased elevation suggests that a shorter growing season is also a factor regulating diversity and is an aspect of climatic rigor. On serpentine soils S_s increases with elevation at both the wet and at the xeric ends of the spectrum, but not in mesic sites. On both wet and dry serpentine sites tree cover decreases with elevation which seems to permit more total species.

It can be seen that H_p declines with increasing aridity on both soil types. On nonserpentine soils H_p peaks in band 2 and then declines with elevation. On serpentine, H_p is generally highest at high elevation, although moisture class B is an exception. I infer that because tree dominance on serpentine in the drier and wettest portions of the moisture gradient declines with ele-

Table 1. Diversity (richness [S values] and evenness [H values] of the vegetation from most mesic (A) to most xeric (E).

Elevation band (meters)	Moisture class A				B				C				D				E			
	S_s[1]	S_g[2]	$\bar{H}$[3]	H_p[4]	S_s	S_g	$\bar{H}$	H_p	S_s	S_g	$\bar{H}$	H_p	S_s	S_g	$\bar{H}$	H_p	S_s	S_g	$\bar{H}$	H_p
Nonserpentine soils																				
850–1040	29.8	72	2.39	3.54	28.0	57	2.08	4.82	27.2	50	2.24	4.55	30.4	45	2.44	4.98	28.0	52	2.26	3.24
1040–1190	35.6	72	2.88	4.44	35.4	79	2.41	5.58	28.5	52	2.03	5.09	29.0	62	2.78	5.19	24.8	50	2.65	3.68
1190–1370	39.6	84	2.76	4.66	29.0	61	2.44	4.05	26.6	46	2.10	2.74	21.8	54	2.39	3.57	23.6	51	2.12	3.21
1370–1550	35.2	77	3.32	4.85	25.0	62	2.58	4.05	25.2	56	2.88	3.67	29.6	55	2.23	2.28	21.2	40	1.74	2.86
1550–1770	27.8	66	2.85	3.81	17.4	33	1.72	2.89	14.4	33	1.88	2.51	16.6	37	1.95	3.27	20.8	41	2.74	3.30
All	33.6		2.84	4.26	27.0		2.25	4.29	24.3		2.22	3.52	25.5		2.36	3.86	23.7		2.30	3.26
Last 3 bands	34.2		2.98	4.44	23.8		2.25	3.68	22.1		2.29	2.98	22.7		2.19	3.04	21.9		2.20	3.12
Serpentine Soils																				
1190–1370	22.2	61	2.81	4.07	32.0	72	3.20	4.90	29.6	55	2.63	3.23	26.4	50	2.23	2.60	19.8	34	2.49	2.78
1370–1550	29.4	82	2.67	4.82	19.8	48	2.52	3.61	27.4	51	2.51	3.62	27.6	45	2.50	3.72	24.4	39	2.93	3.26
1550–1770	31.6	75	2.76	4.92	27.6	65	2.23	3.89	24.4	58	1.98	3.17	31.4	64	3.08	4.65	26.2	50	2.82	4.06
Column means	27.7		2.42	4.60	26.5		2.65	4.13	27.1		2.37	3.35	28.5		2.60	3.66	23.5		2.75	3.37

[1] S_s, a measure of α diversity, refers to the mean number of species per stand.

[2] S_g, a measure of α diversity, refers to the total number of species in a group.

[3] $\bar{H}$, determined using coverage data, refers to the mean of the Brillouin index.

[4] H_p is the Brillouin index pooled per group.

vation, the resultant decline in competition permits a better developed understory. In the dry serpentine sites, S_s and $\bar{H}$ also increase. These effects apparently dominate any temperature effects which are evident on nonserpentine soils. Serpentine soils are more diverse ($H_p = 3.815$) than nonserpentine soils ($H_p = 3.384$) at the same elevations. While this difference is not statistically significant ($P < .10$) it suggests a true biological difference. Higher elevation xeric serpentine sites are more diverse than xeric nonserpentine sites ($P < .05$).

The mean Brillouin index ($\bar{H}$) does not vary as much as H_p and as a consequence, trends are less evident. Nonserpentine samples in the "B", "C", and "D" moisture classes at the highest elevation are the least diverse of any in their respective class. This suggests that environmental harshness acts to limit this aspect of diversity. On serpentine there is a trend ($P < .10$) towards lower diversity in B and C and greater diversity in D and E. This suggests that where the forest canopy is uniform, a short growing season limits diversity of shrubs and herbs but that a discontinuous canopy promotes increased diversity in the lower strata. Trends in $\bar{H}$ between substrates substantiate the greater diversity on serpentine shown by the Hp values. Habitat heterogeneity is thus suggested as a regulatory factor.

Table 2. Concentration of dominance[1] for pooled samples of the vegetation in the Wenatchee Mountains along a moisture gradient from most mesic (A) to most xeric (E).

Soil material elevation (m)	Moisture class A	B	C	D	E
Nonserpentine					
850–1040	.22	.20	.19	.13	.20
1140–1190	.06	.08	.09	.13	.10
1190–1370	.06	.09	.14	.12	.16
1370–1550	.05	.08	.13	.21	.23
1550–1770	.08	.20	.22	.10	.08
Serpentine					
1190–1370	.08	.04	.19	.13	.21
1370–1550	.05	.12	.12	.12	.16
1550–1770	.06	.13	.19	.05	.08

[1] Computed from Simpson's index C using coverage data.

Simpson's index (C) was calculated for each group of stands (Table 2). Only general trends are evident. On nonserpentine, dominance decreases with elevation in most mesic sites, is high at both low elevation and high elevation but low in intermediate sites in classes B and C, and is irregular in the remaining sites. On serpentine, dominance increases in class B sites where forest canopies are fairly well developed and decreases in the driest sites where the forests are depauperate. Dominance increases with increasing soil aridity on serpentine and to some degree on nonserpentine. There is a decline of dominance on both substrates with increasing elevation.

Dominance is more pronounced on nonserpentine soil than on serpentine soil, leading to lower H. While over-all richness is slightly greater on nonserpentine soil than on serpentine, the latter soil has slightly greater richness in comparable moisture classes per given altitude. The way in which Simpson's index varies suggests that it is largely a function of canopy dominance (Table 3). Canopy dominance

Table 3. Percent tree and shrub canopy determined as the sum of individual species' intercepts. Mean for nonserpentine plots is 58.3%, for serpentine plots it is 33.8%.

Elevation band	Moisture class A	B	C	D	E
Nonserpentine					
1	67.4	68.0	62.8	53.9	74.7
2	52.5	49.0	60.6	52.1	60.6
3	37.2	49.2	68.1	60.5	56.0
4	49.5	52.4	57.7	75.8	57.1
5	36.6	69.0	82.2	52.4	53.4
Serpentine					
3	43.1	51.2	30.3	43.3	27.7
4	32.0	49.7	28.8	22.2	26.6
5	32.6	49.3	32.5	31.8	12.5

Table 4. Rate of replacement (beta diversity)[1] of species in composite transects along moisture and elevation gradients in the Wenatchee Mountains.

Moisture-gradient beta diversity:

Soil type	Elevation band Low 1	2	3	4	High 5
Nonserpentine	1.21	1.19	1.04	1.50	2.13
Serpentine	—	—	1.50	1.84	1.01

Elevation-gradient beta diversity:

	Moisture class Mesic A	B	C	D	Xeric E
Nonserpentine	1.34	2.38	1.81	1.37	1.25
Serpentine[2]	0.65	0.45	1.5	1.22	2.00

[1] Computed using density data; units are the number of times 50% of the species are replaced.

[2] Serpentine elevational gradient is only 0.5 that of nonserpentine soils. If this rate of replacement were extrapolated over a similar range, values would be approximately double.

is more pronounced on nonserpentine than on serpentine. It tends to decrease with elevation both on dry sites and very wet sites, and, on serpentine, often declines with drought at any given elevation.

BETA DIVERSITY. Patterns of β diversity are reported in Table 4. On nonserpentine soil, β increases with increasing elevation. This is interpreted as resulting from a response to a more open forest. On serpentine β increases between band 3 and 4, but declines sharply in band 5. This results because microsites in band 5 are not as distinctly differentiated as those at lower elevations, all sites being relatively xeric except wet meadows. Many xerophytic species occurring throughout the coenocline in band 5 are more restricted to band 4. For example, in band 4 *Juniperus communis, Arctostaphylos nevadensis,* and *Agropyron spicatum* are confined to the xeric portion of the gradient while in band 5 they occur throughout. The pattern of β diversity appears to be influenced largely by changes in tree and shrub canopy and thus ultimately by environmental rigor.

Table 5. Growth-form spectra of the flora in various coenoclines in the Wenatchee Mountains.

Parent material	Trees	Arborescent shrubs	Small shrubs	Forbs	Graminoids	Deciduous index[2]
Nonserpentine (174)[1]	13	15	15	120	11	53.5
Serpentine (145)	11	10	14	100	10	53.5
N.S. (3 bands) (152)	13	11	12	106	10	47.2
Elevation transect						
Nonserpentine						
Low (108)	12	11	7	71	7	56.7
(127)	13	15	11	82	6	59.0
Middle (107)	13	11	9	68	6	51.5
(120)	9	10	11	82	8	50.0
High (100)	9	8	11	67	5	50.0
Serpentine						
Middle (123)	10	10	13	84	6	45.5
(114)	10	5	9	82	8	29.2
High (119)	8	4	11	88	8	30.0
Moisture						
Nonserpentine						
Wet (A) (146)	13	14	12	99	8	53.8
(B) (113)	12	11	12	73	5	51.4
(C) (95)	11	12	10	56	6	51.5
(D) (95)	11	11	10	56	7	50.0
Dry (E) (85)	8	10	8	52	7	50.0
Moisture						
Serpentine						
Wet (A) (116)	10	6	11	80	9	18.5
(B) (108)	10	10	13	69	6	37.8
(C) (90)	9	3	10	60	8	22.7
(D) (91)	9	6	8	62	6	34.8
Dry (E) (67)	8	2	5	46	6	20.0

[1] Numbers in parentheses refer to the total number of species present per group.
[2] Percent of all trees and shrubs that are deciduous species.

Within a moisture class a regular pattern of β diversity occurs along a gradient of decreasing temperature on nonserpentine soil. In the wettest site β is low. Species here respond largely to high moisture levels, a condition that does not change dramatically with elevation. In class B communities, β is high, and then declines as conditions become more xeric. Where β is high, forest structure changes considerably with elevation. Under such conditions, both temperature and moisture conditions are changing with elevation at a specific relative position on the moisture gradient.

On serpentine the elevation gradient is not extensive and to compare serpentine and nonserpentine coenoclines, values for the former must be doubled. Values for β are highest in the driest and lowest in class B sites. This reflects minimal structural changes with elevation in the mesic sites, while the driest sites change from tree vegetation that is merely depauperate to a truly desolate condition.

These values for β in moisture gradients are low compared to those of Whittaker (1960) in the Siskiyou Mountains. This may reflect the effects of glaciation in these mountains compared to the more southernly unglaciated surfaces. Time is required for recolonization, soil maturation, and habitat differentiation. These low values suggest that time itself is one factor in explaining diversity differences between regions (cf. Sanders 1969, Whittaker 1969).

GROWTH-FORMS AND TRANSECT RICHNESS. Growth-form spectra and transect richness are important aspects of community structure (Table 5). The percentage of the trees and shrubs that are deciduous is shown for each group. Deciduous trees and shrubs tend to be restricted to fewer elevation bands; although they represent about 50% of the total tree and shrub flora, at a given elevation they may constitute a considerably smaller fraction.

A number of trends is evident. While 174 species were encountered on nonserpentine soils and 145 on serpentine, there are 152 species on nonserpentine soils at the same elevation as the serpentine samples, and richness does not differ greatly between the two substrates. The distribution of species among growth-forms is similar, but on nonserpentine soil the tree and shrub classes contain more deciduous species. No evergreen coniferous species found on nonserpentine soils avoids serpentine, although some, such as *Abies grandis,* are rare.

On nonserpentine soil the number of trees and large shrubs declines with elevation and the number of deciduous species is reduced from 23 to 14. This suggests that shorter growing seasons favor herbaceous plants over woody plants and the evergreen habit in the latter. On serpentine, arborescent shrubs show a pronounced decline with elevation. Forbs are more numerous on serpentine than off, and overall richness in bands 3 and 5 is greater on serpentine. Increasing forb richness with elevation is a predictable consequence of decreasing canopy dominance, if competition for light is a significant factor in diversity.

On both soils increasingly xeric habitats result in declining richness in all groups except graminoids. The proportion of deciduous species on serpentine is lowest at the moisture extremes and is very much lower than on nonserpentine soil. These trends suggest that environmental rigor regulates species richness and that drought is an important influence.

Conclusions. Diversity changes described here are controlled primarily by the degree of environmental rigor which in turn controls the development of trees and shrubs. Trees and shrubs are capable of preempting incoming light and they therefore exert significant control on the structure of the remainder of the community. The demarcation between ''harsh'' and ''mild'' climates is determined by the minimum mildness needed to support a closed tree canopy.

In a rigorous environment, productivity is low and biomass reduced. The reduction of tree biomass leads to open communities and permits forbs and grasses to contribute more to the overall biomass. This results in greater evenness. In such a community, there is considerable habitat heterogeneity generated by patterns of light and shade, zones of root occupation, and levels of competitive intensity. This heterogeneity provides microsites in which less prominent plants may survive. Thus the richness component is also enhanced. At the same time within a harsh environment, increased harshness selects for increasingly generalized species (Levins 1968) which accompanies decreasing diversity.

In a mild environment, conditions permit the development of forests with considerable biomass. In these closed communities, taller species preempt a large proportion of the available light which results in strong dominance and is reflected in a lowering of the evenness component of diversity. If the canopy is closed, sunflecks will be minimal and the rooting volume will be better filled. Under such conditions, micro-habitat heterogeneity will be minimized, and richness will be low. Countering this trend is the ability of more specialized species to occur in an increasingly mild environment (Levins 1968).

This model predicts that diversity is maximized at that degree of harshness which prevents a closed canopy but is sufficiently mild to permit considerable specialization. Overall diversity will be high in very mild environments (NS, class B, low elevation). Diversity will decline as rigor increases until the forest canopy no longer remains intact (NS, class C and D, mid-elevations). Diversity jumps as harshness increases and stands become open (NS, class C and D, low elevation; S, class B, low elevation). As harshness continues to increase, diversity once again declines (NS, class E, low elevations; S, class D and E, low elevation).

This model predicts that fewer species can be sustained in habitats rendered homogeneous by their physical or biotic structural features than in habitats that are more heterogeneous. In the former there is a greater probability of competitive exclusion than in the latter. Recent successional studies in forests indicate that diversity declines as a result of the closing of the canopy (Auclair and Goff 1971). This result supports the above prediction.

The model does not consider what factors govern the absolute number of species in a particular region. Rather, it deals with relative changes within a region. Other mechanisms which may influence the absolute number of species available, such as differences in ecological or evolutionary time, predator intensity, or productivity, do not seem to be involved with the local scale pattern of diversity. These mechanisms may be involved in setting absolute limits to diversity.

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