LIFE ZONES, MODERN ECOLOGY, AND THE FAILURE OF TEMPERATURE SUMMING*

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INTRODUCTION

There is a large degree of confusion as to the relations of life zones as originally described by Merriam, and the plant-animal communities recognized in modern ecology. There are two points of view in the study of distribution: (1) the faunistic-floristic view which bases its principal regions on genera, is purely qualitative and aims at the discovery of facts bearing upon evolution and migration as considered in this field; (2) the ecological point of view which bases its communities (regions) upon species and varieties, is purely quantitative, evaluating all important organisms on the basis of quantity and individual potency, and aims at the discovery of facts bearing on dynamic life relations of all kinds—fluctuations in abundance, competition, invasion, succession, etc. In order to compare this viewpoint with that of Merriam and his followers, it is necessary to go back to the initial thesis of Merriam (1891) and trace its later developments.

FUNDAMENTAL BASIS OF MERRIAM'S WORK

Merriam began his work as strictly a faunistic study. His remarks in his original presentation of his subject were directed mainly as a criticism of Wallace (*Geographical Distribution of Animals*, 1876), whose distribution of regions is shown in figure 29. Zoogeographical regions as worked out by Wallace and many others are based upon genera or families, no consideration being taken of the abundance, habitats, or habitat relations of the animals. The aim was to clarify (historical) evolution, migration, and barriers. Merriam set out to prove that Wallace's mapping is incorrect, constructing a table given below (Fig. 30).

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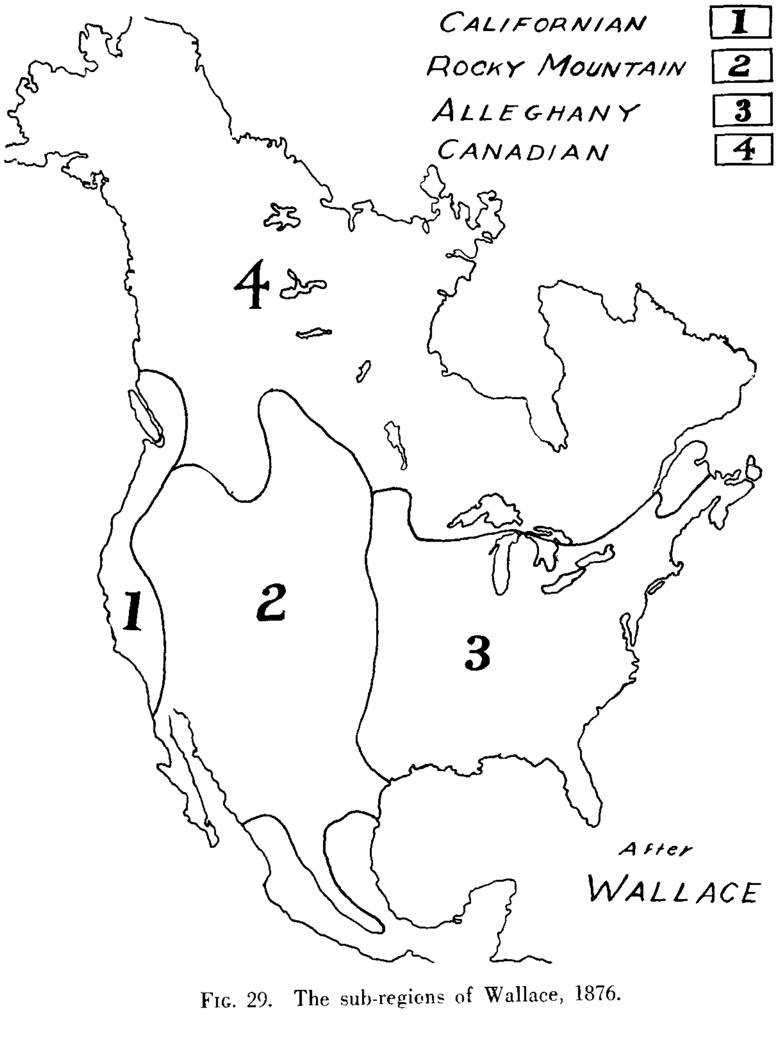

FIG. 29. The sub-regions of Wallace, 1876.

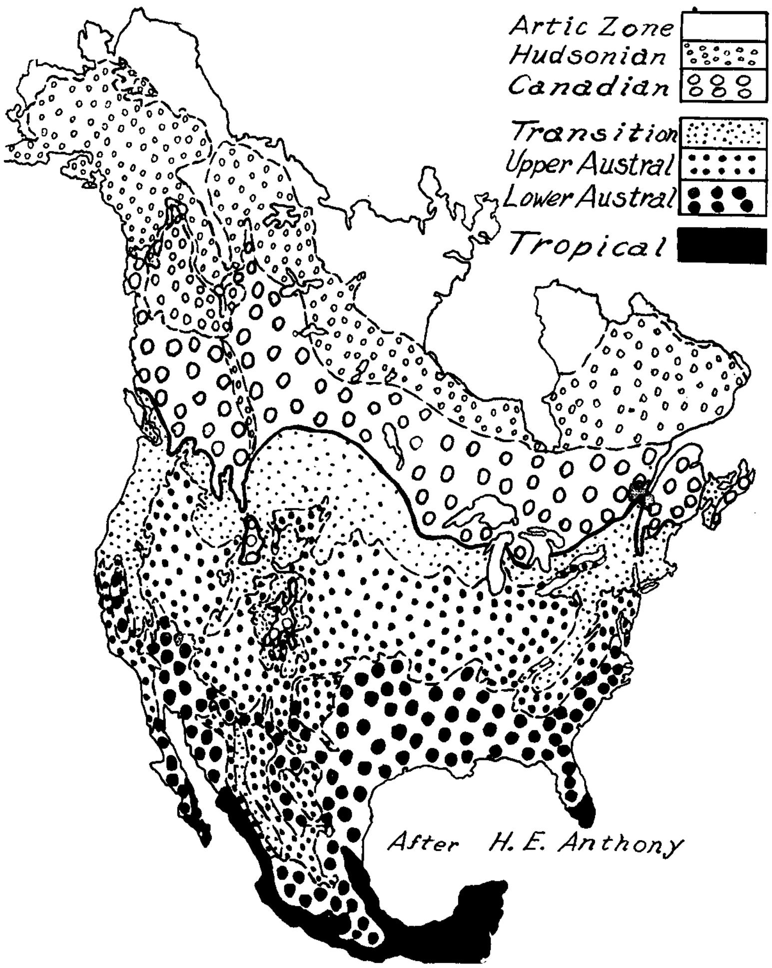

FIG. 30. Merriam's Life Zones, after Anthony.

TABLE I.

Generic Basis of Zones.

	Mammals Families	Mammals Genera	Birds Families	Birds Genera	Total Families	Total Genera
Arid Sonoran distinguished from humid Sonoran by........	1	10	0	24	1	34
Humid Sonoran distinguished from arid Sonoran by..........	1	4	0	7	1	11
Common to both arid and humid Sonoran	13	27	12	31	25	58
Sonoran as a whole distinguished from Boreal by........	8	41	10	100	18	141
Boreal as a whole distinguished from Sonoran by......	6	30	3	40	9	70
Common to Boreal and Sonoran	8	8	....	18	....	26

In this table Merriam showed that more genera are different from north to south than from east to west. The comparison is made between his Boreal and his Sonoran regions for the north and south difference and between the arid and humid portions of the Sonoran for the east and west difference. This agrees with Wallace in one feature of the latter's classification, but disputes his division into Californian, Rocky Mountain, and Alleghanian areas, as shown in Wallace's map (Fig. 29). In other words he practically called Wallace's 1, 2, and 3 (Fig. 30) *Sonoran* and Wallace's Canadian, *Boreal.* He then used these conclusions to disprove the subdivision into Californian, Rocky Mountain, and Alleghanian sections, but presented no table to establish his three transcontinental divisions, namely the Transition, upper Sonoran (or Austral) and lower Sonoran (or Austral). He contended, however, that within the Sonoran zone there are more generic differences from north to south than from east to west. In other words genera, which are the basis of the first subdivision of the large zoogeographical regions, range cross-wise of the North American continent.

RELATIONS TO PHYSICAL FACTORS

1. Merriam's view and method. He had noted correlations between isotherms and distribution limits of birds and mammals, and contended that their limits coincide with certain temperature phenomena, particularly the total temperature above 6° Centigrade (approximately 43° F.). He insisted that temperature is the most important limiting factor, though no experiments were performed and no inquiries as to the method of its operation were undertaken. His sums of temperatures were calculated by the Weather Bureau. Through some error, those given him for publication were not calculated above 6° C. but above zero Centigrade, with all days in which the mean did not reach 6° C., *omitted.* A note was published in *Science* calling at-

tention to this error (Merriam '99), but the new totals were never substituted. The sums published are, therefore, unlike those compiled elsewhere.

This assumption of the sum of temperatures had received considerable attention in the few decades preceding the announcement of the Life Zone idea. Merriam, however, merely took the relation for granted

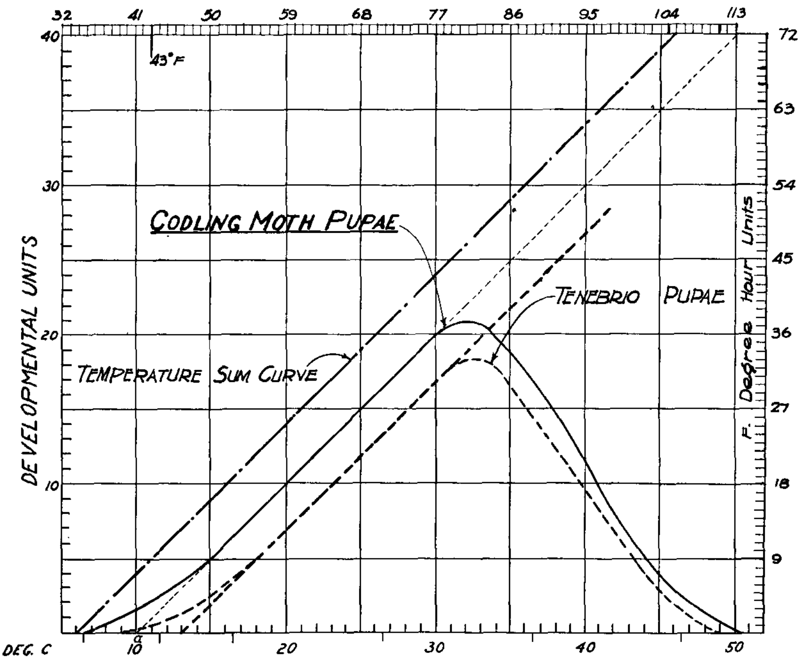

FIG. 31. Developmental curves: The dash-dot straight line is the rate of development curve assumed in summing temperature above 6° C. Compare with the curves of rate of development at different temperaturs for the pupae of the codling moth and the meal worm (*Tenebrio*) at the right. In connection with these two curves for insect pupae, an extension of the straight line portion is shown to indicate the failure of temperature summing. It will be noted that the straight line indicates a starting point marked *a* which is several degrees above the actual threshold, being at 10° for the codling moth and at 13° for the meal worm, while the actual threshold is three or four degrees lower. The velocity figures in Table II are read off on the scale at the left for each temperature on the horizontal scale.

without experimental or direct observational work on birds or mammals or plants, such as described by Kendeigh ('32).

Formulae for estimating daily means above a base, from the maxima and minima readings have long been in use, e. g. Strachey's 1887 formula (see Shelford '29, '30), but apparently were not utilized by Merriam. It is well known that sums of temperature to be of biological significance must be based upon hourly or bihourly readings. The writer has further conducted extensive experiments showing that temperature sums are not a good index to rate of development or of other biological processes (Shelford '29), a fact originally pointed out by Krogh (1914).

2. Comparison of actual developmental rates and rates assumed in summing. The actual rates of development for the codling moth were determined in detail and checked against thousands of cases in nature. Figures 31 and 32 show the actual velocities of development as determined experimentally (codling moth, Shelford '25; meal worm,

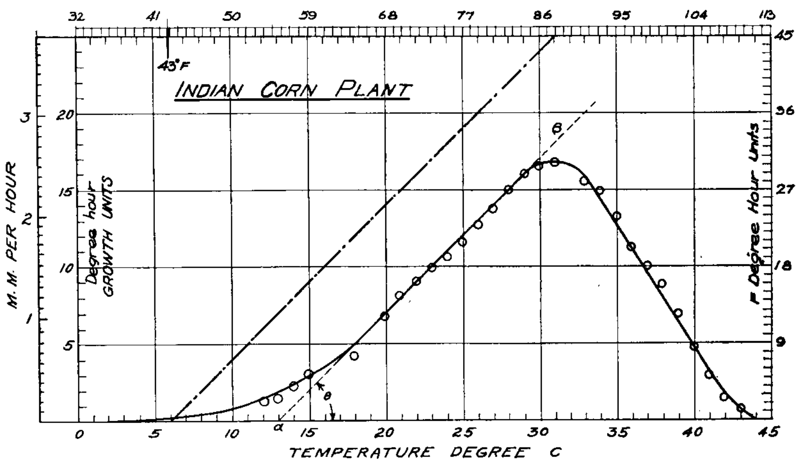

FIG. 32. The 6° summing curve in comparison with the actual rate of growth of the Indian corn plant, according to Lebenbauer (from Shelford '29).

Krogh '14, with extension to conform with the codling moth; Indian corn plant, Lebenbauer '14, and Livingston and Shreve '21). The units shown on the scale at the left equal the effect of one degree (C.) for one hour on all the curves. The straight lines (summation curves) are based on the assumption that the effect of one degree is the same at all temperatures.

The results of summing temperatures and developmental units (Table II) for two weeks, April 3-10 and August 28-September 4 (Fig. 33) are shown in Table III. In this table the sums made by the two-hour mean temperatures of figure 33 are divided by twelve to get the *degree days* and degree day developmental units of Table III.

TABLE II

Table showing the rate of development expressed as the effect of one degree for an hour (developmental units) in the straight line portions of the velocity curves in figures 31 and 32.

°C.	Meal Worm Pupa	°C.	Codling Moth Pupa	°C.	Indian Corn Plant
3	0	3	0	3	0.05
4	0	4	0	4	0.10
5	0	5	0	5	0.2
6	0	6	0	6	0.3
7	0	7	0.2	7	0.4
8	0	8	0.5	8	0.6
9	0	9	1.2	9	0.8
10	0.2	10	1.7	10	1.0
11	0.6	11	2.1	11	1.2
12	1.2	12	2.7	12	1.7
13	1.8	13	3.3	13	2.0
14	2.4	14	4.1	14	2.5
15	3.0	15	5.0	15	3.0
16	3.6	16	6.0	16	3.5
17	4.2	17	7.0	17	4.3
18	5.0	18	8.0	18	5.0
19	6.0	19	9.0	19	6.0
20	7.0	20	10.0	20	7.0
21	8.0	21	11.0	21	8.0
22	9.0	22	12.0	22	9.0
23	10.0	23	13.0	23	10.0
24	11.0	24	14.0	24	11.0
25	12.0	25	15.0	25	12.0
26	13.0	26	16.0	26	13.0
27	14.0	27	17.0	27	14.0
28	15.0	28	18.0	28	15.0
29	16.0	29	19.0	29	16.0
30	17.0	30	20.0	30	16.7
31	17.8	31	20.5	31	17.0
32	18.2	32	21.0	32	16.8
33	18.3	33	20.7	33	15.7
34	17.8	34	19.8	34	14.0
35	17.0	35	18.8	35	12.7
36	15.4	36	17.5	36	11.5
37	14.2	37	16.1	37	10.0

TABLE III

Table showing the application of the Merriam sums (sums above 0 with days at or below 6° C. omitted) of degree days, actual sums above 6° C., the progress of the meal worm pupa, of the codling moth pupa, and the growth of the Indian corn plant. Degree days may be compared with degree day developmental units in the case of the two insects.

	April 3 to April 10, 1916	July 28 to August 4, 1916
1. Sum of temperature (degree days) above 6° which are the assumed developmental units (See 3 and 4)	8.0	154.0
2. Merriam's sum	26.0	196.0
3. Degree day developmental units for the pupa of Tenebrio (See curve Fig. 31)	1.6	97.5
4. Degree day developmental units for the codling moth pupa	4.3	116.6
5. Growth of corn plant in mm.	9.7	326.5
6. Assumed growth for 6° starting point (in mm.)	28.8	554.4
7. Assumed growth under Merriam's calculations (in mm.)	93.6	705.6

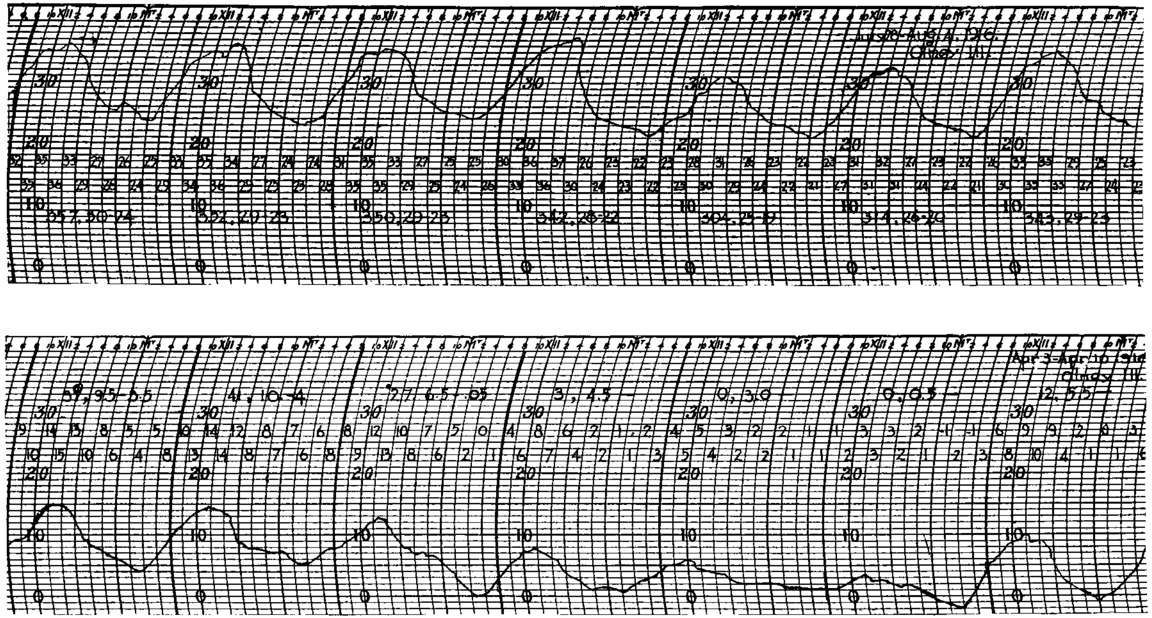

FIG. 33. A thermograph chart for a hot summer week is shown in the upper tracing of the figure. The mean temperature for each two hours is shown in the two-hour spaces. Below in the order named are the sums of two-hour means, the mean, and the mean less 6°. The lower tracing, for a cold week, shows the two-hour means, but the figures above are the sums of two-hour means less 6° for all two-hour periods in which the *mean* is more than 6°; this type of treatment is necessary in days in which there are two-hour periods with means below 6°. The mean daily temperature for this chart is derived as the mean of the maximum and minimum for the day, which is the method used in the U. S. Weather Bureau. The reader will find discrepancies between the mean temperature less 6° and the sum of two-hourly means less 6° divided by 12 to reduce to degree days. For example, on the last day the mean temperature is 5.5 but the sum of bihourly degrees is 12 and 1 degree day was accumulated though none was shown by the mean. In Merriam's accidentally erroneous summing the first three days would be included, but the last four days would not, because their means fall below 6°.

It will be seen from a study of the three rate curves that their form is radically different from the straight line assumption which rises at the same rate as the temperature rises. First the straight line type of curve does not begin until about one-fifth of the temperature range (compatible with growth) above the threshold or starting point has been covered. It then rises directly in proportion to the rise in temperature through about one-third the range compatible with life. The rate is rapidly retarded through the remainder of the life-compatible temperature range (less than one-half of the entire range). The 6° C. starting point is not far from the correct threshold temperature, but the rise in rate of growth or development does not begin to be proportional to the rise in temperature until 7° to 10° higher and ceases to be proportional at about 30° C. (86° F.). Figure 33 shows the bihourly average temperature for the week April 3-10, 1916, Olney, Illinois, and the week July 28-August 4, 1916, Olney, Illinois. For the warm week the sums of the two hourly means are shown for each day. The daily mean and daily mean above 6° C. are derived from the sum. For the cold week the sum of two hourly means *above* 6° C. are given, followed by the mean derived from the maximum and minimum and this mean less 6 degrees. There is considerable difference between this and one-twelfth the sum of two-hour means (see the fourth and seventh days).

The Tenebrio pupa requires 104 degree C. day units for completion and the codling moth 150 degree C. day units. The Merriam sum for the cold week is *fifteen* times as great as the actual progress of the Tenebrio pupa (compare items 2 and 3, Table III). Merriam's sum for the hot week is more than twice the actual progress. Comparing items 5 and 7, Merriam's assumed growth of the corn plant is nearly ten times the actual growth for the cold week and more than twice that for the hot week. The discrepancies due to the error in summing are large and those for the simple summing of temperatures are merely smaller. The sum-of-temperature assumptions are without scientific foundation and must be discarded.

3. Views of students of plants. Livingston and Shreve ('21) after a detailed analysis of climatic conditions (p. 528) in relations to plants, state: "From the preceding discussion, and from considerations presented in Part II, it appears that the system of life zones worked out by Merriam and now rather widely used in a descriptive way, especially by the United States Biological Survey, will require much modification before it may become at all satisfactory to a serious student of etiological plant geography. It is extremely unfortunate

that the actual data on which this system was originally based, and on which its applications are based in current descriptions, do not exist in the published literature. Neither Merriam nor any of his followers has thus far attempted to present the actual basis for the system in form such that a critical study of its good and bad features may be undertaken. Perhaps this may be a main reason why the whole subject of the climatic relations of floral and faunal areas has received so little attention at the hands of students who are able and willing to undertake the complex analyses which are involved in such a subject. The publication of the charts without the data on which they were based, together with the general and official adoption of the system by the United States Biological Survey, have given this important problem the appearance of having been satisfactorily solved —of being a closed subject. Those who have employed this zone system have either refrained from any discussion of its good and bad characteristics, or else they have merely taken the standpoint of advocates, and the lack of numerical data that are absolutely necessary for a critical study has tended strongly to discourage such inquiries. Also, a sort of authoritative atmosphere that seems to hang over government publications in general, together with the apparent authority and dogmatism that invariably go with well-printed (and especially colored) charts, to the exoteric reader, tend in the same direction, to retard real progress. Ecological students should realize that this is not by any means a closed subject, but that it is in a very early, formative stage, and that it requires vastly more critical and original study than has ever been accorded it."

Relations of the Zones to Communities and the Major Facts of Distribution

On his expedition to the San Francisco Mountain in 1889 Merriam discovered the altitudinal zonation of plant and animal communities in that region and named them primarily after the vegetation. He recognized the Alpine Zone, Timber-line Zone, Spruce or Hudsonian Zone, Balsam Fir or Canadian Zone, Yellow Pine Zone, Pinon Zone, and the Desert Zone.

Starting with the San Francisco Mountain and with belts that correspond to vegetation, Merriam carried his zones across the continent on the basis of his temperature theory, cutting the major communities crosswise from west to east. Lengthwise, or from north to south, on the great plains grassland area, the dominant grasses belonging to several genera are distributed throughout. These are divided into three zones. Likewise, the bison, pronghorn antelope, prairie

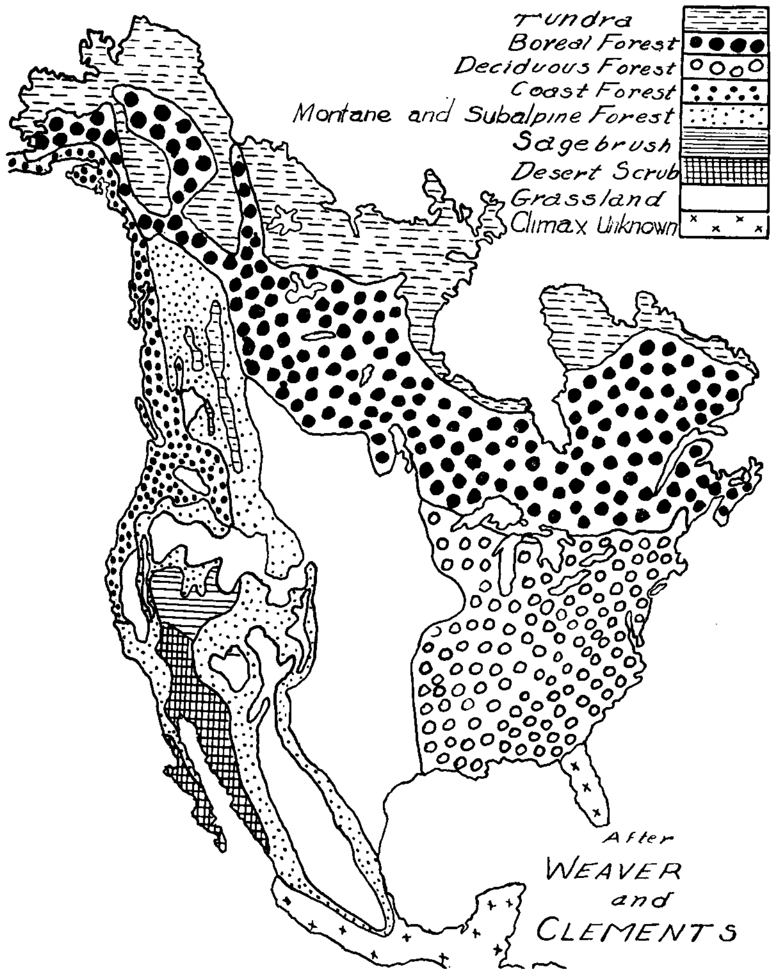

FIG. 34. Map of plant climaxes, modified from Weaver and Clement.

dog, kit fox, in fact, all the more important grassland animals, have their population divided between three zones, though constituting a part of our best known plant-animal formation (biome).

Where the great plant-animal communities are cut across by the life zones, *subclimax plants*, river margin shrubs, and *animals belonging to local conditions* have to be the main reliance as indicators. The trees and shrubs skirting the streams and animals such as the elk and grizzly bear which were found among them occasionally are used though their presence here is governed by soil and water and trees rather than climate. Again in a few cases biotically equivalent varieties of the same species may show relation to life zones. The zonal basis is, however, entirely a secondary matter. Similar violence is done the Deciduous Forest Community. The zones are quite generally out of accord with vegetation areas and natural communities over the southeastern third of North America. The Transition Zone, in particular, includes beech-maple forest, tall and short grassland, poplar parkland, chaparral, yellow pine forest, etc.

Disagreement of the major facts of distribution with the Merriam zones has been indicated by students both with taxonomic-faunistic viewpoint and with a quasi-ecological viewpoint.

Disagreement with the zones is indicated also for mollusca by Pilsbry and Ferriss ('06) in the following terms: "For the student of molluscan distribution, the life zones of the United States as mapped by Dr. Merriam emphasize the secondary and not the primary facts of distribution. The laws of temperature control, which he has developed with keen insight, do not define transcontinental zones of primary import zoologically. These zones are secondary divisions of vertical life areas of which the molluscan faunas were evolved in large part independently."

In his studies of the mammals of the Flathead Lake Region in Montana, Dice ('23B), after pointing out the correspondence of the faunas with those one to two hundred miles away, points out difficulties with life zones (p. 259) in the following terms:

"However, the correlation of these faunas with faunas of more distant regions offers greater difficulties, and little seems to be gained by trying to homologize the faunal area of the bunchgrass near Flathead Lake with the Alleghanian faunal area of the eastern United States in order to form a Transition life zone. The relationships of the lower coniferous forests near Flathead Lake to the Canadian fauna and those of the higher mountains to the Hudsonian fauna respectively of eastern North America are also somewhat remote."

Further, Dice ('23A) takes issue with the life zones in general with reference to the life zones of Alabama (Howell '21). On page 43 he states, "The life zones of Merriam are founded on the belief that there are zones of life extending transversely across the continent of North America, in the south as well as in the north. However, no species of mammal listed in this paper as characteristic of the Upper Austral Zone of Alabama is listed by Hall and Grinnell as characteristic of the corresponding zone in California." On page 47 he states, "The distribution of the species of mammals in the State of Alabama is not well shown by the life zone map presented. Only a relatively small percentage of the species known from the state agree closely in distribution with the boundaries of the life zones as mapped; and the presentation of such a life zone map gives an appearance of finality and precision to the classification of distribution which the facts do not justify.

"The recognition of transcontinental Upper Austral and Lower Austral Zones wrongly represents the faunal relationships of the parts of these zones mapped in Alabama and California respectively."

In the western mountains there is considerable agreement between the plant-animal communities and life zones. Grinnell ('14) has attempted to bring these two systems into harmony and has progressed a long way toward the modern ecological viewpoint, especially from the standpoint of biotic interaction. This would have been impracticable had he not been dealing with a mountain-dominated region, in which the life zones and biotic communities are quite generally in agreement.

As ordinarily presented in America, however, the two systems are so completely out of harmony as to viewpoint, that it is best to leave the life zones to the field of zoogeography, having for its aim the explanation of evolutionary phenomena, but with no ideas of modern community analysis or experimental work. The American life zone viewpoint has been carried so far in the United States Biological Survey that it has faced modern problems of biotic balance, relation to weather and other relations of agriculture, and grazing without suitable scientific foundation.

Modern ecology is concerned with the dynamics of communities. Their development in denuded or other new areas has occupied a large amount of attention and the final stage of this development is taken to stand out as the chief guide to such mappings as are shown in figure 31. Competition between *species*, both plant and animal, control of the habitat by organisms, fluctuations in abundance and their causes, are the chief interests of modern ecologists. Their work has essentially little relation to the mere mapping of regions based upon a record of occurrence of genera, in which abundance, dominance, or influence of species in the community are matters of no concern. Such mapping comes into the field of ecology only when a consideration of the long historical development of the aggregations of species with changes in climate is sought.

European ecologists refer from time to time to North American life zones (Elton, '27, p. 11) as ecological regions. The Russian ecologists (Kashkarov '27, Filipjev '29B, and Kashkarov and Korovin '31) use life zones which correspond to the vegetation. Filipjev has mapped what is essentially the vegetation of Eurasia as *life zones.* The secondary and purely qualitative faunistic character of the life zones recognized in North America by mammalogists and ornithologists and their lack of agreement with natural ecological regions (communities) outside the western mountains has hitherto not been made clear to them.

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