The ranges of many birds seem to conform to the outlines of the area occupied by their preferred vegetational "life form," while others occupy only parts of it and reach either their northern or their southern limits deep within it. This indicates that they are not entirely restricted in their distribution by dominant forms of vegetation. This, then, might leave room within the biotic concept for the application of something like Merriam's temperature concept, or some other modification. Thus it appears that the biome is not much more satisfactory than the life zone in describing bird distribution.

Birds which occupy the developmental stages of a biome are often found in other biomes as well. This is because the life forms of the vegetation that compose the developmental stages of one biome are often duplicated in other biomes. Birds which occupy the climax portion of a biome are most frequently restricted to that biome and are indicators of it. This is because the climax life forms are often peculiar to that one biome.

Birds appear to fit the life zone concept best in climax forest in those areas where temperature agrees with the vegetation, as, for example, in the Canadian and Hudsonian zones.

Briefly, the physical aspects, or "life form," of the vegetation seems to be the most important factor influencing land bird distribution, but this is further modified variously by climatic influences, physical barriers or other geographical factors, interspecific competition, population pressures, and probably also by other less tangible factors.

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PART 6

THE RELATIVE MERITS OF THE LIFE ZONE AND BIOME CONCEPTS

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AKNOWLEDGE of the greatest extent of the biomes, or biotic communities, is a fundamental step in making any comparison of the biome system with the life zone system. Figure 1 is a map of the principal North American biomes with the life zones superimposed. It is similar to the map by Weaver and Clements (1929: frontispiece) of which an earlier modification was published in 1932 (*Wils. Bull.*, 44: 154), but increased knowledge has made further modifications necessary.

To understand the basis for these modifications, the variations within biomes or climax areas * must be taken into account. We are

* In the legends of some maps (for example, the Weaver and Clements map mentioned here) the largest biotic communities are referred to as the "climaxes." "Climax area" would be a better term; thus the *climax area* is the area which it can be predicted will be covered by the *climax community* as shown by studies of succession.

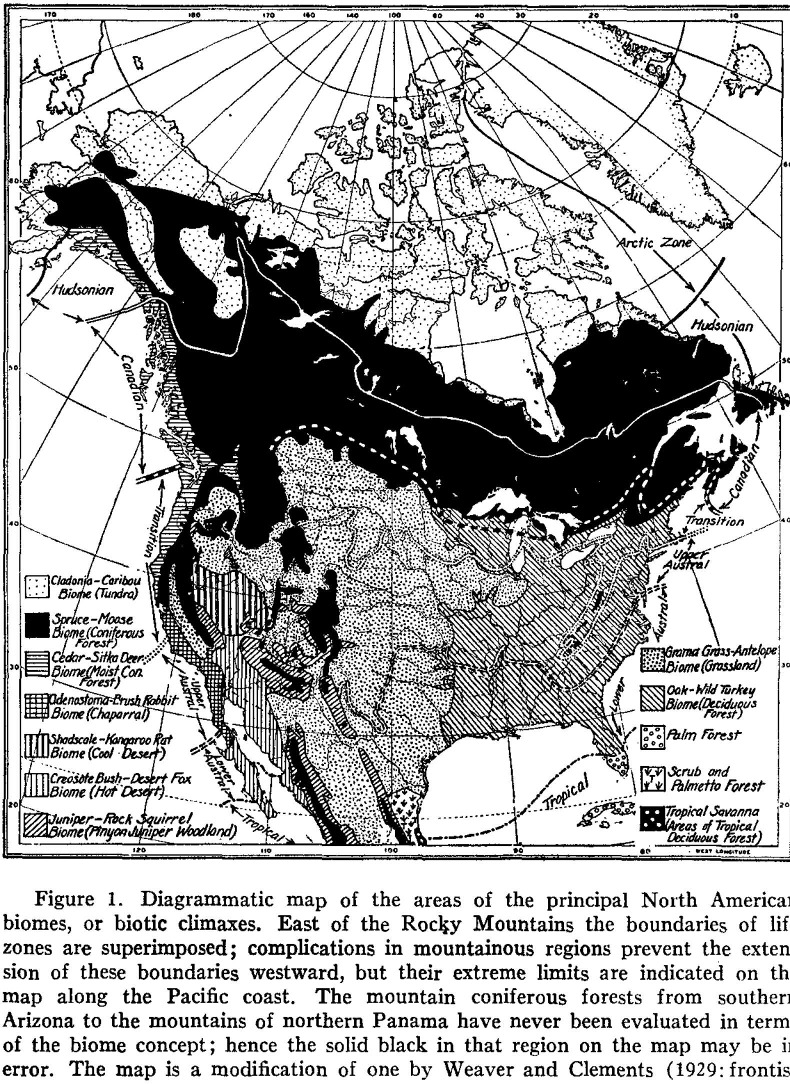

Figure 1. Diagrammatic map of the areas of the principal North American biomes, or biotic climaxes. East of the Rocky Mountains the boundaries of life zones are superimposed; complications in mountainous regions prevent the extension of these boundaries westward, but their extreme limits are indicated on the map along the Pacific coast. The mountain coniferous forests from southern Arizona to the mountains of northern Panama have never been evaluated in terms of the biome concept; hence the solid black in that region on the map may be in error. The map is a modification of one by Weaver and Clements (1929: frontispiece). The ecotones and subclimax areas shown by Pitelka (1941: figure 1) are omitted. For further explanations see text.

all familiar with the several variations of the deciduous forest climax, such as beech-maple, oak-hickory, and oak-chestnut, which are called associations or forest types. Similarly we know the meaning of tall grass, short grass, and mixed tall and short grass types of grassland, also called associations. In plant ecology, associations or types are designated by the plants of outstanding abundance in the aggregations that make up the types or associations. Some of the abundant plants of each association occur throughout the biome (binding species), while others are limited to the associations. However, usually all the most important plants of a biome are of the same "life form"; in the case of the deciduous forest, for example, they are broad-leafed trees. Important animals usually have a distribution within a biome similar to that of the plants. Modifications of the Weaver and Clements map are made necessary because of their failure (a) to include animals and (b) to give full value to life form of vegetation. It has been pointed out in the preceding papers of the symposium that life form characteristics are of great importance in the habitat preferences of birds.

In my modification of the Weaver and Clements map, the lake forest has been combined with the northern coniferous forest because there are no essential differences in the species of important animals in the two areas, and the life form is the same in both the climax and the developmental stages.

Although it could not be shown on the map, the boundary between two biomes is often very tortuous, with narrow extensions ("fingerings") of each biome penetrating the territory of the other. Often this is related to topography, the extensions of one biome being on higher ground than those of the other. A transition, or ecotone, is commonly a complex of these narrow extensions rather than a mixture on the same area of the plant and animal species characteristic of two or three biomes. This is especially true of biome boundaries in the Transition zone area and may be seen also along the boundary between the deciduous forest and grassland. The detail of such fingerings is too great to be shown except on a large-scale map. The small scale of Map 1 made it necessary to omit all ecotones as well as the mountain communities of the western and southern portions of North America. Several other areas, such as the Palm Forest, are small and have been little investigated. These have not been given biome names like those applied to the better-known communities.

In a practical way, biome and life zone systems are to be judged by the advantages or disadvantages of each when used as a guide (1) by an observer in the field; (2) in locating the boundaries of major communities; (3) in selecting indicator organisms; (4) in interpreting interactions, coactions, and reactions; (5) in interpreting community development.

1. Field observation. Since in the biome system, communities are named for the most numerous plants and animals, a student in the field can readily determine his "biological location" by the dominant and influent plants and animals (though the latter must commonly be found by special methods). The names of life zones, however, convey nothing that will help the field naturalist; he has usually to find his biological location on a life zone map. Some life zone students have characterized the zones by forest types but in limited areas only.

2. Locating the boundaries of major communities. The biome usually has quite definite limits which are observable on the basis of life forms. As noted above, a transition area is usually a complex of the narrow extensions of two or more adjoining biomes rather than a mixture of species representative of several biomes. Hence the limits of these major communities may usually be ascertained in the field and mapped to scale. There will sometimes be difficulties because of immature communities, but these can, as a rule, be distinguished by inspection of a considerable area where a series of stages converging to one community type is usually discernible. Outside the mountains, life zone boundaries follow the general trend of the isotherms (since they are based on temperature relations), and in much of the central part of the continent, the traveller cannot tell when he passes from one zone to another. It must be noted that some species are restricted to a portion of a biome on the basis of climatic differences that do not influence other species of the biome. Stevens, for example, in Part 4 of this symposium, has pointed out the limitation of the range of certain song birds to the northern great plains, which would support the idea of a Transition zone. However, the ranges of bison, antelope, and many other important species, such as dominant grasses, show no such relation to life zone boundaries, but are, in fact, cut into three parts by them. The southern boundary of the Transition zone on the great plains is based on species of less than secondary importance.

3. Selecting indicator organisms. Organisms used to indicate biomes are the plants and animals that exert an ascertainable important influence on the biotic community as a whole. They are usually abundant and obviously important so that they can be selected easily. Since they are the plants and animals of the final (climax) stage of the community, they clearly define the biome. Plants used as indicators of life zones outside of the mountains have, on the other hand, frequently been local or have belonged to relatively early developmental stages of biotic communities.

4. The biotic community viewpoint stresses interactions (coactions and reactions) of the various organisms. It carefully considers the function in the community of the population of each species, since each species contributes something to the community and has a definite effect upon it. The number of individuals per unit area is of primary importance. This interaction aspect of community dynamics was largely ignored in life zone work in earlier years, and quantitative data such as the number of animals per unit area is still rarely considered important in listing characteristic species for life zones or in mapping biotic areas.

5. Interpreting community development. The territory of a biome is the area which will be covered by the characteristic biotic climax. Within each biome's territory there are smaller areas with communities in various stages of development toward the climax. The study of

community development (succession) is one of the important features of the biome system. This development is usually ignored by life zone students and has led to confusion in the definition of zone boundaries, particularly in the southeastern United States.

Three other points of view should have brief mention, namely those of plant ecology, plant sociology, and limnology.

Plant ecologists began publication in the field of succession and distribution in terms of large communities in the early 1890's. An occasional writer took notice of animals and referred to "biotic factors," but most of the investigators have discussed plants only. To defend this position, they have relied on the dogma that all animals depend upon plants for food, shelter, and the preparation of the necessary place of abode. They have set up major communities based on plants alone; examples of these are the montane and subalpine forest and lake forests, which are not supported by animal data. The practical problems of grazing and forestry have forced them to give some attention to animals but only very recently.

Plant sociologists have presented admirable statistical methods of dealing with the details of plant populations, usually without reference to animals. A few zoologists have applied the analytic methods of the plant sociologists to animals alone. For example, Gislén (1930), working on Gullmar Fjord in Sweden, recognized more than 40 associations, whereas Peterson's map (1908) showed only 6, classified on the basis of biotic communities. Gislén fails, however, to discuss any features of community dynamics.

Limnologists have worked in great detail and with admirable precision on relatively small bodies of water. However, they have dealt mainly with internal chemical and biological changes—metabolism—rather than with the growth and distribution of communities.

But since none of these schools considers both plants and animals with their dynamic interrelationships, all fail to measure up to bioecological standards.

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