ALTITUDINAL INDICATORS AMONG THE FORMICIDAE

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As long ago as 1917, Wheeler published an account of the ants inhabiting the mountains of western North America, particularly those of the United States, and compared the fauna with that of the eastern states. It was clearly demonstrated that of the four subdivisions recognized (Pacific, Sierra-Cascade, Rocky Mountain, and Eastern) the third or Rocky Mountain area was by far the richest in total numbers and in endemic types. Of the 311 different forms then recorded, 180 are present in the Rockies, and 112 of these are endemic. The eastern fauna is a close second with 124 forms, and 75 endemic. The great abundance of different and peculiar types in the region of the cordillera may be attributed to several factors. It lies between east and west and receives numerous forms from each direction which do not pass beyond its boundaries, and usually enter it from only one or the other side. A relatively few ants are distributed from coast to coast. The mountains act both as barriers to dispersal and as producers of local habitats in which speciation has progressed a long way. Many of the Rocky Mountain ants are only subspecifically different from their relatives, but in addition there is a significant proportion of separate species.

In his treatment, however, Dr. Wheeler dealt in detail with the ants of the mountainous districts, *e.g.*, the Transition and Boreal portions, and the species of the Austral zones were not included. The present report is based to a large extent upon experiences so far encountered in Colorado, and it represents a preliminary examination of the ant fauna of the state, which, it is intended, will be expanded into a more comprehensive study. The statements are not final and may be subject to modification in the light of additional information. I am concerned here especially with the geographic distribution of ants in regard to the different mountain levels and the ecological communities correlated with altitude. Elevations range from less than 3,500 feet in the southeastern part of Colorado along the Arkansas River to some fifty peaks over 14,000 feet. This change of more than 10,000 feet in altitude insures a great variety of ecological niches with attendant differences in climate and biota, within rather short distances. All but two of the zones recognized by Merriam exist with extensive area in Colorado, the Lower Sonoran and Tropical being absent. The taxonomic and ecologic composition of the Upper Sonoran and Transition Zones of Colorado are quite variable both from north to south and from east to west, while the Boreal zones are more uniform. Yet there are general similarities among all sections of

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the Upper Sonoran, as is evident from the animals present and characteristic of it.

As for the ant populations of the state, it seems quite certain that we are dealing with three distinct regions which correspond well to major vegetational changes, but this does not preclude the possibility that further investigation will establish lesser breaks in distribution that fit the five zones based on Merriam's classification. There is already some evidence that a separate foothills or Transition assemblage can be recognized. The principal groupings which now stand out prominently are those of the basal plains, the coniferous forests, and the alpine tundra. The four units or areas thus enumerated are identical with those found to hold for birds, a widely unrelated group when compared with an insect family (Alexander 1937), and no great discrepancy is to be noted between these and the zonational units of plants. This is the more interesting when we recall that plants are the dominant organisms of, and give their names to, the ecological communities described as biomes.

Wheeler pointed out some facts concerning the biology of ants which, I believe, need to be reëmphasized. To quote from his paper of 1917 referred to earlier,

> The great importance of ants in the study of geographical distribution has not been overlooked by students of this fascinating subject. These insects are, indeed, specially fitted for the mapping of geographical areas, for several reasons. They are not, like many other groups of insects, absolutely dependent on specific food-plants, their colonies are stable and stationary entities, chained to the soil or to certain general plant associations, and they are exceedingly sensitive to climate and other environmental influences as shown by the extraordinary development of geographical races (subspecies) and varieties in practically all species of extensive range.

It is felt by some that the nuptial flight of ants, which is also a disseminating mechanism, would counteract the localizing effect of their peculiarities, and result in the wide distribution of the species. Further on Wheeler says,

> It is true that many species of ants have a very wide range, e. g. *Formica fusca*, which is circumpolar . . . , but this is, in all probability, the result of great geologic age, and while we must admit that the nuptial flight of the female ant is practically the only means of rapidly disseminating the species, it is easy to exaggerate its importance.

Others have recorded and I have observed also that winged ants from lower elevations are sometimes found dead in large numbers beneath flat stones on peaks or ridge-tops considerably higher than their colonies are normally found, and this can be attributed to the common, and in fact almost daily phenomenon, of the diurnal up-draft in mountainous regions. But several things should be noted in this connection. The ants are all winged, are dead, and are not succeeding in the establishment of new colonies. Workers of their species are not present, and nests containing live members of the worker caste are not found in the vicinity.

Unless such are located, it is impossible to state that a species has become established at a designated altitude and contributes to the fauna of the corresponding zone. It might be supposed that winged, fecundated female ants, having been transported to a dividing ridge by the convection currents of the daylight hours, might be carried downslope on the other side by the nocturnal drainage that follows, and in this way succeed in spreading the species across an otherwise effective barrier. We cannot claim dogmatically that this does not happen in individual cases, but that it should not occur often enough and in sufficient numbers to enable the ant to overcome the competitive resistance of closely related forms occupying similar niches in the new territory, seems evident from the known distribution of the species and subspecies. When to these facts is added the knowledge that the female ant is a weak flier, is in the air for a very short time out of the total annual period and for only once in her own life span, and that she seeks the earth and concealment soon after mating, it then seems unlikely that she would be subject to drift into another valley by the downdraft. It is possible that the cooling effect of higher elevations and the disappearance of light at sunset may combine to remove the ant from the sphere of air currents. The whole subject of the factors controlling the behavior of the virgin and of the fecundated female needs to be investigated experimentally, for at present we know practically nothing beyond the facts obtained through direct observation.

Despite the fact, as we see above, that the species of ants may be widely dispersed during their nuptial or colonizing flights, their permanent distribution is not necessarily altered. Though landing in many spots, the females are able to gain lasting footholds only in habitats which provide the proper conditions for survival. It may be asked what are the limiting factors. Although Merriam's terminology is freely employed, because the distribution of ants appears to coincide rather well with it, one should not assume that his explanation is either proved or adequate. Certainly, temperature must be a major contributing factor, but other factors, such as moisture relations and soils, exercise profound influences as well. We have descriptive information on the zonal distribution of ants, but to determine the causation of this geographic pattern it would be necessary to eliminate one factor after another through observational correlations and by appropriate field experiments. The determining factors for one species may be quite different for another. (Grinnell 1917).

Inasmuch as ants are all social, living in perennial colonies composed almost entirely of workers, it is necessary only to capture one specimen of this caste to show that the species inhabits a certain zone.[1] Its nest will be in the vicinity whether or not it is located. With nonsocial insects having good powers of

[1] This is true providing the species can be identified from a single specimen. As is well known to systematists, certain castes only or numerous individuals may be needed in "difficult" groups.

flight, the record of a single individual by no means demonstrates that the species belongs to the habitat in question. Of course, human agencies may occasionally transport an individual worker ant beyond its range, but this must be rare, and if one is found it will be, in all probability, the only specimen. Ants usually exist in such enormous numbers (at least all common species) that if one worker is taken, more are sure to be found in the same locality. Cosmopolitan tramp species in well-known cases have been disseminated by man, but these are outside the considerations of this discussion.

The direct effect of plants on ant distribution is negligible since their food habits, as intimated by Wheeler, are omnivorous for the great majority. The catholicity of their tastes makes it possible for them to enter various habitats independent of food requirements, and to be dispersed more with reference to the general ecological (physical and biotic) conditions. One notable exception to this rule is seen in *Myrmecocystus horti-deorum*, the honey ant of the eastern foothills, associated with the belt of scrub oaks where the workers obtain secretions from a species of oak gall as well as from aphids and coccids attached to the plants.

The presence of an ant in one zone does not mean that its occurrence is uniform and continuous over the area. A survey for each species would be a monumental task, but such information as I have been able to gather indicates interesting possibilities. One of the most prevalent factors which complicate distribution is slope exposure, a phenomenon of which botanists are especially cognizant. It is not uncommon to find at the crest of a foothills ridge a warmth-loving, southern or low altitude species with colonies near the top of the open, south-facing slope, while only ten or fifteen feet away in the dense cover of Douglas fir where the north-facing decline begins, a boreal ant will have established its nests. For example, a species of *Pheidole* was abundant in the first location, and a cold-limited *Myrmica* in the latter. Or one may discover that on the relatively level meadows of the tundra, ants are frequent on a gentle eastward slope near timber line, and (as far as could be ascertained) completely absent on a comparable slope looking westward. This was observed along Trail Ridge in Rocky Mountain National Park. In this instance, certainly, the general climate, plant cover, and food conditions are identical, yet some delicately balanced, microclimatic differences of temperature, soil moisture, humidity, etc., may be at work. Such local differences in the distribution of plants are readily observed, but in insects (and other animals) with considerable power of locomotion, striking discontinuities at first are not expected. Sunshine coming at a low angle in the early morning on the east side may be crucial as compared with the western incline where no direct warming light falls until a little later. It may be suggested also that this condition, coupled with the tendency for afternoon cloudiness in mountains, may reduce significantly the total insolation for the daily period on the western ex-

posure. If this is true, it is not consistent with the fact that the western and southern slopes in the Rockies are generally warmer and the zones somewhat elevated as compared to the eastern and northern exposures. The discrepancy outlined, however, was confined to very high altitude, *viz.*, 11,500 to 12,000 feet.

Pogonomyrmex occidentalis, the prairie harvester, is not uniformly spread over the plains. In places its colonies are numerous and distinctly spaced in a sort of territoriality, doubtless conditioned by the foraging activities of the workers, and in other localities it is absent or sparingly represented by poorly constructed mounds. This ant is most often encountered where the soil is heavy and gravelly, the nests being "stuccoed," as it were, with pebbles of approximately equal size. In the sand hill or dune areas, the harvester is an infrequent inhabitant or absent, and nowhere are there conspicuous, conical nests. It is thought that edaphic conditions, such as soil texture, are responsible, as these insects require soil of a consistency which enables them to build structures and hollow seed-storing chambers that will not collapse, especially if dried by summer heat. Food requirements might have some influence here also, since these ants use large quantities of weed and grass seeds, but they do not hesitate to consume insect flesh when it is available.

Between the basal plains and the coniferous forests, the life form of the vegetation changes from that of low herbage to the arborescent type. Along watercourses of the plains and extending into the canyons are cottonwoods, other broad-leaved trees, and shrubbery, remnants of a once more widespread deciduous forest. In southern and western Colorado the oaks are inserted between the yellow pine forests above and the pinyon-juniper woodlands or sage and grassland prairies below. In any case we have a major ecological break, with the usual and varied ecotones between the principal communities. This constitutes the lower timber line, and it occurs from 5,600 to 6,000 feet in northern Colorado, and at 6,500 to 7,800 feet in southern Colorado. An upper timber line varies from 10,900 or 11,500 feet in northern Colorado to 11,200 or 12,000 feet in the south. It happens then, that in different parts of the state the limit of tree growth varies as much as 2,200 feet at the lower levels and 1,100 feet at the higher levels. Rather detailed explanations of this are to be found in Ramaley's papers, Merriam (1890), and Cary (1911).

The ant fauna of the Upper Sonoran Zone is distinct, and rich in species having southern and tropical affinities. Whole genera and even one subfamily are almost entirely limited to it, only ascending above it for a short distance in favorable places in the foothills. Some of the species do not occur east of the Mississippi, but are confined to the high, dry plains between that river and the Rocky Mountains. The same or closely allied species and subspecies swing around the southern end of the mountain chain onto the western slope. While some eastern species

and some ubiquitous forms are to be found, the aspect of the assemblage is definitely western and also has indications of southern origins. Among the adjustments to semiarid and arid conditions, the most remarkable are the seed-gathering and seed-storing habits of *Pogonomyrmex*, and the development of a special caste, the "repletes," peculiar to the honey ants, in whose crops quantities of liquid food are stored.

The Transition Zone occupying the foothills is largely composed of the lower part of the coniferous forests, namely, the yellow or ponderosa pines, and in the south the oaks are considered part of the same zone. The pinyon-juniper might be regarded as part of the Transition, although it was classed with the Sonoran by Cary. Different groups of animals may tend to throw it with one or the other zone, and inasmuch as it has a mixture of life-forms (grassy and arborescent), it may be possible to include it with the yellow pines as a transition region (Daubenmire 1943). However, the climate of the pinyon-juniper belt is hot and dry, and the animals have a decidedly Sonoran aspect. The Transition will doubtless prove to be the richest single assemblage, because, like other ecotones, it receives species from two directions. Boreal ants from the Canadian Zone and southern ones from the Upper Sonoran are easily obtained in the foothills. Some species seem at this time to be rather definitely limited to, or are most abundant in, this zone, and as such tend to substantiate its recognition as an entity separate from the other life belts. Examples of these are the species of subterranean yellow Lasii, *Brachymyrmex heeri depilis*, and *Liometopum apiculatum luctuosum*.

In the needle-leaved forests of the mountain slopes, the fauna is very similar to that of the extensive Canadian forests far to the north and east (Gregg, 1946). There are present species of *Lasius*, *Camponotus*, and particularly *Formica*, only a very few of which are equally at home on the hot mesas and plains. The mountain forests are cool, moist, and have a relatively short growing season. These conditions become accentuated with increasing altitude and reach their most pronounced display in the spruce-fir coverage between 10 and 12,000 feet. The middle elevations are well stocked with ants, but species dwindle somewhat in the luxuriant, subalpine forests. The latter is a notable phenomenon in all cold, moist, coniferous woods, as the author has observed in northern Minnesota and Michigan, in the British Columbia Rockies, and in the exceedingly wet forests of the Canadian coast near Vancouver, as well as in the present studies of the Colorado mountains. As a group, ants are much better developed in warm and dry situations. In the Canadian and Hudsonian Zones there is a definite increase in the use of rotting logs by ants for nest construction, and the large carpenter ants are quite conspicuous owing to the accumulations of sawdust evacuated from their tunnels.

The tundra, though rich in plant life, is drastically impoverished from the standpoint of ants, both in species and in the number of colonies. The sharp

floral break is paralleled by a sharp discontinuity in the Formicidae, but unlike the profusion of highly adapted, stenothermal, cold-limited, flowering herbs which replace the trees, the ant fauna is characterized by a disappearance of nearly all the forms encountered at lower levels, even those occurring a short distance from timber line within the spruce-fir forest. Only two species, *Formica fusca gelida* and *Leptothorax acervorum canadensis*, were discovered with any regularity, and two or three others may be present. These ants are numerous in protected, well-watered pockets with good meadow soil, on the warmest slopes

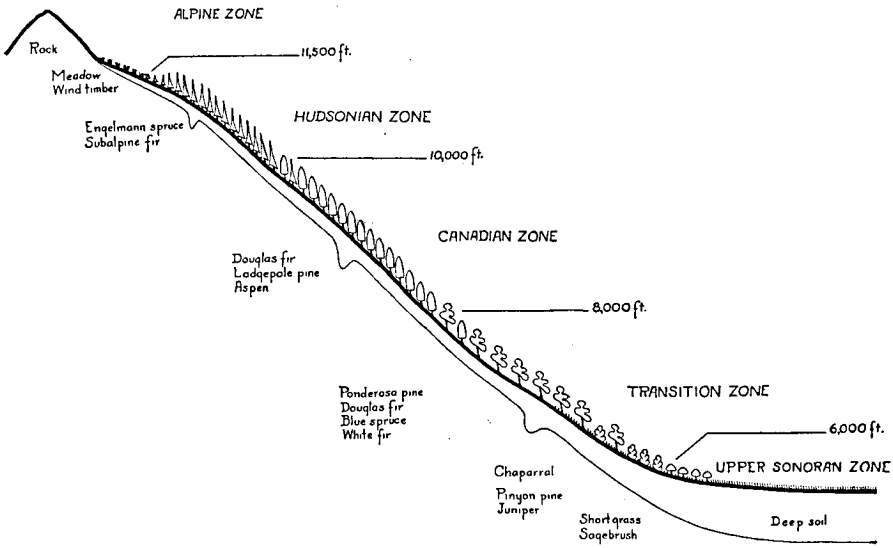

FIGURE 1. Life zones in Colorado. The elevations represent average altitudinal limits. The soil profile is indicated as increasing in depth from the higher to the lower altitudes, and the periodic notches serve to account for local soil accumulations of considerable depth in valley bottoms.

and the lowest levels of the Alpine Zone. This zone is therefore more notable for what is lacking than for what is present. Physical conditions of the tundra are not moderated by perennially aërial vegetation, and the climate becomes exceptionally severe in winter. Mute evidence of this is on every hand in the so-called "wind timber," which marks the actual tree line. The two common ant species are strictly boreal and stenothermal, but they are not characteristic of the tundra in the sense of being found there alone. Their numerous colonies range through the subalpine and montane forests wherever the local conditions provide cool, shady stations.

The following lists of ant species represent the indicators which are correlated

with the zones as recognized above. Some of these are truly stenozonal, warmth-limited, and some cold-limited, but others are euryzonal and range over several life belts. Many more species could be added to the lists if the ants from the mountainous areas of all western states, and if the rarer forms, were included. But for the present we are confined to the commoner species of Colorado. Until the precise elevational distribution of the various species and subspecies is recorded, and plotted on suitable maps, we cannot hope to have a clear understanding of the zonal distribution of all ants. Isolated occurrences, particularly of rare ants, may show that they live in a certain zone and in a special habitat of that zone, but evidence regarding their absence in other levels must be based on rather extensive data. New information is accumulating in our collections, and some of the facts presented may have to be adjusted to them.

In Figure 1, I have represented diagrammatically a profile of the Rocky Mountains in Colorado, including the biotic zones, their average altitudinal boundaries, and the principal plant constituents of each.

UPPER SONORAN ZONE (PLAINS)

Ponera opaciceps
Ponera trigona opacior
Eciton (N.) nigrescens
Pheidole pilifera coloradensis
Pheidole vinelandica
Pogonomyrmex occidentalis
Solenopsis molesta
Solenopsis molesta validiuscula
Monomorium minimum
Crematogaster lineolata cerasi
Myrmica sabuleti americana
Dorymyrmex pyramicus
Dorymyrmex pyramicus niger
Iridomyrmex pruinosus analis
Formica fusca neoclara
Formica cinerea neocinerea
Formica rufa obscuripes
Formica rufa melanotica
Formica (N.) pallidefulva succinea
Camponotus sansabeanus nitidiventris
Myrmecocystus melliger mendax
Myrmecocystus mexicanus horti-deorum

TRANSITION ZONE (FOOTHILLS)

Most of the species in the above list may be found in the lowest level of the foothills, and the present list gives only those that seem to be limited to the Transition or are most abundant there.

Aphaenogaster subterranea valida
Liometopum apiculatum luctuosum
Lasius brevicornis
Lasius flavus nearcticus
Lasius mixtus aphidicola
Lasius interjectus coloradensis
Lasius latipes
Formica rufa haemorrhoidalis
Formica rufa coloradensis
Formica rufa clivia
Formica oreas comptula
Formica dakotensis montigena
Formica ciliata
Formica sanguinea subnuda
Formica (N.) pallidefulva incerta
Polyergus rufescens breviceps
Brachymyrmex heeri depilis

CANADIAN AND HUDSONIAN ZONES (CONIFEROUS FORESTS)

Some of these species may occur in the upper limits of the Transition Zone.

Myrmica brevinodis sulcinodoides
Leptothorax acervorum canadensis
Lasius niger sitkaensis
Formica cinerea altipetens
Formica fusca subaenescens
Formica fusca gelida
Camponotus herculeanus noveboracensis
Camponotus herculeanus whymperi
Camponotus herculeanus modoc
Camponotus laevigatus

ALPINE ZONE (TUNDRA)

Leptothorax acervorum canadensis
Lasius niger sitkaensis ?
Formica fusca gelida

EURYZONAL SPECIES[2]

Lasius niger americanus
Lasius niger neoniger
Formica (P.) neogagates
Formica (P.) neogagates vetula
Formica fusca subsericea
Formica fusca argentea
Tapinoma sessile

In this report I have employed the zonal terminology of Merriam as it appears to be satisfactory for describing the distribution of many animals. For a long time after the publication of Merriam's work his views were accepted and many surveys were based upon them, but in recent years a number of criticisms have been written concerning the zonal concept, especially as it applied to the Austral Region, and a new classification, having for its central idea the plant-animal formation or biome, has been advanced to replace the zones. In a chart (Table 1), the life zones of Merriam, the local terms used by students of mountain ecology, and the plant formations which are apparently identical with biomes (see Clements and Shelford, 1939, p. 20), are equilibrated for ease in comparing one area with another remote from it. The use of plant formation here implies a biotic community and not plants alone. Regardless of taxonomic classification, the table aims to draw parallels between *ecological equivalents*. We do not hesitate to stress the strikingly similar, equivalent, or even identical adaptations of the animals inhabiting the three principal and remote rain forest areas of the globe, so it is only logical to do the same between the Canadian forests or Arctic tundras and like habitats deployed with reference to altitude.

Some of the changes suggested by the newer terminology are much needed improvements, but I believe there is danger of going too far toward the disposition of an old classification in favor of a new one on the assumption that because it emphasizes a newly recognized principle (the plant-animal community), the later system is all-sufficient and more accurate, without realizing that the earlier one included an altogether sound and different aspect of the problem.

There are two important ways of considering distribution. One is classical; the other so-called modern. The former is faunistic, taxonomic, and genetic; the latter is environmental or ecologic. The first is concerned with the origin of groups through the effects of geography on evolution, while the other is concerned with the immediate adaptations of organisms to their habitats and communities in which they live and of which they are a part, regardless of the taxonomic composition and origin of the species.

[2] These species range through three or more life belts, and there are probably numerous others whose precise distribution in Colorado is not yet sufficiently known to justify including them.

TABLE I. *A comparison of methods of classifying biotic distribution*

Ramaley's Zones	Merriam's Zones	Plant Constituents	Plant Formations (Biomes)	Daubenmire's Zones
Alpine	Arctic-alpine	*Alpine herbs Dwarf willows Dwarf birches	Tundra	Alpine tundra
Subalpine	Hudsonian	Wind timber *Engelmann spruce Subalpine fir Bristle cone pine Limber pine	Coniferous forest (taiga)	Spruce-fir
Montane	Canadian	*Engelmann spruce Subalpine fir *Lodgepole pine *Douglas fir White fir *Aspen Alder, Willow, Birch Mountain maple	Coniferous forest (taiga)	Douglas fir
Foothill	Transition	*Douglas fir *Ponderosa pine Blue spruce White fir	Coniferous forest	Ponderosa pine
				Pinyon-juniper
		Narrow leaf cottonwood Box elder Mountain maple Willow *Chaparral Sagebrush	Woodland	Oak-mountain mahogany
Plains	Upper Sonoran	*Pinyon pine *Juniper	Woodland	Grassland and desert
		*Short grasses *Sagebrush Greasewood Yucca, Saltbush	Steppe (semi-desert)	
(Plains) (Desert)	Lower Sonoran	*Mesquite *Creosote bush *Cactus Acacia, Agave Bunch grasses	Desert	

Ramaley did not include the Lower Sonoran in his studies, but presumably would have named that zone "Plains" or possibly "Desert."

* = dominants of the various associations.

Wallace (1876) was the chief exponent of genetic zoögeography, and his division of the United States from east to west into three portions (Eastern or Alleghenian, Rocky Mountain or Sonoran, and Californian) was a recognition of important species differences in the several areas. But greater differences appear to exist if we compare north with south, and these differences are of the order of genera and families. These taxonomic differences are due in part to the geographic origins of the component organisms (Mayr, 1946), and in part also to the adaptations to habitat conditions. Both of these facts must be kept in mind when pointing out the discrepancies between the animals and plants of the western divisions of the Austral as compared to the eastern divisions of the same region. The differences are due not alone to humidity adaptations nor, on the other hand, alone to taxonomic considerations. The fact that many genera do range from coast to coast or nearly so (while species and subspecies usually do not) also would point to the possibly greater importance of latitudinal barriers than of longitudinal ones.

Merriam (1892), extrapolated his zones (which he had first noticed and described in western mountains) to cover the entire country from west to east on the assumption that temperature is more critical than moisture. It is on this point that he has been most seriously challenged. Perhaps it was a mistake to make such sweeping generalizations as implied in his transcontinental Austral zones, and if we are to use them at all in the eastern states, it might be better to speak of the Alleghenian, Carolinian, Austroriparian, and Gulf strip as separate belts with no connection, real or implied, with the Upper and Lower Sonoran of the west. Yet, in fairness to Merriam it must be granted that he did provide for and recognize the great differences produced, particularly in the life forms of plants, by the humid and arid sections of the United States. It is inescapable, however, that if the Boreal Region is distinct, as most persons probably agree, it must be distinct from something to the south of it. This assemblage to the south has been named the Austral Region, and it does have certain features common to its entire width. Many genera could be cited to support this contention, but only a few need be, as, for instance, *Populus* (except the aspen which is boreal), *Quercus*, *Juglans*, *Carya*, *Acer*, among plants, and *Ponera*, *Eciton*, *Stigmatomma*, *Solenopsis*, *Monomorium*, *Crematogaster*, *Pheidole*, *Pogonomyrmex*, *Atta*, *Trachymyrmex*, and *Dorymyrmex* among ants. We have eastern and western robins, bluebirds, meadow larks, flickers, jays, red foxes, gray foxes, bobcats, Virginia and mule deer, etc., with minor differences only correlated with the humid and arid subdivisions. Some plant genera which are now found only in the eastern section are known from fossil evidence to have lived in the west during a humid period in Tertiary times. And this must have been true for associated animal life as well.

It appears then that Merriam's classification comes closer to a unification of

faunistic and ecologic distribution than any other so far proposed. It may never be possible properly to synthesize the two viewpoints, but the life-zone concept may be regarded as a long step in this direction, a foundation upon which to build. The biome concept is concerned only with communities of organisms, and while this is tremendously important, the faunal and floral aspects of distribution are equally important. Grinnell (1914) has made a further contribution toward synthesis. As he points out, anyone who has observed the marked effect of altitude on the dispersal of organisms cannot avoid the reality of major zones at least in mountain regions. He has shown that the distribution of mammals in the Colorado Desert is not uniform over the whole valley (nor should we expect it to be), for the various species are limited rather definitely in most instances to certain plant associations extending inland from the Colorado River, even including the river itself. However, all species which occur in the desert, plant and animal, form a natural unit of larger size than any one association and do not occur in more northern localities or higher altitudes. This natural unit must be recognized and given a name. It has long been known under the appellation Lower Sonoran.

In a discussion of Merriam's zones, Daubenmire (1938), though generally critical of the concept, does admit that the field surveys of Merriam were very accurate, and that the faunal maps of western areas are very useful. Dice (1943) has incorporated zones or life belts into his system of North American Biotic Provinces, but has accorded them a minor position. In speaking of the biotic provinces of Mexico, Goldman and Moore (1945) seem to have no difficulty with the zones and mention them without reservation, even though their boundaries do not coincide with biotic provinces in many places. Various authors have discussed the life-zone concept in an attempt to show its inadequacy. Shelford (1932, 1945), Kendeigh (1932), Daubenmire (1938), Livingston and Shreve (1921), and others have called attention to the fact that Merriam published charts without also giving the numerical data upon which they were based; that he unwittingly employed 0°C. instead of 6°C. as the critical physiological temperature for figuring temperature sums; that a single factor such as temperature could hardly suffice to explain the complexities of organic distribution; that temperature sums are not necessarily the correct aspect of temperature to employ, for maximum and minimum values may be more important (Kendeigh); that what is the critical temperature for one species may be quite different for another; and that in general his zones do violence to the vegetational areas of the continent. Livingston and Shreve in a monographic treatment have tested various criteria for correlation with the vegetation, and have adopted the view that a narrow range or amplitude in a variety of factors, such as number of days in the frostless season, temperature summations, normal daily mean precipitation, precipitation-

evaporation ratio, moisture-temperature indices, humidity, etc., is indicative of causal relationship between climate and the given vegetation area. The logic of this is not questioned, but when the charts for the plant formations are compared with similar ones for the life zones, one notes that some of the factors have narrow and others have wide amplitudes, and there is a generous sprinkling of both, whether we consider formations or zones. These authors also offer a method of temperature summing based on physiological indices that would appear, and is so claimed, to be more in harmony with biological phenomena than that used by Merriam based on temperature remainder indices; yet when the results of these methods are plotted on maps of the United States, the isoclimatic lines thus derived are seen to be remarkably similar, allowing, of course, for minor incongruities (Livingston and Shreve, 1921, Plates 37, 38, 39, 40). These writers do state, nevertheless, that while the work of Merriam will need modification to bring it into line with modern ecology, his was an important beginning, and the field is by no means closed to further investigation.

Notwithstanding the faults of the Merriam system, I wish to submit the following points in its favor. (1) Despite the error in supplying correct figures for temperature summing, the idea seems logical. An adequate series of experiments on many unrelated plants and animals would provide information on a reliable *average* physiological temperature threshold (6°C., 0°C. or some other). (2) Whatever the eventual explanation of zonation, the criteria of Merriam, maximum and minimum temperatures (a valuable suggestion now supported by some experimental evidence from birds by Kendeigh), or a combination of several ecological factors, the fact remains that the vegetation and associated animals (plant formations or biomes) are arranged in a definite, belted or zonal pattern up the slopes of a mountain range. It is this fact of biotic zonation with marked clarity which Merriam observed and described in detail, quite some time before he attempted an explanation, that is usually ignored by those who object to the zone concept. (3) In justice, Merriam did recognize the great importance of moisture in geographic distribution, and did make a distinction between the east and west of his Austral Region. (4) Whether or not the life zones can be used over the whole of North America and other continents without local modifications, it is felt that they are extremely useful in mountainous areas and should be employed to delimit, and in some cases to divide, the biomes there. At least they are directly applicable to the mountains of western North America where the conception was first developed by its author. I believe that careful study has substantiated the zones in the mountains of continents other than North America, with adjustments for the peculiarities of tropical regions. (See Chapman, 1931.) A zonal arrangement, remarkably similar to that of the natural areas of North America, occurs in Russia and Siberia (Marbut, 1931), where the temperature and

humidity boundaries are parallel to each other and separate latitudinal belts from the Arctic Sea to the Himalayas and the Tibetan Plateau.

A legitimate question would be, "Why continue to use life zones if biomes will do as well?" In answer it may be said that, firstly, the zones are practically identical with the biomes in western United States as to cartigraphic extent and as to meaning (a plant-animal community)—for Merriam used criteria from both kingdoms—and have the advantage of prior statement. Secondly, and more important, they do express relationships not stated in other systems, for while the botanist may not see much meaning in the zones, to the zoölogist they describe the ranges of many animals which cut across dominant plant boundaries but which do conform to broad climatic regions. The Grassland Biome of Clements and Shelford (1939) is by no means as uniform as seems to be implied in the concept of a plant-animal formation. To judge from the areas occupied on their map (p. 255), there are actually represented more than one climatic climax, *viz.*, tall grass, short grass, mixed grass, bunch grass, marsh grass, sagebrush, greasewood, mesquite, and creosote bush. These vegetation types would seem to be too unlike to justify their inclusion under one term, unless that be "steppe." But even this is not ample, for some of the climaxes are desert and some are semidesert. Some animals of the area spread widely over most of the territory (bison, prongbuck), but others are distinctly limited. There is an important difference between the more northern sections and the more southern. Heavy snowfall and freezing temperatures in winter are characteristic of the former, while frost is relatively rare in the latter. A great many tolerant tropical and subtropical species, genera, and even some families of mammals are restricted to the hot southern portion (opossum, armadillo, jaguar, ocelot, cacomistle, peccary, and others). The same is true for certain birds. If this region has any uniformity at all, it is a larger unit than a grassland biome, which should be restricted to the areas covered by true grasses and spoken of as subhumid. The term Austral, or better for the west, Sonoran, was applied to this vast region lacking forests in western United States and Mexico. The major differences between north and south in the unit have been described as Upper and Lower Sonoran. It is interesting to note that Thornthwaite's (1931, 1933) classification recognizes these important differences.

The fact that zones are simple and ecologically monophasic in the Boreal Region, while they are complex and polyphasic (with several vegetational types) in the Transition and Sonoran divisions, should not be an insurmountable barrier to their continued service. It is most useful to have a term like Upper Sonoran to express the distribution of certain species of *Pogonomyrmex* in the western states, even though it may embrace a number of plant associations. Lower Sonoran is descriptive of the distribution of certain ant genera which are endemic

to the southwest, and others which have many tropical relatives but which do not push north of the deserts or into upper elevations in the mountains. Examples of these are *Novomyrmex* and *Veromyrmex*, and *Atta*, *Trachymyrmex*, and *Eciton*, respectively. Where plant and animal ranges do not conform, because the animals may have a greater tolerance and spread widely, it is not assumed that the smaller plant zones or associations should be disregarded. On the contrary, they should be conserved as a background of habitats whether or not there are many animals diagnostic of them. The Hudsonian or spruce-fir zone is a case in point, and the Douglas fir zone, the oak zone (chaparral), and pinyon-juniper zone of Daubenmire (1943) are additional examples.

In consequence of their motility, it appears that animals are not as sensitive to some microclimatic differences as are plants and are therefore not as closely limited in occurrence. This holds fairly well even for the soil inhabiting ants. While the specialized alpine flowers are rooted in the tundra and cannot escape its constant impact, many animals take advantage of the rich tundra meadows in summer but retreat to lower elevations in winter. Only a very few are adjusted to spend their entire existence above timber line. Ants have not produced many species which can survive in the tundra winter, and owing to their inability to fly, only these resident colonies are to be found there during the brief summer.

The plant formations, while excellent for general characterizations of life forms on a world-wide, biogeographic scale, are considered too general for the detailed study of a small area such as a state. The classification offered by Daubenmire is strictly botanical, and would seem to fit the plant situation perfectly, but what of the animals? The scheme employed by Ramaley and others for Colorado is applicable and is frequently used by many of us for the local conditions in the northern section of the state, but it has the drawback of emphasizing the physiographic nature of the subject rather than the biotic. For example, "montane" implies mountains, and while most of the zone is in dissected country, some of it includes extensive flat valley bottoms. "Foothills" is really mountainous in a physiographic sense, and while accurate on the whole for the corresponding zone of Merriam, there are large tracts of yellow pines and oak woodland which jut onto the rolling plains southeast of Denver far removed from the foothills proper. Such an area is the Black Forest. The term "plains" is quite acceptable, but does not distinguish desert from semidesert.

As a consequence of these facts, it is felt that Merriam's terminology is the more descriptive, and better permits the direct comparison of biotic communities at least in different parts of the western mountains. When insect distribution is as well worked out as that of vertebrates, the contentions here presented may be further validated or may be subject to considerable modification. The studies on altitudinal ranges of ants are still in an early phase.

SUMMARY

Preliminary studies on the ant fauna of Colorado with reference to altitude show three distinct belts or zones, the basal plains, the coniferous forests, and the alpine tundra populations. A list of twenty-two species is limited or almost limited to the first of these belts, and may be taken as characteristic of it. Another set of ten species is indicative of the cooler, forest-clad slopes, and only two species are at all common above timber line. Many more forms are present in most of the altitudinal levels, but those included are the best indicators of the formicid assemblages. With further examination and careful plotting on maps, it may be possible to show additional distinctions among ant species of the coniferous vegetation. There are indications that the foothills have species not found to any appreciable extent either above or below this zone, and they tend therefore to constitute a separate community. Seventeen forms have been selected as representative of this community, although numerous ants from the coniferous forests and the plains are encountered also in this transitional area. Seven species which are definitely euryzonal have been added by way of contrast. Finally, a critique and possible reconciliation of the life zones of Merriam with the newer biome concept is attempted.

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