DISTRIBUTION OF THE ANT GENUS *FORMICA* IN THE MOUNTAINS OF COLORADO

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The Rocky Mountains afford unusual opportunities for studies in natural history because of the diversity of topography and climate in the region, which are in turn reflected by great complexities in ecological conditions. The botanical aspects of this area (both taxonomic and ecological) have long been investigated and are well known, and the vertebrate fauna too has been examined in detail, so that we are in possession of a large volume of facts about the conspicuous elements of the biological productions in the region. The terrestrial invertebrates (with some exceptions) are more difficult to study and have attracted less attention because of their small size, making them hard to see in the field, the prodigious numbers of their species, and the relatively less mature status of their taxonomy.

Nevertheless, the insect component of the invertebrate fauna is a major portion of the land biota, and there seems to be an almost inexhaustible supply of problems concerning their manifold relationships. This situation should encourage an ever-growing interest in the environmental adjustments of insects.

I have elsewhere (Gregg, 1963) presented a study of a part of the Colorado insect life, namely, the ants, and for the present paper I have chosen to rearrange some of the data from that report and to give them from a different viewpoint. It is interesting to construct a picture of altitudinal distribution as it occurs with a single taxonomic unit, in this case one genus. For this purpose, the genus *Formica* (Family Formicidae) is used as it appears to be particularly suitable. Although some species in this genus nest in soil, the presence of the colony is usually indicated by pellets of excavated earth deposited in the form of a circular, crater-like hill surrounding the nest entrance. Other species tunnel beneath protecting rocks or logs and their presence may or may not be detected easily, depending upon the accumulation of debris at the surface. Some species occupy the galleries in rotting logs or stumps abandoned by carpenter ants. Quite a large proportion of *Formicae*, however, construct mounds of various sorts, such as masonry domes, grassy domes, thatched earthern nests, or thatch piled against rocks or logs, or even nests built entirely of thatch, and these structures can be rather conspicuous features in a landscape. The genus is exceptionally well represented in the area by numerous species, and in addition, the southern portion of the Rocky Mountains especially is a secondary center of speciation as shown by the many peculiar and ecologically interesting taxa. This genus, of course, is also an important one in the temperate portions of the whole Northern Hemisphere, being found in abundance from moderate austral habitats to places with high boreal conditions. It is even known sparingly from cooler subtropical areas on one extreme to the milder parts of the tundra on the other. Since the mountainous areas of western United States embrace a wide selection of environments from hot to cold, and from moist to dry, concentrated in comparatively small geographic areas within each range, we are not surprised to find a rich sample of species of *Formica* distributed among these many types of ecological terrain.

Among 49 species and subspecies of *Formica* known in the fauna of Colorado, 27 have been selected for this study (Fig. 1.). These are representative of each subgenus, and the typical subgenus itself (*Formica*) is represented by at least one species from each species group, except in the case of the *Exsecta* group, which for the purposes of this report did not seem to be necessary. In most instances the data are sufficient to give a clear indication of the altitudinal dispersal and the broad habitat preferences of these ants. The results are the product of many years of field work and appear to be unequivocal. Other species might have been depicted, but would probably not have added anything significant to the pattern. The polygons of the figure were constructed from tallies of collection records that were then plotted on elevation charts showing 500 foot intervals. If a species was found within any 500 foot interval, it was so recorded regardless of what portion of the increment it actually occupied. This is considered admissible since in a chart of this type a compromise of some sort has to be made, but the precise altitude for every collection is recorded elsewhere. Thus, owing to the amount of data available, particularly for common species, it is possible to show more than the mere presence or absence of a form in any altitudinal zone or interval. The polygons mark the segments of a species' range where it is most often encountered, and also where and how its abundance tapers off to the point where it is altogether absent from the available habitats. Two species, *Formica comata* and *F. dakotensis montigena*, are included for contrast, and demonstrate the difficulty of ascertaining the distributional characteristics of a species when only a few occurrences are known. Then it is necessary to employ a straight line and only altitudinal limits can be shown. Relative abundance and importance in various communities cannot even be surmised. Very rare species have been omitted from the figure because the information about these forms is quite insufficient to give reliable indications of their possible true distribution.

Superimposed upon the regular intervals of the distribution chart is an indication of the commonly accepted life-zone boundaries of the

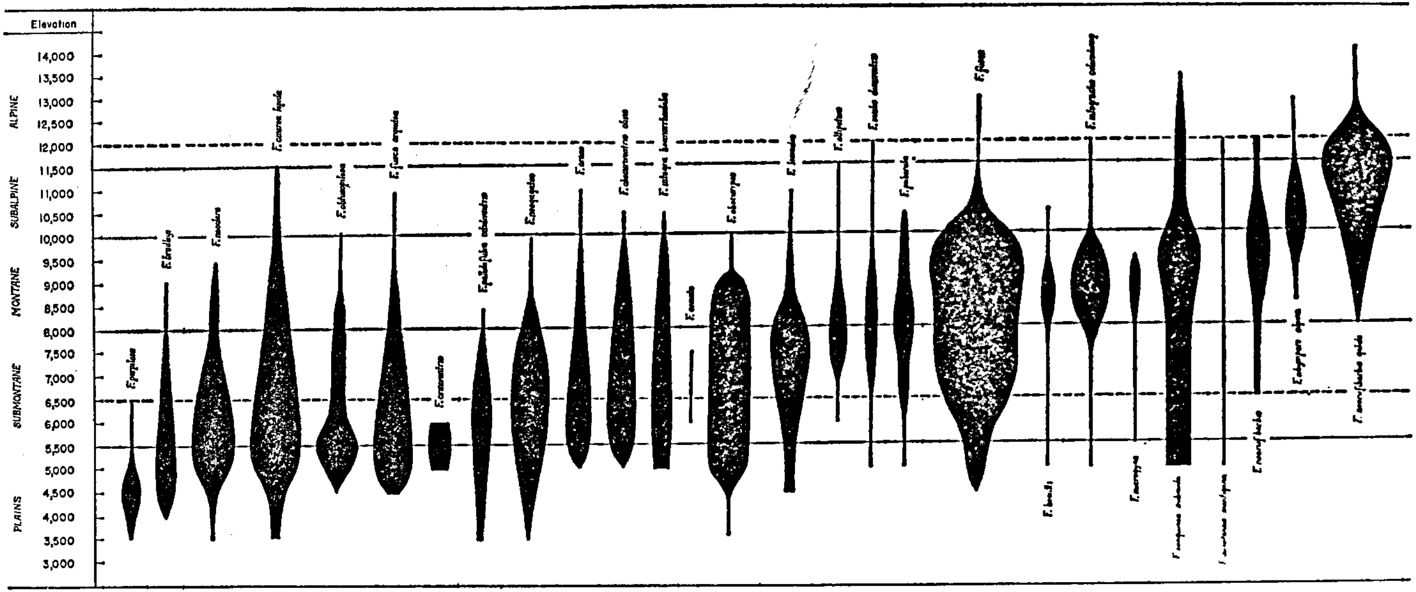

FIGURE 1. Altitudinal distribution of selected species in the genus *Formica*. Solid lines represent average zone boundaries in northeastern Colorado; dashed lines represent average upward displacement of the two most prominent boundaries in western and southern Colorado.—*Formica* (*Proformica*) *lasioides*, *neogagates*; *Formica* (*Formica—fusca* group) *fusca*, *fusca argentea*, *hewitti*, *altipetens*, *cinerea legida*, *neoclara*, *neorufibarbis*, *neorufibarbis gelida*; *Formica* (*Formica—rufa* group) *crinicentris*, *comata*, *obscuripes*, *obscuriventris clivia*, *oreas*, *integra haemorrhoidalis*, *integroides coloradensis*, *dakotensis montigena*; *Formica* (*Formica—microgyna* group) *microgyna*, *rasilis densiventris*, *whymperi alpina*; *Formica* (*Raptiformica*) *bradleyi*, *perpilosa*, *obtusopilosa*, *puberula*, *sanguinea subnuda*; *Formica* (*Neoformica*) *pallidefulva nitidiventris*.

Colorado mountains. The solid lines at elevations of 5,500, 8,000, 10,000, and 11,500 feet separate the five zones, Plains, Submontane, Montane, Subalpine, and Alpine, as they are recognized in eastern Colorado, and especially northeastern mountains such as the Front Range. Actually, these boundaries are not straight and simple as shown here because of the numerous climatic effects of topography (angle of slope, direction of slope, depth of canyons, etc.) which displace the boundaries upward or downward depending upon local conditions. Such complexities are impossible to show in a small diagram. In an area the size of this state, there is enough latitudinal change from north to south and enough climatic difference between the eastern and western sides of the main ranges to produce notable changes in the average positions of the zonal boundaries. The most prominent divisions are those that separate the Plains Zone (otherwise known as the Upper Sonoran) from the Submontane Zone (or Transition), and the Subalpine Zone (Hudsonian) from the Alpine Zone (Arctic). At these points the biological changes are more abrupt and more profound than those which divide the remaining zones. It is at these places too that the effects of latitude and longitude mentioned above seem to show the greatest displacement, for the life-zone levels of the Sonoran and the Arctic belts may be shifted upward as much as 500 to 1,000 feet in western and southern Colorado, and in a few spots as much as 1,500 feet. (Cary, 1911.) I have indicated these differences by means of dashed lines at 6,500 and at 12,000 feet, but have left out any changes for the other zones to avoid undue complication of the chart.

It is evident, of course, that such differences greatly affect the supposed occurrence of certain ants in the highest zone, the alpine tundra. The polygons are based on data from all parts of Colorado, and therefore do not fit any one region perfectly. From our detailed records we know that in reality only these species of *Formica* (*sanguinea subnuda, whymperi alpina,* and *neorufibarbis gelida*) are found as permanent residents in the tundra, and only the last of these with any regularity. The other species which go above 11,500 feet were not taken from alpine locations but instead from stations in central or southern Colorado or from local sites still below the tundra boundary despite their high elevations. On the other hand, the upslope shift of the plains or Sonoran habitats to 6,500 feet would add only three species not already known from the low warm zone, namely, *F. comata, altipetens,* and *microgyna*. In each case, however, the low elevations recorded for these ants are in localities where the zonal interpretation for the site would still place it in the submontane zone or so close as to leave the decision in doubt. In each case also only one or two records are involved. Thus, as to whether a species should be classed as belonging to a particular life-zone depends not alone on the absolute altitudes observed but on what local ecological conditions exist at the collecting site, which are so often modified from the average situation in complex topography. The judgment should also take into account the abundance of the species and its relative importance in the community with which it is associated.

Referring again to the distribution chart (Fig. 1.) we may deduce the following statistics with respect to the altitudinal dispersal of *Formica* as it relates to the various life-zones. Of 27 species treated here, 21 (78%) are in the Plains Zone, 25 (93%) are in the Submontane zone, 24 (89%) are in the Montane Zone, 17 (63%) in the Subalpine Zone, and 3 (11%) in the Alpine Zone.

It can be seen immediately that a great deal of overlap takes place, for some species traverse several zones and certain ones are known in all five zones. Although no species is absolutely restricted to one zone (except perhaps those whose rarity makes it impossible as yet to be sure), there are many with their greatest abundance so confined, or at most having the bulk of their occurrences distributed over two zones. Examples of the former are such ants as *Formica perpilosa* and *F. integroides coloradensis*; of the latter, *F. neoclara, F. obtusopilosa, F. fusca,* and *F. neorufibarbis gelida.* To collect all the species known to live in a given zone, particularly the lower ones, might takes months. But after a reasonable search for them, the Submontane Zone, for instance, is almost sure to yield specimens of *F. fusca, lasioides, obscuripes, neogagates, clivia, neoclara,* or *haemorrhoidalis.* Others may be totally absent, or found there as rarities only after many years of diligent collecting. And it is obvious that ants which are rare or absent at one elevation may be quite common a few hundred or a thousand feet higher or lower as the case demands. It is possible, then, to say that characteristic assemblages of ants do exist and compare well with the usually recognized plant-animal life-zones. No assemblage is "air tight" or pure with regard to its composition, nor should that be expected. The vagilities and ecological tolerances among organisms are so complex and so multitudinous for any community, zone, or ecosystem (or any other unit of classification in ecology) that it is somewhat astonishing to find regularities and groupings among them at all.

Ecological boundaries, such as we are dealing with, without exception show transitional qualities, and though some of these ecotones are remarkably sharp on a geographic scale, they all exhibit intermediate characters to some degree. However, the reality of the altitudinal constellations of forms reported here is supported by the quantitative differences inferred from the changes in abundance of each species, and this can be attested also by the field experience of any myrmecologist familiar with the region. The qualitative differences among the ant inhabitants of the several zones are provided, of course, by the fact that various species and subspecies are involved. A taxonomic control is insured because all the species for this presentation were selected from a single genus. It is clear that these ants show a definite ecological trend from those that are tolerant of warm and somewhat dry conditions in Sonoran habitats (at low elevations) to those that will stand cold and relatively moist or even wet conditions of boreal habitats (at high elevations). It is possible that these species, or some of them, may be not only tolerant but demanding of the indicated environmental circumstances. This is an assumption, however, that would need to be investigated and demonstrated separately for each of the species. The correlations are good and one can make an intelligent guess regarding the requirements of a taxon, but to prove these requirements is much more difficult.

Certainly, there is a decided change in the kinds of *Formica* which appear as one ascends the mountains. The changes involve the addition of new species, the disappearance of other species, changes in abundance, and changes in micro-habitat requirements, although the latter are not evident from the accompanying chart. These changes in ant populations are associated with major differences in vegetation which are much more obvious. Both are accompanied by fluctuations in the cardinal physical factors of the environment, such as temperature, light, and moisture. It is extremely probable that subtle biological interactions (competition, etc.) must be operating also to affect the success of a species in a given ecological milieu. It is further possible that the biological factors may be enormously influenced for the welfare of a particular species by changes in the accompanying physical factors. For example, in addition to its direct influence on the survival of a species, low temperature may differentiate between two species on the basis of which one has a lower temperature threshold for larval development, or which can remain competitively active during low temperatures, or short growing seasons. The combined effect of temperature and moisture seems to control the distribution of many organisms, and it is already known and reported by various authors that warm and moist environments are inhabited by a rich assortment of ant species, whereas cold and moist, or especially wet habitats support very few species, sometimes none at all. The effect of low temperature appears to be exaggerated by excessive moisture. Many ant species thrive in warm dry conditions also, in contrast to the warm and moist, and usually seem to be specially adapted for such environments, but *Formica* is not particularly tolerant of arid situations anywhere. These suggested possibilities show that the surroundings may favor one or another species, and while we have a descriptive understanding of where the forms are dispersed we have yet to learn how and why they occur where they do.

It is interesting to discover that many of these ants can tolerate what are for them extreme conditions, enough to be represented at altitudinally far outposts. In the chart this is shown by narrow extensions of the polygons in most cases to points well above or below the areas of undoubted abundance. In such instances the species seem to be occupying local sites which provide an amelioration of the general environment such that the insects can survive, but they are probably at the limits of their tolerances. Any disturbance in living conditions might eliminate them from the area. The collecting of records like these is hard to explain, and no doubt depends in large measure upon chance; the myrmecologist just happens upon a species rare to the locality, and without suspecting the event. This has been our experience on many occasions, and some of the most stimulating finds and interesting species have turned up in this manner. This phenomenon occurs on a broad geographic scale too, as when ectopic samples are collected well beyond the expected range or general area of known abundance. The situations parallel each other, but are probably more striking in mountainous regions because a few hundred feet of altitude produce environmental changes that correspond with several hundred miles latitudinally among lowland stations. Thus the distributional shifts occur more rapidly and within such short distances in mountains that the boundaries separating groups are rendered more pronounced.

The chart shows that in a region of general aridity (western United States), and of generally high altitude (plains even have an elevation of 3,000 to 5,000 feet), the genus *Formica* exhibits a preference for rather warm habitats and ones also with considerable moisture. It is not overly abundant on the plains, but as soon as foothill (submontane) environments are reached, the incidence of *Formica* and the abundance of individuals (judging from the number of colony records) show a notable increase. Of all the life-zones, the submontane has the greatest number of species. It is warm but not hot, with a rather long open season, and moist but not as wet as places at higher elevation. This affluence of species may be more than an indication of general changes in climatic conditions, and in fact may reflect a significant increase in the number of microsites available to ants as a group, for the zone is generally one of open forests, some dense forests, woodlands, and several kinds of meadow. It is ecologically more complex than grassland.

The Montane Zone still has a respectable ant fauna but slightly diminished as compared to the Submontane. Here conditions are deteriorating from the standpoint of ants, and the downward trend in species richness of these insects has been established. Yet, many species continue to be important constituents of montane communities, and certain forms find optimum conditions for the development of their colonies. A rather wide selection of micro-habitats continues in the montane and considerable heat during the middle of summer, especially in forest glades, permits the growth of ant broods.

In the Subalpine Zone, the number of ant species is markedly impoverished, though the few that exist there may produce thriving populations. The temperature strikes a low average, the growing season is short, and the moisture content is often high in both air and soil. The wetness of the soil and of decaying logs increases the chill of these nesting sites and no doubt makes them unattractive to any but cold-adapted, or at least cold-tolerant species of insects. Since ants as a taxonomic group are thermophilic, it is in keeping with their requirements that only a few species can adjust to subalpine conditions, and only a very few achieve real abundance.

Finally, circumstances in the Alpine Zone are so rigorous that ants are reduced to a minimum number of forms. Most of these are members of the genus *Formica*. The tundra environment is treeless, wide open, brilliantly lighted, but so elevated that the temperature except in direct sunlight drops quite low, and especially at night, even in mid-summer. The season for growth is telescoped into a span of only a few weeks, and the general availability of water is rather low. Life faces severe tests in the tundra, with the result that only the hardiest forms survive. Some may be specially adapted for this environment. Under these circumstances, ants are not good competitors. Only the species *F. neorufibarbis gelida* is to be seen with any consistency, but even this ant will be found usually in the most favorable sites.

Having described the general and zonal distribution of selected species of ants in the Colorado mountains, it will be helpful to consider some of the details of the physical and biological background against which this distribution occurs. A sketch in broad outlines is all that can be attempted, but I hope it will serve to emphasize the environmental intricacies that confront the dispersion of any group. Not only is there a tremendous change in altitude, from as low as 3,500 feet on the eastern plains to over 14,000 feet in these mountains (an amplitude of more than 10,000 feet), but imposed on this complex is a geological history of erosion, uplift, and renewed degradation that has produced a topography of hills, valleys, ridges, canyons, rolling upland, high peaks, and mountain parks. Glaciation has intensified or even altogether changed some features, especially at high altitudes.

Vegetation, being the most conspicuous biological component of the region, shows distinct distributional correlations with this topography and with both the general and the local climatic conditions. Vegetation varies from the extremes of temperate deserts to grasslands, brushlands, woodlands, forests, meadows, wind-timber, and tundra. Most of the river valleys run generally east or west, though other directions are observable, with the result that in this region there are sharp differences often between north-facing and south-facing slopes. The deeper the canyon, the narrower its bottom, and the steeper its walls, the more noticeable are the differences. The phenomenon is known as the "canyon effect." On a north-facing slope many plants and animals typical of high elevations, or the next zone above, may find congenial conditions locally that enable them to descend to altitudes much below their normal range in more open and more horizontal areas. Correspondingly, a south-facing slope may support organisms that are usually confined to much lower altitudes but which can penetrate the mountains or go to a higher zone where local warmth makes such extension possible.

An effort has been made to portray these conditions through an admittedly simplified diagram (Fig. 2.), and of necessity many details are left out. Trees and other life-forms produce the appearance of the landscape, and also create the living conditions so essential to

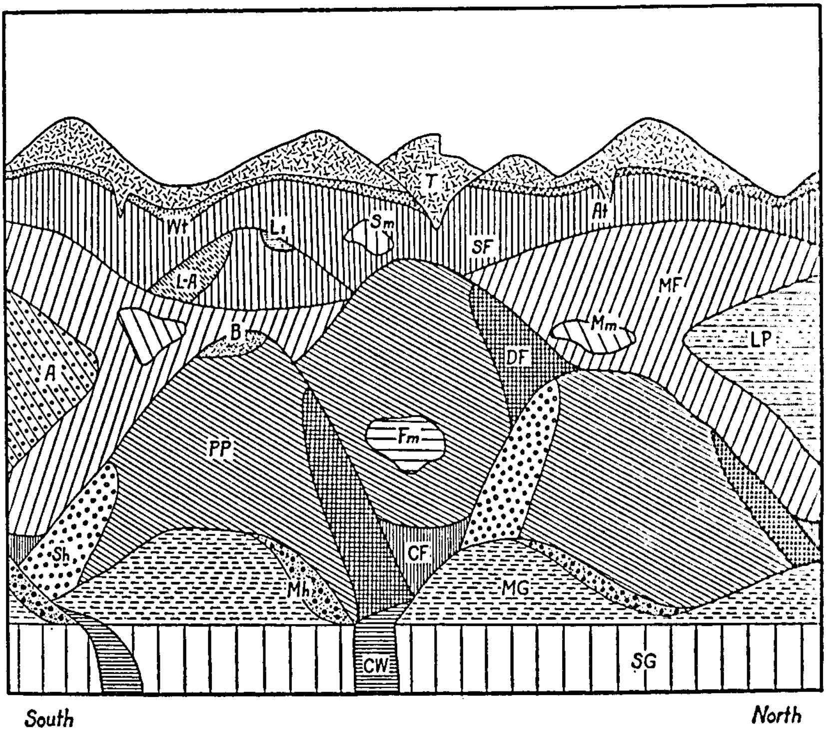

FIGURE 2. Diagramatic distribution of vegetation types in the mountains of the Front Range in Colorado.—SG—Short grass prairie, CW—Cottonwood-willow forest, MG—Mixed grass prairie, PP—Ponderosa pine forest, Sh—Mixed shrubs, grass, and yucca, Mh—Mountain mahogany brush, CF—Canyon forest, Fm—Foothill meadow, DF—Douglas fir forest, MF—Mixed montane forest, A—Aspen forest, LP—Lodgepole pine forest, Mm—Montane meadow, B—Rocky bald, SF—Spruce-fir forest, L-A—Lodgepole pine-aspen forest, Li—Limber pine forest, Sm—Subalpine meadow, Wt—Wind timber, T—Tundra, At—Avalanche track.

animal inhabitants of each area. Thus, a community of plants and animals makes up a complexly integrated unit, and with the addition of the physical aspects of the environment (climate, soil, and so forth) they form an ecosystem. All components of the various ecosystems act, react, and adjust to each other constantly in a dynamic but slowly changing sequence of events. Yet the fluctuations occur about numerous means or average conditions, so that an appearance of long-term stability is presented. Actually, this stability, or homeostasis, is the functional result of myriad interactions that are only partly understood. The boundaries of the several plant types are sharply drawn, and while occasionally rather abrupt borders are found in nature, they more often show some intergradation. The effects of north- and south-facing slopes and of hilltops in contrast to valley bottoms are also included. The site selected could be a view from the plains westward into the features of the Front Range, since this is the most familiar area and the best studied in Colorado. It was not practical to show mountain parks or deserts in this diagram without further complicating the whole pattern of vegetation. The parks can be visualized, however, as extensive grasslands or sagebrush covering the floors of high level basins set amid surrounding mountain peaks, and with at least one drainage channel. The deserts occur on comparatively flat lowlands and plateaus in southern and western Colorado, and contain vegetation composed of sagebrush, greasewood, or saltbush.

The plains vegetation typically is short grass prairie, with cactus, yucca, and many flowering herbs. It is interrupted by cottonwood-willow bottomland forests along streams. In many parts of the region there are also woodlands of pinyon pine and cedar or juniper, but these are absent from the area depicted. In the submontane, forests of ponderosa pine develop, together with meadows and brush of mountain mahogany. Stands of Douglas fir grow on north-facing slopes. Oak woodland occurs in many places, but like the pigmy conifers is almost absent from northeastern Colorado. The montane habitats when mature are usually mixed coniferous forests, but often extensive stands of lodgepole pine or aspen dominate the vegetation. Douglas fir forests grow here also, and there are many sizable tracts covered with montane meadow. The subalpine environment supports lush forest of spruce and fir, and scattered stands of limber pine on exposed locations. It is usually dense and moist, and trees attain their maximum height. At the upper timberline the forest is molded into a spectacular wind timber, or krummholz, which finally gives way to tundra. A lower timberline exists also (partly because of aridity) at the base of the submontane belt, but it shows no physical modification of the trees comparable to the wind timber above. In the alpine tundra trees have disappeared and the vegetation is mostly of low-growing plants exhibiting rosette form or cushion and mat-like growth, and a few are shrubby. A dense turf of grass and sedges and flowering herbs contributes an important component of tundra vegetation as well. In all forested environments there are openings containing grassy meadows, and sometimes bogs and marshes. Many have open lakes. Similar habitats can be seen in tundra and in grassland.

The actual macrosites and microsites where ants are found are therefore very numerous. Species of *Formica* are to be found in virtually all examples of vegetation but not in equal abundance. They tend to favor mixed stands rather than pure stands, especially of coniferous trees, which are quite monotonous. They may be numerous along the margins of different vegetation types. They will be in moist but well drained areas, not marshy or boggy sites, except for members of the *cinerea* complex which can endure such conditions. Rich meadows are particularly suitable locations. The ant populations of all major and many minor vegetation types of the southern Rocky Mountains have been sampled and identified and species lists have been drawn up, but it would be far beyond the scope of this report to include them.

Enough material has been set forth to show that one small section of the Rocky Mountain insect fauna can be ecologically varied and taxonomically interesting. The genus *Formica* has the largest number of species and subspecies of all ant genera in the studied area, so it is the most satisfactory for demonstrating that a group of related taxa of these insects can utilize a wide range of diverse habitats. They appear to show adaptive radiation into many situations, but the adaptations are not special obvious structural modifications, such as for particular foods, for locomotion, for drought resistance, for soil types, or for plant hosts, as is the case with some insects. Rather, these species are omnivorous insects capable of using various foods, able to select suitable nesting sites, to construct a variety of nest types, and to respond satisfactorily to whole environmental complexes available to them. They would appear to possess subtle physiological adjustments toward general ecological conditions, but to learn precisely what these relations are would probably require that each species be investigated experimentally.

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