competition are less common. Active competition in the form of mutual habitat-exclusion has been noted in the cases of flatworms and salamanders. The commonest situation takes the form of niche diversification as the result of interspecific competition. This has been noted in birds, salamanders and other groups of carnivores. Quite likely, host specificity in parasites and parasitoid insects is at least partly due to the influence of interspecific competition.

Of equal significance is the frequent occurrence among herbivores of apparent exceptions to the influence of density-dependent factors. The grasshoppers described by Birch and the thrips described by Davidson and Andrewartha are well known examples. Moreover, it is among herbivores that we find cited examples of coexistence without evidence of competition for resources, such as the leafhoppers reported by Ross and the psocids described by Broadhead. It should be pointed out that in these latter cases coexistence applies primarily to an identity of food and place, and other aspects of the niches of these organisms are not known to be identical.

Kormondy, E.J. 1965. Readings in Ecology.
Prentice-Hall, Inc. NJ. 219 pp.

THE STUDY OF COMMUNITIES

At least as early as the time of Theophrastus it was recognized that different species show particular spatial relationships in groupings of one sort or another. The existence of assemblages and a seeming appearance of pattern in their composition and distribution have provided a considerable arena for ecological investigation.

Stimulated and oriented largely by the Danish botanist Eugene Warming at the turn of the century, the study of communities has been directed primarily towards plants. Considerable effort has been expended in the analysis of vegetational units (composition, physiognomy, stratification, distribution, etc.) and the investigation of such dynamic events as phenological and successional change. These studies on the general nature and composition of the plant community with respect to time and space were involved in reciprocal stimulation from concurrent theoretical developments and philosophical discussions.

Animal community studies were given major thrust by the English ecologist Charles Elton in the 1920's. Elton's concept of key industry animals functioning in integrating the community through a food chain focused attention on the relations of numbers of organisms and the nature of food chains and ecological niches. These aspects of community study are covered in the section on ecosystems.

REPORT ON THE MOLLUSCA AND RADIATA OF THE AEGEAN SEA, AND ON THEIR DISTRIBUTION CONSIDERED AS BEARING ON GEOLOGY

Edward Forbes—1844

Reprinted by permission of the publisher from Report of the British Association for the Advancement of Science for 1843, pp. 130–193, 1844.

One of the earliest clear recognitions of the existence of particular assemblages of different species was in this report by Forbes, who was Professor of Botany at Kings College, London. This study is quite remarkable in its description of spatially distributed communities, or what Forbes called "provinces of depth," and the realization of the dynamic interaction of abiotic and biotic forces in yielding the observed distribution.

The distribution of marine animals is determined by three great primary influences, and modified by several secondary or local ones. The primary influences are climate, sea-composition and depth, corresponding to the three great primary influences which determine the distribution of land animals, namely climate, mineral structure and elevation. The first of these primary marine influences is uniform in the eastern Mediterranean. From Candia to Lycia, from Thessaly to Egypt, we find the same species of Mollusca and Radiata assembled together under similar circumstances. The uniformity of distribution throughout the Mediterranean is very surprising to a British naturalist, accustomed as we are to find distinct species of the same genera, *climatally representative* of each other, in the Irish and North seas, and on the shores of Devon and Zetland. The absence of certain species in the Aegean which are characteristic of the western Mediterranean, is rather to be attributed to sea-composition than to climate. The pouring in of the waters of the Black Sea must influence the fauna of the Aegean and modify the constitution of its waters. To such cause we must attribute the remarkable fact that with few exceptions individuals of the same species are dwarfish compared with their analogues in the western Mediterranean. This is seen most remarkably in some of the more abundant species, such as *Pecten opercularis, Venerupis irus, Venus fasciata, Cardita trapezia, Modiola barbata,* and the various kinds of *Bulla, Rissoa, Fusus,* and *Pleurotoma,* all of which seemed as if they were but miniature representatives of their more western brethren.

To the same cause may probably be attributed the paucity of *Medusae* and of corals and corallines. Sponges only seem to gain by it. The influence of depth is very evident in the general character of the Aegean fauna, in which the aborigines of the deeper recesses of the sea play an important part numerically, both as to amount of species and individuals.

The secondary influences which modify the distribution of animals in the Aegean are many. First in importance ranks the character of the sea-bottom, which, though uniform in the lowest explored region, is very variable in all the others. According as rock, sand, mud, weedy or gravelly ground prevails, so will the numbers of the several genera and species vary. The presence of the sponges of commerce often depends on the rising up of peaks

of rock in the deep water near the coast. As mud forms by much the most extensive portion of the bottom of the sea, bivalve Mollusca abound more individually though not specifically than univalves. As the deepest sea-bottom is of fine mud, the delicate shells of Pteropoda and Nucleobranchiata are for the most part only preserved there. Where the bottom is weedy we find the naked Mollusca more numerous than elsewhere; where rocky, the strong-shelled Gasteropoda and active Cephalopoda. Few species either of Mollusca or Radiata inhabit all bottoms indifferently.

The nature of the sea-bottom is mainly determined by the geological structure of the neighbouring land. The general character of the fauna of the Aegean is in a great measure dependent on the great tracts of scaglia which border it, and of which so many of its islands are formed. The degradation of this cretaceous limestone fills the sea with a white chalky sediment, especially favourable to the development of Mollusca. Where the coast is formed of scaglia numerous marine animals abound which are scarce on other rocks. The genera *Lithodomus* and *Clavagella* among Mollusca, the *Cladocora caespitosa* among Zoophytes, are abundant in such localities only.

In a report on the distribution of British terrestrial and fluviatile Mollusca, which I had the honour of presenting to the Association at Birmingham, I asserted that a remarkable negative influence was exercised by serpentine on the distribution of pulmoniferous Mollusca. This I have had peculiarly favourable opportunities of confirming in the Aegean, where whole islands being formed of serpentine, the almost total absence of those animals which are abundant on the islands of other mineral structure is most striking. But I found further, that not only does serpentine exercise a negative influence on air-breathing Mollusca, but also on marine species. An extensive tract on the coast of Lycia and Caria, indented with deep and land-locked bays, is formed of that rock. In such bays, with the exception of a few littoral species which live on all rocks, we find an almost total absence of Testacea; whilst in correspondent bays in the neighbouring districts, formed of scaglia, of saccharine marble, and even of slate, we find an abundance of Testacea, so that it can hardly be doubted that the absence or scarcity of shelled Mollusca in such case is owing to negative influence exercised by the serpentine. *The outline of the coast* is evidently an important element in such influences, or in modifying it.

Tides and currents in most seas are important modifying influences. In the Aegean the former are so slight as scarcely to affect the fauna; the latter, in places, must be powerful agents in the transportation of species and of the spawn of marine animals. Their action, however, like that of storms, appears materially to affect the upper regions only; the transportation of the species of one region into another seldom extending further than that of the regions immediately bounding that in which it is indigenous. Certain species, such as the *Rissoae*, which live on sea-weed, may occasionally fall to the bottom region, of which they are not true natives, and may live for a time there, but such cases appear to be rare, and the sources of fallacy from *natural transportation* are fewer than might be imagined at first thought, and in most cases have arisen rather from the form of the coast than from currents. Thus where the coast-line is very steep, the sea suddenly deepening to 60 or 70 fathoms close to the rocks, limpets, littoral *Trochi* and other shells, when they die, fall to the bottom, and are found along with the exuviae of the natural inhabitants of those depths.

Several instances of this occurred during dredging.

The *influx of fresh water*, whether continual, as where a river empties itself into the sea, or temporary, as on the coast of Asia Minor during the rainy season, when every little ravine becomes suddenly filled with a raging torrent, bearing down trees and great masses of rock, and charged witb thick mud, frequently modifies the marine fauna of certain districts very considerably. The first generates great muddy tracts, which present a fauna peculiar to themselves; the second, though of short duration, deposits detached patches of conglomerate, and by the sudden settling of the fluviatile mud forms thin strata at the bottom of the sea, often containing the remains of terrestrial and fluviatile animals, soon to be covered over by marine deposits with very different contents. From the influx of a great river we may have tropical or subtropical, terrestrial or fluviatile forms mingled with temperate marine . . . .

PROVINCES OF DEPTH

There are eight well-marked regions of depth in the eastern Mediterranean, each characterised by its peculiar fauna, and when there are plants, by its flora. These regions are distinguished from each other by the associations of the species they severally include. Certain species in each are found in no other, several are found in one region which do not range into the next above, whilst they extend to that below, or *vice versa*. Certain species have their maximum of development in each zone, being most prolific in individuals in that zone in which is their maximum, and of which they may be regarded as especially characteristic. Mingled with the true natives of every zone are stragglers, owing their presence to the action of the secondary influences which modify distribution. Every zone has also a more or less general mineral character, the sea-bottom not being equally variable in each, and becoming more and more uniform as we descend. The deeper zones are greatest in extent; so that whilst the first or most superficial is but 12, the eighth, or lowest, is above 700 feet in perpendicular range. Each zone is capable of subdivision in smaller belts, but these are distinguished for the most part by negative characters derived from the cessation of species, the range of which is completed, and from local changes in the nature of the sea-bottom . . . .

The eight regions in depth are the scene of incessant change. The death of the individuals of the several species inhabiting them, the continual accession, deposition and sometimes washing away of sediment and coarser deposits, the action of the secondary influences and the changes of elevation which appear to be periodically taking place in the eastern Mediterranean, are ever modifying their character. As each region shallows or deepens, its animal inhabitants must vary in specific associations, for the depression which may cause one species to dwindle away and die will cause another to multiply. The animals themselves, too, by their over-multiplication, appear to be the cause of their own specific destruction. As the influence of the nature of sea-bottom determines in a great measure the species present on that bottom, the multiplication of individuals dependent on the rapid reproduction of successive generations of Mollusca, &c. will of itself change the ground and render it unfit for the continuation of life in that locality until a new layer of sedimentary matter, uncharged with living organic contents, deposited on the bed formed by the exuviae of the exhausted species, forms a fresh soil for similar or other animals to thrive, attain their maximum, and from the same cause die off. This, I have reason to believe, is the case,

from my observations in the British as well as the Mediterranean seas. The geologist will see in it an explanation of the phænomenon of interstratification of fossiliferous and non-fossiliferous beds.

AN OYSTER-BANK IS A BIOCÖNOSE, OR A SOCIAL COMMUNITY

Karl Möbius—1877

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By proposing the term biocönosis to describe a "community of living beings," Möbius clearly recognized that the species involved had something in common. Möbius' discussion is decidedly modern in its conception of interaction and regulation within the community as well as between the living community and its nonliving environment; this latter aspect is less well identified, however.

. . . The territory of an oyster-bed is not inhabited by oysters alone but also by other animals. Over the Schleswig-Holstein sea-flats, and also along the mouths of English rivers, I have observed that the oyster-beds are richer in all kinds of animal life than any other portion of the sea-bottom. As soon as the oystermen have emptied out a full dredge upon the deck of their vessel, one can see nimble pocket-crabs (*Carcinus mænas*) and slow horn-crabs (*Hyas aranea*) begin to work their way out of the heap of shells and living oysters, and try to get to the water once more. Old abandoned snail-shells begin to move about, caused by the hermit-crabs (*Pagarus bernhardus*), which have taken up their residence in them, trying to creep out of the heap with their dwelling. Spiral-shelled snails (*Buccinum undatum*) stretch their bodies as far out of the shell as they can, and twist from side to side, trying, with all their power, to roll themselves once more into the water. Red starfish (*Asteracanthion rubens*), with five broad arms, lie flat upon the deck, not moving from the place, although their hundreds of bottle-shaped feet are in constant motion. Sea-urchins (*Echinus miliaris*), of the size of a small apple, bristling with greenish spines, lie motionless in the heap. Here and there a ring-worm (*Nereis pelagica*), of a changeable bluish color, slips out of the mass of partially dead, partially living, animals. Black edible mussels (*Mytilus edulis*) and white cockles (*Cardium edule*) lie there with shells as firmly closed as are those of the oysters. Even the shells of the living oysters are inhabited. Barnacles (*Balanus crenatus*), with tent-shaped, calcareous shells and tendril-shaped feet, often cover the entire surface of one of the valves. Frequently the shells are bedecked with yellowish tassels a span or more in length, each of which is a community of thousands of small gelatinous bryozoa (*Alcyonidium gelatinosum*), or they are overgrown by a yellowish sponge (*Halichondria panicea*), whose soft tissue contains fine silicious spicules. Upon many beds the oysters are covered with thick clumps of sand which are composed of the tubes of small worms (*Sabellaria anglica*). These tubes, called "sand-rolls," resemble organ-pipes, and are formed from grains of sand cemented into shape by means of slime from the skin of the worm. The shell forms a firm support upon which the worms can thus live close together in a social community. Upon certain beds near the south point of the island of Sylt, where the finest-flavored oysters of our sea-flats are to be found, there lives upon the oyster-shells a species of tube-worm (*Pomatoceros triqueter*) whose white, calcareous, three-sided tube is very often twisted about like a great italic *S*. The shells of many oysters upon these beds also carry what are called "sea-hands" (*Alcyonium digitatum*), which are white or yellow communities of polyps of the size and shape of a clumsy glove. Often the oyster-shells are also covered over with a brownish, clod-like mass, which consists of branched polyps (*Eudendrium rameum* and *Sertularia pumila*), or they may be covered with tassels of yellow stems which are nearly a finger long and have at their distal ends reddish polyp-beads (*Tubularia indivisa*). Among these polyps, and extending out beyond them, are longer stems, which bear light yellow or brown polyp-cups (*Sertularia argentea*). Within the substance of the shell itself animals are also found. Very often the shells are penetrated from the outside to the innermost layer, upon which the mantle of the living oyster lies, by a boring sponge (*Clione celata*), and in the spaces between the layers of the shell in old oysters is found a greenish-brown worm (*Dodecaceræa concharum*), armed with bristles, and bearing twelve large tentacles upon its neck. I once took off and counted, one by one, all the animals living upon two oysters. Upon one I found 104 and upon the other 221 animals of three different species. The dredge also at times brings up fish, although it is not very well adapted for catching them. Soles (*Platessa vulgaris*), which seek by jumping to get out of the vessel and once more into the water, stone-picks (*Aspidophorus cataphractus*), and sting-rays (*Raja clavata*), which strike about with their tails, are abundant upon the oyster-banks. Besides those already mentioned, there are many other larger animals which are taken less frequently in the dredge. There are also a host of smaller animals covered up by the larger ones, and which can be seen only with a magnifying glass. Very few plants grow upon the banks. Upon only a single one of the oyster-beds of the sea-flats has eel-grass (*Zostera marina*) taken root. Upon other beds reddish-brown algæ (*Floridiæ*) are found, and, floating in the water which flows over the beds, occur microscopic algæ (*Desmidiæ* and *Diatomaceæ*), which serve as nourishment to the oysters. If the dredge is thrown out and dragged over the sea-flats between the oyster-beds, fewer and also different animals will be found upon this muddy bottom than upon the sand. Every oyster-bed is thus, to a certain degree, a community of living beings, a collection of species, and a massing of individuals, which find here everything necessary for their growth and continuance, such as suitable soil, sufficient food, the requisite percentage of salt, and a temperature favorable to their development. Each species which lives here is represented by the greatest number of individuals which can grow to maturity subject to the conditions which surround them, for among all species the number of individuals which arrive at maturity at each breeding period is much smaller than the number of germs produced at that time. The total number of mature individuals of all the species living together in any region is the sum of the survivors of all the germs which have been produced at all past breeding or brood periods; and this sum of matured germs represents a certain quantum of life which enters into a certain number of individuals, and which, as does all life, gains permanence by means of transmission. Science possesses, as yet, no word by which such a community of living beings may be designated; no word for a community where the sum of species and individuals, being mutually limited and selected under the average external conditions of life, have, by means of transmission, continued in possession of a certain definite territory. I propose the word *Biocœnosis** for such a community. Any change in any of the relative factors of a biocönose produces changes in other factors of the same. If, at any time, one of the external conditions of life should deviate for a long time from its ordinary mean, the entire biocönose, or community, would be transformed. It would also be transformed, if the number of individuals of a particular species increased or diminished through the instrumentality of man, or if one species entirely disappeared from, or a new species entered into, the community. When the rich beds of Cancale, Rochefort, Marennes, and Oléron were deprived of great masses of oysters, the young broods of the cockles and edible mussels which lived there had more space upon which to settle, and there was more food at their disposal than before, hence a greater number were enabled to arrive at maturity than in former times. The biocönose of those French oyster-banks was thus entirely changed by means of over fishing, and oysters cannot again cover the ground of these beds with such vast numbers as formerly until the cockles and edible mussels are again reduced in number to their former restricted limits, because the ground is already occupied and the food all appropriated. The biocönose allows itself to be transformed in favor of the oyster, by taking away the mussels mentioned above, and at the same time protecting the oysters so that the young may become securely established in the place thus made free for them. Space and food are necessary as the first requisites of every social community, even in the great seas. Oyster-beds are formed only upon firm ground which is free from mud, and if upon such ground the young swarming oysters become attached in great numbers close together, as happened upon the artificial receptacles in the Bay of Saint-Brieux, their growth is very much impeded, since the shell of one soon comes in contact with that of another, and they are thus unable to grow with perfect freedom. Not only are they impeded in growth in this manner, but each oyster can obtain less nourishment when placed close together than when lying far apart. . . .

In our seas, with their equitable temperature, a mild winter, followed by a spring and summer with the temperature much higher than usual during spawning time, is especially favorable to the production of a vast number of embryos. All living-members of a social community hold the balance with their organization to the physical conditions of their biocönose, for they live and propagate notwithstanding the influence of all external attractions, and notwithstanding all assaults upon the continuance of their individuality. Although every species is differently organized, in each the different forces act together for the growth and maintenance of the individual, and although each species has from this fact its own

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*From *βιος*, life, and *κοινόειν*, to have something in common.

organic equivalent, yet they all possess the same (balancing) power for the totality of the external conditions of life of their biocönose. Hence all species must respond to a deviation in the conditions of life from the ordinary mean by a corresponding action of their forces, so that their efficacy may increase or diminish uniformly. If favorable temperature makes one species more fruitful, it will, at the same time, increase the fertility of all the others. If more young oysters exist upon an oyster-bed because the old ones receive more warmth and food than during ordinary years, then the snails, crabs, sea-urchins, and star-fish, and all other species living together upon the bank, will also produce more young, as repeated observations have shown to be the case. But since there is neither room nor food enough in such a place for the maturing of all of the excessively large number of germs, the sum of individuals in the community soon returns to its former mean. The surplus which nature has produced by the augmentation of one of the biocönotic forces is thus destroyed by a combination of all the forces, and the biocönotic equilibrium is by this means soon restored again. Where it is possible for one to furnish suitable ground and food for an excessive number of young germs, a greater proportion of them can arrive at maturity than in an entirely natural biocönose . . . .

. . . Every biocönotic territory has, during each period of generation, the highest measure of life which can be produced and maintained there. All the organic material which is there ready to be assimilated will be entirely used up by the beings which are procreated in each such territory. Hence at no place which is capable of maintaining life is there still left any organizable material for spontaneous generation. If, in a biocönose the number of individuals which arrive at maturity would be maintained at the highest point, even though the number of breeding individuals is being artificially lessened, the natural causes which act towards the destruction of the embryos must be diminished at the same time. . . .

OECOLOGY OF PLANTS, AN INTRODUCTION TO THE STUDY OF PLANT COMMUNITIES

Eugene Warming—1909

Reprinted by permission of the publisher from the translation by Percy Groom and Isaac Balfour. Oxford, Clarendon Press, pp. 1–3, 5–6, 12–13, 131–133, 1909.

In spite of the earlier results and suggestions of community studies on animals, the impetus to and direction of community ecology came primarily through the Danish botanist Warming. In his discussion of "Oecological plant-geography" Warming formulated the several basic questions to which community ecology has given much of its attention since the turn of the century.

CHAPTER I. FLORISTIC AND OECOLOGICAL PLANT-GEOGRAPHY

Plant-geography deals with the distribution of plants upon the earth, and with the principles determining this. We may regard this distribution from two different standpoints, and accordingly may divide the subject into two branches, *floristic plant-geography* and *oecological plant-geography;* but these are merely different aspects of the same science, touching at many points and occasionally merging into one another.

Floristic plant-geography is concerned with—

1. The compilation of a 'Flora', that is, a list of species growing within a larger or smaller area. . . .

2. The division of the earth's surface into natural floristic tracts . . . according to their affinities . . . .

3. The sub-division of the larger natural floristic tracts . . . and the precise definition of these.

4. The discussion of the limits of distribution of species, genera, and families. . . .

The thoughtful investigator will not remain content with the mere recognition of facts; he will seek after their *causes.* These are, in part, *modern* (geognostic, topographical, and climatic), and, in part, *historical.* . . .

Oecological plant-geography has entirely different objects in view:—

It teaches us how plants or plant-communities adjust their forms and modes of behaviour to actually operating factors, such as the amounts of available water, heat, light, nutriment, and so forth.

A casual glance shows that species by no means dispose their individuals uniformly over the whole area in which they occur, but group them into communities of very varied physiognomy. Oecology seeks—

1. To find out which species are commonly associated together upon similar habitats (stations). . . .

2. To sketch the physiognomy of the vegetation and the landscape. . . .

3. To answer the questions—

   Why each species has its own special habit and habitat,

   Why the species congregate to form definite communities,

   Why these have a characteristic physiognomy. . . .

4. To investigate the problems concerning the economy of plants, the demands that they make on their environment, and the means that they employ to utilize the surrounding conditions and to adapt their external and internal structure and general form for that purpose. We thus come to the

consideration of the *growth-forms* of plants.

CHAPTER II. GROWTH-FORMS

Every species must be in harmony, as regards both its external and internal construction, with the natural conditions under which it lives; and when these undergo a change to which it cannot adapt itself, it will be expelled by other species or exterminated. Consequently one of the most weighty matters of oecological plant-geography is to gain an understanding of the *epharmony* of species. This may be termed its *growth-form* in contradistinction to its *systematic form*. It reveals itself especially in the habit, and in the form and duration, of the nutritive organs (in the structure of the foliage-leaf and of the whole vegetative shoot, in the duration of life of the individual, and so forth), but shows to a less extent in the reproductive organs. This subject leads us into deep morphological, anatomical, and physiological investigations; it is very difficult, yet very alluring; but only in few cases can its problems be satisfactorily solved at the present time. Thus we impinge upon the problem of the origin of different species.

But difficulty is imparted to the question under discussion by the circumstance that, not only is a species changed in form by external factors and capable of adapting itself to these, but each species is also endowed with certain hereditary tendencies, which, for inherent but unknown causes, evoke morphological characters that cannot be correlated with the present environment and are consequently inexplicable. These inherent tendencies, differing as they do according to systematic affinity, render it possible for different species, in their evolution under the influence of identical factors, *to achieve the same object by the most diverse methods*. While one species may adapt itself to a dry habitat by means of a dense coating of hairs, another may in the same circumstances produce not a single hair, but may elect to clothe itself with a sheet of wax, or to reduce its foliage and assume a succulent stem, or it may become ephemeral in its life-history. . . .

Just as species are the units in systematic botany, so are growth-forms the units in oecological botany. It is therefore of some practical importance to test the possibility of founding and naming a limited number of growth-forms upon true oecological principles. It cannot be sufficiently insisted that the greatest advance, not only in biology in its wider sense, but also in oecological phyto-geography, will be the oecological interpretation of the various growth-forms: from this ultimate goal we are yet far distant. . . .

Growth-forms may be arranged in the following six main classes, namely:

1. Heterotrophic.
2. Aquatic.
3. Muscoid.
4. Lichenoid.
5. Lianoid.
6. All other autonomous land-plants.

Heterotrophic growth-forms are shown by all holosaprophytes and holoparasites, which are undoubtedly derived from autophytes and are degenerate in form and structure. Hemi-saprophytes and hemi-parasites, on the contrary, are under the dominance of chlorophyll and exhibit the same rich diversity of form as other green plants.

Aquatic growth-forms differ from those shown by land-plants so widely as regards their morphology, anatomy, and physiology, that they must be regarded as constituting a separate class.

The muscoid and lichenoid growth-forms are seen, almost only, in mosses and lichens. Their powers of enduring extreme loss of water and of rapidly replacing this by means of absorption over the whole free surface, are oecologically very important. Associated with these characters are a number of others. The distinction between the muscoid and lichenoid types lies in the method of nutrition, as autotrophic and symbiotic respectively.

The lianoid growth-form is mainly determined by social conditions, and shows peculiar oecological and physiological characters. . . . Epiphytes, on the contrary, form an edaphic community of autotrophic land-plants including many different types.

The sixth class includes the growth-forms adopted by all the remaining autotrophic land-plants that contain chlorophyll and, as regards nutrition, are independent of other plants, and are thus *autonomous*. The growth-forms of Pteridophyta are included here, although these differ so widely from those of Spermophyta as regards their reproductive organs. . . .

Oecological botany has further to investigate the natural plant-communities, which usually include many species of extremely varied growth-form.

Certain species group themselves into natural associations, that is to say, into communities which we meet with more or less frequently, and which exhibit the same combination of growth-forms and the same facies. As examples in Northern Europe may be cited a meadow with its grasses and perennial herbs, or a beech-forest with its beech-trees and all the species usually accompanying these. Species that form a community must either practise the same economy, making approximately the same demands on its environment (as regards nourishment, light, moisture, and so forth), or one species present must be dependent for its existence upon another species, sometimes to such an extent that the latter provides it with what is necessary or even best suited to it (Oxalis Acetosella and saprophytes which profit from the shade of the beech and from its humus soil); a kind of symbiosis seems to prevail between such species. In fact, one often finds, as in beech-forests, that the plants growing under the shade and protection of other species, and belonging to the most diverse families, assume growth-forms that are very similar to one another, but essentially different from those of the forest-trees, which, in their turn, often agree with one another.

Oecological plant-geography has also to inquire into the kinds of natural communities in existence, their special methods of utilizing their resources, and the frequent intimate association together of species differing in growth-form and economy. The physical and other characters of the habitat play a fundamental part in these matters. . . .

The oecological analysis of a plant-community leads to the recognition of the growth-forms composing it as its ultimate units. From what has just been said in regard to growth-forms it follows that species of very diverse physiognomy can very easily occur together in the same natural community. But beyond this, as already indicated, species differing widely, not only in physiognomy but also in their whole economy, may be associated. We may therefore expect to find both great variety of form and complexity of inter-relations among the species composing a natural community; as an example we may cite the richest of all types of communities—the tropical rain-forest. It may also be noted that the physiognomy of a community is not necessarily the same at all times of the year, the distinction sometimes being caused by a rotation of species. . . .

The different communities, it need hardly be stated, are scarcely ever sharply marked off from one another. Just as soil, moisture, and other external conditions are connected by the most gradual transitions, so likewise are the plant-communities, especially in cultivated lands. In addition, the same species often occur in several widely different communities; for example, Linnaea borealis grows not only in coniferous forests, but also in birch-woods, and even high above the tree-limit on the mountains of Norway and on the fell-fields of Greenland. It appears that different combinations of external factors can replace one another and bring into existence approximately the same community, or at least can satisfy equally well one and the same species, and that, for instance, a moist climate often completely replaces the forest-shade of dry climates.

It is evident that all these circumstances render very difficult the correct scientific interpretation, delimitation, diagnosis, and systematic classification of plant communities, especially when we consider the condition of our present knowledge—for we have only just commenced to investigate growth-forms and communities, and what we do not know seems infinite. Another difficulty, to which allusion has already been made, is to assign suitable names to the more or less comprehensive, principal or subordinate, plant-communities occurring on the Earth and imparting to the landscapes entirely different physiognomies. Nor is it easy to estimate the true significance of floristic distinctions. . . .

OECOLOGICAL CLASSIFICATION

The foregoing chapters have made it clear that the distinctions between water-plants and land-plants are deep-seated, and concern the external form as well as the internal structure. Plant-communities must therefore be grouped in the first place into aquatic and terrestrial; but between these there is no sharp boundary, for there is a group of plants, marsh-plants (*helophytes*), which, like water-plants, develop their lower parts (roots, rhizomes, and, to some extent, leaves) in water or at least in soaking soil, but have their assimilatory organs mainly adapted to existence in air, as is the case with land-plants to which they are closely allied. Helophytes give rise to special forms of communities. Yet we must include among water-plants all those plants that, like Nymphaeaceae, approximate to land-plants in so far as they have floating-leaves, which are more or less adapted to existence in air, but are nevertheless mainly designed for existence upon water.

It has already been shown that land-plants exhibit many grades of adaptation to their mode of life in contact with air, and that those which encounter the greatest difficulties in regard to securing water are termed *xerophytes;* while others are described as *mesophytes* because in some respects they stand midway between the two extremes, hydrophytes and xerophytes. The differentiation of the land-plant in one or the other direction is decided by the oecological factors, edaphic and climatic, that prevail in the *station* or *habitat*. But edaphic and climatic factors cannot be regarded separately: the plant-community is always the product of both together. The nature of a soil is also influenced by climate, and it is incontestible that climate (rainfall) calls forth the wide differences between, say, desert and tropical rain-forest. But it is far from being true that climate alone calls into existence the different communities of plants which will hereafter be defined as *formations*. Characters of the soil are of supreme importance in determining the production of formations, and they must therefore be the foundation of oecological classification. Clements, with reason, has objected to Schimper's scheme of distinguishing between climatic and edaphic formations, if indeed it was Schimper's meaning that a sharp distinction is throughout possible, and that both groups of factors are of equal potency....

When endeavouring to arrange all land-plants, omitting marsh-plants, into comprehensive groups, we meet with, first, some communities that are evidently influenced in the main by the physical and chemical characters of soil which determine the amount of water therein; secondly, other communities in which extreme climatic conditions and fluctuations, seasonal distribution of rain, and the like, decide the amount of water in soil and character of vegetation. In accordance with these facts, land-plants may be ranged into groups, though in a very uncertain manner. The prevailing vagueness in this grouping *is* due to the fact *that oecology* is *only in its infancy*, and that *very few* detailed investigations of plant-communities have been conducted, the published descriptions of vegetation being nearly always one-sided and floristic, as well as very incomplete and unsatisfactory from an oecological standpoint. . . .

THE ECOLOGICAL RELATIONS OF THE VEGETATION ON THE SAND DUNES OF LAKE MICHIGAN

Henry C. Cowles—1899

Reprinted from the Botanical Gazette 27: 95–117, 167–175, 1899.

Of the several characteristics of communities, the phenomenon of succession has had considerable study and has provided the basis for much theoretical speculation. Cowles' paper is one of the classic early ones dealing with the topic. He recognized succession to be a dynamic process and in this descriptively analytical report he attempts to translate the static scene into an ongoing phenomenon. Cowles, along with C. B. Davenport, C. A. Whitman, and C. M. Child and such graduate students as C. C. Adams and V. E. Shelford, constituted a vigorous "school" of ecology at the University of Chicago at the turn of the century, the influence of which continues in various guises today.

. . . The ecologist employs the methods of physiography, regarding the flora of a pond or swamp or hillside not as a changeless landscape feature, but rather as a panorama, never twice alike. The ecologist, then, must study the order of succession of the plant societies in the development of a region, and he must endeavor to discover the laws which govern the panoramic changes. Ecology, therefore, is a study in dynamics. For its most ready application, plants should be found whose tissues and organs are actually changing at the present time in response to varying conditions. Plant formations should be found which are rapidly passing into other types by reason of a changing environment.

These requirements are met *par excellence* in a region of sand dunes. Perhaps no topographic form is more unstable than a dune. Because of this instability plant societies, plant organs, and plant tissues are obliged to adapt themselves to a new mode of life within years rather than centuries, the penalty for lack of adaptation being certain death. The sand dunes furnish a favorable region for the pursuit of ecological investigations because of the comparative absence of the perplexing problems arising from previous vegetation. Any plant society is the joint product of present and past environmental conditions, and perhaps the latter are much more potent than most ecologists have thought. As will be shown in another place, even the sand dune floras are often highly modified by preexisting conditions, but on the whole the physical forces of the present shape the floras as we find them. The advancing dune buries the old plant societies of a region, and with their death there pass away the influences which contributed so largely to their making. In place of the rich soil which had been accumulating by centuries of plant and animal decay, and in place of the complex reciprocal relations between the plants, as worked out by a struggle of centuries, the advance of a dune makes all things new. By burying the past, the dune offers to plant life a world for conquest, subject almost entirely to existing physical conditions...

A plant society is defined as a group of plants living together in a common habitat and subjected to similar life conditions. The term is taken to be the English equivalent of Warming's *Plantesamfund*, translated into the German as *Pflanzenverein*. The term formation, as used by Drude and others, is more comprehensive, in so far as it is not synonymous. It may be well to consider the individual habitat groups in a given locality as plant societies, while all of these groups taken together comprise a formation of that type, thus giving to the word formation a value similar to its familiar geological application. For example, one might refer to particular sedge swamp societies near Chicago, or, on the other hand, to the sedge swamp formation as a whole; by this application formation becomes a term of generic value, plant society of specific value. . . .

In the following pages an attempt is made to arrange the plant societies in the order of development, the author's belief being that this order more faithfully expresses genetic relationships than any other. In the historical development of a region the primitive plant societies pass rapidly or slowly into others; at first the changes are likely to be rapid, but as the plant assemblage more and more approaches the climax type of the region, the changes become more slow. In the dune region of Lake Michigan the normal primitive formation is the beach; then, in order, the stationary beach dunes, the active or wandering dunes, the arrested or transitional dunes, and the passive or established dunes. The established dunes pass through several stages, finally culminating in a deciduous mesophytic forest, the normal climax type in the lake region. Speaking broadly, the conditions for plant life become less and less severe through all these stages, until there is reached the most genial of all conditions in our climate, that which results in the production of a diversified deciduous forest. On the beach there are to be found the most extreme of all xerophytic adaptations in this latitude, and, as one passes through the above dune series in the order of genetic succession, these xerophytic structures become less and less pronounced, finally culminating in the typical mesophytic structures of a deciduous forest.

A. THE BEACH

As the author hopes to show in a subsequent paper, the beach formations of Lake Michigan are of two distinct types. One may be called the xerophytic beach, the other the hydrophytic beach. . . .

The xerophytic beach is essentially a product of wave action and comprises the zone which is or has been worked over by the waves. Hence the beach may be defined as the zone between the water level and the topographic form produced by other agents; in the region under study the upper limit of the beach is commonly a fringe of sand dunes or a bluff of clay or gravel. The xerophytic beach in its typical expression is very naturally subdivided into three zones, which may be called the lower beach, middle beach, and upper beach. . . .

1. *The lower beach.* The lower beach has been defined as the zone of land washed by the waves of summer storms. It might almost be defined as that portion of the beach which is devoid of vegetation. Perhaps there is no flora in the temperate zone quite so sparse as that of the lower beach, unless we except bare rocks and alkaline deserts. A survey of the life conditions in this zone reveals at once the reason for the scanty vegetation. Land life is excluded because of the frequency and violence of storms; the waves tear away the sand in one spot only to deposit it in another. Even though a seed had the temerity to germinate, the young plant would soon be destroyed by the breakers. Nor is there great likelihood that seeds will find a lodgment in this unstable location. As will be seen later the seeds ripened by tenants of the middle beach are almost entirely scattered away from the lake instead of toward it. The action of both wind and wave tends to carry seeds away from the lower beach. Again, few seeds could endure the alternate extremes of cold and heat, wetting and drying so characteristic of this zone.

Water life is excluded because of the extreme xerophytic conditions which commonly prevail on the lower beach. While algæ may propagate themselves in the shallow pools or even in the wet sand during a prolonged season of wet weather, a cessation of activity if not death itself soon follows the advent of dry weather. . . .

Thus the lower beach is a barren zone between two zones of life. Below it there exist algæ and other hydrophytic forms which flourish in the fury of the breakers; above it there exists the flora of the middle beach, a flora adapted to the most intense xerophytic conditions. At no particular time, perhaps, are the conditions too severe for some type of life; vegetation is excluded because of the alternation of opposite extremes.

2. *The middle beach.* The middle beach is situated between the upper limits of the summer and winter waves, comparatively dry in summer but washed by the high storms of winter. It may also be defined as the zone of succulent annuals. The upper limit of this beach is commonly marked by a line of driftwood and débris. The instability of the beach conditions is often shown by the presence of a number of such lines, marking wave limits for different seasons. A very heavy storm will carry the débris line far up on the upper beach, to all intents and purposes carrying the middle beach just so much farther inland, as the flora of the next season testifies. Another season may be without the visitation of heavy storms and the middle beach will encroach upon the territory of the lower beach. The limits of the middle beach are altered more permanently by changes in the lower beach. In many places the lower beach is growing outwards, reclaiming land from the lake, while at other points the lake encroaches upon the land. Speaking broadly, the middle beach advances or recedes *pari passu* with the advance or recession of the lower beach. To some extent the débris lines register these changes, as their notable departure from persistent parallelism may indicate; however, there is

a considerable lack of parallelism in the débris lines of a single season, owing to variations in the direction of the wind and other factors.

The life conditions in this zone are exceedingly severe, and result in a flora of the most pronounced xerophytic characters. The fury of the winter storms as they wash over the middle beach, tearing up here and depositing there, excludes almost entirely the possibility of survival through that period. In other words, biennials and perennials are practically excluded from maturing flowers and fruits, although their vegetative structures may flourish for a single season. In the summer the xerophilous conditions are extreme. Nowhere in the dune region are the winds more severe than here; the middle beach is close enough to the lake to feel all the force of its winds and yet far enough away for the wind to pick up sand from the lower beach and bring to bear upon the flora the intense severity of the sand-blast. No flora is more exposed to the extreme desiccating influences of the summer sun than that which grows upon the bare and open beach. Even though the roots can readily penetrate to the water level, the great exposure of the aerial organs to wind and sun results in the working out of that most perfect of all xerophytic organs, the succulent leaf. Just as succulent plants inhabit deserts where no other high grade plants can grow, so, too, they are able to withstand the severe conditions of the beach. . . .

3. *The upper beach.* In the strictest sense the upper beach is not a portion of the beach at all, since it is beyond the reach of the waves; it might perhaps be called a fossil beach, but the fact that it is continuous with the beach proper seems to exclude that term, as does the recency of its fossilization. The expression fossil beach will be reserved for a formation of greater geological age and separated from the present beach by other topographic forms. Where dunes are superposed upon the beach, the upper limits of this third beach zone are quite vague, though the theoretical line of demarcation is where the sand is first accumulated by the wind. Where clay bluffs are present at the water's edge, the beach is quite narrow and the upper limit fairly well defined, though at times obscured by alluvial fans. Occasionally the upper beach approaches very close to the water's edge; this is the case where the lower and middle beaches are very narrow because of a high gradient. Sometimes the lower or middle beach zone is replaced by a tiny cliff; in such a case the upper beach may approach to the edge of this cliff. The limits of the upper beach, as of other beach zones, are constantly shifting. The lower limits are carried lakeward or landward by the waves of winter storms, but on the whole the lower limits are pushed out more and more lakeward, keeping pace with the advance of the lower beach. The shifting of the wind causes variations in the upper limits, but on the whole the dunes likewise are commonly formed more and more lakeward, as will be shown further on. The three beaches, then, shift from year to year with apparent irregularity, but there appears to be as a resultant a general progressive movement of them all out into the lake. As a whole the three beach zones slope gradually and somewhat evenly upward, toward the dunes or bluffs beyond; depressions, however, are not at all uncommon, and at times they reach down to the water level, so that a beach pool results.

The life conditions are much less severe than on the middle beach, and chiefly because of the freedom from the wave action of the winter storms. The exposure to the sun is almost as great as on the lower zones, but there is more protection from the wind because of the abundance of driftwood. . . The decay of the driftwood may also add no inconsiderable portion to the food materials of the beach plants.

The flora of the upper beach is much richer than that of the middle beach, both in species and in individuals, but here as there the vegetation is so sparse that the tone to the landscape is given by the soil. . . .

At this point it will be well to emphasize one of the fundamental principles of ecological plant groupings. It is comparatively seldom that any single species can be regarded as perfectly characteristic of a formation, while a group of five or ten species can be so selected as to enable one to detect that formation almost anywhere within a large area. No one of the above six species can be regarded as perfectly typical of the upper beach, although Lathyrus approaches such a type, but together they form an assemblage that cannot be found in any other formation, except perhaps locally on the closely related beach dunes. Even on these beach dunes which grade into the upper beach, the relative proportions existing between the above species are very different from those found on the beach, and, as will be shown later, plant species occur on these dunes which are absent from the beach altogether. . . .

THE ROLE OF ECOTYPIC VARIATION IN THE DISTRIBUTION OF THE CENTRAL GRASSLAND OF NORTH AMERICA

Calvin McMillan—1959

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Although this study is concerned with the nature of the grassland community with focus on the variation from community to community based on analysis of populations, the implications for other communities are patent. By experimental procedure and field observation the relationship of genetic and habitat gradients is assessed. McMillan's discussion should be compared with those of Clements (p. 140), Cain (p. 157), and Whittaker (p. 159). McMillan received the 1960 George Mercer Award of the Ecological Society of America for this paper, recognizing it as the outstanding contribution published by a young ecologist in the preceding two years.

Significant clues to understanding grassland distribution are provided by plant behavior. The interpretation of behavior lies in the separation of the two variables primarily affecting it: (1) the site variable, involving both differences from point to point, microhabitat, and from year to year, annual fluctuation, and (2) the genetic variable, that is, differences in responses to the same habitat due to the different genetic potentials of the individuals involved. Axiomatically, the genetic potential of an individual controls its expression in a particular site, and therefore, an individual may be potentially an early-flowering plant, but whether it flowers or not will depend upon the conditions of its environment. The transplant garden, as employed by Clausen, Keck & Hiesey and others, has been useful in providing a habitat in which the site variable is near the minimum. It has allowed the expression of genetic potentials, particularly of differences in maturity. The greenhouse, representing a minimum in site variable, has been useful in studying the effect of light period on maturity. Observations in the natural habitats have indicated the combined influence of the site variable and the genetic variable in plant behavior. . . .

The goal of the present study is to further understanding of the nature of grassland vegetation, particularly the causes of its continuity over a broad geographic area. The role of ecotypic variation in the distribution of the North American grasslands will be analyzed as the possible mechanism which has allowed an apparently uniform vegetation (i.e., the geographic repetition of combinations of certain species and genera) to be elaborated over an obviously non-uniform habitat. . . .

Studies of ecotypic variation within grassland vegetation indicate that climatic selection has yielded northern communities with individuals that can grow and mature under long day-lengths and short frost-free periods. Progressively southward are communities containing individuals that mature under shorter daylengths and longer frost-free periods. Certain of these studies also have indicated that western sites have selected individuals which can mature under a shorter frost-free period than those of eastern sites. . . .

The present transplant garden and light period studies strongly indicate a genetic basis for differences in flowering time of several species of grasses. These studies support Goodwin in his suggestion that the rate of flower bud development is determined "more by heredity than by habitat conditions." This is not intended to suggest that habitat conditions are totally ineffective, but within the broad limits of the conditions in a number of habitats, the genetic pattern which governs the relative rate of flower bud development is affected but little. . . .

The variable climatic values, different yearly dates of last killing frost in spring, yearly deviations in the precipitation pattern, and fluctuations in the yearly temperature patterns play a vital role in the selection of grassland vegatation. These deviations and fluctuations express the environmental amplitude which an individual must tolerate for continued existence, not necessarily involving reproductive processes, within a grassland community. The marked degree of variability within a species-population in grassland vegetation is a visible response to the highly variable nature of the habitat. . . .

The role of climate in vegetational selection is nowhere more evident than in grassland studies. The community behavior in a northern community (e.g. Devils Lake, N. D.) is obviously attuned to a shorter frost-free period than are communities to the south. The recurrence of a variable frost-free period, shorter in duration than those to the south, has resulted in the selection of populations able to reproduce under these shortened conditions. The climatic variability of late spring frost or early fall frost will result some years in failure to flower or a failure to produce mature seed in a number of populations. This yearly variability will seldom present an extreme that the population cannot tolerate, in part or as a whole. The selection of individuals with characteristics of early maturity in a number of different species and the selection of opportunist species showing early maturity (such as Stipa) allows survival in a habitat where there is a variable but short frost-free period.

The length of the light period has played a role in the latitudinal distribution of the grassland vegetation. Olmsted's work on Bouteloua and Larsen's work on Andropogon have suggested the selective influence of the light period. From their studies, longer day requirements by clones from northern communities and shorter day requirements in southern communities are suggested. The light period studies presented above on a limited number of experimental communities provide further evidence of the selective influence of day length. . . .

The yearly moisture deviations undoubtedly have played a vital role in selection. An extremely variable moisture pattern during the warmer part of the year would favor later flowering among species of characteristic late maturity. This type of selective pressure is more common in southern and eastern communities. The unreliability of a moisture pattern makes the higher average precipitation of these communities deceiving. The northern and western communities with a lower annual precipitation tend to have greater reliability in moisture pattern. The greatest precipitation during the early part of the growing season has aided in the selection of individuals with early maturity.

Less variation in time of flowering is noted both within populations and between populations in areas with a greater likelihood of annual recurrence of similar habitat conditions. The magnitude of the variation is intensified under the extended and erratic moisture patterns of southern communities.

The taller growth form of many species occurs in the southern and eastern communities. For survival in these areas of higher rainfall, the later maturity types have been selected for the advantage of greater vegetative height as well as greater height of flowering culms. . . .

The temperature sequences during the warmest part of the growing season have a remarkable similarity across much of the grassland area. Higher day temperatures may occur in the western sites along with somewhat cooler night temperatures. During July, in the normally hottest week, much of the eastern grassland area has a normal daily range of temperature from 12° to 17°C. Slightly greater temperature variation is shown to the west and slightly less in the southeastern sites.

The communities of the north and west are subjected to cooler night temperatures than are found in the transplant garden. The warmer nights of the garden may have resulted in more rapid development than would have occurred in the native habitat. However, much of the flowering within material transplanted from northern and western communities occurred during June, when the temperature sequence at Lincoln would greatly resemble the July sequence of the northern communities. There is a further possibility that slower activity by southern types resulted from the somewhat cooler temperature sequence of the Lincoln garden.

The selective role of soil is significant within the overall action of climatic influence. Certain local modifications in behavior gradients are undoubtedly affected by soil. While the date of growth resumption in an area may be highly variable from one year to the next, differences in soil may modify time of growth resumption locally in any one year. Although not clearly demonstrated, local soil differences may result in the selection of earlier or later maturing types. The recurrence of edaphically-controlled habitat conditions might be expected to result in genetic adjustments within populations. . . .

These studies of ecotypic variation clarify certain aspects of the nature and distribution of grassland vegetation, for they indicate that a certain combination of species in two areas may result from different phenomena. Through natural selection in different areas, groupings of individuals referable to the same species represent fundamentally different communities. The present studies indicate that the uniformity within a type of grassland community is apparent only as it reflects the geographic repetition of certain species combinations and the continuity of a physiognomic type.

The grassland climax as proposed by Clements, rather than being rendered untenable by studies of ecotypic variation, becomes more easily understood in its application to the present distribution of grasses. The mechanism for the broad distribution of the grassland climax involves the intimate relationship between the genetic gradients within vegetation and the habitat gradients, of which the selective influence of climate is paramount. The recognition of site climax communities as proposed by Whittaker receives additional support through an evaluation of ecotypic variation. The result of selection within the grassland climax has been the creation of geographic continua made up of site climax communities which are self-maintaining and have reached a partial stability and high productivity under the existing habitat pressures.

The origin of grasslands becomes more complex and intriguing in the light of ecotypic studies. Problems of origin are not easily reduced to simple considerations of grassland versus forests. These grassland communities are surviving in North America because grasses, admirably suited to the highly variable nature of the habitat, have received selective preference. The complex nature of grassland vegetation and the selective forces which have produced it indicate a closer affinity than is possible by a relatively simple one factor explanation, such as the creation and maintenance through burning. Although fire has undoubtedly played a significant role in grassland history, the action of fire is not basically directed toward the vital populational processes which have molded grassland vegetation. The patterns of variation within the grassland and presumably within forests have resulted from complex selective processes.

Genetic diversity among members of a species was probably characteristic of pre-glacial grasslands in North America. Toward the north, natural selection had probably favored early-maturing types with an ability to grow and reproduce under long day conditions. With the advance of glaciation, it is likely that these forms did not migrate southward because of the light period conditions and because of the narrow limits of population variation within northern types. It is likely that variants within communities toward the south continued to survive due to their adjustment to southern light period conditions and to their breadth of behavioral variation.

Following the retreat of glaciation, the northward advance of grassland vegetation could be greatly facilitated by conceiving three primary distribution points, a western semi-montane area such as that now found near Colorado Springs, Colo., a southern area such as that in southern Oklahoma and northern Texas, and an area in southeastern United States. The expansion of grasslands into South Dakota, North Dakota, and adjacent Canada would have been greatly facilitated by the availability of western forms with their pre-adaptation to a short growing period. The mid-latitude, semi-montane types, such as those near Colorado

Springs, are able to reproduce under longer light periods and many of these forms could be successfully used to re-populate northern areas with a minimum of selection. From southern communities, adapted to growth under shorter day conditions, but broad in their range of intra-populational variation, could have come material for moving rapidly across Kansas and into eastern Nebraska. From southeastern communities could have come the potential for moving into eastern sites. . . .

The problem of getting a particular aggregation of species together is largely a speculative matter. Often suggestions that a relict community was "left behind" implies that it remains unchanged. To this point the results of this study should be directed. The distribution of grassland vegetation in the past was undoubtedly based on the same fundamental principles which govern its present distribution. The key to its distribution, widespread or in relicts, is undoubtedly due to the variants which make each stand of grassland at a given time fundamentally different from any other stand. . . .

This demonstration of grassland potential is an introductory example of the nature of variation that produces harmony between vegetation and its habitat. It further suggests that as a natural resource, the preservation of grassland potential calls for more than the protection of one large grassland area or even two. It demands the intelligent management of grassland potential by the protection of grassland remnants throughout central North America.

STUDIES ON CONNECTICUT LAKE SEDIMENTS. I. A POSTGLACIAL CLIMATIC CHRONOLOGY FOR SOUTHERN NEW ENGLAND

Edward S. Deevey, Jr.—1939

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The study of the succession of communities in geological time provides still another dimension to ecology. Analysis of pollen provides the basis for interpretation based on a uniformitarian principle of comparable climatic conditions being correlated with comparable plant assemblages in the past and present. Some of the perplexing problems of this aspect of paleoecology are evident in this paper.

The many factors which contribute to uncontrolled variation in single pollen spectra, such as sampling error, local variation in flora, peculiarities in composition of sediment, preservation of pollen, and over-representation of certain species, have been frequently discussed, particularly by Voss, Erdtmann, and Wodehouse, and need not be elaborated here. Most investigators, however, have confined their attention to the retention of pollen by peat, and although Groschopf has considered flotation and lacustrine sedimentation of pollen, differences in permeability to water and sinking speed among various types of pollen have not been adequately studied. It is obvious that conditions in the epilimnia and hypolimnia of lakes are not equally favorable for the preservation of pollen, and it is quite conceivable that the chestnut pollen owes its fossilization in the hypolimnion of Linsley Pond to the low redox potential prevailing in that region. . . .

The over-representation of pine in pollen-spectra, due to excessive production or transportation from afar or both, creates a difficulty which is comparatively easy to circumvent when recognized. Although it has hitherto proved impossible to obtain a quantitative estimate of this disparity, its order of magnitude is indicated by some figures given by Wodehouse, who found that a forest containing 0.2 per cent pine was represented in modern lake sediments by a pine pollen percentage of 25 per cent.

But in spite of all the factors which prevent complete reliance on pollen-spectra as accurate indices of the composition of the surrounding forest, the major postglacial changes in vegetation can be inferred, provided that a sufficiently large number of profiles is available for a region. Since not all changes in vegetation are due to climatic variation, the chronologist must distinguish those events of climatic importance, which may be expected to occur over wide areas, from those of local or edaphic significance. Complete fulfillment of this task is impossible in the present state of North American pollen-analytical research. . . .

HISTORY OF THE CONNECTICUT VEGETATION

In its broad outlines the vegetational history of the New Haven region has already been treated, and the more precise details may be referred to students of plant ecology for elaboration. The need for more exact knowledge of the botanical corollaries of a decaying ice-sheet has been indicated; the relative extent and duration of the late-glacial tundra must be discovered, as well as the center of refuge and speed of migration of the coniferous trees which were the first certainly known invaders of southern Connecticut. With the acquisition of this information ecologists will be in a position to answer the interesting question raised by Flint —whether forests did not grow upon thin stagnant ice near the margin of the waning glacier, as they do today on the Malaspina glacier in Alaska, thus prolonging the period of melting.

Since deglaciation Connecticut has passed through a vegetational stage climatically equivalent to eastern Canada (northern coniferous forest), and through a stage edaphically, if not climatically similar to certain areas in the Lake States (pine climax). Evidence of both periods exists today in relict areas, the most notable examples being spruce-bogs and sandy pine plains or "edaphic deserts." With the onset of favorable climatic conditions the forest gradually acquired its characteristic mesophytism. The subsequent fluctuations in moisture régime, though perceptible in the pollen profiles and evidently general throughout eastern North America, have been of subordinate importance, and quite probably have found floristic expression only in critical localities, where physiography has permitted.

The sequence observed in southern Connecticut, unimpressive though it may be in comparison to the temperature changes attendant upon deglaciation, gains considerable interest from the discussion of the composition of the "original forest type." Bromley and Raup have presented evidence that the New England forest in colonial days

was somewhat less mesophytic than studies of virgin forest remnants suggest. Bromley concluded from a search of the historic records that the pre-colonial type in southern New England was an open oak-hickory forest, and attributed the maintenance of this condition to the frequent fires set by the Indians. Raup, while criticizing Bromley's sources on the basis of unfamiliarity with the interior, and questioning the importance of the aboriginal pyromania, reached the same conclusion after study of the accounts of more adventurous and presumably more reliable observers. He therefore supposed the "xerothermic period of about 3000 years ago" to have been responsible for the inferred xerophytism, and considered that the persistence of the forest until such recent times was due to an inherent stubbornness in the face of a moister climate. Proceeding to a stimulating review of the evidence for a postglacial climatic optimum accompanied by widespread dry conditions, Raup was able to find reasonable arguments for assigning to this period such diverse phenomena as the "Virginian element" in the New England-Acadian marine fauna and the diffusion of Old Algonquian cultures into New York and New England from the mound-builder area.

The concept of widespread and long-continued persistence of forests not adjusted to the prevailing climate logically leads to a negation of ecological theory, and Raup's hypothesis must be construed to include only local areas of relict vegetation. The possibility that such areas were encountered by early American travellers cannot be questioned, whether or not the delay in succession be attributed to fire. That climatic elements propitious for the development of oak-hickory forest obtained in southern Connecticut at the time of the climatic optimum can be determined by reference to the pollen-diagrams. . . .

PLANT SUCCESSION, AN ANALYSIS OF THE DEVELOPMENT OF VEGETATION

Frederic E. Clements—1916

Reprinted by permission of the publisher from Carnegie Institution of Washington Publication 242, pp. 1–512 (pp. 3–4, 6–7, 98–99, 105–107), 1916.

Besides containing an account of the various forces and characteristics in succession, this monograph presents a philosophic viewpoint about the nature of the community which has prompted considerable discussion. In Clements' view, the plant community is an organic entity having attributes describable in terms of an individual (see also Braun-Blanquet, p. 147). Further controversy has arisen over his concept that all succession leads to one climax type in a given area owing to the pervading influence of climate. The major opposing viewpoint to Clements' organismic concept is expressed by Gleason (see p. 153) and Ramensky (see p. 151); Whittaker (p. 159), among others, suggests an alternate theory on the nature of the climax. Professor Clements was one of the most influential early American ecologists both as a faculty member at the Universities of Nebraska and Minnesota and as a research associate of the Carnegie Institution.

CONCEPT AND CAUSES OF SUCCESSION

The formation an organism. The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant.

Universal occurrence of succession. Succession is the universal process of formation development. It has occurred again and again in the history of every climax formation, and must recur whenever proper conditions arise. No climax area lacks frequent evidence of succession, and the greater number present it in bewildering abundance. The evidence is most obvious in active physiographic areas, dunes, strands, lakes, flood-plains, bad lands, etc., and in areas disturbed by man. But the most stable association is never in complete equilibrium, nor is it free from disturbed areas in which secondary succession is evident. An outcrop of rock, a projecting boulder, a change in soil or in exposure, an increase or decrease in the water-content or the light intensity, a rabbit-burrow, an ant-heap, the furrow of a plow, or the tracks worn by wheels, all these and many others initiate successions, often short and minute, but always significant. Even where the final community seems most homogeneous and its factors uniform, quantitative study by quadrat and instrument reveals a swing of population and a variation in the controlling factors. Invisible as these are to the ordinary observer, they are often very considerable, and in all cases are essentially materials for the study of succession. In consequence, a floristic or physiognomic study of an association, especially in a restricted area, can furnish no trustworthy conclusions as to the prevalence of succession. The latter can be determined only by investigation which is intensive in method and extensive in scope.

Viewpoints of succession. A complete understanding of succession is possible only from the consideration of various viewpoints. Its most striking feature lies in the movement of populations, the waves of invasion, which rise and fall through the habitat from initiation to climax. These are marked by a corresponding progression of vegetation forms or phyads, from lichens and mosses to the final trees. On the physical side, the fundamental view is that which deals with the forces which initiate succession and the reactions which maintain it. This leads to the consideration of the responsive processes or functions which characterize the development, and the resulting structures, communities, zones, alternes, and layers. Finally, all of these viewpoints are summed up in that which regards succession as the growth or development and the reproduction of a complex organism. In this larger aspect succession includes both the ontogeny and the phylogeny of climax formations. . . .

Processes in succession. The development of a climax formation consists of several essential processes or functions. Every sere must be initiated, and its life-forms and species selected. It must progress from one stage to another, and finally must terminate in the highest stage possible under the climatic conditions present. Thus, succession is readily analyzed into initiation, selection, continuation, and termination. A complete analysis, however, resolves these into the basic processes of which all but the first are functions of vegetation, namely, (1) nudation, (2) migration, (3) ecesis, (4) competition, (5) reaction, (6) stabilization. These may be successive or interacting. They are successive in initial stages, and they interact in most complex fashion in all later ones. In addition, there are certain cardinal points to be considered in every case. Such are the direction of movement, the stages involved, the vegetation forms or materials, the climax, and the structural units which result. . . .

Developmental aspect. The essential nature of succession is indicated by its name. It is a series of invasions, a sequence of plant communities marked by the change from lower to higher life-forms. The essence of succession lies in the interaction of three factors, namely, habitat, life-forms, and species, in the progressive development of a formation. In this development, habitat and population act and react upon each other, alternating as cause and effect until a state of equilibrium is reached. The factors of the habitat are the causes of the responses or functions of the community, and these are the causes of growth and development, and hence of structure, essentially as in the individual. Succession must then be regarded as the development or life-history of the climax formation. It is the basic organic process of vegetation, which results in the adult or final form of this complex organism. All the stages which precede the climax are stages of growth. They have the same essential relation to the final stable structure of the organism that seedling and growing plant have to the adult individual. Moreover, just as the adult plant repeats its development, *i. e.*, reproduces itself, whenever conditions permit, so also does the climax formation. The parallel may be extended much further. The flowering plant may repeat itself completely, may undergo primary reproduction from an initial embryonic cell, or the reproduction may

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be secondary or partial from a shoot. In like fashion, a climax formation may repeat every one of its essential stages of growth in a primary area, or it may reproduce itself only in its later stages, as in secondary areas. In short, the process of organic development is essentially alike for the individual and the community. The correspondence is obvious when the necessary difference in the complexity of the two organisms is recognized.

Functional aspect. The motive force in succession, *i. e.*, in the development of the formation as an organism, is to be found in the responses or functions of the group of individuals, just as the power of growth in the individual lies in the responses or functions of various organs. In both individual and community the clue to development is function, as the record of development is structure. Thus, succession is preeminently a process the progress of which is expressed in certain initial and intermediate structures or stages, but is finally recorded in the structure of the climax formation. The process is complex and often obscure, and its component functions yield only to persistent investigation and experiment. In consequence, the student of succession must recognize clearly that developmental stages, like the climax, are only a record of what has already happened. Each stage is, temporarily at least, a stable structure, and the actual processes can be revealed only by following the development of one stage into the succeeding one. In short, succession can be studied properly only by tracing the rise and fall of each stage, and not by a floristic picture of the population at the crest of each invasion. . . .

Stabilization. The progressive invasion typical of succession everywhere produces stabilization. The latter is the outcome of greater occupation due to aggregation and migration and of the resulting control of the habitat by the population. In other words, stabilization is increase of dominance, culminating in a stable climax. It is the mutual and progressive interaction of habitat and community, by which extreme conditions yield to a climatic optimum and life-forms with the least requirements are replaced by those which make the greatest demands, at least in the aggregate. So universal and characteristic is stabilization that it might well be regarded as a synonym of succession. It has the advantage of suggesting the final adult stage of the development, while succession emphasizes the more striking movement of the stages themselves.

Causes of stabilization. The essential cause of stabilization is dominance. The latter is partly due to the increasing occupation of a bare area, but is chiefly the result of the life-form. The occupation of annuals in an initial or early stage of a secondary sere is often complete, but the dominance is usually transient. Effective dominance can occur only when the prevailing life-form exerts a significant reaction, which holds the population in a certain stage until the reaction becomes distinctly unfavorable to it, or until the invasion in force of a superior life-form. Dominance is then the ability of the characteristic life-form to produce a reaction sufficient to control the community for a period. Dominance may mean the control of soil factors alone, primarily water-content, of air factors, especially light, or of both water and light. Initial life-forms such as algæ, lichens, and mosses are characteristic but not dominant, since the reaction they produce prevents control rather than gives it. This is the essential difference between the initial and the final stages of succession. While both react upon the habitat, the reaction of the one favors invaders, that of the other precludes them. The reactions of the intermediate stages tend to show both effects. At first the reaction is slight and favors the

aggregation of occupants; then it becomes more marked and produces conditions more and more favorable to invasion. On the other hand, when the reaction is distinctly unfavorable to the occupants, the next stage develops with greater rapidity. Each stage is itself a minor process of stabilization, a miniature of the increasing stabilization of the sere itself. Reaction is thus the cause of dominance, as of the loss of dominance. It makes clear the reason why one community develops and dominates for a time, only to be replaced by another, and why a stage able to maintain itself as a climax or subclimax finally appears. Thus, reaction furnishes the explanation of stabilization, as it does of the successive invasions inherent in succession.

Relation to the climax. The end of the process of stabilization is a climax. Each stage of succession plays some part in reducing the extreme condition in which the sere began. It reacts to produce increasingly better growing conditions, or at least conditions favorable to the growth of a wider range of species. This is equivalent to reducing an excess of water-content or remedying a lack of it. The consequence is that the effect of stabilization on the habitat is to bring it constantly nearer medium or mesophytic conditions. Exceptions to this occur chiefly in desert regions, though they may occur also in water areas, where processes of deposit and erosion alternate. The effect upon the plant population is corresponding. The vast majority of species are not pioneers, *i. e.*, xerophytes and hydrophytes, but mesophytes with comparatively high but balanced requirements for ecesis. For this reason the number of species and individuals grows larger in each succeeding stage, until the final dominance of light, for example, becomes restrictive. At the same time the life-forms change from those such as lichens and submerged plants with a minimum of aggregate requirements to forms with an increasingly high balanced need. The period of individual development increases as annuals are succeeded by perennials and the latter yield to dominant shrubs and trees. The final outcome in every sere is the culmination in a population most completely fitted to the mesophytic conditions. Such a climax is permanent because of its entire harmony with a stable habitat. It will persist just as long as the climate remains unchanged, always providing that migration does not bring in a new dominant from another region. . . .

PRINCIPLES OF CLASSIFICATION OF THE SPRUCE COMMUNITIES OF EUROPEAN RUSSIA

V. N. Sukatchew—1928

Reprinted by permission of the publisher from Journal of Ecology **16**: 1–18, 1928.

Representative of community studies in Russia is this early paper by Sukatchew (or Sukachev) who was associated with the Forestry Institute at Leningrad. The major features of much Russian community study are evident in this paper, namely the relating of narrowly defined associations to environmental gradients as components of ecological series.

. . . we are able to trace the following five typical habitats of spruce forest: (1) more or less nutritive clayey loam or sandy loam soils, well drained in places with sufficiently pronounced relief, in the north for the most part adjoining the rivers, (2) similar soils but becoming already moory, with worse drainage, less developed relief, in the north for the most part situated farther from the rivers, (3) soils still more moory, without differentiated relief, level, situated still farther from the rivers. These three types of habitat form, as it were, a connected series. Besides these there are (4) the bottoms of narrow valleys where there is excessive moisture, but the water is for the most part in motion, and (5) places carrying (for the north) exceptionally rich soils, most often connected with neighbouring limestone rocks.

According to these five fundamental habitats of the spruce we can divide the spruce forest into five types which differ in the phytosociological structure of their communities, as well as in the size of the trees. A conspicuous character is the presence and composition of the lower strata of the community.

Therefore the following scheme of classification for spruce associations may be given:

1. Relief adequately developed; site well drained, soils more or less nutritive, loams, clays or sandy loams, not moory—*Piceeta hylocomiosa*.
2. Relief less developed, sites feebly drained, soils the same, but already somewhat moory—*Piceeta polytrichosa*.
3. Relief undeveloped, surface flat, site not drained, soils moory—*Piceeta sphagnosa*.
4. Bottom of depressions with moory soils, but running water—*Piceeta herbosa*.
5. Sites with nutritive well-drained soils, for the most part in the neighbourhood of limestone deposits—*Piceeta fruticosa*.

Each of these types is composed of a series of plant communities. . . .

Considering the different communities formed by the spruce, we see that the *Piceeta hylocomiosa* represent communities, the interrelation of whose elements is particularly perfect. This type is the most persistent, and must be regarded as the most fundamental of the spruce communities, for not only has the dominant tree a great influence on the rest of the vegetation of the community which is very closely adapted to this influence, but the dominant itself is closely adapted to the conditions so brought about: for instance, the carpet of characteristic mosses is specially suited to the regeneration of the spruce from seed. The closeness of these interrelations of different parts of

the community is the criterion of high social integration, and probably of long duration.

In this respect the first place among all the communities belonging to this group must be assigned to the *Piceetum oxalidosum* and the *P. myrtillosum*. These two, which are, on the whole, near each other morphologically, appear to be also genetically close. The development of phytosociological integration has proceeded in both during thousands of years. But nevertheless the *P. myrtillosum* is the starting point of a series of communities, which departing from *P. oxalidosum* and passing through *P. polytrichosum*, leads to the extermination of spruce forest, a series connected with the process of conversion of forest into bog, and terminating, so far as Piceeta are maintained, with the *P. sphagnosum*, which is, in its turn, followed by the succession to Pinetum, and the ultimate replacement of forest by bog.

This process, the succession accompanying the increasing bogginess of the soil, is observed in spruce forests where the soil is not enriched by springs or the freshets of small rivers and brooks which so abundantly water our northern forests. The most complex of these wet forests and at the same time those in which the growth of the spruce is best is the *Piceetum fontinale* (Russian *log*). The further development of this association has two possible courses. As the river develops its valley and the bed becomes deeper, the soil becomes better drained, and in the course of time the community may pass over to one of the group of *Piceeta hylocomiosa*. In the second case, where the drainage is bad and peaty deposits continue to accumulate, the feeding of the upper layers of soil by springs and floods decreases every year. This causes an impoverishment of the herb stratum, an increased development of the mosses and a worse growth of the spruce, which result in the replacing of *Piceetum fontinale* by *P. sphagnoso-herbosum* (*sogra*), whose natural course of development again leads in the course of time to sphagnum bog with stunted crooked pine. Thus in this second case we have a series of successions analogous with that mentioned above (*P. oxalidosum* to *P. sphagnosum*). The two series in the end lead to the same thing—the extermination of the spruce forests and their replacement by moss bogs. In both cases the process, according to the concomitant external conditions, may proceed sometimes more rapidly, sometimes more slowly, lingering or stopping at certain stages. . . .

From the preceding characterisation of spruce forest it is evident that the fundamental type, in which the most important features of spruce forest are expressed most completely, is the group of *Piceeta hylocomiosa*. The other groups include either communities formed under conditions of excessive moisture, not characteristic of the usual life conditions of the spruce, or under the influence of conditions nearer to those of broad-leaved forest, and consequently also not characteristic of the spruce. We see, as it were, three fundamental ecological series of communities, originating from the group *P. hylocomiosa*. One of them is connected with the beginning of excessive water supply together with stagnation of the water, i.e. a worse supply of oxygen to the roots and deterioration in the supply of mineral food—this is the series *P. hylocomiosa*—*P. polytrichosa*—*P. sphagnosa*. The second series, too, is connected with excessive moisture, but the water is in motion and the roots, consequently, are sufficiently supplied with oxygen, while the mineral food supply is not always improved—this is the series *P. hylocomiosa*—*P. herbosa*. The third series is connected with an improvement of the mineral food supply without a change in the water régime of the habitat or (and this is the commoner case) with a certain increase of dryness and consequently without deterioration and even with improvement of the supply of the roots with oxygen—this is the series *P. hylocomiosa*—*P. fruticosa*.

In each of these groups there is one principal community in which the characters of the group are represented most typically. Next to this come the communities connected with conditions usually already changing in the direction of an approach to the conditions of another group. This leads to an approach of the structure of the community of the given group to the structure of another group. Here within the limits of each group series of two categories are suggested:

(1) *ecological-edaphic series* connected with a change of the nature of the soil within the limits of a definite region.

(2) *ecological-geographic*, or more exactly *ecological-climatic* series.

Each series will represent vicarious associations. . . .

On closer examination of these series we see that they correspond not only with the ecological but also the genetical connections of the communities. The process of succession takes its course along these very series. So the series, let us call it the series A, connected with alteration of the nutritive mineral content of the soil and the absence of excessive moisture is in its essence a succession from oak forest communities to typical Piceeta, being the result of the impoverishment of the soil due to the influence of the forest communities themselves and characterised by the clearing from the Piceeta of the alien elements of broad-leaved forest. This series leads to the formation of the most characteristic association of Piceeta—*P. oxalidosum*.

The series B, leading in the direction of increased moisture and its stagnation, is the succession of Piceeta to bog. If the impulse to its appearance is usually given by external factors, its whole further course is connected with a change of environment produced by the plant communities themselves. Thus their own action on the environment is the chief cause of the succession of communities in this series.

The median series C, on the contrary, has its origin in communities dependent on excessive soil moisture and running water; it is a succession whose fundamental cause is the change in the external factors of existence, the influence of the plant communities on the environment taking no considerable part in the process. In this series, developing parallel to the development of the valley of the rivulet or brook and the deepening of its bed, and hence to the draining of the bottom of the valley, we have a succession to the community *P. fontinale* from communities of the group *P. hylocomiosa* and ultimately from *P. oxalidosum*.

If the succession from *P. fontinale* is determined, not by a gradual drying of the soil, but by impeded flow of water and gradual accumulation of peat deposits, we shall have the series D, i.e. the succession from *P. fontinale* to *P. sphagnosa* and then to pure bog. . . .

If we take into consideration that the series of Piceeta under discussion represent also successive changes of the structure (morphology) of the communities and the interaction of the members of which they are composed, we shall be fully justified in calling them also phytosociological series. . . .

Thus we see that the establishment of ecological series of spruce communities gives us a clear idea of the phytosociological and genetical interrelations between these communities.

Further, the same series allow us to foresee, within certain limits, the character of new communities, not yet known or described, but which may be detected in the future. Thus communities connecting *P. oxalidosum* and *P. fontinale* are not yet known, but no doubt they must exist since there are thinkable transitional natural conditions between those peculiar to these communities in their typical forms. Since we are already acquainted with the extreme members of this series we may in some degree imagine the composition and structure of intermediate links yet to be discovered. The same applies also to the other series, where we are far from knowing all the members.

Hence, it seems to me, it can be seen that the method of ecological series may have a much more extensive significance than that of elucidating the connection of the vegetation series with environment. In its further development it promises to be of assistance in the construction of such a system of communities, as will offer not only a harmonious picture of the phytosociological and genetical interrelations between them, but will allow us to foretell the existence and character of communities not yet described.

REMARQUES SUR L'ÉTUDE DES GROUPEMENTS DE PLANTES

Josias Braun-Blanquet and Ernst Furrer—1913

Reprinted by permission of the authors and publisher from Bulletin Société Languedocienne de Geographie **36**: 20–41, 1913. Translated by Lawrence Wilson, 1964.

The Braun-Blanquet system of plant community analysis views plant associations as having objective reality like a species and as being describable in comparable ways. The major features of the Braun-Blanquet system which are developed in this essay gave rise to the so-called Zurich-Montpellier "school" of phytosociology which continues under his leadership. This tradition of emphasis on floristic composition and "character-species" has had the widest following in Europe and a strong, although frequently modified, influence elsewhere. An opposing view is given by Cain (see p. 157), a reassessment of the Braun-Blanquet system is given by J. J. Moore (1962. *Journal of Ecology* **50**: *761–769*), *and a thorough review of phytosociology is given by R. W. Becking* (1957. *Botanical Review* **23**: *411–488*).

The study of plant groups (*synecology*) embraces four principal points of view: 1. *Descriptive synecology* studies the floristic composition of plant groups; 2. *Physiological synecology*, ecology in the limited sense of the word, explains the relations of cause and effect existing between the groups and the external factors (climatic, edaphic and biotic); 3. *Geographical synecology* is concerned with the distribution of the groups and with their regional and altitudinal differences; 4. *Genetic synecology*, finally, studies the differences existing between present-day groups of plants and their past. It is concerned, therefore, with group evolution.

The only solid basis for any study of this nature is a perfect knowledge of the floristic composition of the synecological unit. This unit is designated as *association* in both French and English, *Assoziation* or *Bestand* in German, and *associazione* Italian. Defined, association "*is a plant group having a determined floristic composition, presenting a uniform physiognomy, growing under uniform stational conditions*" (Flahault & Schroeter), *and possessing one or several characteristic species.*

We have felt obliged to introduce into this definition the notion of *characteristic* species (*Charakterpflanzen*, Gradmann's *Leitpflanzen*). *These are species which are localized without exception, or very nearly so, within a given association;* they may be regarded as the surest floristic expression of the ecology of the group.

The concept of characteristics is not new, but it has been subordinated until now to the notion of dominant species. Now, the dominants are often ubiquitous, growing in very different places; consequently, they tell us very little about the ecological character.

The reverse is true when it is a question of characteristic species. When someone mentions the *Aristida pungens*, *Cardamine alpina*, the *Epipogon aphyllum*, *Vaccinium Oxycoccus*, and *Carex pauciflora*, we know at once that we are dealing with an association of shifting sand, snow coombs, spruce, and sphagnum-bogs. Why? Because he has named characteristics of these associations. Needless to say, the characteristics may be dominants at the same time. . . .

Each site presenting uniform life conditions and bearing one or several characteristic species, realizes, in our opinion, a definite association. The association may be an organized community from which each member benefits, but it need not necessarily be such. It is utterly impossible for us to ascertain just how far the competition among the species extends, just as it is impossible to determine the value of the utilitarian tie which binds the individuals together. Steep rock formations, often considered to be an environment of open vegetation, are sometimes carpeted with lichens, algae, or mosses forming with a few phanerogams living in the tufts of moss or in the clefts of the rocks a close-knit community obedient to the general laws of association. . . .

A balance between plant competition on the one hand and the external factors of the moment on the other marks this more or less lasting stage which characterizes a constituted association. The duration of the state of balance and of the optimum development of the association varies greatly. This duration is almost indefinite for associations due to climate (associations of arctic countries and lofty summits in particular); it is ephemeral in the case of certain transitory associations (the association of *Myricaria* and willows on alluvial lands along rivers), and especially so in the case of cultural or semi-cultural associations (wheat-, flax-, hemp-, etc. fields, forest clearings). The presence of the characteristics, which generally appear only after the complete establishment of the association and which are the first to disappear as soon as the conditions of life undergo a change, allow us to consider the association as definitely established. . . .

It goes without saying that one or several species characteristic of an association in a given region may not be characteristic elsewhere, if the climate differs ever so little. A characteristic species of the second order may become of first order on approaching the limits of its area. *Betula nana*, strictly localised in our high marshes of the Jura and the pre-Alps where it finds its northern limits, grows abundantly almost everywhere in the mountains of Norway and Lapland. . . .

The comparative geographical study of associations must reveal these facts and, at the same time, make known to us the absolutely characteristic species, never going beyond the limits of the area of association.

It is evident that one cannot distinguish all possible associations solely by means of characteristic species. That is possible only in the case of 1) *temporary groupings*, associations on the way to becoming fixed and possessing no characteristic traits; 2) *mixed associations*, the product of a reciprocal penetration by several associations. . . . The associations are infinite, and the phytogeographer may rest satisfied with describing the most apparent of these mixed associations, those which cover a more or less large area. Let us not lose sight of the fact that the primary object in the study of groups is not an inventory of each and every clump of earth, but the search for *a unit comparable to the species, capable of serving as a basis for research in comparative geographical botany*, and for synecological investigations. . . .

As Mr. Flahault noted as early as 1900, the study of associations requires one to take into account not only characteristic species, but also the complete inventory of its flora.

The floristic inventory of the association includes *characteristic* species of the first and second order (*Charakterpflanzen*), *constants* (*Brockmann-Jerosch's Konstanten*) appearing in at least half the surveys of a given association, *accessory* species figuring again in a fourth of the surveys of more or less accidental species. To designate the density of each species in the association, use is made either of the terms *solitariae*, *sparsae*, *coposae*, *gregariae* and *sociales*, introduced by *Drude*, or of the figures 1 to 10. The figure 10 designates the absolute dominance of a species in a closed growth. . . .

As regards a *method* to follow in distinguishing the associations, in individualising and delimiting them, *two procedures* are at the disposal of the beginner who is still unfamiliar with characteristic species. . . .

The first means, *floristic* in character, consists of provisionally delimiting the given stands by the use of one or more dominant species. Nothing is easier than the task of distinguishing and delimiting these stands. . . .

The second method of arriving at a knowledge of associations is essentially *topographic*. The phytogeographer selects well-defined topographical units evidencing a vegetation having the same ecological character: rock formation on the shady side of a mountain, the flood-plains of a river, ponds of stagnant water, the low-water shore of a lake (Gadeceau), stone-falls, etc. He takes an inventory and determines what are the characteristic species for each of these topographic sites. . . .

As regards assigning names to associations, we recommend the practice of Messrs. Flahault and Schroeter who favor using a name drawn from the vernacular, or adding the suffix *-etum* to the generic or specific name of the dominant species. Let us only avoid exaggerating the value of the dominants whose name the association bears. Basically, they represent but one element of the association; wherever they appear *en masse*, one must make certain that the other elements are to be found as well, for only on this condition can one speak of association. The fact that very often the dominant species is at the same time characteristic in no way matters. . . .

Every association is made up of individuals (*Einzelbeständen*, *Einzelassoziationen*) just as the species is composed of individuals which to us seem identical. The two terms are, therefore, philosophical abstractions which must be made to figure in a kind of diagnosis by basing each on the common characters binding individuals of the same type together. There are clearly distinct associations (those of beeches, of *Salicornia*, of *Aristida pungens*); others behave like polymorphous species and their delimitation is difficult. Since one speaks of transitory species, one could speak of mixed associations and indefinite associations. These last cover, even in middle Europe, and there because of man's influence, a considerable area. . . .

The study of the plant groups of limited area must, of necessity, rest upon the fundamental units. "Associations are the solid base of botanical geography" (*Flahault*).

But the study of classification procedures which enable one to draw up a tentative inventory and to outline an initial synthesis of results achieved is to be urged.

One of the most frequently recommended means consists of grouping the associations in keeping with their physiognomic and ecological affinities. The notions of "*formation*" and "*vegetation-type*" in the sense defined by the participants in the Brussels Congress correspond to this tendency.

> After all, it seems that we may consider a formation as a contemporary expression of certain life-conditions which is *independent* of floristic composition (p. 6), and a formation is composed of associations which *differ in their floristic composition*, but which correspond to like stational conditions and assume analogous forms of vegetation.

To Mr. Schroeter's way of thinking and Mr. Warming's, this notion of formation, based solely upon physiognomy and ecology, about corresponds to a kind of systematics.

This last manner of looking at the matter is not ours. For us the method which most nearly conforms with the principles governing this study seems to consist in grouping the associations according to *their floristic affinities* and to reason with respect to the associational groups thus established as one would with respect to the associations themselves. The term superior to the association would then be the associational group, *not given by the same life-form*, but by a *similar floristic composition, by the presence of common characteristics*.

As for the term "formation," also frequently used by German authors to express what we here designate under the name of *associational group*, it seems desirable to us to use it in its original sense. . . .

Formation would then be the physiognomic and ecological expression of the association, as the biological form is the physiognomic and ecological expression of the species. . . .

DIE GRUNDGESETZMÄSSIGKEITEN IM AUFBAU DER VEGETATIONSDECKE

L. G. Ramensky—1926

Reprinted by permission of the publisher from Botanisches Centralblatt N. F. 7: 453–455, 1926.) an abstract by Selma Ruoff of the original Russian article which appeared in Westnik Opitnogo Dela Woronej, 1924. Translated by Edward J. Kormondy, 1964.

The concepts of Clements (p. 140), Braun-Blanquet (p. 147), Sukatchew (p. 144), and others, are developed on the premise of a fundamental unit of natural communities. These association units are considered to be discrete, describable and amenable to categorization and classification into a hierarchical structure. In sharp contrast and dissent are the views of Ramensky and Gleason (p. 153). In this abstract of Ramensky's exposition, the two major principles, that of vegetational continuity (i.e., nondiscrete association units) and species individuality, are succinctly expressed. It is noteworthy that the Russian Ramensky, the American Gleason and the Frenchman Lenoble developed these principles simultaneously yet independently of each other.

. . . The author follows the concept of the coenose introduced by Gams and gives the following definition: "A coenose is an ecologically limited, locally homogeneous plant grouping (the concrete individual coenose) or the totality of plant groups of ecological and floristic delimited similarity (the abstract coenose); the historical and topological resemblance of such groups can be different." He repudiates the phytosociological and plant population viewpoints because of their anthropomorphisms and characterizes the behavior of the coenobiota as decidedly "antisocial.". . .

In considering the moderating law of the coenose one must take into account the production of propagation units (seeds, spores) and their importance for the maintenance of the coenose; in herbaceous coenoses (meadows, steppes and moors) repair appears to follow vegetative processes and the importation of propagation units to play no great part. But this very vegetative propagation often produces a zone of mixing at the limits of two coenoses. In the instance of stenocoenoses, in which the area is segmented into many small lobes or is entirely divided, the influence of these anomalous limits manifests itself mostly over their entire surface; they must not, therefore, be compared directly with macrocoenoses, which homogeneously cover continuously great surfaces (meadows, steppes).

The historical factor is of relevance for a coenose only in the background when an equilibrium is reached between the other factors and the structure of the community, be it a continuous absolute balance (the ideal extreme case) or a dynamic balance which shifts itself slowly in parallel with alterations in external conditions. A diffuse distribution of species is a characteristic of attained equilibrium and at the same time an indication of a high degree of competition among the plants.

The plant cover cannot be understood as a mass phenomenon through the analysis of small parts (neither from uniform coenoses); the ecological moderating law in vegetation composition can be determined only through the summarizing of statistical surveys of greater areas and then the obtaining of averages. The surface appearance of a coenose, that is the minimal area in which the correct moderation law makes itself felt numerically, can be very different. In the smallest coenose the significant factor in development of the surface appears to be frequency, whereas abundance is more important in larger coenoses. . . .

On the basis of his numerous plant surveys coupled with different methods, the author comes to the conclusion that the plant cover modifies itself continuously in space. The sharp boundary between coenoses is an individual instance in need of special explanation (influence of culture, discontinuous alteration of other factors, etc.) The rule of continuity in the three dimensional composition of plant cover will be supplemented and clarified by the rule of ecological individuality of plant species; each species reacts to the other unique factors and occurs as an independent member in the coenose; there are no two groups which end with identical abundance in a coenose. The possible combinations for the association are very great and each one is a group of individual coenoses in which the greatest abundance and the greater annual change is attained.

The kaleidoscopic alteration in the spatial composition of meadows, steppes and low moors (woods and sphagnum bogs appear homogenous) speaks decidedly against a classification of inflexible units. "Groups are not stable, only the rules of plant combinations" and these support research. As a goal of investigation, the author denotes an arrangement of coenoses in ecological sequence with the corresponding abundance curves of their species and according to the coordinates of their factors. The ideal would be the combining of all isolated coenose studies into a uniform coordinated scheme.

THE INDIVIDUALISTIC CONCEPT OF THE PLANT ASSOCIATION

H. A. Gleason—1926

Reprinted by permission of the publisher from Bulletin of the Torrey Botanical Club **53**: 7–26, 1926.

It is Gleason's interpretation that each community is unique, having arisen randomly by environmental selection of those reproductive parts of plants which happen to enter the area in question. In questioning the objective reality of plant associations, Gleason exerted considerable influence, particularly among American workers. His view is inherent in the continuum concept of Curtis (1951. *Ecology* **32**: *476–496) and Whittaker (1951. Northwest Science* **25**: *17–31) and with some emendation in the natural area concept of Cain (see p. 157). In recognition of his outstanding influence in ecology, the Ecological Society of America honored him as Eminent Ecologist in 1959.*

As a basis for the presentation of the individualistic concept of the plant association, the reader may assume for illustration any plant of his acquaintance, growing in any sort of environment or location. During its life it produces one or more crops of seeds, either unaided or with the assistance of another plant in pollination. These seeds are endowed with some means of migration by which they ultimately come to rest on the ground at a distance from the parent plant. Some seeds are poorly fitted for migration and normally travel but a short distance; others are better adapted and may cover a long distance before coming to rest. All species of plants occasionally profit by accidental means of dispersal, by means of which they traverse distances far in excess of their average journey. Sometimes these longer trips may be of such a nature that the seed is rendered incapable of germination, as in dispersal by currents of salt water, but in many cases they will remain viable. A majority of the seeds reach their final stopping-point not far from the parent, comparatively speaking, and only progressively smaller numbers of them are distributed over a wider circle. The actual number of seeds produced is generally large, or a small number may be compensated by repeated crops in successive years. The actual methods of dispersal are too well known to demand attention at this place.

For the growth of these seeds a certain environment is necessary. They will germinate between folds of paper, if given the proper conditions of light, moisture, oxygen, and heat. They will germinate in the soil if they find a favorable environment, irrespective of its geographical location or the nature of the surrounding vegetation. Herein we find the *crux* of the question. The plant individual shows no physiological response to geographical location or to surrounding vegetation *per se*, but is limited to a particular complex of environmental conditions, which may be correlated with location, or controlled, modified, or supplied by vegetation. If a viable seed migrates to a suitable environment, it germinates. If the environment remains favorable, the young plants will come to maturity, bear seeds in their turn, and serve as further centers of distribution for the species. Seeds which fall in unfavorable environments do not germinate, eventually lose their viability and their history closes.

As a result of this constant seed-migration, every plant association is regularly sowed with seeds of numerous extra-limital species, as well as with seeds of its own normal plant population. The latter will be in the majority, since most seeds fall close to the parent plant. The seeds of extra-limital species will be most numerous near the margin of the association, where they have the advantage of proximity to their parent plants. Smaller numbers of fewer species will be scattered throughout the association, the actual number depending on the distance to be covered, and the species represented depending on their means of migration, including the various accidents of dispersal. This thesis needs no argument in its support. The practical universality of seed dispersal is known to every botanist as a matter of common experience.

An exact physiological analysis of the various species in a single association would certainly show that their optimal environments are not precisely identical, but cover a considerable range. At the same time, the available environment tends to fluctuate from year to year with the annual variations of climate and with the accumulated reactionary effects of the plant population. The average environment may be near the optimum for some species, near the physiological limit of others, and for a third group may occasionally lie completely outside the necessary requirements. In the latter case there will result a group of evanescent species, variable in number and kind, depending on the accidents of dispersal, which may occasionally be found in the association and then be missing for a period of years. . . .

Nor are plants in general, apart from these few restricted species, limited to a very narrow range of environmental demands. Probably those species which are parasitic or which require the presence of a certain soil-organism for their successful germination and growth are the most highly restricted, but for the same reason they are generally among the rarest and most localized in their range. Most plants can and do endure a considerable range in their environment.

With the continuance of this dispersal of seeds over a period of years, every plant association tends to contain every species of the vicinity which can grow in the available environment. Once a species is established, even by a single seed-bearing plant, its further spread through the association is hastened, since it no longer needs to depend on a long or accidental migration, and this spread is continued until the species is eventually distributed throughout the area of the association. In general, it may be considered that, other things being equal, those species of wide extent through an association are those of early introdnction which have had ample time to complete their spread, while those of localized or sporadic distribution are the recent arrivals which have not yet become completely established.

This individualistic standpoint therefore furnishes us with an explanation of several of the difficulties which confront us in our attempts to diagnose or classify associations. Heterogeneity in the structure of an association may be explained by the accidents of seed dispersal and by the lack of time for complete establishment. Minor differences between neighboring associations of the same general type may be due to irregularities in immigration and minor variations in environment. Geographical variation in the floristics of an association depends not alone on the geographical variation of the environment, but also on differences in the surrounding floras, which furnish the immigrants into the association. Two widely distant but essentially similar environments have different plant associations because of the completely different plant population from which immigrants may be drawn.

But it must be noted that an appreciation of these conditions still leaves us unable to recognize any one example of an association-type as the normal or typical. Every association of the same general type has come into existence and had its structure determined by the same sort of causes; each is independent of the other, except as it has derived immigrants from the other; each is fully entitled to be recognized as an association and there is no more reason for regarding one as typical than another. Neither are we given any method for the classification of associations into any broader groups. . . .

Let us consider next the relation of migration and environmental selection to succession. We realize that all habitats are marked by continuous environmental fluctuation, accompanied or followed by a resulting vegetational fluctuation, but, in the common usage of the term, this is hardly to be regarded as an example of succession. But if the environmental change proceeds steadily and progressively in one direction, the vegetation ultimately shows a permanent change. Old species find it increasingly difficult or impossible to reproduce, as the environment approaches and finally passes their physiological demands. Some of the migrants find establishment progressively easier, as the environment passes the limit and approaches the optimum of their requirements. These are represented by more and more individuals, until they finally become the most conspicuous element of the association, and we say that a second stage of a successional series has been reached.

It has sometimes been assumed that the various stages in a successional series follow each other in a regular and fixed sequence, but that is frequently not the case. The next vegetation will depend entirely on the nature of the immigration which takes place in the particular period when environmental change reaches the critical stage. Who can predict the future for any one of the little ponds considered above? In one, as the bottom silts up, the chance migration of willow seeds will produce a willow thicket, in a second a thicket of *Cephalanthus* may develop, while a third, which happens to get no shrubby immigrants, may be converted into a miniature meadow of *Calamagrostis canadensis*. . . .

It is a fact, of course, that adjacent vegetation, because of its mere proximity, has the best chance in migration, and it is equally true that in many cases the tendency is for a environment, during its process of change, to approximate the conditions of adjacent areas. Such an environmental change becomes effective at the margin of an association, and we have as a result the apparent advance of one association upon another, so that their present distribution in space portrays their succession in time. The conspicuousness of this phenomenon has probably been the cause of the undue emphasis laid on the idea of successional series. But even here the individualistic nature of succession is often apparent. Commonly the vegetation of the advancing edge differs from that of the older established portion of the association in the numerical proportion of individuals of the component species due to the sorting of immigrants by an environment which has not yet reached the optimum, and, when the rate of succession is very rapid, the pioneer species are frequently limited to those of the greatest mobility. It also happens that the change in environment may become effective throughout the whole area of the association simultaneously, or may begin somewhere near the center. In such cases the pioneers of the succeeding association are dependent on their high mobility or on accidental dispersal, as well as environmental selection.

It is well known that the duration of the different stages in succession varies greatly. Some are superseded in a very short time, others persist for long or even indefinite periods. This again introduces difficulties into any scheme for defining and classifying associations. . . .

The sole conclusion we can draw from all the foregoing considerations is that the vegetation of an area is merely the resultant of two factors, the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment. As a result, there is no inherent reason why any two areas of the earth's surface should bear precisely the same vegetation, nor any reason for adhering to our old ideas of the definiteness and distinctness of plant associations. As a matter of fact, no two areas of the earth's surface do bear precisely the same vegetation, except as a matter of chance, and that chance may be broken in another year by a continuance of the same variable migration and fluctuating environment which produced it. Again, experience has shown that it is impossible for ecologists to agree on the scope of the plant association or on the method of classifying plant communities. Furthermore, it seems that the vegetation of a region is not capable of complete segregation into definite communities, but that there is a considerable development of vegetational mixtures. . . .

In conclusion, it may be said that every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. Its disseminules migrate everywhere, and grow wherever they find favorable conditions. The species disappears from areas where the environment is no longer endurable. It grows in company with any other species of similar environmental requirements, irrespective of their normal associational affiliations. The behavior of the plant offers in itself no reason at all for the segregation of definite communities. Plant associations, the most conspicuous illustration of the space relation of plants, depend solely on the coincidence of environmental selection and migration over an area of recognizable extent and usually for a time of considerable duration. A rigid definition of the scope or extent of the association is impossible, and a logical classification of associations into larger groups, or into successional series, has not yet been achieved. . . .

CHARACTERISTICS OF NATURAL AREAS AND FACTORS IN THEIR DEVELOPMENT

Stanley A. Cain—1947

Reprinted by permission of the author and publisher from Ecological Monographs **17**: 185–200, 1947.

With certain emendations, Cain's viewpoint follows that of Gleason (see p. 153). The value of this excerpt, however, is in its succinct consideration of the limitations of the phytosociological viewpoint (see Braun-Blanquet, p. 147) concerning the objective reality of plant associations. Cain also suggests an alternate conceptual basis for plant community studies.

The drawing of a parallel between associations and species is not tenable. The members of a species are related by descent and reproduce their kind; the members of an association have no such genetic connection. They arrive at their more or less similar state by the successional route from a variety of beginnings, and reproduce their kind only by the most devious and protracted labors. The individuals of the most variable species have nothing like the motley array of antecedents that bring forth the associations. In the work of the phytosociologists there is a grouping of associations into alliances and orders in a manner similar to the grouping of species into genera, families, etc., but if the basic unit lacks objective reality, the hierarchy must be even less sound.

The phytosociologists who have the strongest faith in the integrity of the association believe that the floristic assemblage is the primary feature of the association, and that the association can be studied in terms of its constant species or its characteristic species just as the species can be studied morphologically without preoccupation with its biology or ecology. For the Scandinavian phytosociologists the association is characterized by the constant species, a certain number of species for any association which reoccur in every quadrat and every stand examined with a regularity of 80 to 90 per cent, and usually with a considerable dominance or coverage. These are highly social or gregarious species. For the members of what we may call the Braun-Blanquet school of plant sociology, which includes most of the phytosociologists from Holland to Italy and from France to Poland and the Balkans, the association is recognized by its characteristic species which have a high degree of fidelity to the floristic assemblage which is called the association. These may also be called indicator species.

These investigators only secondarily concern themselves with questions of life form and the physiognomy of the plant communities, and with the relations of the communities to the habitat. Their approach is in the first place a floristic one. Let us examine further whether the association is definable in these terms.

There are certain facts in nature which the plant geographer can study. The species are facts, in most instances at least; and the areas of the species are facts which can be considered with reasonable preciseness. Environments are facts. There are recognizable habitats. They can be rather well described for small enough areas; but we are confronted with merging phenomena and larger areas are progressively more poorly delimitable. The life form of a species is a fact, and the physiognomy of an aggregation of species is describable within acceptable limits. But does the association in the abstract, characterized by its floristic assemblage and the special features of certain of its members have a comparable objective reality? I do not bring into question the reality of the stand, which is the concrete example of an association (the synécie of Gaussen, the association individual of Braun-Blanquet, the fragment of association of DuRietz), but the reality of the abstraction—the association as a composite of the several association individuals.

In nature there is a habitat. It is occupied by plants of a number of species. The number of species composing the community of the habitat and just which ones they are depend upon several factors: the available flora, the ecological characteristics of the species that are available, the chances of and the time which has been available for dissemination into the area of the habitat, the competition among the members, and their life forms. The individual plant community has objective reality—sharply delimited at its borders if the habitat changes strongly in a short space, poorly delimited if the habitat changes gradually over a greater space. But so far as the flora of the community is concerned, it is the result of the superposition of areas of the species. Each species of the stand will have its individual and often quite different total area, and each has a more or less different ecological amplitude and modality. They live together in the particular community because they chance to have overlapping areas and are biologically successful in the particular habitat.

When comparing different stands that are similar, unless one blindfolds himself by preconceptions of the reality of the association in the abstract, it is soon realized that the farther removed one stand is from another the more different are their floristic assemblages, as Gleason emphasized in his paper on the individualistic association. Here arise the questions which have always plagued the phytogeographers: how different can two association individuals be and still belong to the same association? What is to be required in the way of constant or characteristic species?

The investigations of the phytosociologists produce results with the appearance of a high degree of accuracy, with statistical data on coverage, frequency, density, constancy, and fidelity, in impressive tabular comparisons of stands of an association. And yet it seems to me, having tried these methods myself, and without impugning the honesty of the investigators, that there is more artifice here than science in the selection of stands for representation of the association. . . .

My general conclusion is that plant geographers have a largely unfinished task in the adequate study and description of existing vegetation, and that much of their work must be in terms of natural areas. In this connection I am wholly in agreement with Edward H. Graham who says that the term "natural area" is a very useful and realistic one although incapable of exact definition. One virtue of the term is its very indefiniteness. Like the general term "community," it does not commit one to the necessity of certain difficult decisions; but it is an even broader term than community, suggesting a recognition of the simultaneous action of all operative factors and the joint existence of such diverse phenomena as organisms and different physical states of the atmosphere, soil, etc. *A natural area, then, is a geographic unit of any order of size with sufficient common characteristics of various sorts to be of some practical usefulness in biogeography*. Wildlife managers, grazing and forest administrators, and other working ecologists approach such a usage in their common practice.

It does not follow from this argument that students should discontinue

their efforts toward analytic studies of the environment, the fauna and flora, and the communities, nor that efforts toward synthesis and classification are to be abandoned. It is suggested, however, that it be kept in mind that single-factor operation does not occur in biological nature, that the environment apparently can not be completely analyzed, and that diverse analytic data can not at present be synthesized back again into anything like the natural whole of the ecosystem. Elsewhere I have called this the "Humpty-Dumpty problem," and "All the King's horses and all the King's men can't put Humpty-Dumpty back together again." When all these limitations of phytogeographical study are kept in mind, one finds that many useful approximations can be made, coincidences observed between biological phenomena and physical ones, and classifications erected. The temptation of standardization and the erection of supposedly universal systems is more easily avoided and natural objects are not cut or stretched to fit the bed of Procrustes. . . .

A CONSIDERATION OF CLIMAX THEORY: THE CLIMAX AS A POPULATION AND PATTERN

R. H. Whittaker—1953

Reprinted by permission of the author and publisher from Ecological Monographs **23**: 41–78, 1953.

In this well documented paper, Whittaker analyzes the two opposing concepts concerning the nature of the climax community and proposes an alternate. Whittaker views the climax as a population pattern corresponding to the pattern of environmental variables. In certain respects this concept is an amalgam of the monoclimax of Clements (p. 140) and polyclimax concepts; in other respects it brings the study of the community into the framework of the ecosystem approach described in the next section. For a thorough analysis and evaluation of the classification of natural communities Dr. Whittaker's paper (Botanical Reviews **28**: *1–239, 1962) is highly recommended.*

. . . In place of the monoclimax, three major propositions on the nature and structure of climaxes and their relativity may be formulated:

1. The climax is a steady-state of community productivity, structure, and population, with the dynamic balance of its populations determined in relation to its site.

2. The balance among populations shifts with change in environment, so that climax vegetation is a pattern of populations corresponding to the pattern of environmental gradients, and more or less diverse according to diversity of environments and kinds of populations in the pattern.

3. Since whatever affects populations may affect climax composition, this is determined by, or in relation to, all "factors" of the mature ecosystem—properties of each of the species in-

volved, climate, soil and other aspects of site, biotic interrelations, floristic and faunistic availability, chances of dispersal and interaction, etc. There is no absolute climax for any area, and climax composition has meaning only relative to position along environmental gradients and to other factors.

The following secondary or corollary propositions are suggested as of possible significance for synecological research:

A. Propositions of climax determination. Climax composition is determined, as indicated in (3) above, by all factors which are intrinsic to, or act upon, the population on a sustained or repeated basis and do not act with such severity as to destroy the climax population and set new succession in motion. Factors determining climax population will thus include:

1. Characteristics of the populations involved. The balance among populations will necessarily be determined by the kinds of populations entering the community and by the peculiarities of each. The place of a given species in the balance will depend on its ability to maintain a population against environmental resistance, determined by its genetics. Since genetics of species may change along gradients, changing genetics of the species should be part of the background of changing balance among species along gradients. Since a species differs genetically from one place to another, these genetic differences may influence the different places or degrees of importance of a species in climax balances.

2. Climate. All climaxes are adapted to climate (and hence are climatic climaxes); but the climate which acts on and determines a climax population is necessarily the local climate of its site, not the general climate of an area.

3. Site. The climax balance is determined by environment of a specific site, and the climax population has meaning only for a kind of site. For the early assumption that climax was independent of site may be substituted the hypothesis that any significant difference in site implies a difference in climax population. As all climax stands occur on sites having some kind of topographic relation to other sites, all climaxes are topographic, as well as climatic, climaxes.

4. Soil. Soil parent-material, as arbitrarily separated from other aspects of site, is a climax determinant; for the traditional assumption that vegetation on any soil parent-material converges to the regional climax may be substituted the hypothesis that any significant edaphic difference, physical or chemical, may imply difference in climax population. All climaxes are edaphic, as well as topographic and climatic, climaxes. . . .

5. Biotic factors. Natural communities are organic systems of plants and animals in environment; in much of what has been said about the vegetation pattern might be substituted the more awkward phrase natural-community pattern. In the functioning system the balances among plant populations exist in relation to, and are partially determined by, animals acting directly on the plants through consumption and trampling, indirectly through soil, etc. All climaxes are biotic climaxes, balanced in relation to their animal populations. . . .

6. Fire. Periodic burning is an environmental factor to which some climaxes are necessarily adapted. In the absence of fire the climax populations might well develop to something different; but such an ideal climax is not on the ground subject to measurement. The burning may cause some population fluctuation, and it may then be difficult to draw a distinction between fire (and windfall, etc.) as environmental factors to which some climaxes are adapted and as disturbances introducing still greater instability and initiating successions in others. A continuous series from climaxes fully adapted to fire and scarcely affected by a single burn, through climaxes in which minor changes are produced by each burning and those in which the vegetational structure is altered, but not destroyed, to climaxes which are entirely destroyed by a single fire may be expected. Without attempting to draw a clear line where none exists, it may be thought that, in fire-adapted climaxes, fire either does not destroy the dominant populations or does not cause replacement of the dominant growth-form as in other climaxes.

7. Wind. Although wind is a part of the environment of all climax stands, some stands may show marked effect of wind on composition or physiognomy, especially, toward higher latitudes and altitudes and other stands may have windfall permitting reproduction as a normal part of their relation to environment. The combination of sea-wind and salt-spray is particularly effective in producing locally distinctive climaxes along coasts.

8. Other factors. Various other factors may determine locally what self-maintaining or climax populations can exist in a site including, for terrestrial communities, snow-effects, fog as it affects the coastal redwoods, the fog vegetation of the Peruvian desert, and the mossy or cloud forests of many tropic mountains, salt water and tide levels affecting such coastal vegetation as mangrove swamps, although these, not simply seral communities which disappear to be replaced by a climax, may be incompletely stabilized, migratory vegetation in the sense of Crampton, communities of shifting equilibrium in the sense of Alechin.

9. Floristics and faunistics. Climax composition will necessarily be determined by the plant and animal species available in the area. Climax populations in similar environments will vary from place to place for floristic and faunistic reasons, and a recognized climax population type or association will usually have a limited range.

10. Chance. Climax composition must, finally, be considerably affected by chances of dispersal and occupation and of population interactions.

B. Propositions on climax relativity. It has been indicated that the climax population has meaning only relative to the environmental conditions of its site, and the inappropriateness of dichotomous logic has been indicated in several connections. The following aspects of climax relativism are suggested:

1. Climax and succession. There are no distinctions between climax and succession or, more concretely, between climax and seral stands, except those of relative instability and relative significance of directional change. This relativity was expressed by Cowles, "As a matter of fact we have a variable approaching a variable rather than a constant," and has been indicated by various authors.

2. Climax and seral species. There is no reason why some species should not be both seral and climax. Climax species may dominate succession as in desert successions; a species may enter a stand in succession and persist at a different population level into the climax; a species may enter climax stands on one kind of site in an area but only seral stands on another, and may enter climax stands in one area but only seral stands in another. While some species seem clearly seral or climax under specific conditions, for many it is a question of relative position along the time-scale of succession under particular circumstances.

3. Climax and seral types. Types, associations, or stratal communities defined by species may, correspondingly, be seral in one circumstance and

climax in another or may be self-maintaining and successional at different times. Untenable is a familiar kind of logic: Type A (e.g. pines) is being replaced by type B (oak-hickory) on site number 1 (a north slope); therefore, type A growing on site number 2 (a southwest slope) will also ultimately be replaced by type B. Chain-linking of successional observations without regard for site (Type A was seen replacing type B, B replacing C, C replacing D, etc.; therefore, B, C, etc. are all seral to A) is also untenable.

C. Propositions on climax recognition. A number of criteria have been used either explicitly or implicitly in the traditional recognition of monoclimaxes. It may be profitable to examine some of these which seem no longer tenable in this section and to discuss some which seem applicable in the next section.

1. Unity of growth-form. "The first criterion is that all the climax dominants must belong to the same major life form, since this indicates a similar response to climate and hence, a long association with each other." The world-wide occurrence of communities of mixed dominance and of several physiognomic types within a given climatic area may be sufficient commentary.

2. Area of climax. The monoclimax has been thought to be climax of a definite geographic region, so that the climax could be recognized by essential similarity over a large area and occurrence of one or more of the dominants throughout the area. Areal extent is irrelevant to achievement of the climax steady-state, however; and there is almost no lower limit on the area of a climax type. Such restricted types as the summit balds of mountains, Appalachian shale barrens, and southeastern granite flat-rocks, pines on altered andesite in Nevada, stands as limited as the small marsh in a morainic depression and patch of "alpine rain-forest" at the head of a glacial valley described by Ives are, if self-maintaining, climax vegetation. Removal of size restrictions on climax types has, with the variety of populations present, the consequence that distinguishable climax types of the United States are essentially innumerable. While this must certainly be the case, stand types can very well be grouped subjectively into associations-abstract for some purposes.

3. Convergence on different sites. Convergence of different successions to similarity of vegetation on different sites is a criterion based on the first monoclimax assumption. The convergence is only partial, however, leading to climax vegetation which may be expected to differ on different types of sites. Granting the significance of such partial convergence on differing sites as occurs, it is not a basis of recognizing the self-maintaining condition.

4. Upland position. While the vegetation type prevailing on the uplands of an area may be more extensive than other types in the area, it is no more climax than they. Points 2, 3, and 4, may have meaning in relation to the prevailing climax rather than in recognition of the climax steady-state.

5. Physiography. Convergence was achieved through both biological and physiographic processes in the interpretation of Cowles, but physiographic processes act through too long a period to be directly related to the climax as a biological phenomenon. The consequence of erosion of an area down to a peneplain would be not to produce a uniform environment uniformly occupied by one of the vegetation types already in the area, but to produce a less diverse surface of different climate occupied by other kinds of climax stands. In spite of the impossibility of clearly separating biotic and physiographic, autogenic and allogenic succession, it is the former, biological process, and not the hypothetical result of the latter, physical process, which is the concern of synecology. Since some stands, at least, may reach the climax state in almost any area whether physiographically young, mature, or old, occupation of topographically mature sites may bear little relation to climax recognition.

6. Soil maturity. While relations among climate, vegetation, and soil are recognized, these apply more to vegetation as growth-form than to vegetation as populations. As aspects of the ecosystem, vegetation and soil are, together, related to environment and one another, with neither simply determining the other. Soil, vegetation, and environment may consequently be expected to vary together, *pari passu*, through time and space; which is to say that the ecosystemic pattern varies in time and space and hence the coupled aspects of the ecosystem selected for study vary in parallel, though in no simple manner. The alternative definitions of soil maturity, in terms of profile development or of equilibrium with environment, are partially independent, and profile maturity of soil is not in itself a criterion of the climax state. Conditions of some sites in any area and of most sites in some areas may be such as to prevent soils from developing to profile maturity as, in an extreme case, the "infantile" soils of the arctic. Soils in other areas may, in the course of development to the self-maintaining state, become degraded and podsolized so that a less productive vegetation and apparently less mature soil characterize the climax.

7. Mesophytism. The most mesophytic type of an area is no more "the climax" than other, less mesophytic, self-maintaining stands. The course of succession will usually, though not necessarily, lead from apparently less mesophytic to apparently more mesophytic types; but it does not follow that a given xerophytic or hydrophytic stand is becoming more nearly mesophytic. A more mesophytic species is not to be chosen over a less mesophytic one as climax except as it is shown, for a given type of site, that the former replaces the latter. A balance between more and less mesophytic species may exist on sites too dry to support a purely mesophytic stand without implying succession.

8. Tolerance. Succession will often involve more tolerant species replacing less tolerant ones, but in an area the more tolerant species may be climax on one site and the less tolerant ones on another. There is no reason why such intolerant species as the pines should not form climaxes, either in open stands in which they may reproduce continuously or in denser stands in which they may reproduce only periodically. There is no reason why more and less tolerant species should not form mixed climax stands, provided the stand is open enough to permit the latter to reproduce, or is sufficiently opened at times by fires, windfalls, etc., to permit the less tolerant species to reproduce. . . .

9. Higher growth-form. Apart from the difficulty of using criteria of higher and lower growth-forms, vegetational stature, at least, will usually increase through the succession into the climax. There is no reason, however, why heath, bog, or grassland should not in some areas replace forest as climax even though such replacement violates our usual assumptions of trends through succession and of forests as climaxes wherever forests occur. There is no reason why such simple and open communities as those of cliffs, hammadas, alpine rocks and scree, and arctic fjaeldmark should not form self-maintaining stands or why the simple algae of a mountain lake should not form a "primitive" climax.

10. Relation to successional trends. As indicated for stature and soil, so for

productivity, diversity, etc. These features of communities will usually increase through the succession to the climax, but there is no reason why, in a given case, the usual direction should not be reversed. In general, climax status should be determined not by abstract or generalized conceptions of what should be ultimate, but by what populations actually replace other populations and then maintain themselves. . . .

THE CONCEPT OF THE ECOSYSTEM

One of the ends to which science directs itself is the development of an encompassing theory. In ecology, the principle of the ecosystem provides such a unifying framework within which specialized study at the individual, population and community level can be meaningfully conducted.

The concept of the ecosystem as an ecological unit comprising living and nonliving components interacting to produce a stable system is not new. Those who have read more or less consecutively in this anthology have recognized that many ecologists discussed the interrelations of a particular biotic assemblage with its environment and the interrelations of biotic units within the assemblage. However, the theoretical development of the concept and the implementing of studies oriented to its clarification are largely products of the period since 1940, *the major impetus occurring in the 1950's.*