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H.A. Gleason and the Individualistic Hypothesis Revisited

Summary

Henry A. Gleason's individualistic concept has commonly been misconstrued as asserting that the community is a random collection of species, and the species are responding solely to the physical or abiotic envi-

ronment. Neither of these is true, but both persist in the ecological literature as part of a false dichotomy of the nature of community, impeding understanding of ecological communities. This essay reviews some of the misunderstandings of Gleason's concept by ecologists and historians in the context of his ecological work.

In his essay, "Ecological fragmentation in the Fifties," Michael Barbour (1995) described something "profoundly important" in ecology that took place in the 1950s. This "revolution" was a major event in the then long-running, and still very much with us, debate between proponents of the "holistic ecology" of Frederic Clements and the "reductionist," Henry Allan Gleason. According to Barbour, by 1960, the majority of ecologists had changed their concept of community from the "organismic," even "super-organismic," concept of Clements to the "individualistic" concept of Gleason. This revolution was not accomplished without breaking a few eggs, if not hearts or heads. It is certainly true that Gleason's individualistic concept, generally ignored before the 1950s, was resurrected and widely accepted during and after the 1950s, and Gleason's reputation as an ecologist was secured (McIntosh 1967, 1975, 1995, Nicolson 1984, 1990, 2000). The revolution, like many revolutions, was not complete. Adherents of Clementsian-like organismic conceptions persist in ecology, and a preference for holism over reductionism is widely evident, often independently of any direct influence from Clements's writings. Loucks (1998) noted the need to seek an equilibrium between the two, "thus the challenge for ecosystem studies is to balance a desire to explain outcomes by looking at parts of complex systems (reductionist view) against the desire to understand how the parts work together in a fully functioning system (holistic view)."

As is not uncommon in debates about a well-established idea or paradigm and a contrary paradigm, there has been a tendency to polarize the viewpoints (Underwood 1986) and, in some cases, to misinterpret them. The term "paradigm," derived from the work of Thomas Kuhn (1970), has been commonly used to refer to the major positions in this debate, indicating that they are not merely competing scientific theories, but differing conceptions of the nature of the underlying natural reality and the form of scientific practice best suited to reveal it. A persistent theme in the discourse about Clementsian vs. Gleasonian views has been the interpretation of Gleason's individualistic concept in ways that neither Gleason, nor subsequent proponents, ever intended. This has the advantage of simplifying efforts to discredit a position, but does not further the attempt to clarify the differences or advance the argument. The purpose of this essay is to examine ways in which Gleason's individualistic concept has been misconstrued. Some scientific critics of the individualistic concept have said that it held that the ecological community was a random aggregation of species from the available species pool. Other ecologists have asserted that Gleason's concept entailed that the relations among species were due solely to the conditions of the physical (abiotic) environment, and that the interactions (biotic) between and among organisms were not important.

Gleason's work has attracted the interest not only of ecological scientists but also of historians of ecology. It might be supposed that careful historical scholarship would have produced a clear and balanced account of Gleason's views on the nature of vegetation. This has, however, not always been the case. Like their scientific colleagues, historians of ecology have often worked with partial or partisan characterizations. We will comment upon several historian's versions of Gleason's ideas. We will also argue, however, that knowledge of the historical context of Gleason's arguments can help us to interpret his meaning more accurately.

In his earliest expression of his individualistic concept, Gleason (1917*a*) described it as the "Individualistic Concept of Ecology." In both later expositions (1926, 1939), he described it as "The Individualistic Concept of the Plant Association." The latter description limited the sweep of his ideas, and their implications for animal ecology, and ecology in general, were not widely recognized until later (Nicolson 1990, McIntosh 1995). Gleason (1909*a*) was himself quite clear, however, as to the close interrelation between the concepts of plant and animal ecology.

It is likely that the imputation of random combinations of species to Gleason's individualistic concept resulted from readings of his pioneer studies of the distribution of individual plant species within associations (Gleason 1920, 1922*a*, 1925, 1929). In these articles, Gleason seems to indicate that the distribution of species within stands of natural vegetation ("associations" in Gleason's usage) is usually random (Goodall 1952). If this were true, the work of future generations of ecologists would have been greatly simplified. Colwell (1985) noted the shift toward Gleason's individualistic species concept and wrote, "At the very least, the individualistic concept is currently regarded as a kind of null model for community organization . . . ." Other disputes in ecology about assembly rules had posited null models of random combinations of species. Some ecologists have mixed up the null models with Gleason's individualistic concept. Becking (1957) had thought it necessary to caution ecologists against reading the individualistic distribution of species as implying random combinations of species: "However from this the conclusion may not be drawn that tree species are independent of that gradient in the sense that they combine at random." Becking's caution was not always heeded. Many later commentators continued to identify Gleason's individualistic concept with the imputation of random combinations of species within the association, or the primacy of abiotic factors.

Daubenmire (1968), in his well-known textbook on plant communities, denied the individualistic concept, asserting that "no organism lives in a biological vacuum, as implied by the 'individualistic concept.'" He added that accepting it "is to repudi-

ate the thoroughly documented principle of competitive exclusion." Price (1984) wrote, "In ecological time species colonize a patch simply because the conditions are adequate for survival, uninfluenced by the presence of other species on the same trophic level, or by those on levels above," attributing this to the "individualistic response paradigm" proposed by Gleason.

Liss et al. (1986) provided both misunderstandings of Gleason's thought and wrote that, according to the individualistic view, distinct kinds of communities were not evident. "Communities to the extent that they exist at all are little more than random assemblages of populations that colonize and occupy a particular site because of similar habitat requirements." They also commented, "Knowledge of how individual species populations react to the habitat and the physical conditions is of primary importance in understanding a community." The latter point was emphasized by Pound (1988), who wrote, "Simberloff, echoing the writings of phytosociologists (e.g., Gleason 1926), argued that individualistic responses of organisms to physical features of the environment are, along with chance and history, enough to explain community patterns."

Shipley and Keddy (1987) asserted that "The debate concerning pattern (of vegetation) has usually been structured as a dichotomous choice between the predicted patterns of the community-unit and individualistic concepts . . . ." They provided an analysis of numerous articles which, they said, constitute "a large body of evidence which falsifies the causal assumptions of the individualistic concept . . . ." The burden of this evidence, they wrote, is "the importance of both biotic factors as well as interactions between biotic and abiotic factors in determining the structure of such communities." It is clear in Gleason's writings on communities that he recognized the importance of biotic factors and of the interaction of biotic and abiotic factors in community structure, so it is not clear just what was falsified by this evidence.

Noy-Meir and Van der Maarel (1987) took a somewhat intermediate stance on Gleason's individualistic approach. They said he denied the importance of facilitation between species, but "recognized that competition had a role in structuring vegetation." Brown and Kurzius (1987) noted the difficulty of assigning Gleason's concept to the random pole of the debate. "It might seem logical to associate the Gleasonian concept with random assemblages, but as we shall see, species that exhibit a great deal of independence in their distribution can nevertheless show highly non-random patterns of co-existence." Southwood (1987), however, in an essay on community concept, wrote, "The Clementsian view was rejected by their contemporary H. A. Gleason who considered the association to be largely a random assemblage . . . ."

This conflation of the individualistic concept with "random assemblages" ignores the careful observation of vegetational dynamics and structure that is to be found throughout Gleason's ecological writing. It may be based upon a misreading, albeit an understandable one, of his early quantitative work.

Gleason's statistical articles on the distribution of species within plant associations are now upwards of 70 years old, and some historical contextualization is required if we are to interpret them correctly. In several of his papers (1929, 1936, for instance), Gleason stated that, within any given stand of vegetation, species are distributed more or less "at random." He assumed random distribution in order to derive his statistical expressions. However, only on a single occasion (as far as the present authors are aware) did Gleason seek explicitly to justify the conclusion that randomness was the real condition of vegetation rather than merely a heuristic assumption that aided statistical analysis:

> *But are plants distributed within an association merely by the laws of probability and chance rather than by environmental control? The fact that species and area are correlated according to a mathematical formula indicates that the former is the case.* (Gleason 1925)

This argument is obviously erroneous. That a distribution may be described mathematically does not prove randomness, since many other forms of distribution may be equally well mathematically described.

Gleason also implied, on occasion, that distribution was random because dispersal was accidental (1925). However, in his key 1926 paper on the individualistic concept, Gleason provided several telling exemplifications of the problematic relationship between dispersal and ecesis. Thus, he was evidently fully aware that the (partial) randomness of dispersal need not necessarily be reproduced in ecesis, the establishment of the plant. These apparent lapses in the consistency of Gleason's argument are odd, given that his writing is generally distinguished by logical rigor and meticulous accuracy of expression. To elucidate this conundrum, we must examine precisely what Gleason meant when he used the term "random."

Gleason's quantitative papers were remarkable pioneering achievements. However, their author was not well educated in mathematics or statistics (Nicolson 1990). This lack of statistical training reveals itself in the fact that, in contrast to the clarity of his prose, Gleason's mathematical exposition is occasionally difficult to follow. He is also imprecise in his use of the term "random." Gleason's technique of "random" sampling, for instance, involved the first quadrat being "located anywhere" and the others being "located successively in a pre-determined relation to the first," in a straight line or at the corners of a square, a method sometimes called stratified random sampling. This may be an effective and practical way of surveying vegetation, but it is not random sampling as a statistician would recognize it. It should be noted, however, that professional statisticians were themselves divided about the merits and the mechanics of random sampling at this time (Nicolson 1990).

Throughout his many publications on the structure of the association, Gleason failed to make a clear or consistent distinction between the notion of randomness and that of uniformity. Thus, in the same paper (1936), he argued both that:

> *It has long been known that natural vegetation is generally divided into definite areas, each of them uniform, or essentially so, in appearance and structure throughout its entire extent . . .*

And that:

> *Many carefully planned series of observations have shown that, within the extent of a single plant society, the individual plants are distributed at random, or in other words, by chance.*

Statistically speaking, these statements are formally incompatible.

A random distribution is not the same as a uniform one. When applied to the distribution of plant species within an association, the statistical definition of randomness would entail that the probability distribution of the numbers of different species occurring in any given quadrat is the same as that in any other quadrat, *and* that the number of different species in any quadrat is completely independent of the number of species in any other quadrat. In practice, a random distribution of plants in space would not be wholly uniform in appearance. Gaps and clumps would occur. But even if a quadrat could be found with, say, only one species, the probability of finding only one species in an adjacent quadrat would be exactly the same as if one had observed 20 or 30 species in the first quadrat. On the other hand, a uniform distribution, statistically speaking, is one that gives every possible value equal probability. Suppose every quadrat had between 20 and 30 species, and that the probability of those numbers of species occurring in any quadrat throughout the association was the same, then that association would display a nonrandom uniform distribution. Thus, uniformity entails a degree of spatial evenness and homogeneity.

Our statistician colleagues tell us that undergraduate students often find the difference between random and uniform distribution hard to grasp. It is hardly to his discredit that Gleason, who had no formal statistical training, also appears to be somewhat unclear on this matter. With the benefit of historical retrospection, however, we can express Gleason's meaning more precisely than he was able to do. In fact, not much reinterpretation of his writing is required. For example, it is abundantly clear that, in his groundbreaking paper of 1920, Gleason's principal working hypothesis—his null hypothesis—was not randomness within the plant community, but uniformity:

> *The use of a chosen quadrat in representing this structure [of the association] depends absolutely on the theory of the homogeneity of the association . . . . If the association were absolutely homogeneous . . . any quadrat could be chosen to represent the vegetation. Since no association is perfectly uniform, any one quadrat may by its structure accentuate the variability instead of concealing it.*

But in the same paper, Gleason's conflation of uniformity and randomness is also apparent:

> *If plants were distributed absolutely at random over the association, that is if the association were absolutely uniform throughout, separated quadrats would never be necessary.*

The confusion would seem to have sprung from Gleason's failure to appreciate that his biological null hypothesis, that is, uniformity, was different in character from the probabilistic first principles from which he derived, perfectly properly, his statistical indices.

As will be seen most clearly from Gleason (1925), the research question to which Gleason applied his statistical tests was, "Do different species grow together, on a recurring basis, within the association?" Thus, in his actual field practice, Gleason was primarily concerned quantitatively to assess not departures from randomness, but departures from uniformity. On the basis of these observations, Gleason concluded that, within the confines of any given association, species did not grow together in recurring groups:

> *In other words, environmental differences in the aspen association . . . are not of sufficient magnitude to affect the distribution of the species, unless these differences exist within the limits of a single square meter.*

As Gleason pointed out, on several occasions, it is the uniformity of an association that allows it to be visually recognized and described:

> *Homogeneity of structure, over a considerable extent, terminated by definite limits, are the three fundamental features on which the community is based. Without these three features, Grisebach would never have published his statement of a century ago; without them, all our studies of synecology would never have developed . . . Uniformity, area, boundary and duration are the essentials of a plant community.* (Gleason 1939)

It was the distinctive uniformity of the plant community that justified the use of the quadrat method to characterize it.

It should be borne in mind that one of the matters that most occupied Gleason in the formative years of his development as an ecologist was the problem of the interaction between prairie and forest in his native region, the Midwest (Gleason 1909*b*, 1912, 1913, 1917*b*). Here one could see two quite different associations in close proximity, divided by a narrow transitional area. When the ecologist passed from one association to the other, he went from one relatively uniform

form of vegetation, through a zone of very marked discontinuity, to another area of different but equally uniform vegetation. It was under these circumstances that Gleason conceived of relative uniformity as a distinguishing characteristic of the association. As explained above, Gleason's statistical investigations were predicated upon the impulse to characterize and measure this uniformity.

What, according to Gleason, were the causes of this relative uniformity within the association? First, the physical environment of any given association must itself be relatively uniform. However, his experience of the prairie/forest problem had taught Gleason that physical uniformity alone could not be a sufficient cause of vegetational uniformity. In the Midwest, prairie might grow upon soil that had previously supported forest, and forest might encroach upon prairie without any intervening change in the physical environment. Gleason was absolutely clear that what maintained the uniformity of the different forest and prairie vegetations were biotic factors, especially the influence of the dominant upon the subordinate species of each association. The shade cast by the dominant trees excluded the prairie species from the forest floor: the thick sod formed by the roots of the grasses prevented forest species from establishing themselves in the open prairie (Gleason 1927).

Hence the recognition that, when Gleason wrote "random" he often meant "uniform," leads us also to a recognition of the falsity of the assertion, frequently made as we have seen above, that Gleason's individualistic hypothesis ignores biotic factors. On the contrary, Gleason's conception of the association accorded crucial importance to interactions between and among organisms. It was such biotic interactions that imposed and maintained the distinctive uniformity of the association. Thus, he wrote in 1910:

> *The plant itself is in many cases the controlling agent in the environment; the differentiation of definite associations is mainly due to the interrelation of the component plants; and the physical environment is as often the result as the cause of the vegetation.*

And reiterated in 1939,

> *. . . the dominant plants, which are distributed over the whole area of the community, exert such a uniform effect on the other species that discrepancies in the physical environment are more or less smoothed out or obliterated.*

Gleason was, of course, well aware that the uniformity of any association was relative, imperfect, and local.

> *We all readily grant that there are areas of vegetation, having a measurable extent, in each of which there is a high degree of structural uniformity throughout, so that any two small portions of one of them look reasonably alike . . . More careful examination of one of these areas, especially when conducted by some statistical method, will show that the uniformity is only a matter of degree, and that two sample quadrats with precisely the same structure can scarcely be discovered.* (Gleason 1926)

Even within a single locality, variation was continuous:

> *. . . it became evident, from actual field observation, that two separate patches of the same association were never exactly alike, either in component species or in the relative numbers of individuals of any species and that the degree of likeness was roughly inversely proportional to their distance apart.* (Gleason 1953)

Over longer distances, association composition changed steadily, reflecting gradual environmental change. Along the floodplain of the Mississippi, for example, the forest might seem constant in composition for mile upon mile. But:

> *As the observer continues his studies further down stream, additional species very gradually appear, and many of the original ones likewise very gradually disappear. In any short distance these differences are so minute as to be negligible, but they are cumulative and result in an almost complete change in flora after several hundred miles. No ecologist would refer the alluvial forests of the upper and lower Mississippi to the same associations, yet there is no place along their whole range where one can logically mark a boundary between them. One association merges gradually into the next without any apparent transition zone.* (Gleason 1926)

Wiegleb (1989) went beyond the common bipolar representation of the dispute concerning the individualistic hypothesis in posing three hypotheses: H_0, the random assemblage hypothesis; H_1, the individualistic (Gleasonian) habitat response hypothesis; and H_2, the competitive hierarchy response hypothesis with competition an important factor among species. He clearly separated the individualistic hypothesis (H_1) from the random hypothesis (H_0), but its relation to H_2 is less clear. Gleason did not regard interspecies competition as the sole mechanism controlling community competition, as did some later animal community theorists, but he did allow it a place in influencing entrance of individuals of a species into a community and in the composition and structure of the resulting community. He did not believe that the species were responding solely to habitat.

The imputations of random combinations of species and sole response to physical environment for Gleason's concept persist in more recent references. Goldsmith (1993) extended the misinterpretation of Gleason to his successors, and asserted that John Curtis and Robert Whittaker resurrected Gleason's individualistic hypotheses, and that they, and by implication, Gleason, believed that the "biosphere is atomistic and random." He

illustrated this by an analogy of ecological entities behaving "like billiard balls." Fortin (1994) posited an extreme null hypothesis of species independent of one another with no interactions between them, attributing this to Gleason's individualistic concept. Brown (1995) reviewed Gleason's individualistic concept, deeming it to be a logical consequence of G. E. Hutchinson's niche concept, although the reverse would be chronologically true. In noting a tension between community, as seen by Gleason and by Robert MacArthur, whose work was influenced by Hutchinson, Brown commented, correctly, that "it is incorrect to equate Gleasonian individualism with the influence of abiotic conditions and MacArthurian structure with the effect of biotic interactions." However, commenting later on similarities among plants inhabiting mediterranean climates, he noted that "MacArthurian structure is caused largely by biotic conditions," whereas "the Gleasonian individualism can be attributed to adaptations to abiotic interactions," which is clearly incorrect. A slightly different misinterpretation of Gleason's thought appeared in Pulliam's (1997) recollections of his own ecological education. He wrote "A Gleasonian view of the world predominated in which all niches were assumed to be full and all species were thought to be in their proper places." This may have described the view of the animal community theory of Pulliam's graduate days, but it bears little relation to Gleason's thought which had species often not in their "proper place."

Keddy and Weiher (1999) posed the dichotomous approach to communities, noting that "the theme of whether plant communities are discrete communities or random assemblages can be traced back through writings by Tansley, Clements, Gleason, Ellenberg and Whittaker," no doubt putting Gleason at the random pole. More specifically, they commented "that the rejection of Pielou's null model constitutes the first demonstration that communities occur in discrete clusters rather than random (individualistic) associations," erroneously specifying Gleason's concept.

As we have noted, when describing community composition, Gleason may sometimes have used the term "random" when he might more accurately have written "uniform." But it is important to recognize that, in other contexts, he accurately characterized processes that are genuinely stochastic in nature. Clements and his followers tended to view successional changes as proceeding in systematic, ordered series toward a predetermined endpoint. To Gleason, by contrast, succession was the product of the behavior of individual plants and, as such, was highly dependent on accidents of timing and dispersal. As he put it, "the early stages of dune communities are due to chance alone" (Gleason 1926). Succession is, thus, an area in which it is accurate to identify the individualistic concept with random processes of dispersal (Gleason 1927).

Maurer (1999) noted the confusion among ecologists about Gleason's views "Gleason's individualistic concept of community structure is often associated with the idea that interactions among species are not important in establishing the composition of a plant or animal association." Maurer recognized that negative interactions among species did not conflict with Gleason's ideas, although positive interactions did not fit as easily. However, according to Maurer, "regardless of the kinds of interactions among species in a given community, seed dispersal was sufficiently probabilistic that there must always be some degree of chance involved in which a particular set of species was able to establish persistent populations in a given community." This is a fair statement of Gleason's concept, but is, as we have seen, all too frequently extended to an assumption of random combinations of species. In some instances, negation of Gleason's concept took the form of derision. One critic commented "It is not always necessary to destroy old theories in the erection of new ones, as in the current trend to expunge Clements and climax from ecological thought in favor of Gleasonian individualism and perpetual motion" (Johnson 1999).

Many ecologists read Gleason quite clearly, "The significance of the biotic and ecological factors in the environment is acknowledged by Gleason," (Ponyatovskaya 1961). Moore (1990) wrote, "The alternative view (to Clements) pioneered by Gleason, perceives vegetation as an assemblage of individual plants belonging to different species with each species distributed according to its own physiological requirements as constrained by competitive interactions." Taper et al. (1993) reported individualistic responses of bird species, but asserted, "The fact that species respond individualistically does not imply that species do not respond deterministically to abiotic conditions and to other species."

Historians' Gleason

The first writer to write about Gleason from a purely historical viewpoint rather than a scientific one was probably Donald Worster (1977). Unfortunately, Worster rechristened Henry Allan Gleason as "Herbert" and located him at the University of Michigan in 1926, which was seven years after he had left to join the staff of the New York Botanical Garden. Worster's characterization of Gleason's views on vegetation was very concise. The climax community was, according to Worster's account of Gleason's theory, "a haphazard, imperfect and shifting organization," which is at least two-thirds accurate. Oddly, however, Worster suggested that the individualistic concept of vegetation carried the implication that "man need not worry overly much about disturbing" the natural environment. Thus, Worster represented Gleason as an apologist for technology—intensive, exploitative farming. There is nothing in Gleason's published work, nor in the several unpublished sources that are available to historians (Gleason 1944, 1961), nor in what we know of his character as a man who loved plants and the places where they grow, which sustains this view. Worster was unable to present a sympathetic, or even a balanced, assessment of Gleason be-

cause he was, as he made abundantly clear throughout his book, avowedly on Clements' side in the holism vs. reductionism debate. As one of us has argued elsewhere (Nicolson 1988), Worster based his view of the history of ecology upon an oversimplified and unsatisfactory dichotomy between good guys and bad guys.

Ronald Tobey's more detailed study of Clements and his school appeared in 1981. Much of what Tobey wrote about Clements's organicism is of considerable interest, but his account of the views of scientists opposed to Clements leaves something to be desired. Tobey's interpretation of Gleason would seem to be that he held the individualistic hypothesis because he "did not understand" the rich complexity of the Clementsian system:

> *In Gleason's universe . . . there were only individual organisms . . . . This position was philosophically untenable, as any nineteenth century idealistic philosopher would quickly have shown, but Gleason . . . whistled his tune oblivious to the cemetery of buried doctrines similar to his . . . [Gleason] did not recognize the ontological problem with his concept of the species.*

As is exemplified in several of our quotations from Gleason's writings, he did not, in fact, hold that only individual organisms exist in nature. He regularly stressed that plant communities existed, and that their structure was the product of interaction between and among species. He repeatedly acknowledged that plant communities could be studied and mapped in the field. What he did maintain was that associations were not fundamental organic entities. How they were named and classified was entirely a matter of convenience. All the classificatory categories into which vegetation is arranged are human constructs:

> *Different mills produce different qualities of flour from the same wheat. The association concept is a product of our mental mills.* (Gleason 1931)

Far from being overly simplistic, as Tobey implies, Gleason's theory of classification was sophisticated and forward-looking, as Whittaker acknowledged in 1962. It is a tenet of most modern classification theory that whether or not any particular classification should be regarded as valid can only be judged in terms of the practical context within which that classification is deployed (Bloor 1982). This is certainly close to, if not identical with, Gleason's views on the classification of vegetation.

Hagen (1992) provided a more balanced picture of the Clements/Gleason debate than his predecessors. However, he characterized Gleason as an armchair theoretician who "never collected data to support his claims." This is unjustly to ignore Gleason's several very substantial contributions to American field ecology (for instance Gleason 1907, 1909*a*, 1910, 1912, 1918, 1924), all of which are relevant to an understanding of his ideas. The foundations of Gleason's theory lay in his considerable experience of vegetation, both within and outside of the United States (Gleason 1915). The point we wish to emphasize here is that Gleason's papers on the individualistic concept must be understood, and assessed, in the context of the totality of his work in ecology. If this is done, there will be no doubt that his theoretical arguments had a substantial empirical base.

Hagen makes a stronger point when he cautions against making too complete an identification between the individualistic concept and more modern views on vegetational structure. Certainly it would be unrealistic wholly to equate the individualistic concept with advanced niche theory, sensitive as Gleason undoubtedly was to the importance of competitive interactions between species, and the fact that no two species had identical environmental requirements (Gleason 1917*a*). On the other hand, Hagen's assertion that "Gleason did not use natural selection to justify his claim that ecology could be reduced to the activities of independent individuals," would seem to be unfounded. Again, if one considers the individualistic concept against the background of Gleason's work in ecology as a whole, it will be seen that he regarded floristic evolution, adaptation, and migration as among the principal factors that determined the character of long-term vegetational change (Gleason 1922*b*, 1923)

Both Tobey and Hagen criticized Gleason for arguing that the association was not an organism because it did not have definite boundaries. But, in fact, Gleason did not advance any such opinion. He certainly pointed to the importance of recognizing that continuous variation in vegetational composition occurred, such as along the floodplain of the Mississippi. In his view, the absence, in this context, of a definite boundary between very different forms of vegetation was indeed suggestive of the lack of a definite structure to the association. But Gleason knew very well that, under different circumstances, associations might have clear-cut boundaries, as exemplified by the prairie and forest communities of the Midwest. He argued, however, that the existence of these definite boundaries was equally explicable in terms of the individualistic phenomena of plants. The boundary between forest and prairie was not produced by any emergent function of those two associations. Contra Clements, Gleason's consistent thesis was that, whether or not they have definite boundaries, associations have no functional properties beyond the sum of the functions and interactions of their constituent plants.

Gleason's understanding of the relation of plant to environment and other organisms was clear as early as 1910, when he noted that establishment of a plant is conditioned as much by other plants as by the physical environment (Gleason 1910). In the 1917 exposition of the individualistic concept, he wrote, "One of the most important features of the environment is the control of the original physical features by the plant population itself." In the same version, he asserted, "As soon as the ground is occupied competition restricts it (the plant) to its proper proportion." In 1926 Gleason repeated, "it is also a

fact that plants are themselves a part of the environment," and commented that dominants smooth out the physical environment. In each of his three expositions, Gleason was explicit about the effect of, even control of, the physical environment by organisms and of the competitive interactions among the plant species.

Persistence of implications of communities formed as random groups of species without interactions among themselves does not help to resolve the difficult problems of communities and succession facing ecologists. Although Gleason explicitly denied that the plant community, or association, as he called it, was an integrated unit in any sense comparable to an organism, he should not be read as suggesting that it was a random collection of species. He used terms such as "coincidence" and "kaleidoscope" in describing the plant association, and attributed an important component of chance to the arrival of propagules. Vegetation, he wrote, "varies constantly in time and continuously in space," and degree of difference increased with distance. Gleason (1939) wrote, "Into this favorable environment other species also immigrate and from all of the arrivals the environment selects the species which may live and dooms the others."

Typical of the period, Gleason focused his attention on plants. In 1939 he returned to his initial version of the individualistic concept of ecology and briefly included animals. He allowed the different capacities of animal migration, but reiterated the point that only "organisms which have reached a favorable environment are able to continue to live." Thus, species combinations are restricted and by no means a random collection of species. Nor does the individualistic concept preclude pattern in communities. Gleason recognized that differences in a series of communities cumulate with distance "so that the ends of the series may be strikingly different although connected by apparently negligible differences." The search for pattern and rules for its formation in communities was pursued by ecologists, with increasingly involved sampling and analytic technique, and was perpetuated in the work of John Curtis and Robert Whittaker (Barbour 1996). Michael Austin (1985, 1989) has added new insights. Curtis (1959) stated the essence of Gleason's concept, still sometimes misread.

> *It must not be assumed, however, that the vegetation of Wisconsin is a chaotic mixture of communities, each composed of a random assortment of species, each independently adapted to a particular set of external environmental factors. Rather there is a certain pattern to the vegetation with more or less similar groups of species recurring from place to place.*

Or even more succinctly, Curtis wrote of the individualistic hypothesis, "not all things are possible only some."

The belated recognition in the 1950s of Gleason's contributions to ecology by ecologists and, later, by historians, produced extended analysis about the nature of community. Some of the comments by ecologists and historians turned on the debate about the Clementsian organismic concept of the community unit and Gleason's individualistic concept. Austin (1999) lamented the lack of communication between the supporters of different paradigms in community ecology, which, he said, "has led to inconsistencies and lack of progress in ecology." The lack of communication is compounded by misleading communication in the case of Gleason's concept.

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A History of the Ecological Sciences, Part 6: Arabic Language Science—Origins and Zoological Writings

Arabic Civilization, like the Byzantine, was a synthesis; in this case, primarily of Arabic, Byzantine, and Persian cultures (von Grunebaum 1970). Because Arabic and Persian cultures did not emphasize science, and because Byzantine science barely rose above the mediocre level of Roman science, one might guess that Arabic language science would be no better than Byzantine science. Much of it certainly was not better, but a significant portion of it was. The greatest achievements were in mathematics, astronomy, alchemy, physics, and geography. Almost all surveys of Arabic language science have neglected zoology (Anawati 1970, Huff 1993, 2000, Turner 1995, Rashed 1996, Dallal 1999) and sometimes botany; the notable exceptions are by Nasr (1968, 1976) and Sezgin (1970:357–380). Zoology was disseminated mainly through interesting animal stories, but was also pursued through medicine, veterinary medicine, hunting, and pest control (Bodenheimer 1928:128–167, Petit and Théodoridès 1962:171–180, Pellat et al. 1966). Professor Remke Kruk's studies provide the basis for a new synthesis on the history of Arabic language zoology, which we hope he will someday provide.

Alexander the Great had wanted to conquer Arabia, but died in Babylon before he made the attempt. What was there to conquer? Excepting Yemen in the far south, it consisted of oases, camel caravan trails, and desert—not an environment favorable for the flowering of complex civilization. No one had ever united the tribal Arabs, and around the year 600, there was no awareness that anyone ever would. Yet only a decade before, the charismatic Muhammad of Mecca began retreating into a cave to meditate and listen to a voice telling him to lead his people away from paganism to worship the one god, Allah. Muhammad would be Allah's prophet, and the religion he preached would unite the Arabs in religion and would also provide a means for uniting them politically. Although intolerant of paganism (which much later included Hinduism), Muhammad saw himself as the last of the Hebrew prophets (including Jesus), and therefore he tolerated Judaism and Christianity, even though adherents to those faiths paid more taxes and had fewer rights than Muslims.

The Arabs lacked science in their indigenous traditions, but the cultural, political, and military momentum that Muhammad set in motion continued after his death in 632, and Arabs were willing to learn from those they conquered. Within a century, a vast empire stretched from the Atlantic across North Africa, Syria, Mesopotamia, and Persia to the Indus Valley in India. Arabic was the language of Islamic religion, and it also became the language of most of the conquered lands, excepting mainly Iran and, later (after they became Muslims), the Ottoman Empire, although many Iranians and Turks read Arabic. It was too vast an area to govern for long using medieval communications and transportation, and gradually it separated into various states. Not only the Arabic language, but also commerce and culture, persisted over vast regions after the large empire began to break down.

The Umayyad dynasty established the first Muslim Caliphate at Dam-