



CONTRIBUTIONS

Robert Harding Whittaker and the Individualistic Hypothesis

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Robert Harding Whittaker (1920–1980) was one of the most productive and eminent plant ecologists of the twentieth century. His career in research is thus of great interest both to scientists and historians of science. In 1982, Walter Westman and Robert Peet, former students, published a biographical account of their mentor and colleague. As fellow ecologists, they documented Whittaker's many technical achievements in community ecology, as well as in phylogenetic theory and allelochemistry. In particular, they emphasized his contribution to the demise of the community-unit paradigm, the concept that plants grow together in definite, integrated and repeating assemblages, and the acceptance of the alternative individualistic hypothesis of the plant community. This paper is intended as a modest supplement to Westman and Peet's excellent survey. It utilizes some sources that the earlier authors did not use: Whittaker's doctoral thesis (in which he expressed himself, on occasion, even more frankly than he did in his published articles); some relevant archival matter; and an interview that the present author conducted with Whittaker in the course of his own doctoral studies in 1978 (Nicolson 1984). The paper approaches Whittaker's career from the perspective of the history of ecology rather than from within ecology itself. It will also be noted that Henry Allan Gleason remained an important presence within plant ecology into the 1940s, despite his being employed as a taxonomist in the New York Botanical Garden and having ceased field work. Gleason was an important influence on Whittaker, albeit mostly at one remove.

Up until the 1940s, plant ecology in Europe and North America was dominated by the community-unit theory. Natural kinds of vegetation, generally termed "associations" or "formations", were held to constitute the proper subject matter for ecological study, as the plant species provided the proper object of study for taxonomic botany. These units were defined by the American ecologist, George Nichols, thus, "[T]he association may be described as a vegetation-unit characterized by its essentially constant

physiognomy and by its essentially constant floristic composition” (Nichols 1923:171). Between 1917 and 1944, only one American botanist dissented from the general consensus surrounding the community-unit theory, Henry Allan Gleason (1917, 1926, 1927, 1939). In Gleason’s view, the phenomena of the plant community depended entirely upon the behavior of individual plants. Thus, associations or formations did not constitute basic units of which all vegetation was composed. The association was a classifier’s category produced by the activity of classification rather than by the essential reality of vegetation. Its characteristics were dependent upon the priorities and interests of each classifier, “Different mills produce different qualities of flour from the same wheat. The association concept is the product of our mental mills” (Gleason 1931:78).

The year 1947 was a remarkable one in the history of plant ecology. Three articles were published in *Ecological Monographs* which criticized the state of orthodox theorizing in the discipline and, in particular, expressed skepticism regarding the community-unit theory. Two of those papers, by Herbert Mason and Stanley Cain, were first presented at a conference entitled the “Origin and development of natural floristic areas with special reference to North America,” organized jointly by the Ecological Society of America and the Association of American Geographers, in Boston in 1946. Following the hiatus of the Second World War, the meeting represented the resumption of normal research activity in ecological science in the United States and offered an opportunity for the participants to revisit the basic premises of the discipline. Change was in the air; the tide of ecological opinion was beginning to turn in Gleason’s favor.

Herbert Mason was Director of the Herbarium of the University of California, Berkeley. He had trained as a taxonomist and his main interests lay in the evolution and distribution of flora. He argued that, like floras, plant communities were best thought of as assemblages of independent species. The organic functions of the community were confined to the reproductive and genetic activities of intra-specific, interbreeding populations. No integrative processes operated between unrelated populations or above the level of the population. Thus, the plant community cannot be regarded as an interdependent functioning unit. Herbert Mason expressed his agreement with Gleason that the plant community “possesses only coincidental unity based upon simultaneous environmental tolerances for the overall environmental factors” (1947:204).

Stanley Cain, then Professor of Botany at the University of Tennessee, offered his paper as a “twentieth anniversary affirmation of Gleason’s individualistic association hypothesis” (1947:198). He analyzed the abstract concept of the association, as developed in Europe by the Zurich-Montpelier School and in North America by Frederic Clements. He concluded that, when applied in the field, both associational concepts incorporated so many different combinations of species that it was difficult to be convinced of their objective reality as integrated community units. Referring to the identification of associations as then practiced in Europe and North America, he commented, “I will not say that this type of ecology is an art – but it is something less than an exact science” (1947:189). Thus, the scientific validity of ideas of the association as either a super-organism (the view of Clements 1916) or a syntaxon (the view of Braun-Blanquet 1932) was problematic. Species were individualistic in their environmental requirements and distribution, so plant communities must also be individualistic. Their floristic composition was merely the result of the overlap of the areas of distribution of each species.

The third 1947 paper, by Frank Egler, was the report of an extensive field study of the previously undescribed vegetation of the island of Oahu in the Hawaiian Archipelago. The manner in which Egler described

the plant communities was, superficially, quite conventional. But the paper began with a detailed discussion of theory and terminology and it is here that the main thrust of his argument is to be found (1947:387–389). Asserting that American ecology was on “the threshold of fundamental changes in its conceptual structure”, Egler argued that the concepts of “association,” “succession,” and “climax” were no longer useful. His analysis of vegetation was, he asserted, “wholeheartedly and without exception” based upon the “all-but-forgotten” papers in which Gleason set out the individualistic concept of the plant community (1947:389).

In the late thirties and early forties, both Egler and Cain had been frequent visitors to the New York Botanical Garden and had many discussions with Gleason on ecological matters (Nicolson 1990:146,150). Eventually, both were convinced of the validity of the individualistic view and Gleason came to regard them as disciples.

Mason, Cain, and Egler all bemoaned the lack of scientific rigor in the then current practice of field plant ecology and urged that the specialty be modernized in accordance with the best biological practice of the time. Egler repeated these criticisms, even more forcefully, in 1951. However, with the benefit of hindsight, it is clear that what was required to reform plant ecology was not only theoretical arguments or generalized methodological prescriptions but also improved methods of empirical investigation and the original field data that they would produce. Cain effectively recognized this when he complained that there was:

... a surprising paucity of information as to the exact areas of species and particularly on the composition structure and total areas of plant communities. I refer not to the hypothetical and admittedly approximate areas of ‘association types’ ... but to actual concrete specific communities on the ground. (Cain 1947:189)

In 1947, unbeknown to Cain and Egler, a study which did involve a new method of field investigation was already underway. Whittaker, then a graduate student of the University of Illinois, was engaged in an intensive study of the vegetation of the Great Smoky Mountains of Tennessee. As he began the field work, Whittaker was aware that there existed a diversity of opinion as to the structure of vegetation. His principal supervisor was Charles Kendeigh, a zoologist who worked with a concept of the biotic community-unit similar to Clements’s (Westman and Peet 1982). When Kendeigh retired, his role was taken over by Victor Shelford who had worked in collaboration with Clements, and who broadly shared his view of the nature of the community (Clements and Shelford 1939). However, Whittaker had read widely and was aware that European phytosociologists employed units of a different kind. Furthermore, as an undergraduate, he had been taught by Arthur Vestal. Vestal had worked in the field with Gleason, while attending a summer school at the University of Michigan’s Biological Station on Douglas Lake, in 1912. He and Gleason had “counted quadrats all summer” (Nicolson 1990:111). Vestal had remained in close communication with Gleason (Kohler 2002) and, in his lectures, he discussed the individualistic hypothesis fully and sympathetically. According to Gleason’s son, Henry Allan Gleason Jr., his father regarded Vestal as a “crypto-Gleasonian” (Nicolson 1990:150). Vestal certainly introduced Whittaker to Gleason’s publications.

Whittaker went to the Great Smokies determined to devise an objective test that could discriminate between the various theories of species grouping in plant communities. As he stated on the first page of his thesis:

... methods free from the subjective difficulties of conventional ecological procedure were sought in order to analyze the vegetation without reference to preconceived 'associations'. (Whittaker 1948:1)

The technique he adopted was random sampling, which was a radical departure from the accepted norms of ecological field investigation. Indeed random sampling of vegetation had never been done before in North America. It is relevant here that Whittaker was registered as a graduate student in a zoology department. His project was originally intended to be a study of the foliage insect communities of the Great Smokies. It was inadvertent that the preliminary survey of the vegetation grew so large that it eventually constituted the final thesis by itself. As a zoology student, Whittaker had not been intensively trained in the techniques of traditional field ecology so he did not set out primarily to classify the vegetation of his study area:

It [random sampling] appealed to me, first because it was more objective ... Also I didn't know what the natural types were, therefore how could I, why should I, try to sample in terms of them? (interview, Whittaker/Nicolson, 11/29/78, Cornell University, Ithaca, NY)

Using his technique of random sampling, Whittaker came to the conclusion that none of the existing varieties of the community-unit theory was correct. Instead, he described a pattern of continuously changing species composition, along the environmental gradients of elevation and exposure. Whittaker coined the term “gradient analysis” to describe his new interpretation of the structure of vegetation:

Gradient analysis seems one of the most fruitful and realistic means by which the vegetation can be studied. By it the investigator can free his study from the difficulties of preconceived associations and work in terms of one aspect of ecological reality – the actual distributions of community members in the environment and their relative status in different communities. (Whittaker 1948:144)

While a graduate or undergraduate student, Whittaker had received very little training in mathematics or statistics. Nevertheless, among the attractions that gradient analysis held for him were its inherent quantifiability and its statistical nature. It promised the development of a truly quantitative ecology:

The techniques we have been using have become increasingly mathematical as we have been seeking more objective, more efficient, more accurate ways of dealing with vegetation. I think that would be the major change in this area of research. (interview)

To Whittaker, quantification was the necessary condition of a properly scientific field methodology, which could effectively challenge statements about vegetational structure that were based upon subjective judgments:

Daubenmire was saying that because you can see what looks to the human interpreter like a discontinuity, there has to be a discontinuity there and your method is wrong if you can't show that. What I think I see is correct. Of course it's not so – we see what in many cases appear to be well-defined zones on mountains from a distance but when we study them in detail, they intergrade with one another. The findings of quantitative analysis are necessarily stronger than the visual impressions of discontinuity. (interview)

Whittaker concluded that:

In the course of the vegetation analysis the author felt himself compelled by his data to accept fully the individualistic hypothesis of Gleason, and to seek new ways of constructing an understanding of communities from an individualistic beginning. (Whittaker 1948:144)

Whittaker came to this conclusion before he was aware of the fresh support which had recently been given to Gleason by Cain, Mason and Egler, “Independent and spontaneous – you can say what you like about the time being ripe for this.” Whittaker was, however, conscious of the radical nature of his dissent from conventional plant ecology, “I felt very alone – in a position for which Gleason had been castigated.” He was grateful therefore for the early and continued support that he received from Wendell “Red” Camp:

Red Camp found out about my work, was very interested in, and was an enthusiastic supporter. The individualistic hypothesis fitted in with the way he liked to see things. So, yes, I had extensive contact and support from him. (interview)

Having worked in the Great Smokies, Camp had a deep understanding of the floristic and vegetational context of Whittaker’s work (Camp 1931). He was not, however, a plant ecologist and, like Whittaker, he had no disciplinary allegiance to the community-unit theory. He described himself as a biosystematist (Camp 1951, Rickett 1963). Inspired by the neo-Darwinian synthesis, biosystematists employed Mendelian genetics to interpret species variation in the field (Dean 1979). Camp was among the first to develop a genetic understanding of the segregation of ecotypes. Interpreting population phenomena in genetic and physiological terms, Camp’s view of the plant community was virtually identical to that articulated by Herbert Mason in 1947.

Furthermore, Camp was, in the late forties, a member of the scientific staff of the New York Botanical Garden. He was a close colleague of Gleason, with whom he had many discussions on taxonomic and ecological matters. Gleason acknowledged that his views on the species concept had been developed by his discussions with Camp; there is much correspondence between the two men in the Gleason papers in the Archives of the NYBG (Nicolson 1984:374). Camp saw the possibility of using the individualistic hypothesis to aid the interpretation of communities in terms of population genetics. This was very similar, in its emphasis on analysis at the population level, to what Whittaker intended. Whittaker had devised an ecological theory which harmonized with the individualistic hypothesis and the prestigious Neo-Darwinian synthesis, and which Camp was, for several reasons, well placed to understand and support. In 1949, Whittaker wrote to Gleason, acknowledging the inspiration he had derived from his papers on the structure of the plant community, and confidently predicting that the ecological research of the coming decades would be predicated upon an individualistic, population based perspective:

I think, myself, that the future of field plant ecology lies along the lines of population analysis which I am developing and which others of my generation will work out. (letter, Whittaker to Gleason, 6/2/1949, Gleason papers, NYBG Archives)

Whittaker’s Ph.D. thesis was examined and accepted in 1948. However, he was having considerable difficulties finding a satisfactory academic post and getting his Smoky Mountain work published. In the

early fifties, however, he was able to publish two important theoretical papers. In 1951, in an article in *Northwest Science*, he set out a concise summary of the implications of his field work for the understanding of the plant community. If plant species are organized into community units, then that organization should be apparent in similarity of distribution of their constituent species. Random sampling of the vegetation should reveal these groupings. In fact, continuous variation is found, with species distributed not in repeating assemblages but independently of one another along environmental gradients. Whittaker concluded that the “conception of the association as a fundamental unit does not agree with the evidence and must be abandoned.” The interpretation of vegetation presented in Gleason’s 1926 paper was endorsed.

In 1953, in a lengthy, clearly written and wide ranging review of the literature on climax and succession, published in the well-respected *Ecological Monographs*, Whittaker again emphasized the general occurrence of continuous transitions between and throughout those plant communities traditionally regarded as associations. He reconfigured the concept of the climax association as “climax pattern.” However, well-reasoned and forcefully argued as both these papers were, their impact was necessarily minimized by the limited amount of supporting empirical data that they contained.

After several false starts, Whittaker submitted a revised manuscript of his Smoky Mountain field work to *Ecological Monographs*:

I had substantial trouble with the editor, who was H.J. Oosting. I would, in retrospect, concede that Oosting was doing his best to deal fairly with me and that the troubles, as an author, were primarily myself. But anyway it was a long negotiation to get that through some adverse reviews. I was getting some adverse reviews because what I said was unpalatable to conservative ecologists. (interview)

The main sticking point was his sampling technique. Random sampling had by this time become accepted by statisticians as the best means of obtaining unbiased data. However, placing plots at random in a large stand of vegetation is a difficult and time-consuming task, involving much surveying. In fact, Whittaker was vague both in his thesis and in my conversation with him as to how exactly he had located his sample plots. It is likely, indeed, that his sampling method was not strictly a random one, at least by professional statistical standards. Nevertheless, the novel and crucial aspect of his methodology was that he did not locate his sampling sites according to an a priori assumption was to what the vegetation types were. However, to an adherent of the community-unit theory, a sampling technique which was not based upon the identification of associations was necessarily unsatisfactory:

I was told by Daubenmire, for example, that it was not scientifically valid to sample the way I had done because one would get a lot of stands that were intermediate or disturbed and were inappropriate to the recognition of the types one was trying to seek and demonstrate. (interview)

Throughout the 1950s and 1960s, Rexford Daubenmire was one of the staunchest defenders of the community-unit theory (Daubenmire 1952, 1966, Sowards 2015). Whittaker was young, outspoken, and iconoclastic. A certain amount of ill-feeling was aroused.

These men [Daubenmire and Oosting], remember, had devoted themselves to a lifetime of research on vegetation, using a certain set of assumptions and for me to come along and challenge their assumptions did not please them. (interview)

A version of Whittaker's thesis, with most of his field data, finally appeared in *Ecological Monographs* in 1956. It was well received and has since been very highly cited. Daubenmire, however, remained a resolute defender of the reality of community units, arguing that gradient analysis and related techniques inevitably included untypical stands. The areal extent of the ecotones was exaggerated and a false impression of continuous change in floristic composition was created (Daubenmire 1966). But Oosting was eventually converted to gradient analysis and generously acknowledged the impetus that Whittaker's studies in the Great Smokies had given to plant ecological research (Mowbray and Oosting 1968:309).

However, by 1956, the revival of the individualistic hypothesis was already well underway, through the publications of John Curtis and his collaborators at the University of Wisconsin, Madison (Nicolson 2001). In the mid-fifties, Curtis was at a different stage in his career from Whittaker, who had only recently secured a junior post as an Instructor at Brooklyn College, City University of New York. Curtis was already an established scientist and a full professor, having built a substantial reputation as a plant physiologist before he made the shift to ecology. He knew how to please editors and experienced few difficulties getting his papers published. His research was supported by a generous grant from the Wisconsin Alumni Research Foundation and he ran a large and very well-organized team of graduate students, systematically investigating many different aspects of the vegetation of Wisconsin. The comprehensiveness and sophistication of the Madison publications, not to mention their sheer quantity, was very persuasive (Curtis and McIntosh 1951, Brown and Curtis 1952, Curtis 1955, Bray and Curtis 1957, McIntosh 1958, to cite only a few). Curtis was probably broadly justified when, in 1955, he commented that:

... the great majority of investigators [are] rapidly coming around to the Gleason individualistic hypothesis or a reasonable facsimile thereof. The last major holdout appears to be in the group of range managers in the Plains states who are still imbrued with Clementsian doctrine. It is noteworthy, however, that no important papers on vegetation have appeared in the last two years which actually used the Clements system. The old ideas seem to die harder in those who talk about ecology rather than who are actually practicing it. As you have already gathered, we consider ourselves your disciples. (letter, Curtis to Gleason, 1/14/1955, Curtis Papers, University of Wisconsin, Madison, Archives)

However, it should be noted that the first public presentation by the Wisconsin School (as they became known) which explicitly challenged the community-unit theory, and presented new field data to support that challenge, was made by Curtis and his student, Robert McIntosh, to a meeting of the Ecological Society of America in Columbus, Ohio, in September 1950 (McIntosh and Curtis 1950). Having presented the results of their study of the hardwood forest of southwestern Wisconsin, they concluded, "No discernible types or association-like entities could be detected. Rather the stands showed a continuous progression ... [a] vegetational continuum." Whittaker had offered effectively the same conclusion, albeit somewhat differently expressed, with a substantial quantity of relevant data, in 1948. Both Curtis and Whittaker deserve credit for the revival of the individualistic hypothesis and the vindication of Gleason but, strictly speaking, Whittaker and his gradient analysis have priority.

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