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COMMENTARY

ORGANISMIC AND CONTINUUM VIEWS OF PLANT COMMUNITY, THE CENTENNIAL DEBATE OF ECOLOGY

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It is a note to make young ecologists in India and other developing countries familiar with an important and exciting debate in ecology. Social factors have frequently influenced the course of scientific development, and this aspect may interest even to a scientist of other disciplines.

THE DEBATE

In its early formative decades (beginning of the 20th century), plant ecology was considerably shaped by ideas and theories of Frederic Clements (of Nebraska University, USA) about the nature of plant communities, which he pursued with gusto. In a simple term, a community is a group of co-existing and interacting species populations occupying a space. However, the debate on nature of plant community lingered on and keeps surfacing up now-and-again. This article intends to draw attention of ecologists of developing countries to the debate that was generated about the nature of plant communities in ecology during the early decades of the 20th century and the way it still influences some facets of the discipline. Somehow, ecologists of developing countries did not explicitly contribute to the debate. I have also used the debate to highlight some interesting points and patterns that emerged during the course of debate: (i) A view point presented effectively and pursued with gusto may remain shielded from scientific scrutiny for quite some time and arrest the progression of a counter or alternative views. (ii) The acceptance of view point/concept is delayed when it is presented against the existing current, ahead of time. (iii) Occasionally concepts and theories are born simultaneously at widely separate and distant places. (iv) The debate may not subside despite a wide acceptance of new alternative theory, if the old theory replaced has some plausible features. It may be pointed out that this article is not a review on plant communities, it considers only the organismic view of Clements's and continuum view developed from Gleason's individualistic view of species distribution in space and time.

Clements' organismic view of plant communities kept the Gleason's individualistic view sidelined for decades

Ecology had humble beginnings with roots in natural history. However, its subsequent formative period (the early 20th century) was rich and interesting, largely because of the research of Frederick E. Clements and his organismic view of plant communities. The influence of his organismic concept about the nature of plant communities did not allow Gleason's individualistic concept of species distribution to get due attention (Gleason 1917). In fact, Gleason's view of species individuality remained ignored for decades in the USA and other English speaking countries, and got acceptance and recognition only after 1945, the year when Clements passed away. The individualistic view became widely accepted after 1950 as a result of the establishment of continuum view of community by Curtis and his students at the University of Wisconsin, and Robert Whittaker (who called it gradient analysis) at the University of Illinois, USA. Clements recognized plant communities as an integrated discrete unit having emergent properties which were unpredictable from the knowledge of its individual species (Clements 1916) (Fig. 1). It emphasized on

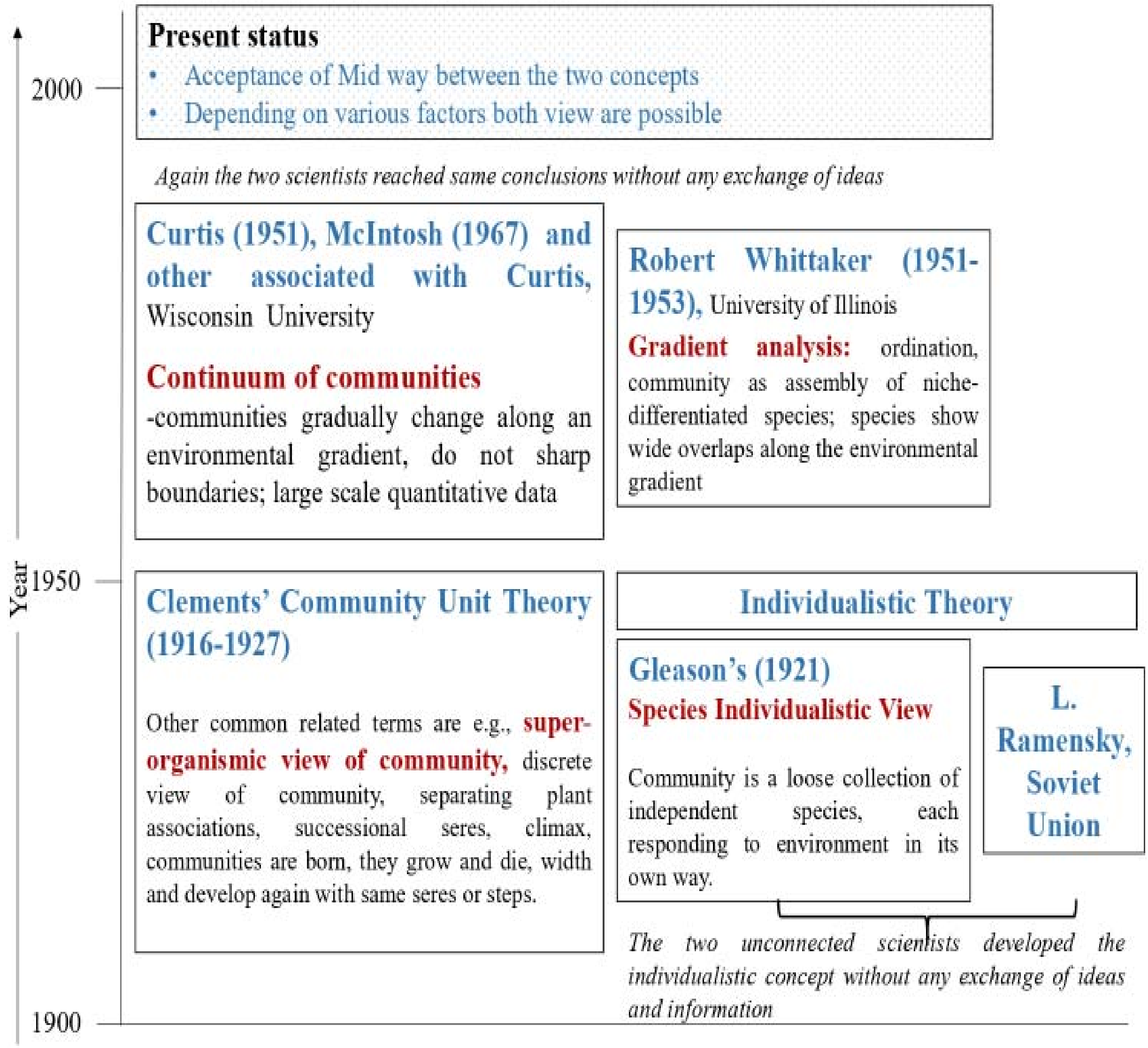

Figure 1. A representation of ecologists involved in debate on plant community in nature.

interdependence among species, and treated a community as a superorganism- "species of a community are integrated as do the organs of an organism". Clements was intolerant of any other view and presented his concepts and ideas in a meticulously organized way, leading to a situation in which there were no takers of Gleason's concept of individualistic species distribution (Gleason 1917, 1939) (Fig. 1). Interestingly, at the same time this individualistic view was being independently developed in the Soviet Union by L R Ramensky but he too was ignored by the then mainstream ecology in this Soviet Union. This situation has been commonly cited as an example of scientific concept developed before its time, resulting in the lack of acceptance by contemporary researchers. The concept of species individuality and vegetation continuity (contrary to Clements' discrete view of community) that Gleason and Ramensky developed were very similar and claims of "clear priority" for Ramensky was advanced by Sobolev and Utekhin (1973). The two researchers gave similar ideas without any interaction.

In Frederic Clements' view, a community is a super-organism. Thus plant communities are made up of interdependent species and they are highly organized unit of vegetation- a kind of super-organism. Succession was key to his view, and according to Clements' communities are born (pioneers), develop (sequence of seral stages), attain climax and eventually die. There are definite sequences by which "climax" is formed. In a given habitat type all successions would end up in one climax. Many of these ideas were considered rigid and dogmatic.

As shown in Figure 2 when species importance values, such as density and cover are plotted against a spatial gradient (e.g. soil moisture or soil pH) or temporal gradient, a group of species show parallel distribution, their density or biomass rising and falling together with change in environment, and forming sharp boundaries with other group of species. They were called associations by Clements. In other words, whenever that requisite habitat conditions occur, the same species group will appear. So communities are discrete and can be identified and named. Thus tightly linked species within communities complement each other for the benefit of the whole association/community. The famous British ecologist Sir Arthur George Tansley (1920) also thought that associations become mature, integrated, self-maintaining quasi-organism. Having somewhat a similar view Braun-Blanquet (1932) of European School of Vegetation Science described the association as having concrete reality.

Clements was passionate and accomplished field researcher who gave considerable importance to quantification of species for which he used a quadrat (a square). He worked almost alone (but was greatly benefitted by his wife Edith) (Fig. 3). He established well developed field stations and his Alpine lab was visited by many scientists from different parts of the world.

Clements' climax theory (a stable plant community at which succession eventually terminates) dominated ecological thought in America and other English speaking countries long after his death and was used though in a bit different words by Odum (1971) while mainstreaming the ecosystem concept in ecology. The importance of diverse species in making an ecosystem was recognized by Odum and is integral to Gaia hypothesis. Though ridiculed by several ecologists later on, Clements' discrete community view keeps on surfacing even today in various ways.

In Uttarakhand Himalaya, tilonj oak (*Quercus floribunda*) forms dense forests (just above 2000 m), often with over 80% crown density. However, I have come across three deeply shaded sites, located in hollows in which the top canopy consisted of widely

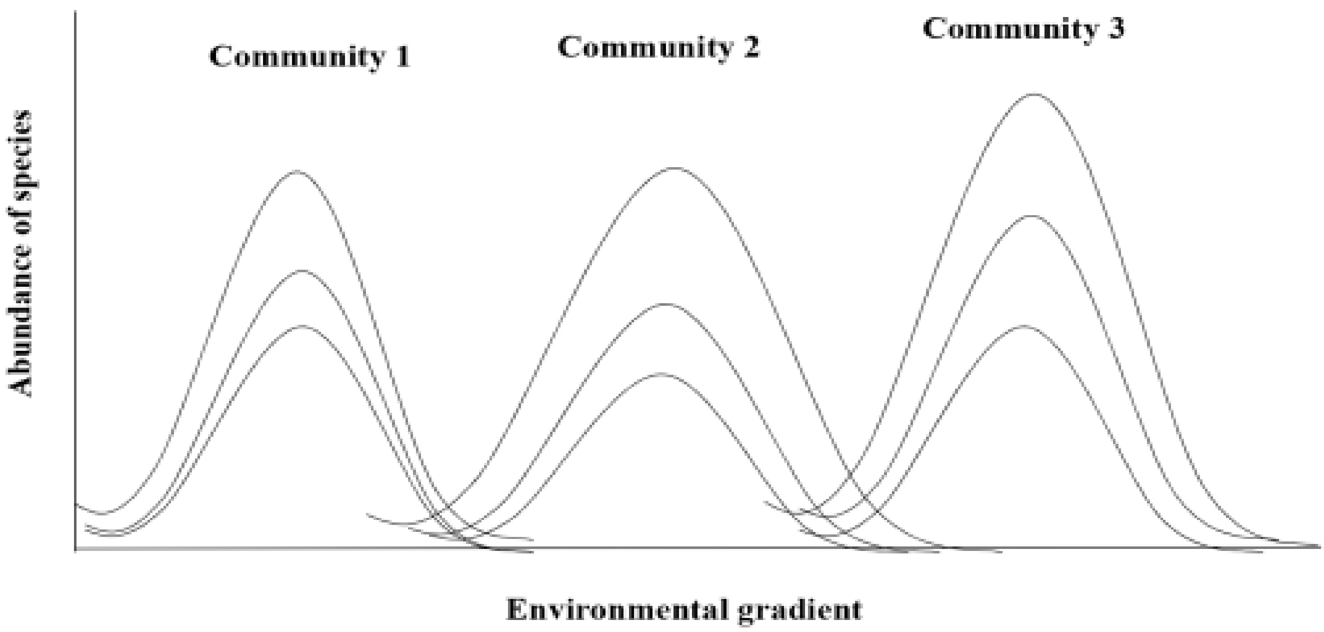

Figure 2. Pattern of species distribution along an environmental gradient as predicted by the discrete view of association or organismic view of Clements', species population curves of a community have a similar pattern of rise and fall and those of different communities form sharp boundaries along the environmental gradients (from Singh et al. 2017).

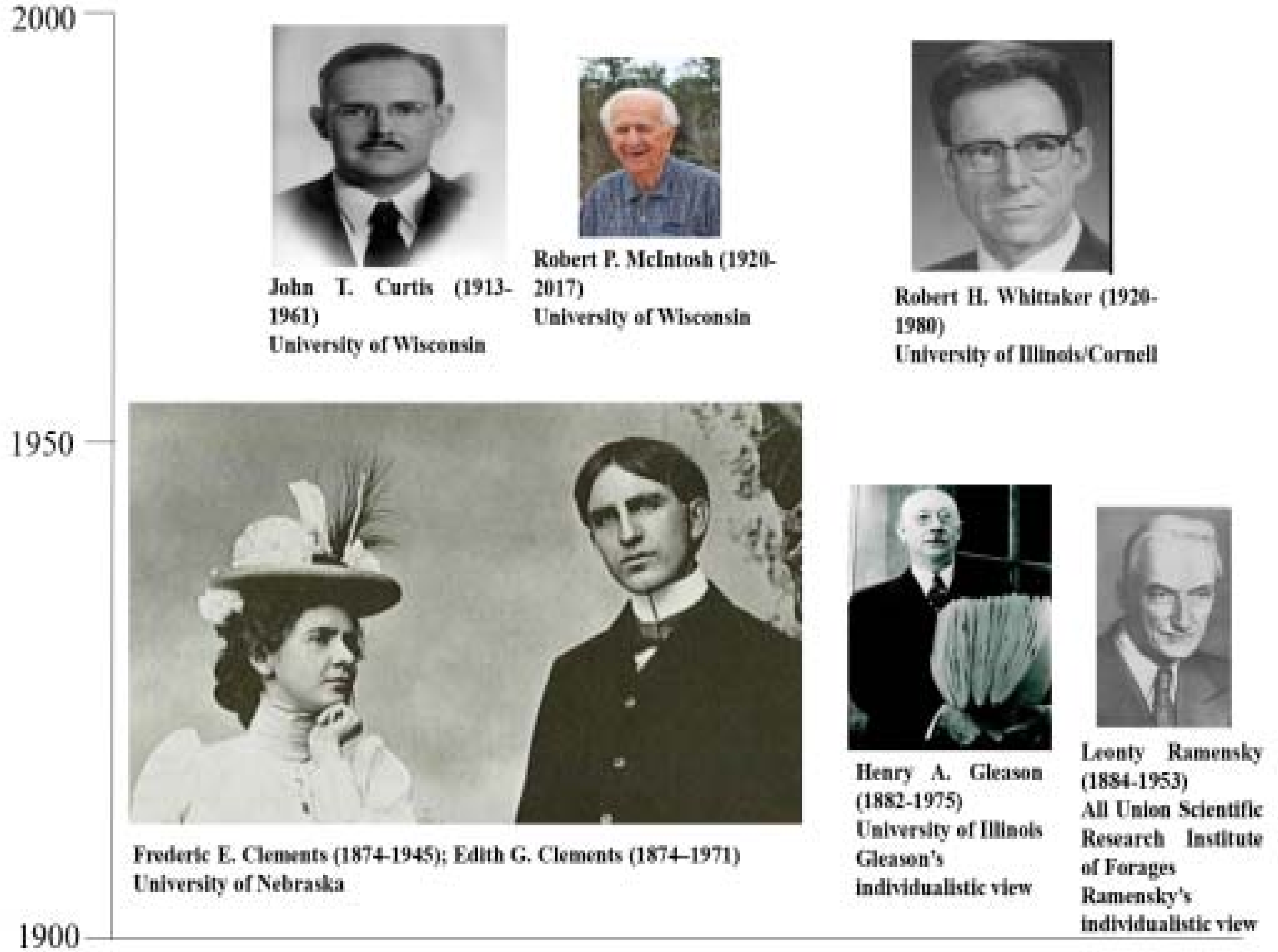

Figure 3. The major players of the debate on the community theory. Edith G. Clements (the wife of Clements') (pictures extracted from Google) "unsparkingly devoted her unusual ability as an illustrator, linguist and botanist" to become life-long collaborator on research and books.

spaced trees with less than 30% crown density, while undercanopy of *Machilus duthei* was continuous without any break. The sites are several hundreds of kilometer apart. It seemed that by restricting the growth of canopy species the deep shade of the hollows allowed the more shade-adapted *M. duthei* to over-express itself. While passing by them, I am reminded of Clements' observation that the same species composition reappears when its habitat repeats itself. In the Uttarakhand's tilonj oak stands, not only species composition but physiognomic modifications that the shade caused are the same at widely distant sites. This kind of repeatability of species association and structure is not common in Himalayas. However, the relationship between slope direction and species composition can be shown by repeated appearance of one forest type on one aspect and that of another type on its opposite aspect. To a great extent, the issue is of degree of tightness of species combination.

Gleason's individualistic concept and the establishment of continuum view of communities

According to this view, species are distributed individualistically along the environmental gradients, or no two species respond in the same way in space and time to a changing environment. So, communities are only a loose collection of species living together at a particular place. Locally, a chance factor is very important as it decides whether a seed lands at a given place. Chance factor can be important even at a regional scale. For example, cactus family originated in America, so there the desert communities have species of cactus family. Deserts communities in India do not have them. The Kashmir valley does not have either *Pinus roxburghii* or *Quercus leucotrichophora*, which extensively dominate much of the western and central Himalayas. According to this view species, not community is the basic unit of vegetation.

The species individualistic view eventually led to the birth of **continuum view of community** which subsequently was widely accepted. However, there are some ecologists (Wilson and Andrew) who think that Gleason's community concept was essentially not much different from Clements' community concept (also see Leibold and Mikkelson 2002). They believe that being basically a taxonomist, Gleason was confused by super-organismic terminologies given by Clements, but most of the points he made were essentially identical to those of Clements.

Continuum view of community

From species individualistic hypothesis was born the continuum view of community in 1950s soon after the World War II. Ecologists at Wisconsin University under the leadership of John Curtis (1951) and Robert Whittaker (1951, 1953) at the University of Illinois, the USA independently propounded continuum view by actually quantifying pattern of changes in vegetation along environmental gradients. They investigated the nature of plant communities using well designed and objective approaches through field sampling and data analysis (Nicolson 2001). According to McIntosh, who was among the earliest PhD students of Curtis (Fig. 1), his teacher had begun doubting about the organismic view of plant communities soon after joining the Wisconsin University. That was also the time when ecologists had begun to recognize the importance of objective sampling in a field, and a large scale data collection using appropriate techniques, particularly for ordinating data collected from vegetation sampling. Curtis gave emphasis on examining variation in vegetation by extensive and intensive data collection on species importance values, such as density, and cover. One of the distinct features of McIntosh' PhD thesis (under the supervision of Curtis) was the large scale of data collection from Wisconsin forests, which led to ground breaking paper with Curtis in 1951. The paper on Wisconsin forests showed that there existed continuous series of overlapping species along environmental gradients (Fig. 2). Following the continuum view the species population curves were generally unimodal and species did not show similar patterns of rise and fall in importance values along the environmental gradients like declining moisture or increasing elevation (Fig. 4). That the importance value curves of species were not identical along the environmental gradients and that they did not form sharp boundaries, supported the individualistic view of species, described several decades ago by Gleason and Ramensky independently.

In the Wisconsin forest species distribution curves were overlapping and species composition changed continuously (McIntosh 1967). Furthermore, the species optima were scattered, they did not form

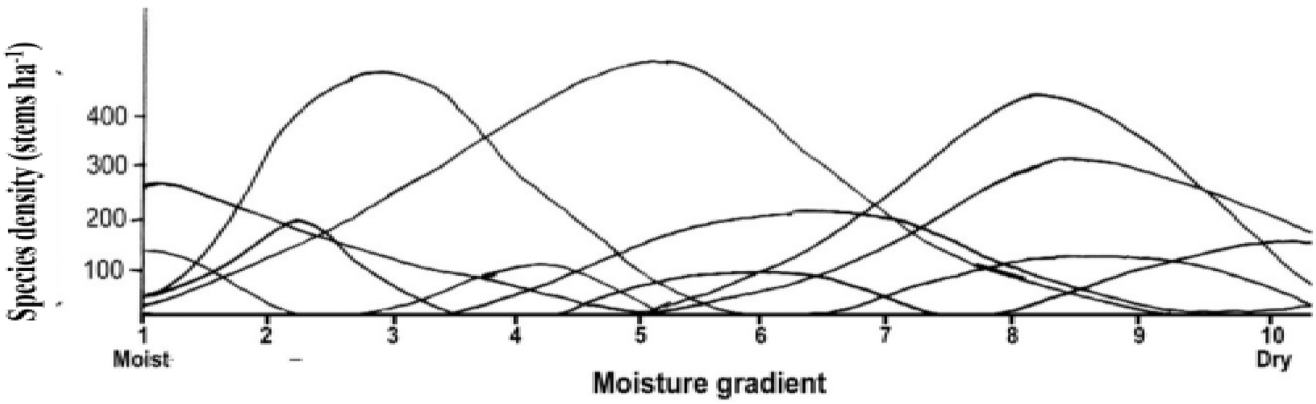

Figure 4. A representation of distribution of tree species populations along moisture gradient according to continuum view. Species population curves (generally unimodal) do not have similar pattern of rise and fall, and do not form sharp boundaries along the environmental gradient (from Singh et al. 2017).

clusters (Fig. 4). Oblivious to research of Wisconsin team similar approaches, ideas and terminologies were being developed by Robert Whittaker at the University of Illinois. Whittaker's studies were on trees and insects along elevation gradients in the Great Smoky Mountains. He used the word *Continuous* for overlapping series of species populations along the elevation gradients and gradient analysis for the method. At Wisconsin, the Curtis school used the term *gradient analysis* and coined the term "continuum" for "continuous changes in vegetation" (McIntosh 1967). Whittaker like Curtis emphasized that their findings were consistent with Gleason's concept.

Strangely, Curtis and Whittaker developed the continuum concept and the corresponding methods of sampling and data analysis (ordination and gradient analysis) independently, without any interactions until 1950. Moreover, Curtis helped Whittaker in getting his work published, as journals were not inclined to accept continuum concept (unfortunately both Curtis and Whittaker died of cancer prematurely in 1961 and 1980 at the age of 48 and 60, respectively). So it is a strange coincidence that the individualistic concept and continuum concept that was born from that, were developed independently and simultaneously by different groups/individuals.

Connected to the establishment of continuum view is the emphasis on quantification and data analysis in vegetation ecology. The emphasis on quantification was apparent in the publication and teaching of Curtis, McIntosh, Whittaker, and their followers. In Braun-Blanquet School, as an example species were assigned to cover classes, such as 50-75% cover. Data used for gradient analysis pertained to the precise measurement of species frequency, density, stem basal area and plant cover. Subsequently, quantification of species importance value became of standard practice in the USA.

The debate of community nature is centennial and still puzzles ecologists.

Most ecologists subsequently accepted the continuum view of community, however, currently there is some tendency to take a middle position between Clements' and Gleason's views. **Echoes of the controversies** between the Clements' and Gleason's views of community continue to influence ecology even today. It may be pointed out that Clements was misunderstood to an extent. Several ecologists ridiculed the organismic view of community that Clements passionately put forth. Partly, the problem with Clements was that ecologists often over-paid attention to his terms like community as "super-organism" or "climax concept", paying little attention to space he allowed for several deviations from his central ideas. Some of the ecologists seemed to deliberately chose those writings of Clements that would underpin their assumption that Clements' ideas were dogmatic. Clements presence, however can be seen in debates in several areas pertaining to ecosystem properties and management of natural resources, such as forests. To manage forests, practically one requires to classify them, as an example.

Whether one is against or for Clements' community unit theory, debates in ecology that have historical ingredients generally continue to refer to Clements. Community patterns along environmental gradients continue to draw attention of ecologists even after a century of debate and research (can be considered to have started in early decades of the twentieth century, Clements 1916, 1936; Gleason 1926). The two views are considered to be irreconcilable (McIntosh 1967). However, using a multi-species competition model, Liautaud et al. (2019) emphasized that community unit (organismic view) and individualistic view represent two limiting states along a continuum of outcomes. When the strength of the competition varies widely, a community unit emerges. On the other hand, when species interactions are weak and uniform, gradual changes in species composition occur (follows the continuum form). Liautaud et al. (2019) emphasized the importance of species interactions to understand and predict the species responses to environmental changes. Thus the study reframes the debate between community unit and community-continuum views by demonstrating that both can emerge at different models within a same theoretical ground. In this species interactions and species dispersal considered to play critical roles.

CONCLUSIONS

The debate did not touch Indian ecology

The centennial debate of the nature of the community-super-organisms vs a collection of loosely interdependent species has been dramatic and colorful. Somehow, we Indian ecologists hardly participated in this debate. Continuum was not a familiar term in Indian ecology, for a long period after its wide acceptance. I still remember one day in 1979, I sat with Prof. J. S. Singh in his small room with a mesmerizing view of lake Nainital (Kumaun University), to discuss continuum view in the context of forest community of Himalaya, which eventually resulted in the first Ph.D thesis based on ordination techniques and continuum view. It was of Jeevan Tewari, my first Ph.D scholar, who worked on forest vegetation along an elevation gradient from the sal forests of Chorgalia to oak forests in Nainital catchment. Since then, many Indian ecologists have used ordination techniques, but the debate on community theory remained sidelined. In high ranges of Himalayas, mature forests are quite common, and they seem to provide evidences for both communicating views.

The domination of Clements' organismic view for decades, and utter disregard for the Gleason's individualistic view indicates that scientific mechanisms to address controversies have been at least ineffective. The ecology text books also played a role in the widespread acceptance of Clements' organismic view of community. The domination of Clements and Odum can be seen in Indian ecology, and in this text books played a key role. Not many Indian students know about Whittaker, the proponent of continuum view as his book was much less accessible than of Odum in India. However, the concepts and ideas of Clements were not entirely wrong, they had enough substance to persist in some form in ecology.

The development of individualistic concept, almost identical, in two widely different countries, the Soviet Union and USA simultaneously with no exchange of ideas is rather strange. Strange is also the development of continuum view and the associated ordination techniques independently at the same time in 1950s in the USA. Interestingly, almost all important ecologists of these decades had something to say about the debate. With the widespread acceptance of continuum view in the late half of the 20th century is associated with rapid development of quantitative measurement at a large scale in vegetation ecology. Generation and analysis of data began to occupy central stage in ecology.

Treeline a physiognomic discontinuum (?)

Responses of treeline to climate change is a relevant area of research in this regard as, treeline is a physiognomic discontinuum. The repeated occurrence of birch (*Betula utilis*), fir (*Abies spectabilis*) as a canopy species and *Rhododendron campanulatum* as an undercanopy species can be seen at many treelines in the Western Himalayas. The birch occupies the moist north aspect, and blue pine (*Pinus wallichiana*), treeline is often confined to the drier south aspect. However, these heat-deficient sites can have other species too, such as evergreen broadleaved oak (*Quercus semecarpifolia*) and deodar (*Cedrus deodara*). Blue pine is an effective colonizer of slopes released by glaciers. However, birch too is a colonizer. Succession and mature communities are difficult to separate in such a stressful environment.

The results of giving importance to making ecology quantitative and multidisciplinary by Clements and subsequently, Curtis could be seen in recent growth of ecology and conservation as a quantitative science dealing with the analysis of large datasets (Anderson et al. 2021), focusing on global issues and increasingly using statistical modeling meta-analysis and phylogenetics.

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COMMENTARY

ORGANISMIC AND CONTINUUM VIEWS OF PLANT COMMUNITY, THE CENTENNIAL DEBATE OF ECOLOGY

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It is interesting that you are unearthing this debate, the same one we had in class in graduate school in 1965. Probably there is no way to get data that would satisfy the people who care about it, as I speculate later in this note.

COMMENTS

First, I think there are two questions here: Do species act individualistically? And, does vegetation always exist as a continuum, or do distinct communities exist in some circumstances? In my opinion, people conflate Gleason's contention that species behave in an individualistic manner with the idea that vegetation occurs as a continuum, with no biological basis for dividing it into distinct communities. I think these are separate questions, and that individualistic species behaviour does not necessarily result in a vegetation continuum.

Communities develop in response to a variety of factors, which vary with time and place and plant age, and just because the properties of species we measure result in an individualistic mixture among species, this does not mean that the environmental factors and plant responses that actually determine what is growing together now and in one place will be responding to all those properties. Maybe the various species that grow together are similar in the properties that determine where they can live in those conditions of environment, competition and plant age. Thus, species that appear individualistic in all the properties we measure may be similar in the few that limit their success in one set of conditions. And, some species that have a broad tolerance range to abiotic factors grow primarily near the edge of it, as they cannot compete elsewhere, for example. I do not have any easy solution to what to say about this.
I do know that the multiple herbs we study at Mount St. Helens do each act/look differently than all the others. But they also grow together in somewhat predictable combinations, it seems to me. So, I think there is lots of evidence for species being distinct from one another. But I am quite nervous about assuming that species individualistic nature necessarily will prevent them from developing discrete community types or force all vegetations in a landscape to exist as continuum.

Having separated those phenomena of the nature of species from the nature of communities, I will comment about the argument about the nature of plant communities, in particular those developing long enough to have come into some type of equilibrium with their environment (which can include small disturbances). I am no expert on this topic, but I have been observing and teaching and getting some research results that bear on these matters for a long time. I have not read recent writing about this topic, but I am happy to hear that people are talking about a more nuanced view than the old dichotomy

Here are some comments:

- Most ecologists of my generation (1960s onward) accepted the continuum idea just as thoroughly as their predecessors had swallowed the ideas of Clements. And, for most, probably with as little data or experience or thought about it. I was lucky; my Prof. H.J. Oosting knew many of the principal figures in the debate and worked on succession, but had no hard position to try to defend. We read the papers he provided, listened to his presentation of their context, and drew our own conclusions.

- Clements' idea of vegetation as organism keeps surfacing anew. I have reviewed papers that "discovered" the idea, apparently, with no reference to this debate or history. Even the earth (Gaia) is said to be like an organism, I believe.
- Much of what one sees in terms of community pattern, discrete communities vs. continuum, depends on where one looks and what he chooses to see...or rather, looked, and saw. See some of the points below.
- Reading Rexford Daubenmire, Plant Communities textbook 1968, and an exchange with McIntosh in Science, I think, about that same time, gives a very useful third view re. what is (or was) really out there...where he worked, which applies to my area also.
- Daubenmire, in Idaho and Washington, worked with old communities that had been little affected by people, and identified discrete communities. In contrast, by the time Curtis et al. started studying Wisconsin vegetation, it had been mostly cut over or farmed for at least 50 years.
- Succession produces a gradient through time. If you sample a variety of forest types of a variety of ages in each type, I think one should expect to find vegetation that one was call a continuum. This was the situation in Wisconsin.
- Daubenmire based his concepts on old stands that were selected to represent the minimal amount of recent disturbance giving time for older communities, more adapted to their environment, to develop.
- Across Wisconsin, topography is gentle, climatic gradients gentle. In the Rocky Mountains (and the Cascades) steep mountains produce sharp gradients in microclimate, including elevational changes, rain shadows, and deep valley microclimates like the Himalaya. Thus, the nature of environment probably contributed to what the ecologists found in the vegetation.

I have tried to produce a Whittaker-type curve using substantial sets of vegetation data, and did not get anything like the smooth curves the continuum people publish. And they never provided the data points they used to draw those nice smooth curves. My former colleague was a grad student with one of the key gradient people, saw the original data, and did not think that they justified such a smooth curve as was published. So finding a continuum may also reflect one's willingness to see a simple pattern among the messy data.

So, for what it is worth, these are some things I think one should be exposed to and think about as he ventures into this type of consideration. Gaining any certainty (i.e., appropriate data) may be impossible now. I suspect that there are few if any places left in the temperate forests where one could sample forests to try to test these models. Disturbance by civilization is almost everywhere, and there may not be enough left in the fragments of really mature forest to test what forests will become with age. Rapid climate change may have already disrupted the relationships of plants to environment that existed when old stands established. If one is just saying that existing forests are mostly a continuum, that seems likely to me...but that does not answer the debate that Clements, Gleason, Curtis, Whittaker, Daubenmire, et al. were having.

It is interesting to think about these things. I have not read any of this literature for years. But from our work at St. Helens, and combining it with work of others there, it is clear that the process of succession and long-term community development is diverse and not modeled effectively. The end points of succession will probably be even harder to understand, if there is enough such vegetation left to allow a conclusion.

Prof. Don B. Zobel is professor in the Department of Botany and Plant Pathology, Oregon State University. He kindly responded to Prof. S.P.Singh's commentary. Prof. Zobel taught ecology at the height of the debate and he has added an important point to the debate that "individualistic behaviour of species does not necessarily result in a vegetation continuum."