

Method and metaphysics in Clements's and Gleason's ecological explanations

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Abstract

To generate explanatory theory, ecologists must wrestle with how to represent the extremely many, diverse causes behind phenomena in their domain. Early twentieth-century plant ecologists Frederic E. Clements and Henry A. Gleason provide a textbook example of different approaches to explaining vegetation, with Clements allegedly committed, despite abundant exceptions, to a law of vegetation, and Gleason denying the law in favor of less organized phenomena. However, examining Clements's approach to explanation reveals him not to be expressing a law, and instead to be developing an explanatory structure without laws, capable of progressively integrating causal complexity. Moreover, Clements and Gleason largely agree on the causes of vegetation; but, since causal understanding here underdetermines representation, they differ on how to integrate recognized causes into general theory—that is, in their methodologies. Observers of the case may have mistakenly assumed that scientific representation across the disciplines typically aims at laws like Newton's, and that representations always reveal scientists' metaphysical commitments. Ironically, in the present case, this assumption seems to have been made even by observers who regard Clements as naïve for his alleged commitment to an ecological law.

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1. Introduction

Plant ecologists face a considerable challenge in explaining how vegetation develops over long periods, in that extremely many and diverse causes substantively affect every outcome, confounding hope for explanatory laws associating one or a few causes with particular outcomes. This state of affairs is often illustrated in ecology textbooks by the moral tale of Clements and Gleason. Frederic E. Clements, perhaps the first American theoretical plant ecologist, in 1916—so the tale goes—naïvely advanced a law of plant succession despite this complexity. The law stated that climates compel a single kind of vegetation, inevitably. For Clements, climates are like genomes, and vegetation is like an organism whose characteristics its genome determines. Though broadly influential for a time, this law and its associated theory were roundly defeated by a scientist sensitive to the real complexity of vegetation in a way Clements was not—Henry A. Gleason. Gleason understood that vegetation is comprised of individual plants in complicated

begin page 86

relationships with local environments, acting freely of laws. And so, newly acquainted with causal complexity, plant ecology marched on to a Gleasonian future. So the story goes.

One of my contentions here is that the caricature of Clements widely presented in histories, textbooks, and science articles, as naïve about complexity and committed to a deterministic law, is mistaken. Clements offered a sophisticated approach to ecological explanation uncommitted to laws. By characterizing Clementsian explanation more fully than usual, I hope to demonstrate that what has appeared to many readers a law is not one.

Making that argument invites the question how so influential a scientist as Clements could have been widely misread. Part of the explanation lies in Clements's works having been narrowly anthologized, with emphasis on portions fostering the impression that he believed in a law. But furthermore, this selective reading itself reflects a common commitment to what Richard Lewontin (2003) calls the Newtonian Ideal—that science above all aims at 'the formulation of some principle of great generality, if not universality, a law or small set of laws that applies at all times and in all places'. Readers of science have often approached it with the assumption that scientists' ambitions to general theory are automatically ambitions to meet the Newtonian Ideal. Ironically, in accounts of Clements this ideal appears to have been assumed as an interpretive framework for science even by those who would consider it naïve as an interpretive framework for all of nature. How this might have come to be raises my second main contention, which concerns their pairing.

Gleason was one of Clements's many critics; others included English ecologist A. G. Tansley and American R. H. Whittaker (Tansley, 1920, 1935; Whittaker, 1951). What has made Clements and Gleason a pair—what has made their theories jointly a benchmark episode in the history of ecology—is the ease with which they have been identified with extreme opposite views on the metaphysics of vegetation, and at times even with opposing views of *nature*. Opposite views of nature pique the imagination, but here especially because they bring plant ecology into the historical narrative of twentieth-century physics. Since 1900, physics has drawn a universe decreasingly resembling Newton's straightforward, law-governed one. Correspondingly, historians, philosophers, and others writing about science having increasingly regarded the Newtonian Ideal as a naïve one for all science—perhaps one arising from the modernist impulse to impose strict order on messy nature. Within this narrative (without calling it in question), Gleason, the denier of Clements's laws and entities, and recognizer of complexity, easily assumes the role of progressive antagonist.

The problem is that Clements (1916, 1936) does not assert a law of vegetation. In contrast, I argue, Clements and Gleason largely agree on what controls vegetation. But, in their work, interestingly, causal understanding does not determine the structure of explanation. The scientists adopt quite different strategies for constructing explanations from similar causal backgrounds. Their differences lie in methodology, not metaphysics.

The phenomenon Clements and Gleason theorize about is plant succession—the development of vegetation in an area through time, especially following a disturbance. After a fire, for example, removes plants from some area, vegetation grows back not through a sudden reappearance of what was there before, but through a series of stages. Such series are instances of succession. Historians and ecologists have attributed to

begin page 87

Clements variations on two main theses about successions: (1) vegetation develops in any given area as a *unit* and in a way analogous or literally identical to the development of an individual *organism*, and (2) the development of vegetation in an area *must* culminate in a particular type of vegetation determined by local climate and called a *climax*. Gleason has been associated with the rejection of these theses, and with an alternate theory privileging the interactions of independent *individuals* with their environments over the integrated, holistic dynamics of Clements's theory. Here, representatively, ecologist Michael Barbour summarizes Clementsian ecology:

Clements had argued that natural vegetation tended over time to become organized into discrete units separated by narrow or broad ecotones. These units, which he named formations or associations (and which others have come to call communities), are uniform over large areas. Each area has its own characteristic climate. That is, every climatic region will over time (other factors not interfering) develop its own association vegetation type, and that association is in balance with the climate. Factors that interfere include unique geologic substrates and drainages and episodic disturbances. Associations are as natural as species or atoms; they are fundamental units in the hierarchy of life and not mere human constructs. The floristic composition within any community is homogeneous throughout its range, he wrote, because the component species are tightly interdependent upon each other. Moreover, if an association is disturbed by fire, logging, grazing, cultivation, or flood, it recovers its original species composition and appearance over time (once the disturbance ceases) in a process he called succession. The path of succession leads faithfully back to the regional association because only this community is in balance with the climate. Clements called this final phase of succession a climax. A single climatic region, Clements wrote, has only a single possible climax. Thus all successions should ultimately, with sufficient time, lead to the same end point, whether time zero starts on bare rock, on the lee slope of a hill, or at the edge of a pond. This is the 'monoclimax' corollary to Clements's basic hypothesis about vegetation. Because each unit is so constant, its boundaries so discrete, its location with respect to the regional climate so predictable, and the path of succession so reminiscent of the ontogeny of an individual from conception to maturity, Clements equated these units with organisms.¹

Note that Barbour emphasizes the apparent determinism of single outcomes by climates, and a homology between this production and organisms' development. He then attributes further theses to Clements, such as that climax associations stand in 'balance' with local climates (though it is not clear what that means), that they are natural kinds, that they are adamantly real—not postulated—entities, that they are internally homogeneous across broad areas, and that their constituent parts are tightly integrated and interdependent. All this quotes only the second line of Clements's 1916 *Plant succes-*

begin page 88

¹ Barbour (1996) pp. 234–235.

tion.²

Barbour then presents in contrast a version of Gleason likewise conforming to the usual tale:

In 1917 and again in 1926 and 1939, Gleason published his theory of vegetation, which he called the 'individualistic concept'. According to this theory, formations and associations are not real, natural units; they are merely artifacts and human constructs or abstractions. Groups of species do not appear and rise and fall in abundance synchronously across the landscape; entire collections of co-occurring species are not interdependent. Rather, each species spreads out as an independent entity, individualistically distributed according to its own genetic, physiological, and life-cycle characteristics, and according to its way of relating both to the physical environment and to other species.³

For Barbour, Clements's realities become Gleason's mere constructs, and determining laws become uncoordinated interactions. Gleason denies the theses attributed above to Clements, and finds in individual and independent interactions the causes of vegetation. Barbour's subsequent discussion further identifies Gleason's theory with reductionism and Clements's with holism, Gleason's with sensitivity to complexity and heterogeneity, and Clements's with a remarkable simplicity. Clements's theory becomes an object of mild derision, of wonder at how a generation of scientists could have believed, in the face of ubiquitous counterevidence, a theory so naïve. 'The subjective, simplistic Clementsian landscape', Barbour writes:

can only be circularly 'proven' to be real by the use of subjective, simplistic sampling techniques. It is not real; it is not nature. If one wishes to recognize associations, perhaps on the basis of the presence of certain dominant species, one can do so and even draw lines on maps; but this activity must be recognized as arbitrary, subjective, and a gross simplification of nature.⁴

I quote Barbour at length to avoid erecting a strawman of the legend. When analysis of Clements refers to Clements's writing at all, it typically refers only to the first pages of his 1916 major work on succession, *Plant succession*, or, more often, only to his late 1936 article, 'The nature and structure of the climax'. That this paper is the one piece of his voluminous output widely anthologized has, I suspect, led many readers to misjudge how climaxes fit into the full theory. Variations on the tale have been offered by individual writers, but typically as extensions of these two basic theses. Environmental historian Donald Worster, in his well known history of ecology text, attributes Clements's naïveté to extra-scientific faith, writing that,

begin page 89

undoubtedly the explanation for Clements' emphasis on the serene and its climax lies in his underlying, almost metaphysical faith that the develop-

² The other two sentences cited as "Clements (1916), pp.3" actually appear nowhere in Clements's 1916 text, as verified by a full-text electronic search at the Library of Congress. Ibid.

³ Barbour (1996) p. 237.

⁴ Ibid.

ment of vegetation must resemble the growth process of an individual plant or animal organism.⁵

He attributes Gleason’s dissent to similarly submerged motives:

There were a number of scientists, too, who found the anti-technology implications in the climax ideal hard to accept. From this objection, as much as from any purely scientific quarrel with Clements, there emerged in the thirties an ‘anti-climax’ party. Earliest to join issue with Clements on this point was Henry Gleason of the University of Michigan.⁶

Further reiterations with variations have been offered by historians Ronald Tobey (1981) and James Malin (1961) ecologists Frank Golley (1996), Robert P. McIntosh (1975, 1985), Charles J. Krebs (1972) and Paul Colinvaux (1978), biology textbook authors Joy Tivy (1972), Robert Ricklefs (1997) and Michael Begon, J. L. Harper, and C. R. Townsend (1990), philosopher of science Richard Looijen (1998), early environmentalist Paul Sears (1949), and even literary scholar Debra Journet (1991), among many others. Though they are overlooked by many accounts, Joel Hagen (1988, 1992) has made some important corrections to thesis (1) attributed to Clements, the thesis concerning the organismic analogy; I mention them later. I focus here on correcting thesis (2), concerning Clements’s alleged climax law.

2. From physiological ideals to successional dynamics

A better account of Clements’s ecology begins where he did, with experimentation on plant physiology. Opening *Plant physiology and ecology* (1907), Clements writes that ‘the proper task of physiology is the study of the external factors of the environment or habitat in which the plant lives, and the activities and structures which these factors call forth’.⁷ That is, with respect to an individual plant, its ‘environment’ can be understood as a set of factors which influence its ability to survive—‘water, soluble salts, humidity, light, temperature, wind, soil, pressure, physiography, gravity, polarity, and biotic factors’.⁸ For Clements, the key to understanding the internal physiology of a plant is knowing what kind of environment it *normally* lives in, which is to say, what ranges of these external factors it is normally exposed to (e.g how much water, how much wind, what parasitic fungi, etc.). A plant’s physiology consists of three degrees of ‘responses’ to external factors.⁹ First, the overall structure and functioning of a plant typically reflects its evolutionary response or ‘adjustment’ to a kind of environment. Xerophytes,

begin page 90

⁵ Worster (1994) p. 211.

⁶ Ibid., p. 238.

⁷ Clements (1907) p. 1.

⁸ Ibid., p. 3.

⁹ Clements includes under ‘response’ (sometimes ‘reaction’) to environmental stimuli both ‘adjustment’, which is ‘functional’ response, and ‘adaptation’, which is ‘structural’ response. Suggesting that it is ‘convenient’ to distinguish them, he treats them as continuous with each other. While focusing extensively on both adaptations and adjustments themselves, understood as mechanisms for handling environmental variation, he remains silent in (1907) about the mechanisms ultimately producing them, whether Darwinian, Lamarckian, developmental, or otherwise. He focuses, instead, on reading function into observed structure and behavior. In (1929), with Weaver and Hanson, in the context of discussing the role of competition in community structure, he suggests ‘adaptation or modification is the regular if not universal outcome of competition’.

for instance, are those plants adapted to little water; hydrophytes, to much water.¹⁰ Second, environmental changes of great intensity and duration (e.g. in humidity), can cause at least those plants whose growth permits some plasticity to adjust developmentally, by, for instance, producing fewer leaves or longer stems. Third, in more superficial and ephemeral respects, how a plant is functioning reflects its present environment. For example, changes in humidity cause plants to adjust the amount of water they evaporate. At all three levels, understanding an individual plant's physiology requires knowing which external factors have acted and are acting on it, in evolutionary time, in its lifetime, and currently. Brief and minor environmental changes elicit functional responses, enduring or severe changes elicit structural responses.¹¹ From this account of the physiology of individual plants (focusing on adjustment to their environments) emerges Clements's account of their interactions—his ecology of vegetation. It consequently emphasizes the adaptation of component plants to particular environments, and the population dynamics which occur in response to environmental changes.

We gain further insight into how individuals' physiologies structure Clements's ecology by noticing him calling some functions and adjustments *normal* and *abnormal*. 'Normal function', he writes, 'is physiological, and abnormal function is pathological'.¹² Because species of plants are adapted to the environments in which they normally occur, understanding their physiologies (which is to say, the successful functioning of their adaptations) requires paying attention to the environment or environments of their usual ranges. Plants migrating to new environments, or whose habitats have been severely modified, will often be poorly adjusted to their new circumstances. 'A plant', Clements remarks, 'that is more or less hindered in carrying out its usual functions ... exhibits abnormal adjustment'.¹³ In an environment to which it is not adapted, that is, a plant functions pathologically, requiring severe adjustments in form or function to survive. Strained by dehydration, a plant may drop most of its leaves, which behavior, though normally detrimental, may allow it to survive drought, albeit in pathological condition. When a plant's capacities for even pathological adjustments—for making severe adjustments to survive—is inadequate to the threat, it will die. If understanding the various factors comprising plants' environments is crucial for understanding their physiologies, knowing which plants function normally in which environments is essential to characterizing the ecology of any area (that is, which organisms occur there, what environments they thrive in, and what effects they have on each other's abundance, functioning, and survival).

Having distinguished normal from pathological with respect to functioning and adjustment, Clements concedes 'there is no hard-and-fast line between the two, since any plant is acted upon by abnormal stimuli while it is getting established in a new habi-

However, he immediately expresses skepticism about whether 'such changes are fixed', and suggests 'there is no proof ... that Darwin was correct in thinking that competition is the mechanism for accumulating minute variations', (p. 322). I have not found other conclusive evidence of his views on the mechanism by which characteristics are acquired. Tobey (1981) proposes that Clements 'never abandoned his neolamarckism', though the evidence he offers there is not compelling, (p. 87). Hagen (1988) argues from correspondence that Clements increasingly preferred Lamarckism as he aged.

¹⁰ Clements (1907) p. 155.

¹¹ Ibid., p. 3.

¹² Ibid., p. 6.

¹³ Ibid.

tat, but these same stimuli become entirely normal when the plant has become adapted to them'.¹⁴ He moreover concludes that the distinction serves little explicit purpose in botany: 'in studying the behavior of plants, it is both illogical and inconvenient to separate the normal and the abnormal'.¹⁵

But why bother with 'illogical and inconvenient' terms at all? Aware of difficulties, Clements uses 'normal' sparingly. But later he applies it ecologically to the sequence of succession: 'normal succession is unit succession, that is, the development from an initial bare area to a climax'.¹⁶ We can perceive in his willingness to employ 'normal' and 'pathological'—logical flaws notwithstanding—the conceptual starting point of his ecology. Normalcy is a way of characterizing a fit between particular species of plants and particular environments due to physiological adjustment and structural adaptation. Plants have a range of circumstances in which they thrive. Towards the edges of this range they struggle, and outside it they die. Given a knowledge of physiology, we can identify for any environment which species will thrive in it, these being 'normal' for it just in that reductionist, physiological sense. Normal successions will accordingly be *physiologically ideal*, best fit sequences for average conditions in a place. Moving into ecology, however, we must remember that ideals are not always, nor even typically, realized. 'Normal' for Clements may not mean 'quantitatively typical'.

If physiology concerns ideal environments for particular species, succession extends the idealization to dynamic environments of shifting suitability. Clements associates potential environmental changes with sets of species adapted to particular environments—those for which ranges of conditions are *physiologically ideal*—and calls them 'communities'. After a major disturbance like fire, what grows is typically a function of what can migrate into the area and survive in the new conditions. Species comprising this 'pioneer' community can modify their environments so that conditions become more physiologically suitable to another set of plants than themselves. The arrival of plants viable in the new conditions but not in the old marks a second stage. Eventually, if abiotic influences in the environment are stable, some residents can cease modifying the local environment in ways unfavorable to their own reproduction; for instance, they may be able to survive in their conspecifics' shade. Under average conditions and absent abiotic changes, the discontinuation of biotic modifications of an environment can produce this equilibrium 'climax community'. Because of the physiological fit that defines it, it can be replaced only by abiotic disturbance, meaning significant change in conditions. This idealized endpoint culminates a unit succession, an individual instance of the developmental process from pioneers to climax, called a 'sere'.¹⁷

begin page 92

The complete process of adjustment by best fit species to stable environmental conditions, the ideal sere, thus obtains where most occurring environmental changes are due to inhabitants themselves, against relatively stable background environments. Where conditions do not remain within an historically average range, climaxes will often not be

¹⁴ Clements's use of normalcy here incorporates some circularity, whether pernicious or not: normal functioning is defined relative to normal environment, but (1) environments change as individual species become adapted to them and modify them, and (2) which habitats are normal for a plant changes as a function of the ability of a species to function normally in it.

¹⁵ Ibid.

¹⁶ Clements (1916) p. 169. I will set out shortly how the concepts of normalcy and pathology function centrally in his theory, if less so the terms.

¹⁷ Ibid., p. 4.

avored. 'Normal' successions derive their constituencies from long evolutionary histories of competition among individual plants and adaptation to environments, but, given the reality of environmental variation in both time and space, these are ideals very unlikely to be realized widely or enduringly. This contrasts with caricatures of Clements which would have it that linking regional climates to climax regions entails assuming, very implausibly, no abiotic environmental changes or local heterogeneity.

Clements avoids this assumption. He establishes up front that behind successions stand a whole variety of conditions external to the component plants and comprising their environments (equivalently called their 'habitats'). Indispensably among these factors are climatic ones, meaning those aspects of the environment relatively fixed for any region.¹⁸ But by definition climate cannot control succession. As succession amounts to a series of changes through time, the set of factors controlling it shifts in composition and in the relative significance of each component. Among these, climatic factors assume robust influence by setting the general parameters of environmental variation; no matter how much a patch of grass in Antarctica might adjust its environment, orchids will never establish there under the present climate. But equally indispensable are the aspects of a habitat modifiable by its residents, including expendable resources like nutrients and adjustable features like shade. Any actual succession will be affected, too, by unmodifiable factors, both local (like where rocks are) and regional (like actual rainfall or storms). Clements divides the suite of factors directing succession into four kinds, which correspond to different parts of the process in time (though not exactly to the 'stages' of succession mentioned above). They are 'initial causes', 'ecesis causes', 'reactions', and 'stabilizing causes'.

Initial causes instigate succession. Initial causes include any events or circumstances creating bare areas, and those which (where they are not already suitable) modify bare areas in such a way that they become suitable for colonization by pioneer species. Areas where succession is possible are either originally bare (such as where volcanic action creates lava deposits which newly protrude from water), or bare by denudation (as where some event like flooding or glacier scouring has removed some or all vegetation). Initial causes further include any circumstances necessary for vegetation, like that the soil remaining after the flooding has a particle size conducive to ranges of water saturation consistent with plant establishment.¹⁹ After initial causes create the possibility of succession, ecesis causes and reactive causes control the development of vegetation. *Ecesis causes* comprise the activities and adjustments of individual plants which directly shape vegetation. They are the attributes of plants influencing their success at invading. Among them are dispersal capacities, capacities for migration into an area, and capacities for growth and reproduction under certain circumstances. Also among them is ecesis itself—the degree to which an individual plant can adjust to and thrive in a given environment, and ultimately reproduce in it.

begin page 93

¹⁸ The relative importance of climatic factors, both among environmental factors and therefore also in general, leads Clements occasionally to refer to them elliptically as the cause determining climax formation, though usually not of succession entirely. So, e.g., 'the degree of departure from the climatic mean controls the life history and determines the number of stages possible between pioneer and climax formations', (ibid., p. 35). He does the same with 'habitat', which is a more general category than 'climate': 'the underlying causes of the complete development of the formation are to be sought in the habitat', (ibid., p. 125); and 'the habitat is the basic cause, and the community ... the effect' (ibid., p. 123).

¹⁹ Ibid., p. 46.

Ecesic causes interact dynamically with *reactions*, the third category, which are the characteristics or activities of resident plants which alter their environments, and thus also the environment facing any plants attempting to migrate into an area. Examples are adding or subtracting soil, adjusting the water content of soil, adding or decreasing nutrients or toxins, encouraging or discouraging soil organisms, and reducing the wind and light exposure of, or adjusting the humidity around, newly germinating plants. Reactive causes and ecesic causes interact to form the stages of successions. For example, the (ecesis) success of plants growing in the bottom of ponds can contribute to the shallowing of those ponds (a reaction), making the environment hostile to plants rooted on the bottoms, and more amenable to the establishment (ecesis) of floating plants.²⁰

A final class of causes is *stabilizing causes*, which are the capacities of particular species to alter their environments in such a way that further invasion is prevented. For instance, tall trees may screen out light so thoroughly in areas below the canopy that species other than mosses and lichens are unable to take hold, as is typical in mature forests. Clements describes this prevention of subsequent invasion as the *dominance* of the species reacting on their environments in this way. Preventing the development of new vegetation, stabilizing causes encourage the entrenchment of plants producing them, which consequently define the climax formation for the area.

3. Clements's alleged law

So, Clements recognizes a variety of primary causes. But if he does, what is the status of the putative law that climates beget climaxes, necessarily and universally? Clements certainly makes comments which appear to support attributing a law to him. He writes in 1916 that 'the explanation of the universal occurrence of a climax in succession lies in the fact that the succession is reproduction. The reproductive process can no more fail to terminate in the adult form in vegetation that it can in the case of an individual plant'.²¹ Elsewhere, he declares that 'every sere must begin with a denuded area and end in a climax'.²² Such comments have produced two kinds of misunderstandings. The first, that Clements believes actual successions have only one cause, that they are 'monocausal', is partly undermined by the multiplicity of causes just reviewed.²³ The second misunderstanding, not yet addressed, is that they have only one outcome, a 'monoclimax'.²⁴ These misunderstandings dispatched, it will remain to explain the real significance of Clements's apparently lawlike generalizations.

begin page 94

If sometimes Clements writes as though climaxes develop under the sole control of local climates, this amounts to an oversimplification when read, as has been standard, as a generalization across actual successions. This misplaced interpretation is the one indicated by Ronald Tobey when he writes that 'an essential principle of Clementsian theory

²⁰ Ibid., p. 82.

²¹ Ibid., p. 106.

²² Ibid., p. 63. And see also, e.g. 'Every complete sere ends in a climax', (p. 105).

²³ E.g. Tobey (1981) p. 103. His early (1907) list of 'laws of succession', presenting ideas much more fully developed in (1916), offers a potential counterexample. I suggest that these claims function for Clements as definitions, and that it in presenting the more mature version in the following years he drops the word 'law', for good reason.

²⁴ e.g. McIntosh (1975) p. 255.

was that every succession was headed toward a climatically caused monoclimax'.²⁵ One way of understanding 'climate' is as a relatively permanent or slowly shifting range of conditions in a particular area. That is how Clements apparently intends 'climate' in writing that 'it is axiomatic that all forest climaxes are indicators of forest climates'.²⁶ Here the climate is something relatively stable across years and seasons for a wide area. In this sense of the term, climate does play a particularly strong role in Clementsian succession; it constitutes the limits of environmental conditions facing potential immigrants and current residents, which may need to adjust to them or evolve in order to remain.²⁷

But any *actual* instance of succession is controlled by many other factors, many of which are among the four main classes of causes, some of which are not. For one example, consider that Clements writes that 'water-content is the controlling factor in all succession'.²⁸ That is to say, after succession is instigated by disturbance, the factors exerting the most influence on the outcome will often be climatic ones, and among these water-content exerts the strongest influence. Clearly, actual water-content of soil and air is not at any given time entirely a function of climate in the sense above, though the wider 'climate' may be understood as defining its limits. This wider sense of 'climate' is different from the sense Clements apparently intends in writing '*Reaction upon local climate*.—Plant communities react upon the air above them by transpiration and by lowering the temperature'.²⁹ Here, 'climate' means the actual local environment which can be reacted upon by plants and exhibit significant short term variation. This sense of 'climate' cannot determine a climax in so far as climaxes are (relatively) stable types determined by the average conditions or range of conditions in a larger area.

Thus, when actual climaxes arise, they do so not as nomic consequences of either sense of 'climate', but as culminations of successional sequences jointly produced by initial, cesic, reactive, stabilizing, and potentially other causes. *Actual* successions are not monocausal. Are their outcomes monoclimatec?

The constituents of climax types are simply those species best able to establish in an area where the immediate environment tracks a sequence of conditions typical for the region. Clements identifies such sequences in given areas with the particular vegetation types observed to outcompete others frequently under typical local conditions, and names them by their dominant species. As an example, 'moss-spruce burn succession' names the following ideal sequence of species occurring in the Rocky Mountains of Colorado and well adapted to burned areas:

Bryum-telmatium; moss meadow formation.
Aster-Chamaenerium-poium; aster-fireweed meadow formation.
Deschampsia-Carex-poium; hairgrass-sedge meadow formation.
Salix-Betula-helolochmium; willow-birch meadow thicket formation.

²⁵ Tobey (1981) p. 104.

²⁶ Clements (1920) p. 345.

²⁷ Though not the environments entirely, in so far as reactions effected by resident plants are themselves precisely adjustments of environments. Also, the point made in this sentence makes sense with respect to both evolution by natural selection and the Lamarckian evolution which has, as noted, been attributed to Clements.

²⁸ Clements (1916) p. 164.

²⁹ *Ibid.*, p. 94.

Populus-hylium; aspen forest formation.
Picea-hylium; spruce forest formation.³⁰

Here, spruce forest is the climax. As such, it represents the last part of an ideal sequence reflecting sets of organisms occurring in the area which are frequently able to (individually or as groups) successively out-compete other organisms over a series of local environmental changes. After the initial causes, environmental changes supporting this ideal sequence are those caused by the plants themselves and varying within the limits of the regional climate. When a burn occurs, and when individuals of these species live nearby enough to immigrate into the burn area, they may invade and then successively out-compete each other over changing conditions.

But an enormous variety of factors can, and frequently do, prevent such a sequence from obtaining. Immediately after writing one of the apparently deterministic statements often cited as supporting monocl原因, that 'the reproductive process can no more fail to terminate in the adult form in vegetation than it can in the case of an individual plant',³¹ Clements writes,

In both instances it may fail under abnormal, i.e., unfavorable, conditions. The lack of light in dense thicket or woodland will prevent the maturing of herb or woody plant, as it will of aquatic and amphibious plants when too deeply submerged. An excess of water will have similar effects, while a deficit often suppresses the vegetative stages in large degree. The action of man or animals may keep the plant in an immature condition throughout its life history. While the response is usually more complex, the behavior of the formation is strictly comparable. Natural or artificial factors may hold it almost indefinitely in an imperfect condition of development, i.e., in practically any initial or medial stage, or may cause reproduction of little more than the adult stage alone. Man in particular may cause a developmental stage to become permanent, or to recur so constantly that it appears to be fixed.³²

Clearly, the stages of normal succession do not *always* obtain; 'natural or artificial factors', (meaning non-anthropogenic and anthropogenic factors) may cause a successional sequence not to develop along idealized lines. In addition to becoming stuck at an intermediate level, as the above passage suggests may occur, succession may also not follow the usual course if its species components are not migrating into the area, or if other, more better adapted are:

begin page 96

The habitat may be modified in the direction of the successional reaction and correspondingly hasten the rate of development, or contrary to the reaction and thus reduce the rate, fix an earlier climax, or change the direction. In the case of invasion it is obvious that the failure of the dominants

³⁰ Ibid., p. 225.

³¹ One could interpret this as a definition, but there is another reason that this particular statement might be understood as not asserting a necessity. It asserts a determinism just as strong as that of maturation for an individual plant, which is itself not necessarily very strong! Much can interfere with an individual's development, too.

³² Ibid., p. 106.

of a particular stage to reach the area would produce striking disturbances in development. Likewise, the appearance of alien dominants or potential climax species would profoundly affect the usual life history.³³

Climaxes do not appear to be inevitable. However, commentators who have thought Clementsian succession to be fairly deterministic have sometimes recognized that normal pathways of succession bear exceptions. Worster (1994) calls them 'freakish', with the implication that exceptions to normal successional sequences are statistically unusual. So, does Clements admit deviations only to treat them as rare or inconsequential, so as to save his deterministic law from falsification?

With respect to the influence of disturbances on usual climax sequences, Clements writes that departure from climax sequences due to them are more common than progress along the normal lines. 'Disturbance', he writes, 'is to-day a practically constant feature of most climaxes'.³⁴ And referring to a particular instance, he remarks, 'like most climax units, they have been modified by disturbance in some degree'.³⁵ Overall, Clements's characterizations of actual vegetation dwell as much on alternate states departing from normal successional sequences towards climaxes as on the states themselves comprising the normal sequences. 'Unlikeness and variation', he writes, 'are universally present in vegetation'.³⁶

Clements describes two typical kinds of deviations from normal successional avenues:³⁷ factors interfering with the development of seres, and factors producing variation within areas of vegetation comprising them. Factors interfering with the development of seres change the course of development, so that instead of an expected type of community (which is to say, a set of species sharing habitat requirements, characterized by a dominant species) appearing in sequence, another type appears. 'As has been seen', Clements writes, 'various agents may interpose to prevent complete development. The result is to produce apparent climaxes of greater or less duration'. These apparent climaxes, differing from the normal climaxes are called 'subclimaxes'. Clements remarks, 'various causes produce subclimaxes. Such are (1) soil, (2) reaction, (3) competition, (4) migration barriers, and (5) man. In spite of the greatest difference in their action, they agree in preventing development by handicapping or destroying some stage, usually a climax one'. Examples include vegetation of the Great Basin where 'the climatic formation is that of sagebrush (*Artemisia tridentate*), but vast alkaline stretches will be covered by *Sarcobatus* and *Atriplex*',³⁸ and across much of the United States, formations due to grazing or cultivation. Likewise, 'potential climaxes', 'preclimaxes', and 'postclimaxes' are all alternate stages which may be produced by changes in conditions. The terms characterize commonplace departures from normal climaxes.

begin page 97

Alternately, environmental heterogeneity within a region can produce variation, so that though a type like 'spruce forest' may be applied to a region, nobody imagines

³³ Ibid., p. 33.

³⁴ Ibid., 262.

³⁵ Ibid., p. 275.

³⁶ Clements (1907) p. 289.

³⁷ That there are three general kinds is a function of my meta-classification of Clements's own classification of exceptions. I make it as a first step towards describing the various classes of exceptions which he classifies individually himself.

³⁸ Clements (1916) p. 107.

it uniformly occupied by spruce. Associations are rarely just their dominant species. Dominants are such when they control (in a local sense, subject to the constraints of climate and other factors) the conditions of growth of *other* plants, for instance by shading or by altering soil chemistry. And species cluster to some degree, owing to the contingencies of smaller scale environmental variation, of migration and dispersal methods and routes. At most scales, both composition of species and the abundance of each usually varies.

Two important patterned kinds of variation are 'alternation' and 'zonation'. Alternation is any response to unlikeness of physical factors in habitats.³⁹ It represents mixtures of small bits of formations due to differences in habitat or competition. 'Different habitats nearby one another', Clements writes, 'cause alternation fundamentally and universally'.⁴⁰ Another kind of heterogeneity, 'zonation', is 'the common response to plants to the way in which physical factors are distributed through a habitat or a series of them'.⁴¹ Continuous variation in bands or gradients, as for instance graded diminution of moisture with increasing distance from a lake, produces zonation. These variations are so common that 'the structure of all formations rests on two principles, zonation and alteration'.⁴² The various climax departures, zonation, and alternation are each ways that Clements recognizes nonconformity with simplified climax types. Whatever the homogeneous monoclimate is, it is not Clements's belief about nature.

4. Integrating diverse causes

That Clements recognizes multiple causes and multiple effects does not, however, free him from the charge that he defends a naïve law. One of Gleason's criticisms of Clements's account of succession is that it adopts excessively many new terms; these terms may represent insulation against falsifiability. Karl Popper (1968) famously worries about Freud's theory that it neutralizes exceptions through merely *ad hoc* amendments; when a predicted disorder does not manifest, it is called 'repressed'. Clements's excessive terms may play this role, if he expresses a law *simpliciter*, and then assigns terms to abundant exceptions. Exceptions could be introduced to save the law by subsuming exceptions under insubstantial names, amounting to vacuous *ceteris paribus* qualification. We could understand Clements as arguing that climaxes obtain except when something causes a disclimax, subclimax, or the like, where this exception is as vacuous as a *ceteris paribus* clause because the surplus language is invoked whenever predictions fail. However, Clements's adoption of new terms is, from the outset, methodological and substantive.

Clements introduces terms primarily in three classes, each with particular purposes. Terms for describing the stages of normal successional processes include 'reaction', 'ecesis', 'climax', 'colony' (a group of two or more species which develops in a denuded area),⁴³ 'seres' (a unit succession from pioneer to climax species),⁴⁴ 'consere' (a series of

begin page 98

³⁹ Clements (1907) p. 289.

⁴⁰ *Ibid.*, pp. 290–291.

⁴¹ *Ibid.*, p. 294.

⁴² *Ibid.*, p. 289.

⁴³ Clements (1916) p. 129.

seres in the same place),⁴⁵ 'formation' ('the climax community of a natural area in which the essential climate relations are similar or identical'),⁴⁶ and 'association' (the various 'climax communities which are associated regionally to constitute the formation').

A second class of terms is needed because actual areas of vegetation are heterogeneous, not pure instantiations of their types. Terms describing this variation including 'consociation', (a unit of the association limited to an area in which a single species exerts pure dominance),⁴⁷ 'society' ('a community characterized by a subdominant or sometimes by two or more dominants'),⁴⁸ 'clan', (a small group of individuals of a non-dominant species), 'mictium' (the temporal overlapping or mixture of two stages dominated by different species),⁴⁹ 'zonation' (continuous variation along an environmental gradient), 'aspect', (a group of species exerting more dominance through some part of annual seasonal variation), 'layering', (vertical variation, from e.g canopy to soil), and 'serule' (a small unit of vegetation due to small scale variation like 'earth, duff, litter, rocks, logs, cadavers, etc').⁵⁰ For a typological theory like Clements's, such local heterogeneity is explained by particular disturbing conditions—deviations from average conditions. For instance, in an area of ten square meters dominated by a particular sedge, mosses' domination of several square meters covered by boulders is a variation explicable by deviation.

Clements also treats stronger disturbing conditions as producing not just heterogeneity within a fixed type, but sometimes also a change in type. He creates for such vegetation a type defined by the nature of its departure from the normal seral type, and explains it by appeal to the action of disturbing conditions. A third class of terms is thus required to characterize deviation which rises to the level of difference in type. Several terms describe delayed succession—the long establishment due to disturbance of a vegetation type treated as antecedent to the climax type. One is 'subclimax':

Various causes produce subclimaxes. Such are (1) soil, (2) reaction, (3) competition, (4) migration barriers, and (5) man. In spite of the greatest difference in their action, they agree in preventing development by handicapping or destroying some stage, usually a climax one.⁵¹

Similarly, a 'serclimax' is 'a seral community usually one or two stages before the subclimax, which persists for such a period as to resemble the climax in this one respect', for instance, a reedy swamp which persists where drainage is inhibited.⁵² Alternately, 'disclimaxes'

chiefly ensue in consequence of a disturbance by man or domesticated animals, but they are also occasionally produced by mass migration. In some cases disturbance

begin page 99

⁴⁴ Ibid., p. 4. The following usages are the 1916 and 1936 ones, rather than the earlier, often different ones of 1905, 1907, etc.

⁴⁵ Ibid.

⁴⁶ Ibid., p. 126.

⁴⁷ Ibid., p. 129.

⁴⁸ Ibid.

⁴⁹ Ibid., p. 140.

⁵⁰ Clements (1936) p. 279.

⁵¹ Clements (1916) p. 107.

⁵² Clements (1936) p. 264.

and the introduction of alien species act together through destruction and competition to constitute a quasi-permanent community with the general character of a climax.⁵³ So, where disturbing conditions exert sufficient influence that they can no longer be understood as producing mere heterogeneity, but rather change in type, these types demand a third class of terms, of which these are the most frequently used.

All this discussion of terms serves to demonstrate that Clements's method includes adopting so many terms for states of vegetation because he attempts to develop a *comprehensive* theory of vegetation, one that should explain everywhere why plants occur in particular places, and to some degree predict what plants will occur there in the future. To do so adequately, it needs to account for the ubiquity of variation and change. Clements's solution is to establish for each area an *ideal sequence* of vegetation types against which such variation stands out. The sequence for each area will certainly not be arbitrary; each is comprised of species known to occur in an area that have the physiological capacities to outcompete each other sequentially in that general climatic area, by affecting habitat and resources (or, through 'reactions', in Clementsian language). But a sequence is *expected* not to develop always, and where it does, it will typically not cover an area in a uniform way.

Though 'normal succession', for Clements, is 'unit succession, that is the development from an initial bare area to a climax',⁵⁴ this pattern is not normal in a distributive sense. Rather it is a product of what Clements regards as physiologically normal for individuals, as an ideal type determined by evolutionary optimization. Actual succession, in contrast, is frequently 'abnormal' and subject to significant variation. Accordingly, the abundant terms serve substantive strategies for explaining variation.

5. Clementsian explanations

The usual error of mistaking climax sequences for laws produces a misunderstanding of Clementsian explanation. On the usual understanding (e.g. Barbour's, Worster's, McIntosh's, Tobey's) a Clementsian explanation of instance of vegetation *v* would have this form:

- (1) *v* is the climax type for the area in which it occurs, or
- (2) *v* is part of the sere (the series of types) leading up to the climax type, or
- (3) *v* is the consequence of some freakish, unusual circumstances.

If climax sequences commonly fail to obtain, this explanation strategy must commonly fail. It suggests that where vegetation appears that is a part of neither a climax type nor a sequence leading up to one, a Clementsian ecologist has little to say, except perhaps to invoke an *ad hoc* escape term.

But this account fails to capture how Clements approaches actual instances of vegetation, and the theoretical resources he develops over the course of a long series of articles and monographs. More accurately, in case *v* is part of a climax sere, a Clementsian explanation takes the following form:

⁵³ Ibid., p. 265.

⁵⁴ Clements (1916) p. 169.

- (1) a neutral initial cause disturbed vegetation;⁵⁵
- (2) typical ecesic causes contributed to immigration and establishment of the best adapted plants;
- (3) if these plants, exercising typical reactive causes, alter conditions enough to allow the establishment of other species better suited to the new conditions, their immigration is facilitated;
- (4) when some plants' stabilizing (e.g competitive) causes are sufficiently strong to prevent their displacement under a typical range of conditions, they remain;
- (5) *v* is thus comprised of species best physiologically adapted to some of the conditions in this sequence and able to competitively displace other species in them.

The general placeholders in this explanation may always be replaced by particulars, since the proximate cause of vegetation is that some set of environmental variables has particular values. But these values themselves are also, or arise through the action of, causes classified as initial, ecesic, reactive, and stabilizing.

However, when *v* is not part of a climax sere, far from retreating to *ad hoc* terminology, Clementsian explanations are just getting started. Conditions are frequently not normal, typical, or ideal. Deviation from average environmental conditions, or the addition of further causes, or the presence of different species than those historically adapted, can each produce vegetation different than that assigned to the climax sere. Clements believes that variation in each of these factors may even be traced well enough that actual vegetation *indicates* its causes. His 'method of indicators' is advanced in his major work *Plant indicators: The relation of plant communities to process and practice* (1920). Essentially, the method entails 'reading off' causal factors from actual vegetation by appealing to a theoretical understanding of how the former give rise to the latter. For instance, the presence of particular pines in the Rocky Mountains can indicate that fire occurred a certain number of years before. The presence and condition of plants with certain requirements for water indicate how much water a wetland area has been exposed to over recent years. Instances of vegetation may indicate not only the normal range of conditions in an area, but also the environmental conditions preceding and simultaneous with their development.

The method of indicators works because not only do climax seres have particular species assigned to their stages, but also particular subclimaxes and disclimaxes obtaining in response to certain disturbances do as well. For example:

Examples of subclimax are legion, the outstanding cases being mostly due to fire, alone or after lumbering or clearing. Most typical are those composed of 'jack pines' or species with closed clones that open most readily after fire. Each great region has at least one of these, e.g *Pinus rigida*, *virginiana* and *echinata* in the east, *P. banksiana* in the north, ...⁵⁶

⁵⁵ Here I mean an initial cause which is neutral with respect to subsequent development, one which merely clears an area to some degree. The significance of this qualification will be clear shortly.

⁵⁶ Clements (1936) p. 263.

These species of jack-pines occur after fire disturbances in some places, and their presence, with other species, indicates conditions an ecologist familiar with the area can use to explain their presence, and that of other vegetation, present and past.

begin page 101

Filling out the Clementsian’s explanatory resources, each class of successional causes—initial, reactive, ecesic, and stabilizing—has a range of ways it can deviate from normality. This provides a basis for the indicator method. Each kind of disturbance has a knowable direction of effect, observable in resulting vegetation. An initial cause must minimally ‘accomplish two results: it must produce a bare area capable of ecesis, and it must furnish it with physical factors essentially different, in quantity at least, from the adjacent areas’.⁵⁷ When it does nothing more—where it is neutral—and they are available, pioneer species are expected to arrive, and normal succession, to obtain. But a catalog of other factors may interfere.⁵⁸ Therefore, ‘the *degree of departure* [of various factors] from the climatic mean *controls the life-history* and determines the number of stages possible between the pioneer and the climax vegetation’.⁵⁹ One particular kind of interference for example—earthquakes—often produces ponding or draining (the accumulation or dispersal of water);⁶⁰ and then,

the effect of drainage upon the course of development is determined by the degree to which the water is removed. If open water with a depth not greater than 12 meters is left, the normal water succession is initiated. Later stages are initial at the respective depths less than this, until a point is reached where drainage completely removes the surface water. This permits the soil to dry more or less rapidly and to become quickly covered with a growth of mesophytic ruderals or subruderals. This is typically the case in areas drained artificially.⁶¹

Or, for an anthropogenic example, ‘the primary activities by which man produces denuded areas are burns and clearings’; and the method of clearing determines whether soil is disturbed or not, which in turn affects the nature and course of the subsequent succession.⁶² Even when causes have not been directly observed, vegetation can suggest them, because *considered as sources of deviation*, rather than as causes simpliciter, causes have definable, testable effects. Indeed, much of Clements’s empirical research (and research program) amounts to testing how particular causes, like different degrees of light reduction, deflect vegetation from climax seres.

Clements is able to characterize the influence of disturbing factors and conditions just *because* he treats them as disturbances on idealized sequences. They become disturbances by being excluded from (in some cases) the set of conditions, or departing from (in others) the values of conditions, standing behind normal sequences. Ironically, establishing a set of normal conditions for each area, and assigning particular kinds of vegetation to them (as determined by physiological adaptation), permits recognizing the influence of an enormous range of interfering factors precisely enough to

⁵⁷ Clements (1916) p. 34.

⁵⁸ These are classified according to the various classes disturbing agents, in Clements (1916) pp. 35–62.

⁵⁹ *Ibid.*, p. 35; italics mine.

⁶⁰ *Ibid.*, p. 54.

⁶¹ *Ibid.*, p. 51.

⁶² *Ibid.*, p. 59.

incorporate them into explanations.

6. Gleason's criticisms and individualistic explanations

In 1909 Henry Gleason's understanding of succession strongly resembles Clements's. Consider this passage:

begin page 102

Within every complex of related plant associations, there are one or more definite orders of successions, leading from pioneer to climax associations. The steps in the succession follow each other in regular series and constitute what may be called a normal succession ...⁶³

We recognize 'related plant associations', 'definite orders of succession', 'pioneer[s]', 'climax[es]', and the 'regular series' of steps or stages. Moreover, Gleason's topic is the 'normal' or original, pre-settlement vegetation of the Illinois plains, and the structure of 'normal succession' of prairie in that area, in contrast with the 'abnormal' successions observable where forest has invaded prairie and where prairie has been cultivated. Gleason, à la Clements (1916) surveys available historical records of original vegetation and its successional patterns. But his message in 1909 is that little research so far reveals these facts, and that much remains to be learned, especially about the vegetation edges where prairie merges into forest, and where vegetation has converted from one to the other.

Gleason's 1912 study repeats these questions, but answers them by inference from observations of contemporary vegetation in central Illinois. He presents the explanation for the occurrence of particular species primarily as a matter of geography and topography—principally, the relation of a plant's location to water in ponds and sloughs. Based on observations of present vegetation in the study area, he attempts to reconstruct the pre-settlement vegetation of the state, and determines that its current forest distribution reveals a three-stage successional history, 'beginning with the oaks and hickories at the south, passing through the bur oak stage at the center, and ending with the red oak stage near the north end'. He lends the series a squarely Clementsian explanation: 'This succession is the usual one for central Illinois, and is caused, at least in part, by the gradual accumulation of humus and decrease in light. There are many other places in the state where the same series may be observed under different ecological circumstances'.⁶⁴ While forest has advanced into areas covered by prairie, its advance has been confined by 'the advent of man', producing 'the virtual cessation of the struggle between forest and prairie', which is to say, the stable entrenchment of red oak forest.⁶⁵

However, by 1917, in 'The structure and development of the plant association', Gleason, writing one year after Clements's major work, *Plant succession* (1916), begins to express doubts about Clements's approach. He remarks that Clements's work 'enriched' the ecological literature, but also that he cannot accept all its claims. He especially advances four objections. First, he resists units of vegetation being organisms. Second, he rejects Clements's enlarging the unit of vegetation to include the climax and the series

⁶³ Gleason (1909) p. 270.

⁶⁴ Gleason (1912) p. 45.

⁶⁵ Ibid., p. 49.

leading up to it. Third, notably, he dislikes that the course of vegetative development is represented as being so complex a process that many new terms are required to describe it. Finally, he insists that 'several apparent exceptions have been excluded by definition'.⁶⁶

These objections suggest departure from the Clementsian trajectory of Gleason's early career. But Gleason is usually credited with an understanding of succession opposite of Clements's—what Gleason calls 'the Individualistic concept of ecology'. Opposing the Clementsian use of organism similes, Gleason proposes (1917) an account of vegetation according to which,

begin page 103

the phenomena of vegetation depend completely upon the phenomena of the individual. It is in sharp contrast with the view of Clements that the unit of vegetation is an organism, which exhibits a series of functions distinct from those of the individual and within which the individual plants play a part as subsidiary to the whole as that of a single tracheid within a tree.⁶⁷

Gleason's most widely reprinted, 1926 article, 'The individualistic concept of the plant association', presents a stronger version of this objection. It argues that while there are certainly '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', uniformity is nonetheless only a matter of degree. The incompleteness of uniformity leads ecologists to differ on how they establish the identities of associations.⁶⁸

Moreover, two further problems impede tying environments to particular vegetation types. First, even where environmental diversity has been significantly reduced, which species appear varies. Second, associations under the same name often appear in differing environments. Denying the identification of locations with vegetation types, Gleason argues, 'individual plants' physiological response is not to geographical location or surrounding vegetation per se', he says, but rather to 'more particular factors', such as particular environmental conditions.⁶⁹

For Gleason, these facts and the vagueness of association boundaries undermine 'the integrity of the association concept'. Doubt is cast on both the usefulness of the association concept to identify a discrete entity and the possibility of treating units of vegetation as having normal sets of constituents, as Clements does. Gleason concludes that 'an appreciation of these conditions leaves us unable to recognize any one example of an association type as the normal or typical'.⁷⁰

While Gleason's 1917 objections attack Clements's method, they do not reveal the deep differences from Clements's understanding of vegetation which legend suggests and Gleason implies. The primary way the later Gleason departs from Clementsian theory lies in his mounting reservations about the usefulness of the Clementsian explanatory apparatus, including its organism simile. Overall, I contend, their writing

⁶⁶ Gleason (1917) p. 463.

⁶⁷ *Ibid.*, p. 464.

⁶⁸ Gleason (1926) p. 9.

⁶⁹ *Ibid.*, p. 17.

⁷⁰ *Ibid.*, p. 19.

supports not deep differences in understanding of which causes produce vegetation, but rather significant differences in strategy for assembling those same causes into unified explanatory frameworks. Gleason's first objection denies that vegetation formations are organisms, but this concern is misplaced in so far as Clements claims at best that plant formations are like organisms in some respects only and never that they are organisms. Joel Hagen (1988, 1992) has treated this disagreement more accurately than others, noting that Clements cannot have intended plant formations to resemble complex, higher order organisms, but rather something like protists. The analogy (never homology), as useful as it was for inspiration and pedagogy, breaks down because in Clements's account—unlike cells and organs—ecological interactions among plants are indirect, effected through habitat modification. Hagen (1988) notes that the organism analogy was a common explanatory device around the turn of the century, and so could easily play methodological and explanatory roles for him.⁷¹ But if pedagogically crucial, the organism analogy applies to so little about causation that it commits Clements to nothing about the causes of vegetation that Gleason would reject. Next, in light of the above understanding of how Clementsian climaxes and vocabulary function, Gleason's second and third objections, too, are revealed as resisting Clementsian methodology much more than his causal understanding. Finally in the fourth objection, exceptions Clements excludes by definition he excludes from the climax *sere*, not from his explanations. The remaining 1926 objections concern the usefulness of Clements's explanatory strategy. Though Clements never suggests that associations have sharp boundaries in space or time, the vagueness of these boundaries in some places might well render the concept challenging to use. The potential difficulties Gleason himself experienced in (1909) with identifying best adapted vegetation may well render the Clementsian apparatus too difficult to employ. But these disagreements concern the usefulness of explanatory concepts and methods. In contrast, when Gleason describes his own 'individualistic view', he writes little Clements would object to.⁷² Consider the above quotation, that 'individual plants' physiological response is not to geographical location or surrounding vegetation *per se*, but rather to 'more particular factors'; Clements would adamantly agree.

begin page 104

Yet, there are differences. Gleason sets out as his core positive thesis about plant succession that it results from environmental sorting of potential immigrants. When seeds (or other reproductive structures) arrive someplace, local environment determines which germinate and survive, and which fail to. So far this is indistinguishable from Clements's core thesis. Both understand environmental selection of potential immigrants as the mechanism of succession. They differ in emphasis, in their prioritization of causal factors. While Clements emphasizes *environmental* sorting among potential individual immigrants, Gleason emphasizes environmental sorting among potential individual *immigrants*. That is, Gleason posits that one cannot look first to environment

⁷¹ Hagen (1988) pp.264–265. Agreeing with Hagen on the analogy's methodological role, I depart from him on its role in at least causal explanation. Its explanatory role for Hagen lies in unifying concepts, but that is explanation *qua* pedagogy, not explanation *qua* revealing causes.

⁷² I use the subjunctive because Clements never that I know of published a response to Gleason. One might attribute this to his arrogance, but this discussion suggests that, though Gleason implies otherwise, they largely agree on the causes of vegetation, and we know Clements preferred his own strategy for assembling them into explanations.

to determine the development of succession in some area; which species are available to immigrate from nearby populations is the more influential cause. Clements treats immigration potential as a central ecocic cause, and, as quoted above, he agrees that if species with adapted, competitive advantages do not arrive, or if better adapted species do, succession will proceed differently; 'the appearance of alien dominants or potential climax species would profoundly affect the usual life-history'.⁷³ (Of course, enduringly present 'alien dominants' would become part of the usual life-history—of the climax sequence.) But Clements believes that habitat, both independent of and as affected by resident organisms, is a more significant cause than species availability. There is a disagreement here, but it is not even about which causes are responsible; it is about which bears slightly more responsibility, where both theorists agree that both kinds of cause are essential and primary.

begin page 105

It remains now to describe how, now quite differently than Clements, Gleason proceeds from this shared understanding of the mechanism of succession to a strategy for explaining vegetation. Gleason never explicitly spells out in his papers a statistical explanation of vegetation, but he hints at strategy. Gleason works from the Clements friendly idea in 1917 that 'the phenomena of vegetation depend completely on the phenomena of the individual', to the claim in 1926 that the composition of organisms appearing in an area is a matter of mere 'coincidence'.⁷⁴ He suggests that the structure of vegetation may be merely random to the point of sounding Heraclitan, as in this remark:

Suffice it then to repeat that on every spot of ground the environment is continually in a state of flux, and that the time-period in which a certain environmental complex is operative is seized on by the particular kinds of plants which can use it. The vegetation of every spot of ground is therefore also continually in a state of flux, showing constant variations in the kinds of species present, in the number of individuals of each, and in the vigor and reproductive capacity of the plants.⁷⁵

Taken at face value, this does not leave much room to develop explanatory theory about vegetation. But Gleason does allow that organized processes work to give rise to vegetation, the same causes Clements focuses on—environmental sorting of available immigrants and seeds.⁷⁶ One could conclude that Gleason thinks any general explanation laid on top of this mechanism is impossible, and the best he offers is that 'the laws of mathematical chance' might characterize vegetation.

In trying to realize this as a strategy for explaining vegetation, the best one could presumably do, given that Gleason agrees that species composition is regionally stable in the long term,⁷⁷ is work from statistical descriptions of past vegetation to statistical estimations of future vegetation. Note, however, that we are now in the realm of prediction. When Gleason offers an explanation, we find not statistics but environmental sorting of available immigrants:

⁷³ Clements (1916) p. 33.

⁷⁴ Gleason (1917), p. 464; (1926), p. 160.

⁷⁵ Gleason (1939) p. 99.

⁷⁶ Gleason (1926) p. 21, and (1938), p. 101.

⁷⁷ Gleason (1939) pp. 103–105.

I have seen this variable result of the interaction of migration and environment beautifully illustrated along the shore of a lake, where winter storms and ice action keep the shore denuded of permanent vegetation. Each spring some storm washes on the beach a long strip of flotsam, twigs, fragments of bark, and dead leaves, and in it seedlings develop. Some years the strip of drift is marked by hundreds of seedlings of willow, at other times by seedlings of elm, and again by seedling red maples. In each case the environment is the same. The difference is caused by migration.⁷⁸

If the causal difference-maker here is migration, what does it make a difference to? It affects the very local establishment of individual plants under high disturbance conditions. This is not the sort of thing the climax sere directly explains. For Clements this would be explained by these particular initial conditions, and by the availability of certain immigrants (the particular ecesic causes), as they *differ* from typical regional conditions, perhaps even in a way typical to lakeshores in that area. Gleason, meanwhile, explains by chance only this very local variation *within* a plant association of defined membership, and within which migration is the most significant cause of individual-organism-scale variation. (Eliding a reference to chance),

begin page 106

All these facts warrant the general conclusion that, within the limits of a single plant association, the environment, while possibly presenting observable differences, is essentially homogeneous for each species ...and that the number of individuals of a species, other things being equal, is an index to its adaptation to the environment.⁷⁹

In the end, adaptation, for Gleason, too, explains occurrence, but when the explanandum changes from regional vegetation (explained for both by adaptation) to local variation, Clements reasons from adaptation and particular conditions (represented as deviations) to vegetation, while Gleason reasons from adaptation to statistical abundance to vegetation.⁸⁰ Noticing their main arguments are pitched at different scales, we see precisely where they switch to different explanatory strategies from (largely) shared understanding. And ironically (for legend, anyway), we find Clements developing explanations from complex causes, while Gleason promises generalizations holding 'other things being equal', and to that degree insensitive to causal complexity.

7. Method, not metaphysics

A standard account has it that in contrast to Clements's naïve assumptions of organization and order, Gleason was sensitive to complexity and disorder. Gleason fancied himself an iconoclast in the face of Clementsian orthodoxy. And so we imagine he was sensitive to a kind of complexity that Clements failed to observe or ignore. Revisiting Clements suggests that, whatever the merits and deficiencies of his explanatory strategies, he was quite sensitive to complexity and heterogeneity, and organized

⁷⁸ Ibid., p. 100.

⁷⁹ Gleason (1925) p. 74.

⁸⁰ This is the theory, anyway, though in particular cases like the previous quotation, he does not.

his theory specifically to address those features of ecological systems. I have argued that Clements's views have been disfigured in their reception, and that Clements has a more sophisticated approach to vegetation systems especially than Worster's caricature of 'metaphysical faith' in vegetation as organism or superorganism. Where Gleason has been understood as his definitive critic, two dimensions of Gleason's criticism have usually been emphasized—the organism (and its putative connotations) and the climax 'law'. In turn, the essential features of Clements's ecology have been mistakenly identified with what Gleason rejects, as brought out in contrast by the lamp of criticism. The ecologists do disagree, primarily on the appropriateness and utility of employing the ideal developmental sequences Clements compares to organisms. But we accept a diminished version of Clementsian ecology when we treat it as just what has been called out for criticism by the present historical victor.

begin page 107

One conclusion, then, is historical. Although certain accounts of Clements, like Joel Hagen's (1988, 1992) and of Gleason, like Nicolson and McIntosh's (2002) have made helpful corrections on the common tale, typical renderings (e.g. Barbour's) of one of the most often recounted episodes in the history of ecology continue to include skewed readings of each participant's work. Sharon Kingsland (1995) has observed that twentieth-century ecology saw recurring episodes of polemical dispute, especially between mathematical modelers and natural historians, but also that the rhetorical distance between positions was typically exaggerated. Divisive rhetoric obscures how much, for example, Robert MacArthur, the consummate theoretician who also knew his warblers, and natural historians, caricatured as antiquarians but 'just as much interested in generalizations and the testing of hypotheses as the scientist', share in common.⁸¹ I suggest this general lesson of *Modeling nature* applies equally to Kingsland's own earlier (1991) passing remark about Clements and Gleason being opposites. Similarly, Joel Hagen's careful analysis of Clements's use of the organism concept revises our understanding of that aspect of Clements's ecology, and represents a radical advance in accuracy over other presentations, including subsequent ones. But Hagen's account retains Clements's 'sweeping generalization about climax vegetation', the 'claim that succession is always a linear process, progressing to award a uniform climax'.⁸² This generalization equally deserves the re-examination Hagen lends the organism analogy.

Through all this we should see that what seems to be a law is not always one. Though the current may be shifting, twentieth-century philosophy of science fostered the habit of scrutinizing theories with law divining rods, as though all science was aiming for Newtonian regularities or something like them. In plant ecology we find a domain where explanatory, strict laws are unlikely, and yet there is sophisticated understanding of component causal processes, even as of a century ago. The ecologist's challenge lies in moving from that understanding to explanatory theory, and in the example of Clements and Gleason we find science where the shape of explanatory theory is underdetermined by the mutually acknowledged underlying mechanisms. Clements assembles causes into theory without explanatory laws, while Gleason adopts statistical laws as desiderata. Their resulting representations therefore differ in interesting ways, but not in the way they appear to if we assume Clements shared the Newtonian Ideal,

⁸¹ Kingsland (1995) pp. 205–209.

⁸² Hagen (1992) p. 48.

that he advocated laws and a supporting account of nature as rigidly structured and law governed. Clements and Gleason's quite different theoretical structures grow out of diverging methodologies, not metaphysics.

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begin page 108

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