Contributions

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History of Ecological Sciences, Part 54: Succession, Community, and Continuum

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Introduction

Names and classifications of groups of organisms are based upon reality, but which reality? Like blind men encountering different parts of an elephant and announcing wildly different descriptions, ecologists (even if not blind) can see groups differently and then construct names and classifications differently. To some extent, it is a matter of convenience and convention—not a discovery comparable to finding that a water molecule consists of one atom of hydrogen combined with two atoms of oxygen. Agreements on names and definitions of groups of plants has been just slightly less difficult than getting agreement among blind men about what an elephant is like.

Plant ecologists developed the ecological concepts of *succession*, *community*, and *continuum*, which later were expanded to include animals. An exception was Karl Möbius' concept of "biocönose" to describe animal communities on mudflats where oysters dominated (Möbius 1877, 1880:721–729), since plants on mudflats were inconspicuous phytoplankton. Conversely, the balance of nature concept had developed with only animals as examples, until Carl Linnaeus expanded that concept to include plants in his version of it, "oeconomia naturae" (Linnaeus 1749, 1755:39–129, Egerton 1973:335-337).

Ordinary language divides our environment into forests, prairie, savanna, marsh, swamp, lake, seashore, and other entities, and sometimes subdivides these entities, such as into pine forest, oak forest, rain forest. Science moves beyond ordinary language when its concepts and objects are unnamed in ordinary language or need defining more precisely, requiring technical terms. However, the three ecological terms in the above title were all borrowed from ordinary language and given special meanings. Two early plant ecologists, Eugenius Warming (1895, 1909) and Frederic Clements (1916), coined a number of ecological terms, some of which continue in usage. An important aspect of the study of succession and community has been the names and terms involved. For the 1900s, Robert ("Mac") McIntosh provided clarification in "The Succession of Succession: a Lexical Chronology" (1999).

Part 54 goes beyond my previous writings on the history of plant succession studies and formalizing plant ecology (Egerton 2009, 2013), and when touching upon topics previously discussed, I have new things to say. The concern here is not merely with who stated that a group of organisms form a distinct entity, but on how the investigator thought that entity was organized and functioned. The history of plant ecology is supported by surveys with bibliographic guides. Frederic Clements' chapter 2: "General Historical Summary," in his *Plant Succession* (1916:8–32) focused on studies published from 1685 to 1914. Narrower in scope, but including far more detail, was Rudy Becking's "The Zürich-Montpellier School of Phytosociology" (1957), which mentioned Humboldt, Schouw, and Heer, but focused upon studies published after 1850. Broader in scope than either Clements or Becking's surveys was Robert Whittaker's "Classification of Natural Communities" (1962), which mentioned a few works before 1850, but emphasized works published after 1850. David Shimwell's *The Description and Classification of Vegetation* (1971), focused upon works published after Grisebach's *Die Vegetation der Erde* (1872). Most of the 20 papers in *Ordination and Classification of Communities*, edited by Whittaker (1973), have historical discussions. The title of Maarel's "The Braun-Blanquet Approach in Perspective" (1975) seems to indicate a narrower scope than it has: its historical background has general interest. Malcolm Nicolson's articles on the history of plant ecology (1987, 1989, 1990, 1996, 2013), begin mainly with Willdenow, and are substantial contributions to topics discussed here. (Ecosystems will be discussed in part 59 of my history.) Michael Barbour, Jack Burk, and Wanna Pitts, *Terrestrial Plant Ecology* (edition 2, 1987:12–25) has a chapter on history, with illustrations, beginning with Willdenow. Paul Keddy wrote "Milestones in Ecological Thought—A Canon for Plant Ecology" (2005) that has echoes in his textbook, *Plants and Vegetation: Origins, Processes, Consequences* (2007), with historical discussions in chapter 2 and also in 17 "Enrichment Boxes" that are primarily historical, distributed throughout the chapters. Keddy was misled in Box 4.1, "The Discovery of Carnivorous Plants," by the lack of a historical introduction in Darwin's *Insectivorous Plants* (1875) into thinking that Darwin had discovered carnivorous plants. In fact, William Bartram (1739–1823) reported (1791) that Venus flytrap, pitcher plants, and sundew all catch insects (Egerton 2007c:261).

Animal ecologist Frank Golley compiled a collection of 21 reprints (1901–1973) on *Ecological Succession* (Golley 1977), by both animal ecologists and plant ecologists, though the latter's reprints predominate. He divided his selection into five categories and provided an introduction for each category.

Historical survey

We begin with early observations on bogs, because some bogs were known to have gradually come into existence or gone out of existence, and others had been drained to create dry land. Studies of bog vegetation, therefore, could potentially give rise to the botanical concept of succession.

Gerrit/Gerard Boate (1604–1650), a Dutch physician living in London, did not use a technical vocabulary in *Irelands Naturall History* (London, 1652), when he divided the lands into three groups: moory or boggy heaths, dry heaths, and wet bogs (Gorham 1953:259–261, Egerton 2009:44). He did not choose between the terms "moory" and "boggy," and this kind of heath included "dry, or red bogs."

But since he had originally divided lands into heaths and bogs, it is illogical to next subdivide one kind of heath into categories that included a kind of bog. Boate studied plants, but only categorized and described bogs and heaths. He discussed different kinds of vegetation without specifying what species of plants it included.

Thirty-three years later, Boate's countryman, William King (1650–1729), Anglican clergyman in Dublin, wrote "Of the Bogs, and Loughs of Ireland" (1685) to assist in draining bogs. He divided bogs into quaking bogs and drier turf bogs, the latter being the same as red bogs. He thought that when seeds of bog-moss fell on dry land, it produced heath. Nevertheless. King gave "a clear and definite statement of succession, beginning with the mineral soil, passing through grassy quaking bogs, and growing into turf bog" (Gorham 1953:262). He saw (King 1685:950–951) that bogs are "generally higher than the land about them, and highest in the middle: the chief springs that cause them being commonly about the middle." A third Irishman, John Honohane, reported to the Royal Society of London (1697) that heavy rains caused a bog near Charleville, Limerick County, to slide down a slope and cover a meadow, in some areas 16 feet deep. A diagram—perhaps the first ever having ecological relevance—showed the direction of slide, from south to north (reproduced in Egerton 2009:46). Boate, King, and Honohane provided good general observations on bogs without observations on bog plant species.

France's leading naturalist of the 1700s, Georges-Louis Leclerc de Buffon (1707–1788), before turning to his great natural history of quadrupeds (mammals) and birds, was interested in forestry (Roger 1970, 1971:527–584, 1989:66–70, 1997*a*:426–474, 1997*b*, Magnin-Gonze 2004:136–137, Egerton 2007*b*, 2012:see index). His "Mémoire sur la culture des forêts" (1742) contains "the first clear record of the succession of forest dominants, and of the effect of light and shelter on the process" (Clements 1916:9). He saw that seedlings did not do well in bare fields. One should imitate nature and (Buffon 1742:234, translated in Clements 1916:9):

> *…plant shrubs and bushes which can break the force of the wind, diminish that of frost, and moderate the inclemency of the seasons. These bushes are the shelter which guards the young trees, and protects them against heat and cold. An area more or less covered with broom or heath is a forest half made; it may be ten years in advance of a prepared area.*

He continued, that after young trees "passed the first few years in the shade and shelter of the others, they quickly stretch up, and suppress all the surrounding plants" (Buffon 1742:238, from Clements).

Carl Linnaeus (1707–1778), Buffon's Swedish rival, was foremost a botanist (Hagberg 1952, Blunt 1971, Morton 1981:259–276, Koerner 1999, Magnin-Gonze 2004:120–128, Nicolson 2013:96), but also a naturalist with broad interests (Egerton 2007*a*). He developed the first explicit version of ecology, named "oeconomia naturae" (Linnaeus 1749, [English, 1759, French, 1972], Egerton 1973:335–337, 2007*a*, 2012:see index). In that essay, which one of his students, I. Biberg, translated from Swedish into Latin as a doctoral dissertation, Linnaeus described plant succession from practically bare rock with lichens through a series of plant stages culminating in a forest, followed by death and decay of trees and the use of decaying wood by fungi and beetles to create a revolving cycle of nutrients. In another essay, which A. Hedenberg turned into Latin as a doctoral dissertation, *Stationes Plantarum* (1754), Linnaeus sought to distinguish between *station* (habitat) and *habitation* (range). On station he wrote, "the native places or

Fig. 1 (a) Georges-Louis Leclerc, Comte de Buffon. By François-Hubert Drouais. Web. (b) Carl Linnaeus. Web.

stations of plants respect the country, climate, soil, and situation, nature of the ground, earth, and mould" (Linnaeus 1775:368), which is clear enough, but then he confused the issue by adding this definition to that of habitation: "along with latitude, altitude, and topography" (Linnaeus 1775:369–371). Linnaeus' list of stations of plants was: maritime or saline, marine, freshwater, damp regions, prairie, cultivated, rocky, sand, sterile soil, rubbish piles, forest, bushes and hedges, subterranean, mountain, parasitic, and saprophytic. Competition and avoidance of extinction were themes of *Politia Naturae* (Linnaeus 1760, [English, 1781, French, 1972]), which H. Wilcke turned into Latin as a doctoral dissertation. (*Extirpate* rather than *extinguish* is the term chosen by English translator Brand, but the context indicates that extinguish is what was intended: Linnaeus 1781:132.) Linnaeus realized that species produce more offspring than can survive, which produces "a war of all against all!" (Blair translation in Hagberg 1952:183). Despite that predicament, he believed the balance of nature was preserved, and he also explained how God had provided means of survival (a theme first addressed by Plato [Egerton 2001:96]) by what we call *ecological diversity*, as a way of reducing competition between species. Sweden had about 1300 plant species, but only about 50–100 live in any one place (Linnaeus 1781:133). All these changes occurred within a static system: Linnaeus assumed species were static until his later years, when he began to doubt their stability (Egerton 1973:335–337, 2007*a*).

Swedish plant ecologist Einar du Rietz (1957) surveyed Linnaeus' observations and comments on peat bogs in some two dozen of his publications, 1742–1773, and also included those of some of his predecessor, students, and associates. This is Du Rietz's "Summary of Linnaean Contributions to Paludology" (du Rietz 1957:68):

1. *The statements about the habitats of various mire plants in Linnaeus's Flora Lapponica and Flora Svecica seem to be the first in botanical literature.*

2. *Linnaeus seems to have been the first author to describe mire vegetation with lists of species. During the eighteenth century his descriptions were surpassed in exactitude and clearness only by his pupil [Pehr] Kalm, who published the first vegetation analyses with notes on the quantity of various species. Linnaeus's and Kalm's descriptions of bog vegetation were more correct and full of information than any others for nearly a century or more, i.e. at least until Grisebach (1845) published his descriptions of bog vegetation in NW Germany. In his* Skånska Resa *(1751) Linnaeus gave the first description of hummocks and hollows on a bog.*

3. *Stenius (1742) published the first description of differences between fen and bog vegetation. The first lists, however, of species characteristic of fen (Paludes) and bog (Cespitosae Paludes) vegetation were given by Linnaeus 1751 in* Philosophia Botanica.

4. *The domed shape of bogs was first described in print by King (1685 from Ireland). It was rediscovered by Linnaeus in Sweden and described by him in print 1747 and 1751. Similar observations were printed in Germany by Bansen 1753 and in Denmark by Borgen 1762. The first measurement of the convexity of a bog was printed by Carleson 1756 (from Sweden).*

5. *The lagg surrounding a bog was first mentioned in literature by King 1685 (under the name of "the bounds of the bogs") from Ireland. It was rediscovered by Linnaeus in Sweden and described in his* Skånska Resa *1751.*

6. *The vegetable origin of peat was clearly stated by King (1685) and Linnaeus (1735). The part played by various plant species in peat formation was first elaborated by Linnaeus (1745b, 1747, 1749, 1750, 1751b, 1753c, 1755) and Kalm (1753).*

7. *Different plant species were first mentioned as indicators of different habitats (in mires and elsewhere) by Linnaeus (1737, 1747, 1751*a *and* b*).*

8. *By these contributions Linnaeus has well deserved an honorary position in the history of paludology as one of the chief founders of this science.*

Du Rietz expanded all of his above brief citations in his bibliography.

Berlin botanist-physician Karl Ludwig Willdenow (1765–1812) knew Linnaeus' works, which is evident in his *Grundriss der Kräuterkunde* (1792), which became the standard textbook of the time (Bylebyl 1976, Nicolson 1987:172–174, 2013:96, Magnin-Gonze 2004:155–156). Linnaeus' influence is evident in this passage from the English translation of Willdenow (1811:422, from Buell 1949):

> *Naked rocky places, on which nothing can grow, are, by the winds, covered with the seeds of Lichens, that by means of the accustomed showers in Harvest and Spring are induced to germinate. Here they grow, and the rock is spotted with their coloured frond. In time the winds and weather deposit small dust in the rough interstices of the rock, and even the decaying lichens leave a thin scurf.*

Much more of it Buell quoted, without realizing Linnaeus' influence. Nicolson (2013:96) quotes another relevant discussion. Alan Morton (1981:314) judged Willdenow's textbook as "the first attempt to explain the world distribution of species in a scientific manner."

It is surprising that Clements (1916) did not discover Willdenow's contribution, since Willdenow's textbook exerted a strong influence on botany students. However, forest ecologist Stephen Spurr (1952) cited eight sources on forest succession, 1792–1860, only one of which Clements had cited, and several times I mention here succession studies which Clements cited in his book, but not in his historical summary (chapter 2).

A Genevan natural philosopher living in London, Jean André Deluc (1727–1817), mainly studied geology, meteorology, and physics (Beckinsale 1971, Carozzi 1987:207–219). He discussed peat formation in a lengthy letter which he wrote in January 1806 to Rev. R. Rennie, for quotation in Rennie's *Essays on the Natural History and Origin of Peat Moss* (1807–1810); Deluc's letter shows he was "the keenest and most indefatigable of early students of peat-bogs….He was probably the first to make use of the term *succession*, and certainly the first to use it with full recognition of its developmental significance" (Clements 1916:10). Rennie quoted from Deluc's letter at several places in his book, but most crucially on pages 137–141, which so impressed Clements that he included 1.5 pages of abridged quotation (Clements 1916:11–12) from Rennie's own quotation, on the six stages of succession when vegetation invades shallow lakes and convert them into peat bogs.

An important source of plant ecology from the 1800s was phytogeography (Browne 1983, Lomolino

Fig. 2. (a) Karl Ludwig Willdenow. Web.
(b) Jean André Deluc. Web.

Fig. 3. (a) Göram Wahlenberg. Web. (b) Joachim Frederick Schouw. Web.

et al. 2004), beginning with Alexander von Humboldt (1769–1859) and his colleague Aimé Bonpland (1773–1858), who spent five years (1799–1804) exploring Latin America (Nicolson 1987:174–186, 1996:290–292, 2013:96–97, Egerton 2009*b*, 2012:121–125). For present purposes, the most important of their sources is *Essai sur la Géographie des Plantes* (1807, also in German), in which some authors have credited Humboldt with using the term "association" to designate different kinds of vegetation. In fact, he was not trying to establish a vegetative terminology; he was merely using common language, as in: "Ces plantes associées sont plus communes dans les zones tempérées que sous les tropiques…" (Humboldt and Bonpland 1807:15). On the same page he also wrote: "D'autres plantes, réunies en société comme les fourmis et les abeilles…" Humboldt's important study on isothermal lines (Humboldt 1817; Robinson and Wallis 1967), which was translated into English (1820–22), was significant for phytogeography, if temperature could correlate with species distributions.

Humboldt became a famous scientist who exerted a strong influence upon others (Braun 1954:7–13 + 3 plates, Jahn 1965), some of whom followed him into plant geography. Among them were especially Scandinavian botanists. Göran Wahlenberg (1780–1851) studied medicine and botany at Uppsala University and spent his career there (Lindroth 1967, II:424–429, Eriksson 1976). His Scandinavian botanical explorations began in 1799, before Humboldt's influence touched him, and in 1811 he extended his explorations into central Europe, becoming friends with Willedenow when he visited Berlin. He published a series of floras of regions he explored (Pritzel 1872:336–337), with plant geography studies in their introductions. For his *Flora Carpathorum Principalium* (1814) he also inserted an early contour map of the Tatra Mountains (Szaflarski 1959).

Danish lawyer-botanist Joachim Frederick Schouw (1789–1852) was another Humboldtian disciple (Christensen 1924–26, I:253–276, Sanders 1975*b*). In 1812, he accompanied Norwegian botanist Christian Smith on an expedition into Norway's mountains, where Schouw was impressed by the vegetation growing in definite zones up the sides of mountains (comparable to what Humboldt and Bonpland had published concerning South America in 1807). He wanted to study the causes, and in 1816 he earned a doctorate in botany at Copenhagen University, where he remained for the rest of his career. In 1822, Schouw was first to name plant associations by attaching the suffix *-etum* to the end of the genus name of the dominant species (Whittaker 1962:9, Nicholson 1996:293, 2013:97). Schouw explored Italy's vegetation and climate on two expeditions, in 1817–1819 (when he met his future wife) and in 1829–1830. After the first expedition, he published a survey of principles of phytogeography: *Grundtraek till en aimindelig Plantegeographie* (1822, viii + 466 pages, German, 1823, French, 1824). In 1839 he published *Tableau du Climat et de la Végétation de l'Italie*, volume 1. Malcolm Nicolson (1996:293) saw reference to volumes two and three, but was unable to locate either. In fact, Carl Christensen's bibliography for Schouw (1924–1926, II:165–179), with 96 titles, lists no volumes 2–3; instead, it lists a series of papers published in 1841–1849 on Italian plant geography.

Genevan Augustin-Pyramus de Candolle (1778–1841), became one of Europe's foremost botanists (Pilet 1971*b*, Dajoz 1984:13–19, Magnin-Gonze 2004:165–166, Drouin 2008, Egerton 2010:26–29, 2012:132–136). His treatise on phytogeography clarified the distinction between Linnaeus' station and habitation (Nelson 1978:280–281). Lomolimo et al. (2004:28–48) mistook a 20-page English summary in Candolle and Sprengel 1821:263–283 as an English translation of an 88-page French text. Candolle recognized the importance of competition in determining the extent to which a species grows (1820:384, translated by Lyell 1830–33, II:131, with a phrase Lyell dropped added in brackets):

All the plants of a given country, [all those of a given place,] are at war one with another. The first which establish themselves by chance in a particular spot, tend, by the mere occupancy of space, to exclude other species—the greater choke the smaller, the longest livers replace those which last for a shorter period, the more prolific gradually make themselves masters of the ground, which species multiplying more slowly would otherwise fill.

Candolle's "war one with another" echoes Linnaeus' *Politia Naturae* (quoted above), but Candolle first explained its dynamic significance. Perhaps he was influenced to pursue this thought by his familiarity with the French edition of Malthus' *Essay on the Principle of Population* (1809), translated by his former philosophy professor (Egerton 2010:29). Candolle actually met Malthus during his 1816 visit to England (Candolle 2004:318). English botanist William Hooker (1785–1865)—professor of botany at Glasgow (1820–40) and Director, Royal Botanic Gardens, Kew (1841–65) (Allan 1967, 1972, Pilet 1971)—wrote an article on plant geography for a geographical encyclopedia (1834); he followed rather closely Candolle's 1820 article (as Hooker acknowledged). Hooker distinguished range and habitat in this sentence: "Botanical geography is constituted by considering plants in relation to their *habitation*, region, or the country in which they grow, and in regard to their locality or particular *station*…" (Hooker 1834:228).

Early attempts to understand vegetation and its changes included rather isolated contributions, with later commentators sometimes unaware of important literature relevant to their concerns. The French scholar Adolphe-Jules-César-Auguste Dureau de la Malle (1777–1857) managed crops, meadows, and woodlands on his Bocage Percheron estate (Drouin 1994:149–150). He got the idea of plant succession not from Buffon or Deluc, but from an English author, Arthur Young, writing on crop rotation. Yet he based his report on succession (1825) upon his own experience during 30 years of planting crops and harvesting timber. Clements (1916:13–14) summarized Dureau de la Malle's article and translated his conclusion:

The alternance or alternative succession in the reproduction of plants, especially when one forces them to live in societies, is a general law of nature, a condition essential to their conservation and development. This law applies equally to trees, shrubs, and undershrubs, controls the vegetation of social plants, of artificial and natural prairies, of annual, biennial, or perennial species living socially or even isolated.

Later authors did cite this article, showing its influence (Drouin 1998:15–16).

In 1830, German botanist-physician and Humboldt protégé Franz J. F. Meyen (1804–1840) traveled as physician on the royal cargo ship *Prinzess Louise* during a world cruise lasting almost two years (Querner 1974, Nicolson 1996:294–295). He published an account of his voyage in 1834–1835, followed by *Grundriss der Pflanzengeographie* (1836, English, 1846, 1977). In the English edition, the distinction between habitat and range was drawn in these words: "The station (*statio*) of plants denotes the relation in which plants stand to the situation in which they always grow; or we understand by it, the locality…. The distribution of plants (*extensio plantarum*)…signifies the whole range of their stations…" (Meyen 1846:88). He went on to describe plant stations under two headings, aquatic and land plants, each of which in turn was subdivided further (Meyen 1846:50–61). His aquatic stations were: marine, fresh-water, submerged, floating, lake, ditch, river, fountain, saline, amphibious and inundated, maritime and shore, and mangrove forests; this was not logically satisfactory, since floating, lake, ditch, river, and fountain plants should fall under the "fresh-water plants," and the remaining groups could have followed "marine plants." His subdivisions of land plants were even more complex. Besides such stations as heath, bush, forest, land plants also included bog and marsh plants. Next, he discussed "Social Growth of Plants," called social if individuals of a species grow together, and otherwise "unsocial or solitary" (Meyen 1846:80), following Humboldt (Humboldt and Bonpland 1807:15). Meyen sometimes added an emotional response to his accounts (Meyen 1846:80):

> *Sphagnum palustre and Dicranum glaucum are extremely social plants; they often cover the moors of the north with so thick and uniform a covering that seldom any other plant grows up amongst them, and the plains have thence a very dreary appearance.*

When Göettingen botany professor August Grisebach (1814–1879) used the term "formation" to distinguish different groups of vegetation (1838:160), he was not deliberately replacing Humboldt's term "association," since Humboldt had not established association as a technical term, though Schouw had (see above). Grisebach became a leading phytogeographer (Wagenitz 1972, Magnin-Gonze 2004:202, Egerton 2013:343–344), and two of his reports on advances in botanical geography, for the years 1842–1843 and 1844–1845, were translated into English (Grisebach 1846, 1849, 1977). He was best known for *Die Vegetation der Erde nach ihrer Klamatischen Anordnung* (1872), which included a colored map of world vegetation.

University of Zurich Professor Oswald Heer (1809–1883) was a well-rounded naturalist who taught botany and entomology, and had a strong interest in paleobiology (Tobien 1972). Concerning his doctoral dissertation, *Die Vegetationsverhältnisse der südostlichen Teiles des Kantons Glarus* (1835), Becking (1957:415) wrote that Heer seems to have been first to apply "numerical values to species abundance and sociability," and Maarel (1975:215) stated in more detail that this same monograph

> …had a clear notion of the plant community as a type, its interrelations with the environment and the diagnostic value of plant species with a fidelity to one particular type of environment. Heer distinguished 30 "localities" (vegetation-site complexes that resemble our present-day ecosystems!). Each locality type is characterized by certain environmental characteristics, which may be found back in the type's name and characteristic species. It often can be recognized easily as a modern association….Heer also paid attention to the performance of species, particularly their sociability, for which he used a ten-point scale.

By 1842, Europeans had published a good number of studies on peat bogs, which mostly emphasized (excepting Linnaeus) fuel and drainage and conversion into meadows. Sometimes, asking new botanical questions led to new answers. Danish naturalist Japetus Steenstrup (1813–1897) started his career as a school teacher, but his published biological discoveries won him a professorship at the University of Copenhagen (Christensen 1924–25, I:464–472, II:230–231, Spärck 1932, Müller 1976, Egerton 2009:49–52, 2012:193). He dug into Danish forest bogs and discovered layers, each of which had different kinds of vegetation than layers above and below it (Steenstrup 1842, Clements 1916:14–16). He discovered that the peat layers not only had evidence of bog plants of different periods, but also evidence of forest trees surrounding bogs. In fact, the evidence on forest changes was more dramatic than that on bog changes. His conclusion from this investigation was, in part ([a prior paragraph to that

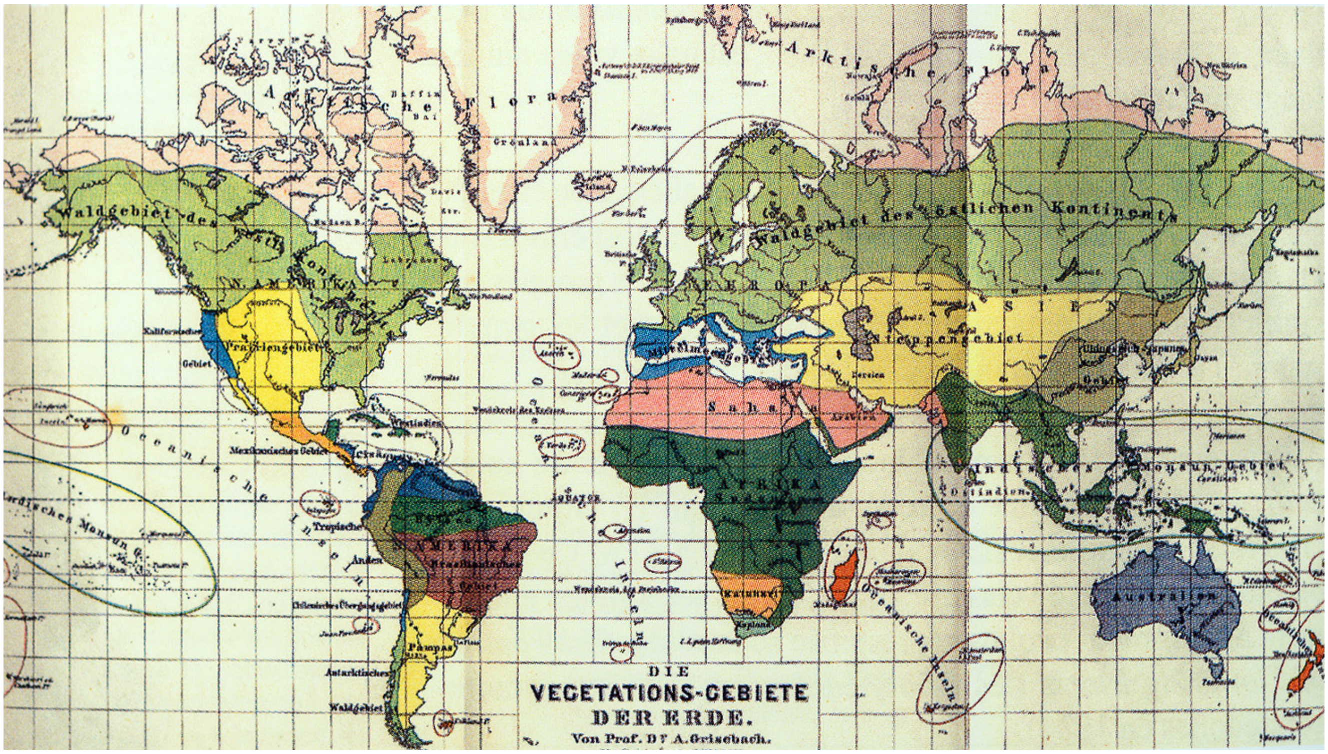


Fig. 4. Grisebach's map of world vegetation (1872). From Magnin-Gonze 2004:202.

Fig. 5. (a) Oswald Heer. Web. (b) Henri Lecoq. Virville 1954:242.

quoted below is in Egerton 2009:52] translated in Clements 1916:16):

> *…these two moors* [Vidnesdam, Lillemose] *have developed during a period in which several forest vegetations have arisen and disappeared. The aspen forests may be regarded as preparatory to the pine and oak forests, which probably dominated the region for thousands of years, but have practically disappeared from the country to-day. While these forests, as well as the moor vegetations, belong in a definite time sequence, it is practically impossible to assign any absolute time for any or all of the layers.*

Thus began paleoecology, which eventually added a time dimension to vegetation studies. Assigning definite dates to peat layers became possible after World War II, using radioactive carbon decay measurements.

French Professor and Director of the Jardin des Plantes of Clermont-Ferrand, Henri Lecoq (1802–1871), published an important study (1844) which "developed a quantitative measure which was essentially a combined cover-abundance estimation" (Maarael 1975:215). Darwin consulted it when writing his *Origin of Species* (Stauffer 1975:613, 671). Still more important was Lecoq's *Étude sur la Géographie botanique de l'Europe* (9 volumes, 1854–58). Maarel (1975:215) claimed that in 1854 Lecoq defined "association végétale" "along the lines Braun[-Blanquet] elaborated later, including the use of faithful species." Nicolson (2013:97) claimed that Lecoq (1854:58–90) "clarified the distinction between '*sociabilitié'* —many plants of the same species living together—and '*association*'—many plants of different species living together."

School teacher Jules Thurmann (1804–1855) was born in a town in Alsace, France, and received his B.A. degree from the University of Strasbourg, but his widowed mother raised him in Porrentruy, Switzerland, and that remained his home town. He earned scientific recognition in both geology and botany from his publications, despite his death from cholera at middle age. Plant ecology historian Malcolm Nicolson quoted (in translation, Nicolson 2013:97) Thurmann's 1849 distinction between flora and vegetation: "A land's flora and its vegetation are two quite different things which should not be confused: the first means the numbers of the distinct plant species which one observes, the second their proportions and associations." Since Alexander von Humboldt published on both flora and vegetation, this distinction should have been clear around four decades earlier, but Thurmann and Nicolson nevertheless thought it worth reminding some readers of the distinction.

Dr. Siegfried Reissek gave a talk in Vienna in September 1856 about his study of islands and vegetation formations in the Danube River—summarized in the October 1856 issue of *Flora*. Clements (1916:16–17) summarized *Flora*'s summary of Reissek's article, and I summarize Clements' account. The islands grew from sand bars, and their vegetation emerged in a regular pattern. Willows—usually *Salix purpurea*—were first established, and their hummocks caught sand from water and helped islands grow. *S. riparia* and *Myrica germanica* came next, followed by *Alnus incana*, *Populus alba*, and *Cornus sanguinea*. After the latter three came *Fraxinus excelsior, Ulmus campestris, Acer campestre, Quercus pedunculata, Pirus malus, P. communis*….willows died off as soon as the trees of the second stage developed much shade…" (Clements 1916:17).

The next year, Danish botanist-forester, and former student of Steenstrup, Christian Theodor Vaupell

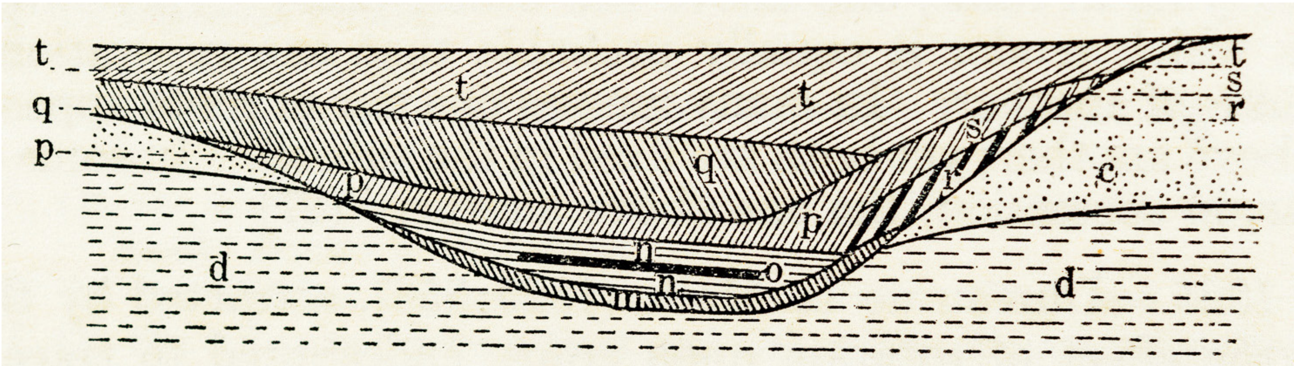


Fig. 6. Section of Lillimose Moor, Denmark, showing central and marginal layers of an ecosere (Clements' term). After Steenstrup. From Clements 1916:15.

(1821–1862), published *Bøgens indvandring i de Danske Skove* (Invasion of Beech into Danish Forests, 1857). He had examined the fossil record of Danish forests and found no evidence of beech before recent times, and therefore he concluded it was a recent arrival from France and Germany as Denmark's forests became drier than before (Clements 1916:17, Christensen 1924–1926, I:472–492, II:288–292). Vaupell concluded that beech could displace formerly common birch and pine except in marshy or sterile soils.

Another isolated observer, Henry David Thoreau (1817–1862), a New England naturalist (Egerton 2011, 2012:151–156), spoke in 1860 to an agricultural society on "The Succession of Trees," which was published in the *Transactions of the Middlesex Agricultural Society* and also in a New York newspaper (Thoreau 1980). Clements' search of scientific literature did not uncover this talk. Thoreau saw that when pines were logged, oaks replaced them, and when oaks were logged, pines replaced them. He explained that pines could not replace cut pines because oak seedlings were already growing, and pine seedlings could not grow in shade. Squirrels buried more acorns in pine forests than they ever recovered in winter. Pine seeds blew annually into oak forests, and when oaks were cut, pine seedlings flourished in the sunlight. He also saw that birds eat cherries from trees and later expel the seeds elsewhere in their droppings.

Not isolated was Austrian botanist Anton Kerner (1831–1898), whose *Pflanzenleben der Donauländer* (1863, English, 1951) is discussed by Nicolson (1996:297–298) and Egerton (2013:342–343). He used Grisebach's formation concept to describe the vegetation of the Danube valley: Juniper Formation, Oakwoods, Poplarwoods, Riverbank Forests, Swamps, Formations on Soils with Efflorescent Salts, How a Swamp Becomes a Meadow, Draining of Swamps, Plant Formations of Dry Lands (Kerner 1951:ix). For the adjacent Carpathian Mountains he distinguished Deciduous Forests, Coniferous Forests, Elfinwood Formations, and Meadow Formations. For the adjacent Hercynian Mountains, he distinguished Beechwoods and Pinewoods, and Sprucewoods and Birchwoods. For adjacent Alps, including Achen and Oetz Valleys, he distinguished Evergreen Shrub Formations, Woodlands, and Alpine Meadows. In chapter 24, "The Genetical Relationships of Plant Formations," he discussed "Development of the Azalea Formation." Kerner's final chapter is "Plant Formations of the Oetz Valley" (Kerner 1951:206–227). It introduces some subdivisions not previously mentioned, although Oetz Valley was already discussed with Achen Valley. Some of these subdivisions are named formations, as "Calluna Formation," while others seem to be formations in content, if not in name, as "Alder Woods." Why did he chose this valley for more detailed treatment than the rest of his area? The answer seems to be: "No other Tyrolean valley can boast so rich a literature as this one" (Kerner 1951:206). Having more data from there to work with, he carried his analysis to finer detail than anyone did elsewhere. Clements (1916:484) cited Kerner's book, but did not discuss him as an early investigator of succession.

Clements (1916:21–23) helpfully, but briefly, discussed several European contributors to plant succession observations during the 1870s and '80s, two of whom are also discussed here: Blytt and Hult. (Danish botanist Eugenius Warming was older than both Blytt and Hult, but his earlier work was not as relevant for plant ecology as his work during the 1890s, and so he is discussed below, after them and some others.)

Norwegian botanist Axel Gudbrand Blytt (1843–1898) was son of Professor Matthias Nums Blytt (1789–1862) at Christiania University (now University of Oslo). In 1863, Norway bought Matthias Blytt's personal herbarium, and in 1865 Axel Blytt became conservator at the Christiania University Herbarium, and in 1880 he became a professor. Axel continued work on his father's Norway flora and published volumes 2 and 3 (1874, 1876). In 1876, Axel published his own most important work, an essay on the immigration of the Norwegian flora during alternating rainy and dry periods, which was also published the same year in English. Blytt "advanced the theory that since the glacial period the climate of Norway has undergone secular changes in such fashion that dry periods of continental climate have alternated with moist periods of insular or oceanic climate, and that this has happened repeatedly. "As long as land connections permitted a mass invasion, continental species entered during one period and insular species during the other" (Clements 1916:21). Clements' summary on Blytt provides other details, including a correlation between Blytt's findings in Norway with Steenstrup's in Denmark.

Finish botanist Ragnar Hult (1857–1899) studied at Uppsala University and did research for several years in Blekinge, southern Sweden (Collander 1965:74–77). "In his important *Försök till Anallytisk Behandling af Växtformationerna* (Attempt at an Analytical Treatment of Plant Formations, 1881) he introduced a new analytical method of studying plant communities…" (Fries 1950:70). Clements praised Hult for "being the first to fully recognize the fundamental importance of development in vegetation, and to make a systematic study of a region upon this basis" (1916:22). Clements based his

Fig. 7. (a) Axel Gudbrand Blytt. Web. (b) Ragnar Hult. Collander 1965:facing 80.

claim upon Hult's "classic investigation of the vegetation of Blekinge" (1885) and upon his tracing "the development of the alpine vegetation of northernmost Finland" (1887). Hult's work was also important for the emergence of the geography discipline in Finland (Rikkinen 1988).

Blytt and Hult's work, in turn, stimulated two Swedish botanists, Andersson and Sernander, to continue their research. Gunnar Andersson (1865–1928) studied at Lund University and in 1909 became Professor of Economic Geography at the Stockholm Commercial College (Fries 1950:75). (Johan) Rutger Sernander (1866–1944) studied at Uppsala University and spent his career there. Clements (1916:492–493) cited 28 of Anderson's publications and 21 of Sernander's—making them among his most cited authors—but he discussed neither in his survey on the history of succession studies. However, both were discussed briefly in Robert Fries, editor, *A Short History of Botany in Sweden* (1950) and in more detail by Thomas Söderqvist's history of Swedish ecology. Söderqvist (1986:47) translated this passage from Andersson 1890:492:

> *A viewpoint of vegetation which seems to have forced its way through during the last years of the 1880s is that in order to understand the life of the individual species it is necessary to consider it in relation to those species which occupy the surrounding places. Thus the study of vegetation becomes the study of the plant community.*

Elsewhere, Söderqvist (1986:52) stated that Andersson and Selim Berger (1912) published a "vast inventory of the flora of northern Sweden…combining the immigration historical problem with extensive discussion of the ecological factors responsible for the geographical distribution of plants."

Sernander studied at Uppsala University. He wrote a doctoral dissertation on the "Evolution of the Vegetation of Gotland" (translated title, 1894), which earned him a title of docent of phytogeography. In 1908 he became a professor of plant ecology, possibly the first ever, three years before Henry Cowles achieved this title at the University of Chicago. Frederic Clements, Professor of Botany at the University of Minnesota was a de facto professor of ecology there, 1907–1917 (Ewan 1971). Sernander became "founder of the Uppsala school of plant geography and plant sociology, the institutional center for Swedish plant ecology from the 1930s to the 1960s" (Söderqvist 1986:44). He did research on palynology and extended Blytt's chronology back into the last ice age. Sernander also studied Scandinavian plant geography. Clements (1916:380–382) quoted in English translation (from German summaries) passages from Sernander papers of 1890 and 1891.

German botanist (Carl George) Oscar Drude (1852–1933) studied under Grisebach at Göettingen and received his doctorate in 1873 (Egerton 2013:345–346). In 1879 he settled at the Dresden Polytechnikum (now Dresden Technical University), where he spent his career (Magnin-Gonze 2004:203). As Grisebach's student, it is not surprising that Drude published a *Handbuch der Pflanzengeographie* (1890, French 1892), followed by *Deutschlands Pflangengeographie* (1896). What is surprising is that this second book (Tobey 1981:52):

> *…revealed the qualitative character of quantification in plant geography at the moment that Pound and Clements jumped to fully numerical quantification. Drude distinguished between five grades of abundance: social, gregarious, copious, sparse, and scarce (in order of decreasing abundance).*

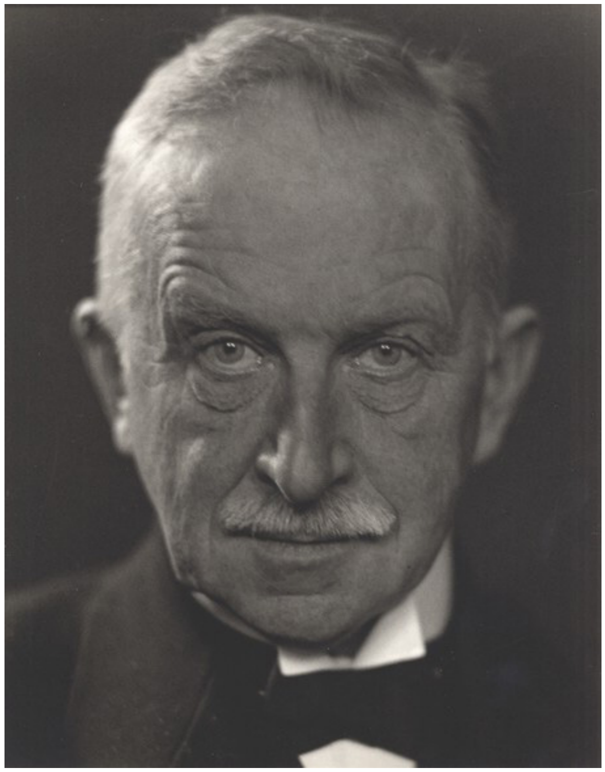


Fig. 8. (Johan) Rutger Sernander.

Drude's text for German plant geography provided guidance for these plant geographers on the Nebraska prairie, Clements and Pound (Egerton 2013:358–360), though Tobey's characterization of their work as quantified is an exaggeration (Nicolson 1988:194). Drude's *Die Ökologie der Pflanzen* (1913) was perhaps the third plant ecology textbook, counting Warming's as first (see below) and Clements' *Research Methods in Ecology* (1905) as second.

Plant ecology, animal ecology, limnology, and marine ecology during the later 1800s developed independently (Egerton 2013, 2014*a*, *b*, *c*), yet there were some parallels. Developments in animal ecology and marine ecology during that time had parallels with plant ecology. Karl August Möbius (1825–1909) developed a community concept, "biocönose," while studying oyster beds in Kiel Bay, Germany (1877) that was to be important enough to translate into English (1880; partly quoted in Allee 1949:35–36, Egerton 2014*a*:62). He noted that oysters and particular other species were found only on sandy bottoms, and that muddy bottoms had a different set of species (Reise 1980, Kölmel 1981, König et al. 1981). He suggested that a particular example of either group was a biocönose (translated as "community" in the English edition). Retrospectively, this was an important concept, but at the time of translation, the concern was care of oyster beds.

However, there were marine forerunners to that concept, which Möbius might not have known, but can be noted here. English zoologist Edward Forbes (1815–1854) was certainly studying marine ecology—though lacking the name—when he reported on the different zones of marine algae and invertebrate animals found at different depths along the coasts of Britain (1840) and in the Aegean Sea (1844) (quoted in Egerton 2010:182,184, 2012:135–138). Observing species in different zones is not a community concept, but a step toward it, and Warder Allee (1949:34) thought that Forbes was first to explore ecological dynamics in his Aegean discussion.

Continuing that tradition was an American professor of zoology at Yale University, Addison Verrill (1839–1926), who in 1871 began research for the U. S. Fish Commission at Woods Hole, Massachusetts on the marine fauna in that region (Egerton 2014*c*:359). It led to his voluminous "Report upon the Invertebrate Animals of the Vineyard Sound and the Adjacent Waters, with an Account of the Physical Characters of the Region" (1873) and to subsequent studies at Woods Hole into the 1880s (Coe 1932, Shor 1976). Allee (1949:32) also recognized the value of *Des Sociétés animales* (1878) by Alfred Espinas (1844–1922), but failed to note that Espinas was studying societies of single species of social insects, which were fundamentally different from communities of different species (Egerton 2014*a*:59–60). Somewhat more substantial than philosopher Espinas' book was one by zoologist Karl Semper, *Animal Life as Affected by the Natural Conditions of Existence* (German and English editions, 1881), discussed by Allee (1949:22) and Egerton (2014*a*:60), but Semper did not describe animal communities.

An American zoologist probably influenced by Möbius was Stephen Forbes (1844–1930, no known kinship with Edward Forbes), a professor at the University of Illinois (Croker 2001:126), who was also among the first to refer to his research as ecological. A passage in "Some Interactions of Organisms" (Forbes 1880:3, 1977) noted that significant changes in the fortunes of a single species could "initiate some other form of change, the disturbance thus propagating itself in a far extending circle." That statement indicates a path of his thinking that became the focus of his talk, "The Lake as a Microcosm" (1887, cited from 1925 reprint). In more recent terminology, one could call a lake an ecosystem. Logically, his talk was a contribution to limnology, but in reality François Forel was developing limnology simultaneously in Switzerland with no awareness of Forbes, and therefore Forbes' 1880 and 1887 contributions were to general ecology, not directly to limnology (Egerton 2014a:64–66, 2014*b*).

An American mammalogist, C. Hart Merriam (1855–1942), with a medical degree, worked for the U.S. government in the Department of Agriculture, studying birds and mammals, 1885–1910 (Sterling 1977, 1997). In 1889 he and other personnel in the USDA Division of Ornithology and Mammalogy surveyed the San Francisco Peak and nearby Little Colorado River, Arizona (Sterling 1977:204–240, Egerton 2014*a*:65–69). He explained his choice for a survey (1890):

> *San Francisco Mountain was chosen because of its southern position, isolation, great altitude, and proximity to an arid desert. The area carefully surveyed comprises about 13,000 square kilometers (5000 square miles), and enough additional territory was roughly examined to make in all about 30,000 square kilometers (nearly 12,000 square miles), of which a biological map has been prepared.*

He published no climatological data (as Humboldt had, in 1807), but he found that he could correlate vegetation with elevation to define seven "life zones" for that region (1890:plate 1), ranging from an Alpine Zone above 3000 m (11,500 feet) down to a Desert Zone at 1200–1800 m (4000–6000 feet). He then matched his mountain life zones with lowland vegetation to construct a "Provisional Biological Map of North America Showing the Principal Life Areas" (1890:map 5). Later, ecologists found fault with his life zones as simplistic (Shelford 1932, Sterling 1977:25), though Rexford Daubenmire (1938) praised his use of both plant and animal data in constructing life zones, and life zones have continued in use in western mountains as a system of convenience (Barbour et al. 1987:17–18).

The earliest plant ecology textbook was (Johannes) Eugenius (Bülow) Warming's *Oecology of Plants: an Introduction to the Study of Plant Communities* (English version, 1909), which in its first two versions (Danish, 1895, German, 1896, Polish 1900, Russian 1901) was still within a phytogeographical context (Christensen 1924–26, I:776–806, II:367–399, Müller 1976). Warming (1841–1924) had interrupted his studies at Copenhagen University in 1863–1866 in order to serve as secretary to zoologist–paleontologist Peter W. Lund (1801–1880) in a tropical savannah–woodland in Brazil, where Lund had moved permanently in 1833 (Jensen 1932). Those years in Brazil were "most significant for [Warming's] scientific development" (Christensen 1932*b*:156; see also Christensen 1927, Tansley 1927, Goodland 1975).

Warming taught the first known course in plant ecology. His *Plantesamfund* did not show any influence from the above-mentioned zoologists. In 1884 Warming had surveyed the physiognomy of north European Spermophyta, "which he arranged in fourteen chief groups with many sub-groups, based upon morphological and biological characters" (Warming 1909:4). He began the English edition of his textbook by explaining the distinction between floristic and ecological plant geography (Warming 1909:1–2). Clements (1916:23) praised Warming for being "first to give a consistent account of succession on sand-dunes, and his pioneer studies in this field have served as a model for the investigation of dune seres in all parts of the world." Warming's discussion of plant communities (Warming 1909:12–13), although brief, focused plant ecologists' attention on this level of study much as Möbius' discussion did for animal ecologists. When he surveyed the earth's vegetation, he used

Grisebach's term, "formation," as in "Lithophytes: Formations on Rocks." However, his last section on "Struggle between Plant Communities," consisting of chapters 94 to 100, included 96, "Changes in Vegetation Induced by Slow Changes in Soil Fully Occupied by Plants," and 97, "Changes of Vegetation without Change of Climate or of Soil," which Clements (1916:25) praised as a very helpful introduction to the study of plant succession.

In contrast to Warming's treatise, which lacked illustrations, was the encyclopedic *Pflanzengeographie auf Physiologische Grundlage* (1898) by Strasbourg botanist Andreas Schimper (1846–1901), which (at least in the English edition, 1903) contained author's portrait, 4 maps, and 497 other illustrations. Like Warming, Schimper had also traveled to the tropics to study vegetation (Sanders 1975*a*, Cittadino 1990:97–115, Matagne 2009:see index). Clements (1916:26–27) summarized Schimper's theoretical ideas and found them less compelling than Warming's. Dwight Billings (1985:5) praised the publications of both Warming and Schimper, but thought that Schimper's *Pflanzengeographie* "was a valid beginning of modern physiological ecology." However, R. J. Goodland (1975:243) accused Schimper of quoting "extensively from more than fifteen of Warming's works and even reproduced Warming's figures" without acknowledgment.

Just as Drude's treatise provided guidance for Clements and Pound at the University of Nebraska, so Warming's book provided comparable guidance for another American, Henry Cowles (1869–1939), at the University of Chicago (Tansley 1940, Sears 1958, Tobey 1981:104–108, Cittadino 1993, Burgess 1996:31–32, Cassidy 2007). In a published paper from his doctoral dissertation, Cowles expressed (1899:97–98)

> *...his great indebtedness to Dr. Eugen Warming, professor of botany at Copenhagen; his textbook on ecology and his treatises on the sand-dune floras of Denmark have helped greatly to make clear the true content of ecology, and they have been a constant incentive to more careful and thorough work.*

Cowles cited three of Warming's studies in addition to his textbook, all in Danish. These works were so important to Cowles that he learned Danish (Cittadino 1993:534, Cassidy 2007:28). Warming's discussion on plant succession on coastal dunes covered 10.3 pages (262–272), and Cowles' discussion covered 118 pages, including 26 photographs.

It is fitting that Cowles studied the Indiana Dunes along the south shore of Lake Michigan, 1896–1898, which are about 25 miles across, because they are the largest dunes in the world (Cassidy 2007:31). Cowles had actually gone to the University of Chicago to study under glacial geologist T(homas) C(hrowder) Chamberlin, and although he switched to plant ecology, his subject of study drew upon both his geological and ecological knowledge. The oldest dunes are farthest inland and the newest ones are closest to the shore. Therefore, the earliest vegetation is closest to shore and the oldest farthest from shore. Cowles' challenge, therefore, was to understand what changes occurred and why, moving from shore outwards. Eugene Cittadino (1993:536) summarized Cowles' findings

> *Community replaced community in an orderly sequence; xerophytes and hydrophytes gave way to mesophytes, so that where once there was only drifting sand and dune grass, now there was a luxuriant oak forest or, better yet, the stately beech–maple forest, pinnacle of succession.*

Going beyond his dissertation publication, Cowles provided a broader panorama in "The Physiographic Ecology of Chicago and Vicinity" (1901) in the *Botanical Gazette* and a shorter version in the *Bulletin of the Geographic Society of Chicago*.

Cowles achieved greater generalizations in "The Causes of Vegetative Cycles" (1911), in which he argued that there are vegetation cycles in which "there is a period of youth, which is characterized by vigor of development and by rapidity of change; in each there is a period of maturity, and finally one of old age, which is characterized by slowness of transformation and by approach to stability, or at least to equilibrium….the final vegetative aspect varies with the climate, and hence is called a climatic formation." He thought that the "climatic plant formation is the most mesophytic which the climate is able to support in the region taken as a whole."

Clements, in his historical summary on the development of succession understanding, stated (1916:27) that Cowles' 1899 paper, along with Warming's discussion, "served as a model for the investigation of dune succession the world over." Concerning Cowles' 1911 paper, Clements (1916:31) stated that it was discussed at some length in his chapters 7–9, and he merely mentioned (p. 31) that Cowles had called attention to the three great cause of succession: climate, physiography, and biota, and he also listed the seven topics which Cowles (1911) covered. One of the topics, "The Development of Dynamic Plant Geography," contains a brief history of such studies, which provided the start for Clements' own historical chapter. Clements thus acknowledged the substantial contributions which Cowles made to succession understanding.

Two zoologists who received Ph.Ds from the University of Chicago and studied partly under Cowles were Charles Adams (1873–1955) and Victor Shelford (1877–1968); both published noteworthy books on animal ecology in 1913 (Croker 1991, Harmond 1997). Adams' small *Guide to the Study of Animal Ecology* was perhaps the first attempt to describe in some detail the scope of this science. The book is an introduction to that literature, which Adams organized to accompany his course on animal ecology. Most relevant to ecological communities was his discussion and bibliography, "The Dynamic Relations of Associations and Aggregations, with Special Reference to Animal Associations" (1913:130--141). However, he contributed nothing of his own to this topic, for his introduction to it is a quotation from Stephen Forbes, followed immediately by a bibliography in chronological order that began with Möbius on oysters, then Forbes on "The Lake as a Microcosm," and so on.

Shelford's *Animal Communities in Temperate America, as Illustrated in the Chicago Region* (1913) is a very substantial original work. Its 15 chapters include six articles he previously published, reworked as chapters. It helped that he had studied some communities from the same sand dune communities at the south end of Lake Michigan that Cowles and his plant ecology students had been studying since the 1890s. Shelford's chapters included 10 on the animal communities found in nine kinds of environments: large lakes, streams, small lakes, ponds, between land and water, swamps and floodplain forests, dry and mesophytic forests, thickets and forest margins, and prairies. His last chapter, "General Discussion," included sections on "Agreement between Plants and Animals," "Relations of Communities," and other topics generalizing from the diverse preceding chapters.

Although food chains had existed in the natural history literature since the early 1700s (Egerton

2007), and Semper (1881:51–52) had discussed a hypothetical food web, Italian entomologist Lorenzo Camerano (1856–1917) diagramed two barely comprehensible food webs in 1880, which may never have influenced anyone else (Egerton 2007*d*:53, 2014*a*:62–63). The earliest clear diagram of a food web is perhaps the one by USDA entomologists Dwight Pierce and colleagues in 1912 on the cotton boll weevil and its enemies (illustration reproduced in Allee 1949:53, Egerton 2014*a*:68), followed in 1913 by two by Shelford (1913:70, 167, reprinted in Egerton 2007*d*:54, 55). Shelford's two diagrams (aquatic and terrestrial) have nothing in common with the boll weevil one; he did not cite Pierce et al. 1912, and he did not discuss boll weevils.

Pennsylvanian Edgar Nelson Transeau (1875–1960) had been a graduate student under Cowles, 1900–1901, before earning his Ph.D. at the University of Michigan (1904). After holding several other positions, he settled at Ohio State University in 1915 (Burgess 1996:106). Clements (1916:495) cited six of Transeau's articles, two of which were on plant succession (1909, 1913), without including him in his historical summary on succession. Transeau's most notable study was on the prairie peninsula (1935).

Detroit native William Skinner Cooper (1884–1978), as a child, loved flowers, and his mother bought him a copy of Asa Gray's *Manual of Botany*. At Alma College, ecologist Transeau "influenced my scientific development more than any other person" (Cooper 1994:130). In graduate school at Johns Hopkins University, he became interested in relationships between glacial geology and vegetation (Buell 1963, McCormick 1994, Burgess 1996:29–30). After transferring to the University of Chicago, he discovered he had learned Cowles' teachings from Transeau. However, geologist Rollin Salisbury, at Chicago, "was the greatest teacher I have ever studied under." Cooper's doctoral dissertation, "The Climax Forest and Its Development," he published in six papers, 1912–14, two of which Clements (1916:477) cited (and I reprinted, 1977), but, as with Transeau, Clements omitted Cooper from his historical summary.

Clements had studied ecology simultaneously with Cowles, but at the University of Nebraska (Tansley 1947, Clements 1960, Tobey 1981:76–87, Hagen 1988, 1992:20–28, 1999, Burgess 1996:26–27). Clements' early publications were empirical studies, in which theory was inconspicuous. He more than kept abreast of Cowles' publications with his own, for where Cowles was publishing important papers, Clements was publishing respectable books. Clements' *Plant Succession* (1916) was the foremost of his contributions, though not his last book. It is a very detailed synthesis on the subject and therefore exerted a strong influence. Nevertheless, it had two controversial assumptions, one of which Tansley (1916) and Cowles (1919) identified in their reviews: that succession is always toward a climatic climax, which can be specified. Both reviewers found otherwise in their own studies. Clements' other controversial idea was already stated in his *Research Methods in Ecology* (1905:199)

> *The plant formation is an organic unit. It exhibits activities or changes which result in development, structure, and reproduction. These changes are progressive, or periodic, and, in some degree, rhythmic, and there can be no objection to regarding them as functions of vegetation. According to this point of view, the formation is a complex organism…*

Having established this latter point to his own satisfaction, he merely referred the reader of *Plant Succession* (Clements 1916:3) to his earlier book for his reasoning. If he had offered both his climatic climax and community-as-organism as hypotheses instead of as pronouncements, he would have been within sound scientific practice, and he or someone else might have realized the difficulty of testing if a community is an organism.

Cowles exerted more influence as an educator of plant ecologists than any other American in early decades of the 1900s (Sprugel 1980). However, his and Arthur Tansley's reviews were unable to discredit Clements' influence (which they were not attempting to do, anyway) during the first half of the 1900s in America. Clements' dogmatic statements did not discredit his own careful observations and his mastery of a vast literature. Reviewers are apt to find something to complain about in any large-scale synthesis (whether fairly or not). Since one cannot defeat something with nothing, one needs a competing hypothesis with evidence to challenge an established perspective. That competing hypothesis was developed almost simultaneously by an American and a Russian.

The American was Midwesterner, Henry Gleason (1882–1975), from a small town in Illinois, who earned his B.S. and M.S. degrees (1901, 1904) from the University of Illinois and his Ph.D. from Columbia University (Nicolson 1990, Burgess 1996:46). "Between 1917 and 1945 only one major ecologist in the whole of America dissented from the general consensus surrounding the reality of [Clementsian] vegetation-units—Henry Allen Gleason" (Nicolson 1990:93). Often, biologists begin publishing descriptive papers, with their interpretive accounts coming later. That was true of Gleason, and Clements (1916:480) cited six of his papers (one was coauthored). Clements (1916:215–216) briefly summarized Gleason (1907), stating that he "described the successional relations of the bunchgrass, blow-sand and blow-out associes, and the black-pack forest associes of Illinois," and reproduced a successional diagram from Gleason's paper (also in Egerton 2009:57–58, 63). The terminology Clements used, however, was his own. Clements continued: "Gleason (1910) has made a comprehensive study of succession on the inland sand deposits of Illinois, in which prairie and forest are the climax stages." These papers did not, however, earn Gleason recognition in Clements' list of his predecessors in his historical summary on succession studies.

Gleason began expressing his differences with Clements in his "Vegetation of the Inland Sand Deposits of Illinois" (Gleason 1910, Nicolson 1990:107–108), but that context was observational, not theoretical, and besides, neither his nor Clements' interpretations were well known and appreciated that early. In 1916, a month before *Plant Succession* appeared, Clements and Gleason met on a field trip which the new Ecological Society of America sponsored near San Diego (Nicolson 1990:111–114). Their major differences emerged, and Clements expressed hope that his book would change Gleason's mind. Clements made his theoretical understanding quite clear and conspicuous in his *Plant Succession*, which became Gleason's opportunity to explicitly explain his dissent, as he did in "Structure and Development of the Plant Association" (1917). His theoretical understanding was then as clear as Clements' was, but the plant ecology community barely noticed. Why? The Torrey Botanical Club's *Bulletin* was undoubtedly little read in Europe, but was read in America. A major problem was that Gleason's 19-page article could not discredit a theory in Clements' impressive 525-page book. Clements' *Plant Succession* was a paradigm for organizing a young science, and Gleason's article was not.

Gleason's biographer, Malcolm Nicolson, pointed out (1990:115–119) that neither in America nor in Europe was Clements' theoretical understanding fully accepted. However, other plant ecologists did not have to choose between Clements and Gleason. They found various other understandings than Gleason's

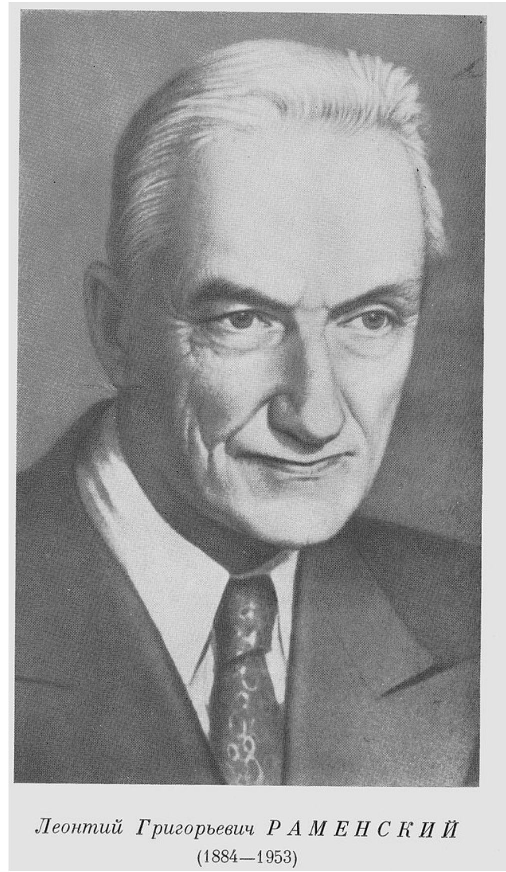


Fig. 9. (a) Henry A. Gleason. Web. (b) Leonty G. Ramensky. Wikipedia.

for their dissents from Clements' theoretical claims. A Canadian, George Fuller (1869–1961), who earned his Ph.D. (1913) under Cowles and remained at the University of Chicago (Nicolson 1990:119, Burgess 1996:44), pointed out, in his "Units of Vegetation and Their Classification" (1918) a range of opinions between Clements and Gleason, so Gleason was not entirely ignored, but also not endorsed. In 1926, Gleason returned to a defense of his "individualistic concept" of plant communities. He had more data than he had had a decade earlier, and ecologists had not reached a consensus on how to describe units of vegetation. He invited them to reconsider his concept in an article about the same length as in 1917 and published in the same journal. He did not have much more success then than before—Clements was still defending his own ideas—but this time Gleason's ideas were not forgotten and were destined to exert a significant influence after World War II (Nicolson 1990:130–136).

The Russian who developed an understanding similar to Gleason's was plant ecologist Leonty G. Ramensky (or Ramenskii, 1884–1953), who graduated from Petrograd University in 1916 and earned his Ph.D. in 1935 (Wikipedia). In 1911–1928 he worked at the Research Institute of Voronezh Gouvernement (later, Voronezh State University), and from 1928 at the Grassland Institute (later, All-Union Scientific Research Institute of Forages). He argued that biotic communities consist of species behaving individualistically (Sobolev and Utekhin 1973, McIntosh 1983, Ramensky 1983), and Wikipedia claimed that politically powerful V. N. Sukachov and his colleagues saw communities as super-organisms (influenced by Clements?), and Ramensky was marginalized until "rehabilitated" posthumously. There is some truth to this claim, but the situation was more complex than indicated. Douglas Weiner stated (1988:186)

> *Of the opponents of the closed, self-regulating biocenosis, among whom Leontii Grigor'evich Ramenskii, Aleksei Porfir'evich Il'inskii, A. A. Elenkin, and Academician Vladimir Leont'evich Komarov were the most prominent, it was the last who best articulated this current of thought.*

In other words, in 1988, Weiner did not view Ramensky as an isolated prophet crying in the wilderness. Komarov was a very prominent botanist, honored by the naming for him of a botanical institute (Shetler 1967). Later, however, Weiner stated (1999:375):

> *Since 1910 the [skeptical] approach had been championed in Russia by Leontii Grigor'evich Ramenskii, but it had made little headway against the holistic, superorganismic model of the biogeocenosis (ecological community plus abiotic environment) championed by Sukachëv and his many allies.*

Ramensky's earliest landmark paper was published in Russian in 1924, with excerpts translated later into English (McIntosh 1983). This was a case of simultaneous discovery in science, as no evidence indicates that either Gleason or Ramensky was influenced by the other's ideas.

Russian mathematically inclined ecologist, Georgii Gause (or Gauze, 1910–1986), is mostly remembered for *The Struggle for Existence* (1934, to be discussed in part 55 of this history). He saw the difficulty of resolving the controversy between Clements' community concept and Gleason's individualistic concept of plant associations by verbal arguments, and he explained (1936) how to make quantitative measurements to resolve this conflict. He did not cite Ramensky, apparently being unaware of his work.

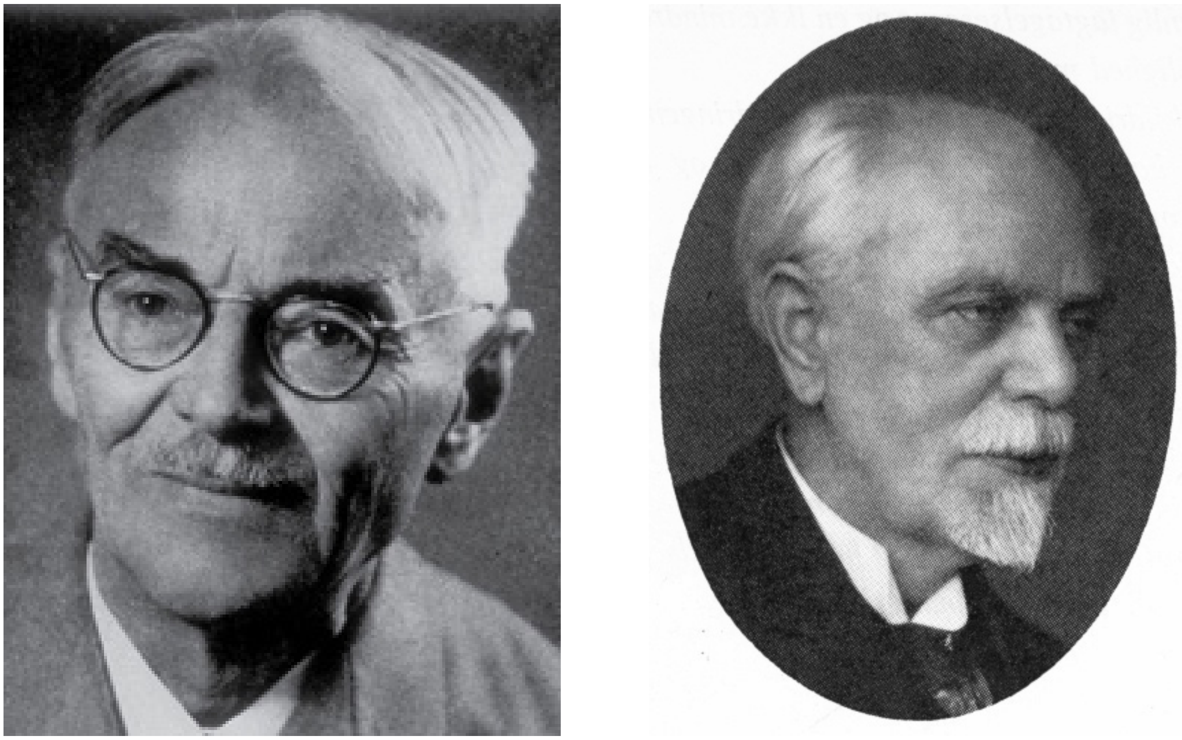


Fig. 10 (a) Josias Braun-Blanquet. Web.
(b) Christen C. Raunkiaer. Web.

Plant ecology historian Malcolm Nicolson (1989) has compared the approaches of Clements and Josias Braun-Blanquet (1884–1980) and viewed their differences as representative of American and French plant ecology. His discussion of their work is fine, but offering them as examples of national styles is problematic. Nicolson knows quite well that Clements' American contemporaries, Cowles and Gleason, had significant differences with him, and so he did not represent an "American system" of plant ecology. Josias Braun (who added Blanquet to his name when he married) was Swiss, and as an undergraduate studied plant ecology under Professor Carl Schröter and other botanists at the University of Zurich (Acot 2008). He did earn his Ph.D. under French botanist Charles-Henri Flahault at the University of Montpellier, but since Braun-Blanquet was from the Zurich-Montpellier school of plant ecology, as Nicolson acknowledged, it seems odd to name him a representative of "French" plant ecology.

However, the differences between Clements' and Braun-Blanquet's plant ecology were substantial. Braun-Blanquet synthesized his early studies in *Pflanzensociologie: Grunzüge der Vegetationskund* (1928, English, 1932). His later work appeared in French or German (Maarel 1975:218, Nicolson 1989:181). Maarel (1975:213) compared Braun-Blanquet's role in the history of phytosociology to the role of J. S. Bach in the history of European classical music. Maarel thought Braun-Blanquet's phytosociology was a "synthesis, a completion of ideas and methods from the beginning of the 19th century," from Humboldt's work to that of European botanists (named) in the early 1900s. By 1921, Maarel (1975:214) judged that Braun-Blanquet had achieved his three "principles of a systematics of plant communities on a floristic basis," which Maarel explained. An American comment on Braun-Blanquet: he "developed his methods of community sampling, data reduction, and association nomenclature that dominate much of plant community ecology today" (Barbour et al. 1987:23).

Danish plant ecologist Christen C(hristensen) Raunkiaer (1860–1938) would follow Warming as professor of botany (1912–1923) at the University of Copenhagen (Adsersen online pages 15–16, Wikipedia). He married an artist, Ingeborg (1863–1921), who accompanied him on his study trips to the Virgin Islands (1905–1906) and Mediterranean shores (1909–1910) and illustrated his publications before their divorce in 1915. Although older than Braun-Blanquet, Raunkiaer's publications were little known outside Denmark until collected and translated into English (1934). "He developed a life form classification that is still widely used…and a quantitative method of sampling vegetation whereby data could be treated statistically without bias" (Barbour et al. 1987:22). "*Life form*, by Raunkiaer's definition, was basically the position of the plant part which survived the most severe season in any area" (McIntosh 1985:135).

"…around 1915–1920 an observer of Swedish botany could discern two qualitatively different approaches to the field study of plant-environment relations, i.e., the Uppsala school and the Stockholm school" (Söderqvist 1986:106). Uppsala had field observers and Stockholm had experimentalists. Their competition continued through the 1920s and came to a climax in 1934 when Einar Du Rietz (1895–1967), at Uppsala, and Henrik Lundegårth (1888–1969), in Stockholm, competed for the botany chair at Uppsala. Du Rietz won; Lundegårth would surely have ended the distinctive Uppsala school. This reminds us in a general way of the competition which Ron Tobey (1981) discussed between plant ecology schools at Nebraska and Chicago. In neither of these cases was the outcome based upon one school being right and the other wrong. It was a matter of each school having a distinct approach to plant ecology, and one could choose which to support, based upon various considerations. Both Swedes were active researchers and publishers. Söderqvist (1986:89–94) apparently wrote the most extensive discussion of Du Rietz's contributions; Anthony Larkum wrote "Contributions of Henrik Lundegårth" (2003). Lundegårth's subsequent research emphasized plant physiology.

At the ESA and AAAS meetings in December 1916, Clements spoke on "The Development and Structure of the Biotic Communities" and coined the terms *biotic community* and *biome* which he also defined (quoted from Croker 1991:65):

> The biotic community is regarded as an organic unit comprising all the species of plants and animals at home in a particular habitat….The biotic community, or *biome*, is fundamentally controlled by the habitat…

Clements did not focus on the biome in his own research, but Shelford studied animal communities, and they had a meeting of minds in their *Bio-Ecology* (Clements and Shelford 1939). *Bio-Ecology* synthesized their researches since the early 1900s, and they cited a vast literature which they had consulted. They even included a historical survey of previous studies on both plants and animals in communities, beginning with Möbius (1877). He had used the term *biocenose*, which he only used regarding oysters, though others used the term to designate both plants and animals (Clements and Shelford 1939:6–19). They mentioned that they had been reporting on bio-ecology in the yearbooks of the Carnegie Institute of Washington from 1926 to 1934. Clements had continued along the lines laid out in his *Plant Succession* (1916), but Shelford had greatly expanded the scope of his investigations. With and without his students, he explored very widely in North America, including Mexico and even Panama (Croker 1991:55–119). In 1918 he began spending alternate summers at the Puget Sound Biological Station, where he taught and researched. With other colleagues there he wrote "Some Marine Biotic Communities of the Pacific Coast of North America," a 105-page synthesis in *Ecological Monographs* (Shelford et al. 1935). Later, he summarized that study in the final chapter of *Bio-Ecology* (Clements and Shelford 1939:313–353).

E(mma) Lucy Braun (1889–1971) was a lifelong resident of Cincinnati, Ohio, and earned her three degrees at the University of Cincinnati (B.A., 1910, M.A. in geology, 1912, and Ph.D. in botany, 1914). She joined that university's faculty in 1910, was professor of botany, 1927–1946, and professor of plant ecology, 1946–1948 (Stuckey 1973, 1994, 1997, 2001, Braun 1994, Burgess 1996:18). Her studies on vegetation in Ohio and Kentucky culminated in her *Deciduous Forests of Eastern North America* (1950). She continued researching and publishing, and her later works included "The phytogeography of Unglaciated Eastern United States" (1955), *The Woody Plants of Ohio* (1961), and *An Ecological Survey of the Vegetation of Fort Hill Memorial* (1969). She served as vice-president of ESA in 1938 and as president in 1950—the first woman in either office. She was one of 50 botanists awarded a Certificate of Merit by a jubilee committee of the Botanical Society of America (BSA), "for her contribution to our knowledge of the origin and structure of the Eastern American deciduous forest" (Meyer 1958:16). The BSA jubilee volume included her paper, "The Development of Association and Climax Concepts, Their Use in Interpretation of the Deciduous Forest" (Braun 1958). Her biographer, Ronald Stuckey (1994:5) judged her "One of the most original thinkers for the developing field of plant ecology during the first half of the twentieth century in North America." However, she was not a revolutionary.

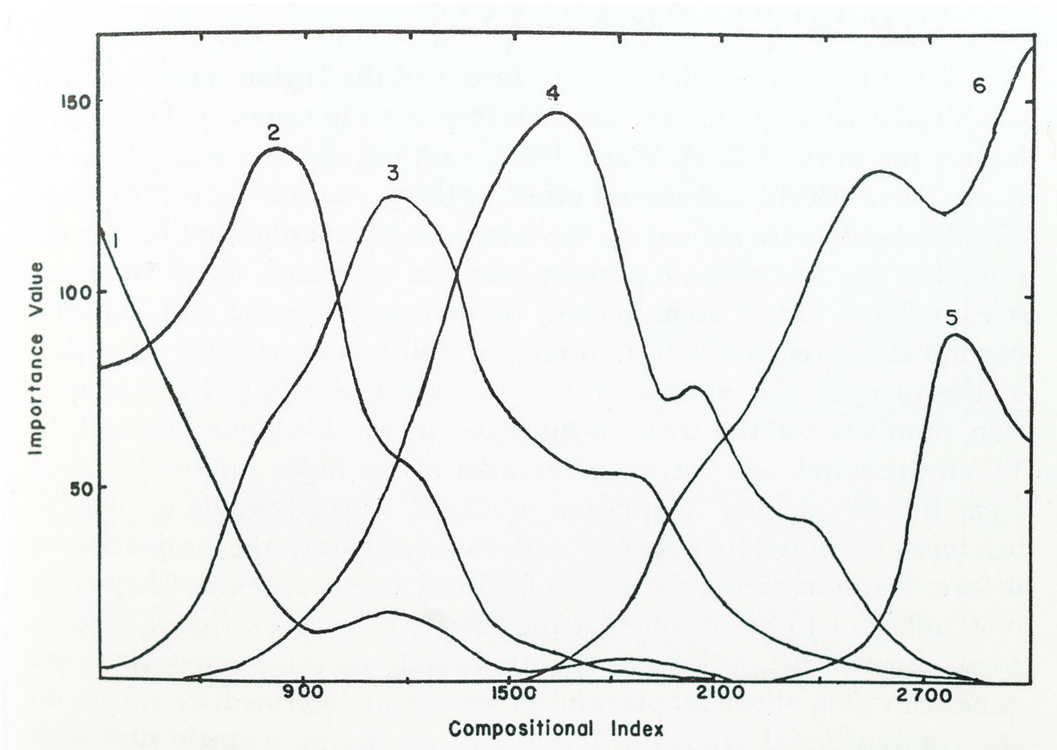


Fig. 11. Behavior of major tree species on compositional gradient of southern upland forest. 1. Bur oak *Quercus macrocarpa*, 2. Black oak *Q. velutina*, 3. White oak *Q. alba*, 4. Red oak *Q. borealis*, 5. Beech *Fagus grandifolia*, 6. Sugar maple *Acer saccharum*. Curtis 1959:97.

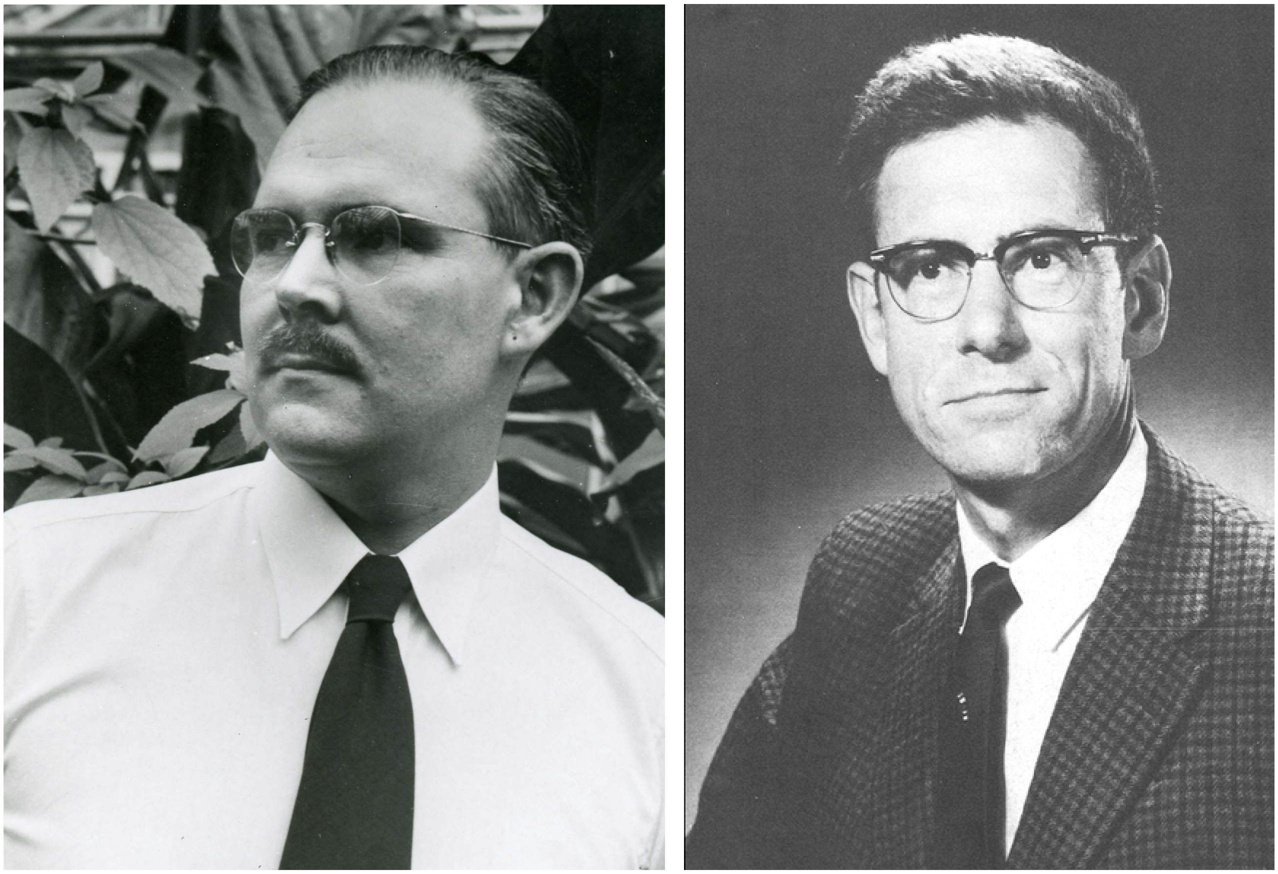


Fig. 12 (a) John T. Curtis. Hunt Institute for Botanical Documentation. (b) Robert H. Whittaker. Westman and Peet 1982:97.

Clements' concept of plant community was challenged, and largely superseded, by Gleason's continuum concept, for several decades, thanks mainly to John Curtis, and to some extent to Whittaker (see below). John Curtis (1913–1961) was born in Waukesha, Wisconsin, 20 miles west of Milwaukee—now more or less a suburb, but it was not in 1913. He did well in public schools and in 1930 entered Waukesha's Carroll College, where he studied biology and chemistry, and was most influenced by the professor of plant physiology (Burgess 1993:1–4, 1996:33). After graduating in 1934, he was accepted as a graduate student in the Department of Botany, University of Wisconsin, Madison. He majored in physiology and minored in pathology. He never took an ecology course. He spent the summer of 1935 at the university's Trout Lake Biological Station, where he collaborated on algal research with university limnologist Chancey Juday, with Curtis as senior author in reporting their findings (Curtis and Juday 1937).

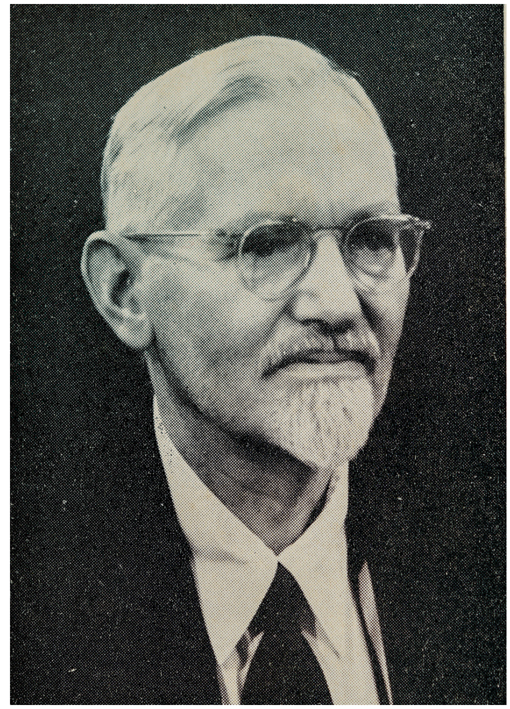
Both Curtis' M.S. and Ph.D. (1937) dissertations were on orchid seed germination. In 1937 he became an instructor in botany at U.W.-Madison, and in 1938 he married botany student Jane Kurtenacker, who researched orchid–mycorrhizal relationships. In 1938 he also began teaching a joint course with two other botany faculty, on physiology, morphology, and ecology. In 1940, he was appointed director of research at the University of Wisconsin Arboretum. In 1941, he won a Guggenheim Fellowship for a year to study Michigan, Wisconsin, and Minnesota forests. After two months, his fellowship was interrupted by World War II and he accepted research directorship of the Société Haitiano-Américaine de Dévelopement Agricole, working in Haiti with the Rubber Development Corporation at an experiment station, to obtain rubber latex from *Cryptostegia* vines (commercially unsuccessful). He had joined the Ecological Society of America in late 1941 or early 1942.

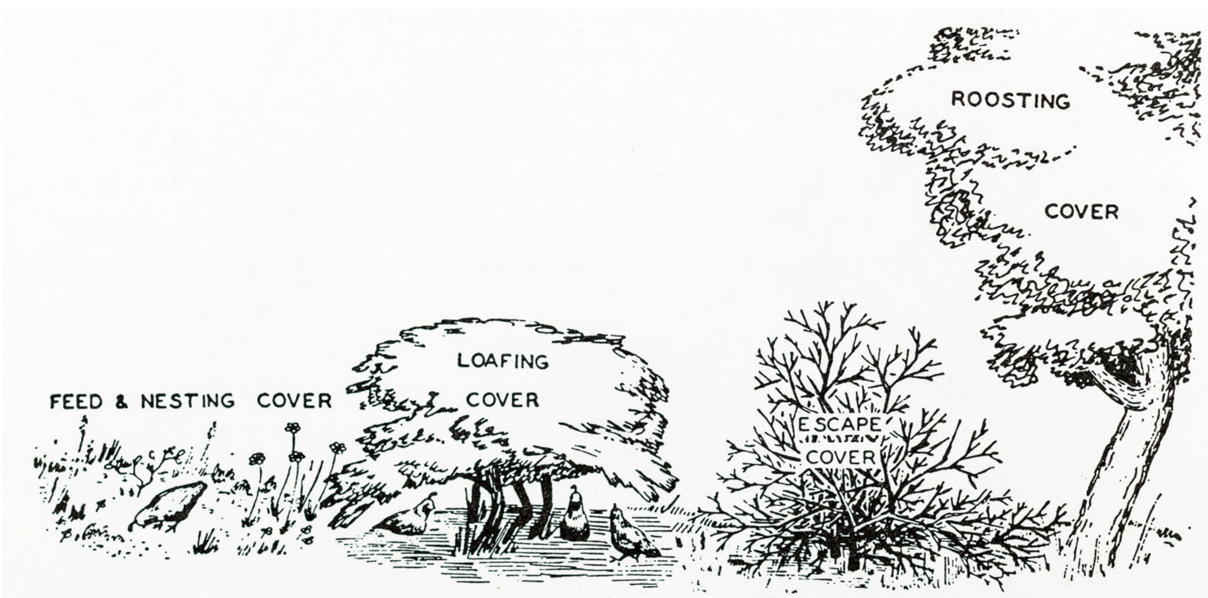
After returning to the University of Wisconsin in 1946. Curtis began research on the vegetation of Wisconsin, which became his major life's work. In 1947, articles by Braun, Cain, Egler, and Mason in *Ecological Monographs* showed movement away from Clements' paradigm, which must have set Curtis thinking about how to organize his own research. There was nothing attacking Clements in the four doctoral dissertations completed under Curtis in 1949: by Cottam, Partch, Stearns, Whitford (McIntosh 1993:97). However, the Curtis school of continuum ecology evolved from Gleason's individualistic concept, in which each species' distribution differed from other species with which it associated. Continuum studies by him and his numerous graduate students culminated in Curtis' *The Vegetation of Wisconsin* (1959, 657 pages). Curtis's legacy in American plant ecology may be comparable to that of Cowles.

Clements and Shelford's *Bio-Ecology* (1939) did not lead many other land-focused ecologists to study biomes. They continued to be primarily plant ecologists and animal ecologists. American botanists Henry Oosting (1903–68) and Rexford Daubenmire (1909–95) wrote textbooks focused on plant communities (Oosting 1948, Daubenmire 1968, Burgess 1996:34, 83). Animal ecologists could not slight plants to the same extent that plant ecologists could slight animals. In their encyclopedic *Principles of Animal Ecology* (1949), Chicago area ecologists Clyde Allee, Alfred Emerson, Orlando Park, Thomas Park, and Karl Schmidt entitled one of the five sections into which it was divided "The Community" (pages 436–597). Five of six chapters in that section were written by Orlando Park, and the sixth was coauthored by him and Schmidt.

Aquatic ecologists, whether limnologists or marine ecologists, were similar to land animal ecologists

Fig. 13 (a) Lee Raymond Dice. ESA Bulletin December 1952:cover. (b) Four types of cover needed by California Valley quail. Emlen and Glading 1945. Cited from Dice 1952:420.





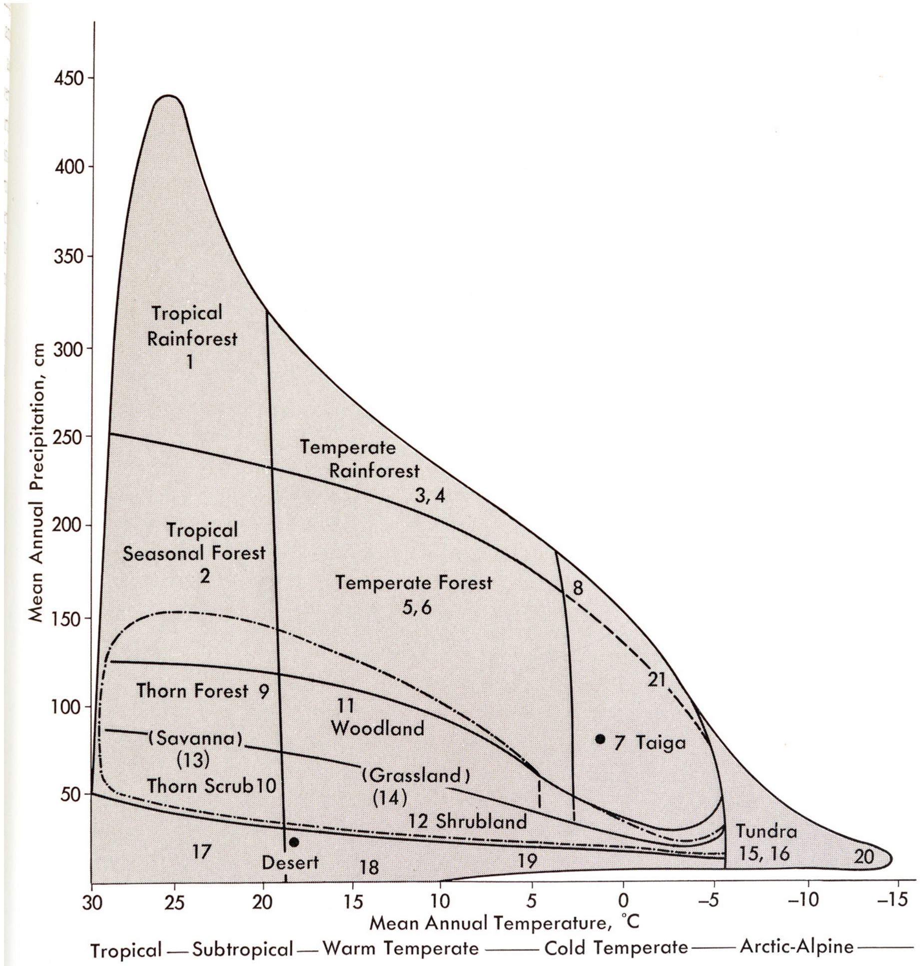


Fig. 14. World formation types in relation to climatic humidity and temperature. Not indicated are Whittaker's five hydric community biomes. Whittaker 1970:65.

in considering plants. Even when aquatic animals were more conspicuous than plants, one could not adequately discuss animal communities without also discussing aquatic plants. Franz Ruttner published in German the first edition of his *Fundamentals of Limnology* in 1940. The third edition, translated into English in 1963, devoted 101 pages to the aquatic environment and 145 pages to biotic communities, which included 70 pages on plankton, and 75 pages on vascular plants, animals, and decomposing organisms. George Reid's *Ecology of Inland Waters and Estuaries* (1961) devoted some 200 pages to aquatic environment and 130 pages to aquatic life, which subdivides into 15 pages on protista and plants, and 113 pages on animals and aquatic communities. Robert Wetzel's *Limnology* (1975) devoted 280 pages to aquatic environment, and 370 pages to plants, animals, and communities.

Professor Lee R(aymond) Dice (1887–1977) had a very peripatetic education and early job career, though he paused at the University of California, Berkeley, long enough to earn M.S. and Ph.D. degrees (1914, 1915). During summer, 1919 he finally settled at the University of Michigan, where he remained. He served as vice-president (1938) and president (1952) of ESA, and he was ESA's Eminent Ecologist for 1964, so his books undoubtedly attracted an attentive audience. One major theme in his researches was on the biotic relationships and distributions of species. His main publications on this theme were: "Life zones and mammalian distribution" (1923), *The Biotic Provinces of North America* (1943), and *Natural Communities* (1952). *Natural Communities* was a landmark synthesis. Perhaps it contained no new theoretical insights, but it was a well-organized summary of contemporary knowledge. Even so, it was only one landmark in a long slog toward consensus. Donald Strong, Jr. et al., edited *Ecological Communities: Conceptual Issues and the Evidence* (1984), which led a book reviewer to conclude (Southward 1985:872): "mechanisms underlying the structure of animal communities will not be easily revealed."

Kansan Robert Whittaker (1920–80) was son of a zoology professor, and he majored in zoology at Washburn University in Topeka (B.A., 1942), then joined the Army Air Force for 3.5 years (Westman 1982, Westman and Peet 1982, Whittaker 1994, Burgess 1996:113). He served as a meteorologist in England, and in his spare time read works by Clements, Weaver and Clements, and Shelford. He thought Shelford's book was "rather awful" (Whittaker 1994:617)—probably Shelford's *Animal Communities in Temperate America* (1913, reprinted 1937) rather than his *Laboratory and Field Ecology* (1929). Departing the Air Force, he applied to the Department of Botany, University of Illinois for graduate work. He was rejected for not having taken enough botany courses as an undergraduate. However, he was accepted by the Department of Zoology, and in March 1946 began studies under Shelford, who retired in June, and then Whittaker studied under Charles Kendeigh. However, he was influenced as much or more by Illinois plant ecologist Arthur Vestal (1888–1964), who was skeptical of Clements' concepts and instead defended those of Gleason. Whittaker was interested in Hart Merriam's life zone concept, developed for western mountains, and Kendeigh suggested studying communities in the Great Smoky Mountains for a dissertation. Whittaker agreed and studied there both insect and plant distributions and relationships. He unexpectedly confirmed Vestal's concepts, and for his dissertation only found time to work up his vegetation data, thus receiving a Ph. D. (1948) in zoology with a plant ecology dissertation, which he finally got published in 1956 in *Ecological Monographs*. He promised to his doctoral committee to work up his insect data after receiving his degree, and he published that study in *Ecological Monographs* in 1952. He was one of the few ecologists who studied both plant and animal ecology (Vestal was another).

By 1956 Whittaker was a sufficiently well known ecologist to be invited to be one of forty authors who provided articles for the Golden Jubilee Volume of the Botanical Society of America (celebrated in 1956, published in 1958). His "Recent Evolution of Ecological Concepts in Relation to the Eastern Forests of North America" (1958) follows immediately after Lucy Braun's "The Development of Association and Climax Concepts: Their Use in Interpretation of the Deciduous Forest" (1958), in which she offered mild criticism of two of Whittaker's earlier papers and praised his "Vegetation of the Great Smoky Mountains" (1956). His 1958 paper focused mainly upon a critique of Clements' vegetation units, but he also evaluated Braun's modifications of Clements' system. He concluded that her system was an improvement over Clements', but that it did not go far enough (toward Gleason).

Whittaker had a very broad vision and was a vocal critic of ecological theory. An example of his broad vision was his 230-page historical survey, "Classification of Natural Communities" (1962, 1977), which began with Humboldt and ended with Braun, Braun-Blanquet, himself, and others who published in the 1950s. Yet his penchant for criticism did not lead to his championing a particular classification system. An example of his criticism was his "Gradient Analysis of Vegetation" (1967, 2004). In it he explained that gradient analysis "seeks to understand the structure and variation of the vegetation of a landscape in terms of gradients in space of variables on three levels—environmental factors, species populations, and characteristics of communities" (Whittaker 1962:207). He thought gradient analysis had "changed the conception of vegetation as much as research on the genetic basis of variation and evolution has changed the concepts of plant species."

Whittaker's *Communities and Ecosystems* was a concise account of his understanding of these subjects by 1970. His chapters covered "Community Structure and Composition," "Communities and Environments," "Production," and "Cycling and Pollution," emphasizing terrestrial communities. He included a vegetation map of the world's lands (Whittaker 1970:154–155), with a dozen types of vegetation formations indicated. However, his list of the world's biomes amounted to 25, because he subdivided some vegetation types: two kinds of temperate rainforests, two kinds of thorn woodlands and scrubs, distinguishing between subarctic and subalpine taiga, Arctic and alpine tundra, four kinds of deserts, and five kinds of hydric communities (1970:52–64).

In 1980, shortly before Whittaker died, a ESA committee notified him that he had been chosen for an Eminent Ecologist award for 1981 (Westman 1982).

Plant ecologist Paul Keddy has argued (2007:497) that one need not assume that Gleason was entirely correct and Clements entirely wrong. Vegetation in different regions can exhibit different degrees of interdependency, and therefore the hypotheses of Gleason and Clements can themselves be seen as different positions on a continuum between randomness and structure.

Eugene Odum's textbook, *Fundamentals of Ecology* (1959, edition 3, 1971) broke new ground in discussing both plants and animals, within the ecosystem context, which will be discussed in part 57 of this history (2016).

Conclusions

The history of studies on succession, community, and continuum is primarily within the domain of plant ecology, which seems appropriate, considering that plants form 99% of the earth's biomass. It is the story of many worthy observers of nature, but with just a few who steered this science in new directions. Foremost among the earlier observers was botany professor Carl Linnaeus at Uppsala, the first theoretician in natural history since Aristotle and Theophrastos, who developed the concept of "oeconomiae naturae." A worthy successor was Alexander von Humboldt, who also collected numerous scientific data, with which he constructed a correlational science that explained how environmental factors affected species distribution. Humboldt also exerted a strong influence upon ecological botany during the remaining 1800s. Anton Kerner had undoubtedly been influenced by Humboldt, but he also went his own way in defining different communities, or formations, in a part of the Danube Valley. Edward Forbes, Karl Möbius, and Addison Verrill were marine zoologists whose researches focused upon near-shore animal communities in which animals were more conspicuous than associated plants. Danish botany professor Eugenius Warming notably provided the first comprehensive synthesis of plant ecology (1895). American plant ecologists Henry Cowles and Frederic Clements advanced the study of both plant community and succession; Clements' dogmatic pronouncements dominated for several decades, but were ultimately rejected as a paradigm. Henry Gleason and Leonty Ramensky, on opposite sides of the earth, concluded that plants species have unique requirements which determine their distribution, rather independent of other neighboring species, and therefore co-habiting species did not constitute actual communities. Neither botanist achieved a large following, but John Curtis was more successful in gaining a substantial following for the continuum concept, and Whittaker also assisted.

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