ORIGINS AND DEVELOPMENT OF ECOLOGY

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INTRODUCTION

How did ecology develop as a distinct science? What distinguished it from already existing sciences? Why did it develop when it did? Although ecologists seem largely unaware of his work [Loehle, 1987; Krebs, 2006], I will use two concepts developed by Charles S. Peirce (1839–1914) to examine the origins and development of ecology: (1) his concept of abduction, *i.e.*, hypothesis generation; and (2) his concept of convergence. For Peirce, it is the collective judgment of a scientific community that will eventually determine which hypotheses have been sufficiently confirmed by observation and/or experiments to be accepted as beliefs. This is what he meant by convergence. An outline of Peirce's philosophy of science can be found in his two seminal essays, "The fixation of belief" and "How to make our ideas clear," which were published in 1877 and 1878, respectively, in the *Popular Scientific Monthly* [Hartshorne and Weiss, 1931–1935]. For an alternative take on the development of ecology, see Graham and Dayton [2002] who examined the evolution of ecological ideas using Kuhn's concept of paradigm shifts.

Abduction is basically guessing or conjecturing what is responsible for (*i.e.*, explains) an observed pattern. For Peirce, abduction is the only mechanism that produces new knowledge or insight, and he proposes a number of characteristics that make hypotheses plausible, including consistency with already confirmed hypotheses, simplicity, and generality. What were the abductions that resulted in the development of ecology? What was so novel about them that they could not be accommodated by existing sciences?

For Peirce, the scientific community's evaluation of the correspondence between the observations predicted by an abduction (hypothesis) and the actual field or experimental observations resulting from studies designed to test the hypothesis determines if a hypothesis has been confirmed or not. Thus critical scrutiny by the scientific community results in an increasing or decreasing probability that a hypothesis has been confirmed. Hypotheses that have been repeatedly confirmed eventually become beliefs. Ecology, like any other science, is ultimately a set of beliefs. In effect, convergence toward a set of confirmed hypotheses and the elimination of unconfirmed hypotheses are the marks of a mature science. Convergence

is scientific progress for Peirce. Has there been a convergence in ecology? Does it have a well confirmed and universally accepted set of hypotheses?

It is my claim that a new abduction or novel hypothesis that falls outside the scope or form of those in existing sciences can trigger the development of a new branch of science. When novel hypotheses are proposed that do not conform to the kinds of hypotheses that scientists perceive to be relevant to their discipline, they can respond in three basic ways: (1) they ignore such hypotheses, at least in the short term; (2) they expand the boundaries of an existing science in order to accommodate them; or (3) they begin to develop a new branch of science based on them. For a new branch of science to develop, a new abduction must be not only novel but scientifically productive. In the case of ecology, it must be applicable to a wide variety of geographic situations and/or to many kinds of organisms and thus be potentially relevant to many biologists and other scientists. In this chapter, I am specifically concerned with identifying and characterizing those abductions that triggered the development of ecology as a distinct discipline and that established its initial research agenda. I will also briefly examine the role of convergence in ecology.

It is not my claim that *only* novel abductions will lead to the development of a new science. For example, many scientific disciplines that overlap with ecology (forestry, fisheries biology) or subdisciplines of ecology developed because of the common interest of a group of scientists in some organism, *e.g.*, plants (plant ecology) or insects (insect ecology), or some natural system, *e.g.*, lakes (limnology), grasslands (rangeland ecology) or wetlands (wetland ecology). In some cases, these overlapping disciplines, *e.g.*, forestry, became organized prior to ecology.

There were also many hypotheses that were already well established prior to the development of ecology that were simply assimilated by early ecologists because they were relevant to their interests [Park, 1946]. A good example of such a hypothesis is that population sizes of organisms are always limited by predation, disease, starvation, etc. As Charles Darwin (1809–1882) emphasized in *The Origin of Species* [1859], the various factors that control population sizes are responsible for natural selection [Stauffer, 1960]. By the first-half of the nineteenth century, the first mathematical models of human population growth had already been developed such as the geometric growth model of Thomas Robert Malthus (1766–1834) and the logistic growth curve of Pierre-Francois Verhulst (1804–1849); the latter emphasized that there was an upper limit to the size of human populations. The Darwinian hypothesis of natural selection and hypotheses about population regulation were both important hypotheses that were assimilated into ecology, but they were not the novel hypotheses that triggered the development of ecology. In short, early ecologists continued to accept and utilize hypotheses that they had acquired as part of their training in botany or zoology.

Ecology is known to be polyphyletic [McIntosh, 1985]. Most early ecologists were trained primarily as botanists and zoologists. Thus plant- and animal-oriented ecologists were usually hired and housed in different university departments or research institutes [McIntosh, 1985; Kingsland, 2005]. Some pioneer ecol-

ogists were primarily interested in terrestrial systems (forests, grasslands) while others were interested in aquatic systems (initially primarily oceans and lakes). The later division is largely due to the different techniques used to sample the dissimilar organisms that dominate terrestrial (vascular plants, mammals, birds, insects, etc.) and aquatic (algae, aquatic invertebrates, fish, etc.) systems. Some of the earliest scientists who are now recognized as proto-ecologists include oceanographers like Edward Forbes (1815–1854) because of his studies on marine benthic invertebrates and limnologists like Francois-Alphonse Forel (1841–1912) because of his studies on Lake Léman (=Lake Geneva) [Acot, 1998a; Elster, 1974; McIntosh, 1985]. Geographic influences also had some bearing on the polyphyletic nature of ecology. Oceanographers were, not surprisingly, found at institutions on or close to a coast while early terrestrial ecologists, at least in the United States, were at institutions in the Midwest (especially in Nebraska and Illinois) about as far from any ocean as it is possible to get in North America. Consequently, the novel ideas that triggered the development of ecology would arise more or less simultaneously in a number of different disciplines and locations.

In this chapter, I will specifically address five questions concerning the origins and development of ecology: (1) What were the novel abductions or hypotheses that set ecology apart from existing sciences? (2) What was the origin or inspiration of these hypotheses? (3) How much have these initial hypotheses affected the subsequent development of ecology? (4) Who exactly constituted the community of pioneer ecologists? (5) How much convergence towards a consistent and widely accepted set of hypotheses has occurred? To keep the task manageable, I will restrict myself to the very earliest stages of the development of ecology in the nineteenth and early twentieth centuries in Europe and North America and to an examination of a limited number of hypotheses concerning topics identified by pioneering ecologists as central to ecology. For more detailed historical accounts of the origins of ecology, see Worster [1977], McIntosh [1985], Acot [1988, 1998a], Cittadino [1990], Golley [1993], Hagen [1992], Kingsland [1985; 2005], and Egerton [2008]. The original works of early ecologists can be easily accessed through compilations such as Kormondy [1965], Egerton [1977], and Acot [1998a].

1   WHAT WERE THE NOVEL ABDUCTIONS OR HYPOTHESES THAT SET ECOLOGY APART?

It is possible to identify the core interests of pioneer ecologists by examining the contents of early ecology texts. Because I am focusing on the origins of American and British ecology, Charles Elton's [1927] *Animal Ecology*, one of the first animal ecology textbooks, and Frederic E. Clements [1907], *Plant Physiology and Ecology*, an early plant ecology text, were selected. Elton [1927] covers topics such as environmental factors limiting growth, distribution of organisms, community organization, food chains, and succession. Clements [1907] covers much the same ground, but he emphasizes the importance of plant adaptations to various environmental conditions for understanding their distribution. This reflects his reliance

on late nineteenth-century German physiology and ecology texts for much of the material in his book. Why and how did pioneer ecologists develop an interest in these topics (limiting factors, adaptations and distribution, community organization, food chains, and succession)? I will examine in some detail each topic to determine if an interest in any of them developed because of a novel hypothesis. From here on, any novel hypothesis that triggered the development of ecology will be designated a "defining" hypothesis to distinguish it from other novel and established hypotheses that ecology assimilated more or less unmodified from other scientific disciplines.

1.1   Factors Limiting Growth

Justus von Liebig (1803–1873), whose studies of plant nutrition were made possible by early nineteenth-century advances in chemistry in Germany, proposed what has become known as the law of the minimum in 1840: plant growth is limited by that required nutrient whose supply in the soil is least adequate [Blondel-Mégrelis, 1998, pp. 311–313]. Liebig stressed that the soil has only a limited supply of available nutrients and that nutrients removed from the soil due to the harvesting of plants by man or by domestic animals like cows and sheep can eventual limit the growth of these plants unless these nutrients are replaced. The basic concept of a soil nutrient budget and nutrient cycles were established in the 19th century by Liebig and other European scientists who recognized that the store of soil nutrients is limited, that plants are nutrient pumps that reduce the stocks of nutrients in the soil, that animals obtain their nutrients from plants that they eat, and that the return of nutrients to the soils is through litter decomposition and that this could take a long time. Liebig and other soil scientists of his era were largely concerned with maintaining soil fertility at levels needed for the growth of crops by farmers.

Liebig's novel hypothesis was that plant growth is a function of the amount of the most limited nutrient present in the soil, regardless of what it is. In other words, plant growth can be stunted by an inadequate level of just one nutrient even if all the other nutrients and requirements for growth like water, light and air and soil temperature are at optimal levels. This and his other discoveries put agriculture on a more scientific basis and stimulated the use of fertilizers to restore the fertility of crop fields. Liebig's hypothesis was not so radical, however, that it resulted in the development of ecology. What is striking about Liebig's work and those of his fellow nineteenth-century soil and crop scientists is that early ecologists would ignore their major findings and insights about limits to primary production, nutrient budgets, litter decomposition, and nutrient cycling for nearly a century. Liebig was, in effect, a proto-ecosystem ecologist. There are some echoes of Liebig's ideas about the importance of nutrient limitations and cycles in the later part of the nineteenth and early twentieth century among scientists studying freshwater and marine systems, who in hindsight are considered to be proto-ecologists. For example, Francois-Alphonse Forel describes in some detail the carbon cycle in Lake Léman [Acot, 1998b, pp. 163–164].

The idea that the growth of organisms can be limited by the absence of only one necessary factor was eventually taken up and expanded by animal ecologists to provide a framework for explaining animal distributions. In a 1911 paper and in his 1913 book *Animal Communities in Temperate America*, Victor Shelford proposed a generalization of Liebig's hypothesis in the form of his law of tolerance: an organism can only persist or remain in a given environment, which is characterized by a complex set of physical and chemical factors, if all these factors are within the tolerance range of that organism and, if any one factor exceeds its minimum or maximum tolerance, it will fail in that environment. Shelford's law of tolerance had a profound impact on the development of animal physiological ecology [Feder and Block, 1991]. It is this reformulation of Liebig's hypothesis to explain plant and animal distribution that first found its way into ecology.

Although the law of the minimum was a novel hypothesis when proposed by Liebig and it was eventually taken up by ecologists, it was not a defining hypothesis of ecology. If it had been a defining hypothesis, ecology would have begun to develop many years earlier than it did and it would have been much more focused in the nineteenth century on primary and secondary production and nutrient cycling than it was.

1.2   Adaptations and Distributions

During the 19th century, Germany was the major center for advances in all aspects of botany, not just crop production and nutrition. Major advances were also made in plant anatomy/morphology and many areas of plant physiology such as water relations [Cittadino, 1990]. During this period, German botanists had access to the best and latest technology, especially high resolution microscopes, and German physiologists benefited from rapid advances in analytical chemistry. In reaction to earlier, more speculative botanical theorizing that was largely based on vitalism and idealism, German botanists were the first to begin to apply more rigorous "scientific" or mechanistic approaches to the study of plants. Prior to 1850, botany in Germany, as elsewhere in Europe, had been largely descriptive studies of plant tissues and cells, classificatory studies of plant species, and descriptive studies of plant distribution. Among the last, one of the most influential was Alexander von Humboldt's (1769–1859) *Essai sur la géographie des plantes* [1805–1807] in which he emphasized that botanists should study the physical factors that control plant distribution. This largely descriptive and correlative approach to plant geography reached its ultimate form in August Grisebach's (1814–1879) *Die Vegetation der Erde nach Ihrer Klimatischen Anordnung*, a two volume set published in 1872. (Nicolson [1996] provides a excellent overview of European plant geography during the nineteenth century and the development of several different European schools of vegetation studies.)

Establishing mechanistic relationships between plant adaptations and plant distributions began in the mid-1870s with the anatomist/morphologist Simon Schwendener (1829–1919) and his students as well as other German botanists [Cit-

tadino 1990]. Schwendener's work established that morphological and anatomical adaptations had physiological consequences for plants. Gottlieb Haberlandt (1854–1945), one of Schwendener's students, published his *Physiologische Pflazenanatomie* in 1884. In it, he stressed that to understand plants you had to study the functions of their tissues and organs. Plants have to exploit and cope with their environment. What adaptations do they have to do this? Haberlandt introduced Darwinian thinking about natural selection into botany. In his book and other writings, Haberlandt provided mechanistic explanations, putatively the result of natural selection, for functional adaptations of plants. His emphasis on natural selection and how it produced plant adaptations to environmental conditions stimulated an interest in the study of plants and their environments where they naturally grew. Haberlandt, like many German botanists in the late 19th century, began to travel outside of Germany, and in 1891–1892, he traveled to the Indo-Malaysian tropics to study the adaptations of leaves of tropical plants.

Georg Volkens (1855–1917), who like Haberlandt was a student of Schwendener and who was also interested in the ecological significance of plant adaptations, conducted a study of the anatomical-physiological adaptations of desert plants in Egypt. This study was undertaken because Schwendener had proposed that plant adaptations to environmental conditions could best be studied under extreme climatic conditions. Volkens' book *Flora de ägyptisch-arabischen Wüste* [1887], although more focused on taxonomy than ecology, is among the first scientific works that could be described as ecological. In retrospect, he himself viewed it that way "...[my book] helped found and develop a special discipline of botany, the ecology of plants." (quoted in Citadino [1990, p. 66]. Volkens' book, however, was of minor significance compared to those shortly to be published by Andreas Schimper and Eugenius Warming.

Because of his travels in the Caribbean in 1881–1882 to study epiphytes, Andreas F. W. Schimper (1856–1901) began to recognize that factors other than plant adaptations to environmental conditions like light, temperature, and moisture were responsible for the distribution of epiphytes on Caribbean islands, including distance from the continent, ocean and wind currents, and bird migration patterns. On a later trip to Brazil, he studied the interactions of ants and trees. The ants protect the trees from other herbivores and in turn are supplied with food by the trees in the form of special structures at the base of their leaf petioles. In 1898, Schimper published, *Pflazengeographie auf physiologischer Grundlage*. There is a strong natural selection-adaptationist slant to his book. As the title implies, Schimper stressed the importance of plant physiological adaptations for understanding the distribution of plants. There are 170 pages on environmental factors (temperature, soils) and other factors (animals) as well as 600 pages on the relationships between plants and environmental conditions. In effect it is one of the first ecology textbooks. The first so-called ecology text, however, was written by Eugenius Warming (1841–1924) who is often recognized as the founder of plant ecology. Warming was a Dane who was trained in Germany. In 1895, he published a book in Danish, *Plantesamfund*, which was quickly translated into German as

Lehrbuch der ökologischen Pflanzengeographie; eine Einführing in die Kenntniss der Pflanzenvereine [Warming, 1896], and eventually into English much modified as the *Oecology of Plants* [Warming, 1909].

The novel hypothesis developed by Schwendener and his students that plant adaptations to environmental conditions can explain plant distributions was a defining hypothesis of ecology. This hypothesis is the central hypothesis of both Schimper's and Warming's books. Botanists who saw the implications of this hypothesis quickly began to do studies of plant distribution from a physiological perspective all over the world. These were the first ecologists. The rapid adoption of this defining hypothesis in the United States is reflected in the establishment in 1903 of the Desert Laboratory in Tucson, Arizona, by the Carnegie Institution of Washington. The primary focus of studies at the new Desert Laboratory was the physiological basis for the distribution of desert plants [Craig, 2005]. The new field, however, was still trying to decide on an appropriate name [McIntosh, 1985]. Most early plant ecologists viewed what they were doing as an extension of plant physiology [Clements, 1905; 1907]. In the 1890s and early twentieth century, however, ecology began increasingly to be viewed and described as a new field distinct from the established fields of plant physiology and plant geography.

1.3   Community Organization

A second novel hypothesis that became a defining hypothesis for ecology was proposed in a paper on ways to improve oyster cultivation by Karl August Möbius (1825–1908). Over-exploitation had led to a decline in oyster and mussel beds off the German coast, and Möbius was charged with studying the feasibility of promoting oyster and mussel farming. His studies resulted in Möbius proposing that an oyster bank is a biocönose (biocenose) or social community by which he meant "a community of living beings where the sum of species and individuals being mutually limited and selected under average external conditions of life, have, by means of transmission, continued in possession of a certain definite territory." (English translation in 1880, p. 723 [Acot 1998a, p. 228] of Möbius [1877, p. 76]). When environmental factors are altered or new species invade, the composition of the biocenose or community changes and a new equilibrium community develops. He also points out that the over-exploitation of a target species can result in its extinction locally from a community and its replacement by other species. "If in a community of living beings the number of individuals of one species is lessened artificially, then the number of mature individuals of other species will increase." [Möbius, 1880, p. 726]. In fact Möbius had introduced the same idea under a different name, "Lebensgemeinschaft" or "life community", in an earlier publication [Acot, 1998b, p. 156].

Möbius' novel hypothesis is not that organisms are found in communities or that there are species interactions within these communities. These were already well established concepts. His novel hypothesis is that, because of their interactions, species in a community are in dynamic equilibrium with each other and

thus form a stable community. The community will remain unchanged as long as nothing disturbs this dynamic equilibrium. This hypothesis in less explicit form, the balance of nature, can be found in earlier natural history writings often more as a theological than an ecological concept [Egerton, 1973] but it is also found in Darwin [1859] as resulting from the "struggle for existence" among organisms. Möbius' claim is that this equilibrium occurs even at the scale of a square meter or less. Another formulation of this hypothesis was proposed in 1887 in the writings of another early ecologist, Stephen Forbes (1844–1930). Forbes [1887, pp. 86–87], in his most famous and influential paper, "The lake as a microcosm", views a hypothetical lake as being a microcosm in equilibrium and that this equilibrium is the result of interactions among the organisms, particularly predator-prey interactions. "The interests of both parties [prey and predator] will therefore be best served by an adjustment of their respective rates of multiplication, such that the species devoured shall furnish an excess of numbers to supply the wants of the devourer, and that of the latter shall confine its appropriations to the excess thus furnished." "We see that there is a close *community of interest* between these seemingly deadly foes." Forbes views this community as being a product of natural selection. As with Liebig's studies of nutrients in soils, the studies of aquatic communities by Forbes and Möbius can also be viewed as precursors of ecosystem ecology. However, their preoccupation with explaining distribution patterns of organisms made pioneering ecologists overlook the functional implications of the Möbius-Forbes hypothesis.

The Möbius-Forbes hypothesis that organisms are found in communities that are in, or tend toward, equilibrium is one of the defining hypotheses in ecology. It introduced into ecology a more holistic perspective that has had a profound impact on its development. Nevertheless, like the German physiological ecologists, who wanted to provide mechanistic explanations for plant growth and plant distribution, Möbius and Forbes seemed to envision that it is mechanistic species interactions that result in a community tending toward equilibrium. Disputes about the nature of communities and community equilibrium, however, would dominate much of plant ecology in the first half of the twentieth century, especially when theories about the development of equilibrium communities (succession) began to be proposed [Worster, 1977; McIntosh, 1985]. See section 1.5.

1.4   Food Chains

The concept of food chains was already established prior to the development of ecology [Egerton, 2007]. Darwin's *The Origin of Species* [1859] described a now-famous food chain in rural England: red clover, bumble bees, field mice and cats. More detailed studies of food chains were done later in the nineteenth century by Stephen Forbes who studied the importance of aquatic invertebrates in fish diets and published a monograph on the topic, *The Food of Illinois Fishes* [1878]. His data were derived primarily from studies of fish stomach contents. He similarly studied the diets of birds in order to discover whether their predation of insects

was beneficial to farmers or not [Croker, 2001]. From these studies, Forbes began
to understand the central importance of food (energy) in ecology because this
was one key link between plants and animals and among animals themselves.
However, Forbes and his contemporaries never quantified their studies of food
(energy) uptake.

Closely related to the Möbius-Forbes hypothesis, especially Forbes' version of
it, was a novel hypothesis about energy losses along food chains proposed by the
German zoologist, Carl Gottfried Semper (1832–1893), who worked primarily in
the Philippines. Semper [1881, p. 52] hypothesized that inefficiencies in the trans-
fer of energy from one feeding or trophic level (plants, herbivores, carnivores) to
another limited the number of organisms at each feeding level or, in other words,
limitations in energy transfer were a major factor controlling the types of species
and their abundances in communities. Semper proposed a hypothetical commu-
nity in which there were only 1,000 units of plant food and that only 10% of this
food could be transferred to herbivores. This means that this community can only
sustain 100 units of herbivores. Assuming the same transfer efficiency from her-
bivores to carnivores (only 10%), this community could only sustain 10 units of
carnivores. It was Semper's novel hypothesis that a community like Forbes' micro-
cosm is structured in large part by energy losses from one trophic level to another
and that this limits the number of herbivores and carnivores in any given area. In
effect, Semper had interjected thermodynamics into ecology. Although Semper's
trophic hypothesis in the form of the pyramid of numbers was popularized by Elton
[1927] and it strikingly presages Lindeman's [1942] trophic-dynamic hypothesis, it
was not one of the defining hypotheses of ecology. Although it is closely related to
the Möbius-Forbes community-equilibrium hypothesis, Sempers' hypothesis had
little impact on late nineteenth and early twentieth century ecology. The ineffi-
ciencies in energy transfer along food chains that Semper highlighted would not
become relevant to ecologists until the latter half of the twentieth century when
ecosystem energetics became a major research agenda. Like Liebig, Semper was
ahead of his time.

1.5   Succession

Initially ecologists were concerned primarily with trying to explain spatial patterns,
i.e., plant and animal geographic distributions. Nevertheless, many observers had
noted that temporal changes in vegetation or succession often occurred locally
[Clements, 1916; Acot, 1998]. Clements [1916] reviewed the early literature on
succession and found numerous descriptions of temporal changes going back to
the seventeenth century. (See also Egerton [2009] for a recent review of succession
studies.) A couple of examples will illustrate the character of these observations.
The French writer Dureau de la Malle (1777–1857) in 1825 published a paper
primarily on crop rotation that describes the succession of species in forests and
meadows. He concludes that changes in plant species "est une loi générale de
la nature" [Acot, 1998, p. 130]. Likewise, Henry David Thoreau (1817–1862) in

1860 gave an address on "The succession of forest trees" in which he describes changes in forest vegetation that he had observed in New England [Spurr, 1952]. Thoreau "recognized the effects of wind-throw and fire in the forests found by the original European settlers, and distinguished between successional trends in small clearings, following cutting, following single fires, and as a results of agricultural use" [Spurr 1952, p. 426]. Such observations, however, had little influence on early ecologists. Although Warming [1895, 1896] had previously described the phenomenon of succession and even postulated some rules that govern it, the studies of succession that most influenced the development of ecology were those of Henry Chandler Cowles (1869–1939). Cowles described succession, more correctly a chronosequence, in the sand dunes along the south shore of Lake Michigan in a series of papers published in 1899. (For a detailed account of Cowles life and works, see Cassidy [2007].) Cowles was able to place the vegetation types observed into a crude chronological sequence because the dunes became older as you moved inland from Lake Michigan. He interpreted this chronosequence as a putative successional sequence from pioneering dune to mature forest vegetation. Cowles describes the various kinds of vegetation found in the dunes in considerable detail, but he does not hypothesize much about the patterns observed beyond noting that physiographic (landscape) position and dune age are correlated with vegetation types. In short, Cowles' study is transitional in that it focuses primarily on the distribution of vegetation types and only secondarily on temporal changes. It was the temporal dimensions of his studies, however, that were to have the most lasting influence on the development of ecology in the twentieth century [McIntosh, 1985; Cassidy, 2007]. Early animal ecologists, most notably, Victor Shelford (1877–1968) quickly picked up the concept of succession first from Cowles and later from Frederic E. Clements [Croker 1991].

In 1917, Frederic E. Clements (1874–1945) published a massive monograph on succession in which he proposed another defining hypothesis of ecology: succession is the development of a climax formation [Clements, 1916]. A climax formation (a vegetation type defined by the growth form of its dominant species, e.g., deciduous trees) was in equilibrium with its climate and thus was able to persist until the climate changed. A formation is for Clements an organism that "arises, grows, matures, and dies." In short, a climax formation has both an ontogeny and phylogeny just like an individual plant. Like the ontogeny of a plant, succession is directional and irreversible (progressive in Clements' words). Nevertheless, Clements also recognized that succession was much more "complex and obscure" than the development of an individual plant and his descriptions of specific vegetation changes are often highly mechanistic. In short, Clements' novel hypothesis is that a climax formation is a "super-organism" and that its ontogeny is the result of succession. Clements makes the claim that there is a strong but not perfect analogy between an individual organism and a formation. Nevertheless, he seems to be making a metaphysical claim that there is a level of biological organization, the climax formation, above the species level and that formations have characteristics, e.g., an ontogeny, similar to those of individual organisms.

In Chapters 1 and 2 of *Bio-Ecology* [Clements and Shelford 1939], one of Clements' last major works, Clements and Shelford review various hypotheses about the nature of communities and defend in considerable detail Clements' hypothesis that communities are "complex" organisms (formerly super-organisms). In this work, Clements and Shelford now call the endpoint of succession a "climax community" rather than a climax formation. "One of the first consequences of regarding succession as the key to vegetation was the realization that the community ... is more than the sum of its parts, that it is indeed an organism of a new order" [Clements and Shelford, 1939, p. 21]. They continue "... it is essential to bear in mind the significance of the word "complex" in this connection, since this expressly takes the community out of the category of organisms as represented by individual plants and animals" [p. 21]. They try to clarify their definition of complex organism again by analogy and state that it bears "something" of the same relation to the individual plant or animal that "each of these does to the one-celled protophyte or protozoan". In other words, the formation is a real entity, but one that is not as integrated as a higher plant or higher animal. Not surprisingly, the exact metaphysical status of Clements' complex or super-organism is still being debated [Eliot, 2007].

According to Clements, ecology is fundamentally a holistic science [Clements 1935]. The Möbius-Forbes hypothesis about communities tending toward equilibrium had holistic overtones, but it did not necessarily imply that communities are metaphysically distinct entities. Clements' critics like Henry Gleason [1917], who saw communities as groups of overlapping populations of species, believed that Clements confused change [*e.g.*, in species composition] with development. Nevertheless, Clements' novel succession/super-organism hypothesis was to be one of the most important defining hypotheses in American ecology in the first half of the twentieth century [Worster, 1977; McIntosh, 1985; Kingsland, 2005].

1.6   Defining Hypotheses

Only three of the topics emphasized in early ecological texts seem to have had their origin in defining hypotheses: the adaptation-distribution, community equilibrium, and succession/super-organism hypotheses. The law-of-the-minimum hypothesis of Liebig and the trophic-limitation hypothesis of Semper were not influential enough in the nineteenth century to require a new discipline, although both would eventually play a major role in shaping ecological thinking and research agendas in the second half of the twentieth century. Many other hypotheses were assimilated unchanged by pioneer ecologists from existing disciplines, *e.g.*, various hypotheses about factors controlling populations sizes in animals.

2   WHAT WERE THE ORIGINS OR INSPIRATIONS OF THESE DEFINING HYPOTHESES?

In general early ecologists acknowledged to only a limited extent the sources or inspirations for their hypotheses. In the case of the adaptation-distribution hypothesis, however, a number of its sources are obvious and are acknowledged by its originators. These include the studies of various plant geographers [Coleman, 1986; Nicolson, 1996] and Darwin's *The Origin of Species*, especially through Darwin's influence on German morphological/anatomical studies, which began to focus on the functional significance of plant adaptations [Cittadino, 1990]. As noted, many of these nineteenth century German scientists were also reacting against the vitalistic and idealistic biology that had dominated German biological thought in the early nineteenth century. Consequently, the adaptation-distribution hypothesis which developed when plant physiology and plant geography began to overlap, was formulated as a mechanistic/reductionistic hypothesis.

Some aspects of the origins of Möbius' concept of the biocoenosis have been examined by Nyhart [1998]. Based primarily on an examination of Möbius earlier writings and his professional activities, Nyhart concludes that the concept of an equilibrium community was shaped in large part by his teaching, previous research on marine fauna, civic experiences, and work with culturing marine organisms in aquaria. What Möbius did in his 1877 monograph on oysters was to propose a Greek neologism, biocönose, to make his hypothesis of a living community in equilibrium appear more significant and profound to the scientific community of his day. What is missing from Nyhart's account of influences on Möbius is an assessment of the general intellectual milieu in which he worked.

Hagen [1992, pp. 4–7] has pointed out that Forbes' concept of the microcosm seems to be based on Hebert Spencer's (1820–1903) evolutionary philosophy. Spencer proposed that all things in the universe are a product of evolution. For Spencer evolution always involves the transformation of the homogenous into the heterogeneous and progress toward heterogeneity is inevitable at all levels of organization from the molecular to cosmological (see Freeman [1974] for more detail about Spencer's philosophy of evolution). However, evolutionary progress need not be continuous. Spencer believed in a "moving equilibrium." For Spencer equilibrium is the result of a temporary balance of the forces of evolution and dissolution. In the case of biological systems, external forces, *e.g.*, changes in environmental conditions, can result in dissolution. Changes in environmental conditions, for example, can have an adverse effect on the production of plants. This in turn will adversely affect the herbivorous animals that depend on these plants for food and this will affect the predators and parasites of the herbivores and so on. Internal evolutionary forces, in this case the development or acquisition of morphological structures that enable the plants to cope with the new environmental conditions, will result in the establishment of a new equilibrium. Although Spencer was interested primarily in human societies, his ideas about the nature and development of human societies are not only reflected in Forbes' community equilibrium hypoth-

esis, but even more so in Clements' succession/super-organism hypothesis.

In a paper entitled "The Social Organism" [1860], Herbert Spencer outlined how human societies developed much like organisms. He admitted that this organic analogy was not exact, but that there were many similarities between the development of organisms and societies. Worster [1977, p. 212] and Tobey [1981, pp. 64–85] point out that Frederic E. Clements was familiar with the works of Spencer. He discussed Spencer's ideas with his colleague Roscoe Pound and Spencer's work is cited in *Bio-Ecology* [Clements and Shelford, 1939, p. 24]. Moreover, Tobey [1981] makes the point that both Herbert Spencer and the pioneer American sociologist, Lester Frank Ward (1841–1913), both of whom conceived of human societies as super-organisms, influenced Clements, but that this conception can also be traced back to German idealistic plant geographers like Oscar Drude (1852–1933). More than any other pioneer ecologist, Clements was conscious, if perhaps only in hindsight, of his intellectual influences. Spencer's ideas of inevitable progress and moving equilibrium seem to be the philosophical underpinnings of Clements' concept of succession. In his *Principles of Biology*, Spencer [1898–1899] states that evolution is responsible for the increasing integration of the plants and animals and their increasing mutual dependence on each other. Spencer's increasingly integrated assemblage as Worster points out bears a strong resemblance to Clements' climax formation. Clements *et al.* [1929, p. 314] quote from Spencer's writings: "Spencer has discussed the concept of the social organism with special clarity, and the student of community development can still turn with great profit to his treatments of this theme [1858, 1864]. It is both interesting and suggestive to find that he anticipated certain axioms of plant succession by the statements 'Societies are not made but grow' and 'Man may disturb, he may retard or he may aid the natural process of organization [development], but the general course of this process is beyond his control.'" Thus it seems that Herbert Spencer and his evolutionary philosophy played a major role in the development of both the equilibrium community and the closely related succession hypotheses.

Prior to the nineteenth century speculations about human societies had been part of philosophy [Tucker, 2002]. Spencer's writings as well as those of other early sociologists like Henri Saint-Simon (1760–1825) and Auguste Comte (1798–1857) provided early social scientists and ecologists with concepts and terms for describing social groups and the development of such groups, particularly the organic analogy between the organization of human societies and organisms [Hagen, 1992]. There were many interactions between early ecologists and sociologists. For example, the sociologist E. A. Ross and Clements were at the University of Nebraska at the same time and, according to Ross' biographer Gross [2002], Clements and Ross became friends at Nebraska and they continued to correspond for several decades after both left Nebraska. Clements' contacts with sociologists were strong enough that he had several papers [*e.g.*, Clements 1935, 1943] published in social science treatises. Clements [1905, p. 16] actually has a short section in his textbook, *Research Methods in Plant Ecology*, on sociology in which he notes that plants and humans are subject to the same "laws of association." In turn,

Clements and other early ecologists influenced the development of some schools
of sociology, particularly the "human ecology" of R. D. McKenzie. McKenzie's
[1943] *Readings in Human Ecology* has selections from the writings of a number
of American and British ecologists: plant communities (W. B. McDougall), ani-
mal communities (Charles Elton), competition (Clements, Weaver and Hanson),
plant dominance (McDougall), and animal dominance (C. C. Adams). By the
mid-1920s, the tables had turned and sociologists were now looking to ecology
for inspiration; for example, the development of human societies is now being
compared to Clements' succession/super-organism hypothesis [McKenzie, 1924].

3   HOW MUCH HAVE THESE INITIAL HYPOTHESES AFFECTED THE SUBSEQUENT DEVELOPMENT OF ECOLOGY?

All three defining hypotheses to this day continue to shape ecological thought and
research agendas as is illustrated in many of the other chapters in this book and
numerous books on the history of ecology [Worster. 1977; McIntosh, 1985; Acot,
1988; Hagen, 1992; Golley, 1993; and Kingsland, 1985; 2005]. Both plant [Lam-
bers *et al.*, 1998] and animal [Feder and Block, 1991] physiological ecologists have
continued to study the physiological significance of adaptations and their utility
for understanding plant and animal distributions. Their techniques and tools have
become more sophisticated but the core topics that dominate these fields today
would be familiar to their nineteenth and early twentieth century predecessors.
The long-lasting impact of this approach can be seen in comparing major mono-
graphs on aquatic plants: Agnes Arber's *Water Plants* [published in 1920], C. S.
Sculthorpe's *The Biology of Aquatic Vascular Plants* [1967], and Julie Cronk and
Siobhan Fennessy's *Wetland Plants* [2001]. Although all three books cover many
aspects of the morphology, taxonomy and ecology of aquatic plants, anatomical
and morphological features (adaptations) that control their distribution within and
among wetlands are a central focus of all three. Because organisms have to cope
with more than just their physical environments, by end of the nineteenth cen-
tury, the inadequacies of the adaptation-distribution hypothesis had already been
noted by Schimper. Consequently, topics like chemical defense mechanisms against
predators or pathogens and adaptations to disturbances became more prevalent
in the twentieth century. This defining hypothesis, however, continues to be in-
fluential. This general approach to understanding and predicting the distribution
of plants and the composition of plant communities gained new life in the works
of J. P. Grime [1979]. He emphasized the importance of three kinds of plant
adaptations: to environmental conditions (stress), to periodic disturbances, and
to competition.

Whether communities actually are in, or tend to, equilibria as proposed by
Möbius and Forbes is still being debated by ecologists. Prior to World War II,
this was primarily in the form of a debate about Clements' holistic and Gleason's
reductionistic ("individualistic") hypotheses about the nature of plant communi-
ties (associations) [McIntosh, 1985, pp. 263–267]. One attempt to resolve this

debate was made by Arthur Tansley [1935] who proposed the term "ecosystem" as a less extreme holistic formulation of communities (associations) than that proposed by Clements. Tansley's ecosystem has much in common with Möbius' biocenose. During the middle years of the twentieth century, this debate about the nature of communities sparked a series of field studies by plant ecologists, most notably Robert H. Whittaker (1920–1980) [McIntosh, 1985]. These studies collectively resulted in what Simberloff [1980] called the "materialistic and probabilistic revolution" in ecology that overthrew Clements' succession/super-organism hypothesis, at least among plant community ecologists. However, the debate about the nature of communities did not end. In the 1960s and 1970s, the debate over the equilibrium theory of island biogeography of MacArthur and Wilson [1967] was another version of it, primarily among animal ecologists, and this sparked a secondary debate about the role of competition in structuring communities. Its most recent incarnation has been the debate over biodiversity and community or ecosystem stability [Naeem, 2002]. This version of it began in the 1970s and then re-emerged in the 1990s [McCann, 2000].

Although Clements' succession/super-organism hypothesis was quickly challenged by H. A. Gleason [1917; 1926] and others, Clements' holistic claims about the nature of communities and succession were and continue to be immensely influential in ecology as has been well documented in Worster [1977], Simberloff [1980], McIntosh [1985], Hagen [1992], Golley [1993], and Kingsland [2005]. By the middle of the last century, a new succession theory began to develop among plant ecologists based on the individualistic hypothesis of H. A. Gleason. Glenn-Lewin *et al.* [1992] provide a detailed treatment of post-Clementsian succession theory. Nevertheless, Clements' succession/super-organism hypothesis has not been completely abandoned. In E. P. Odum's paper "The strategy of ecosystem development," he reformulated Clements' hypothesis about succession as a hypothesis about ecosystem development [Odum, 1969]. Among ecosystem ecologists it continues to have traction [Golley 1993] and applied ecologists (see section 5).

4   WHO EXACTLY CONSTITUTED THE COMMUNITY OF PIONEER ECOLOGISTS?

Ecology was proposed as the name for a discipline that was needed but did not exist by Ernst Haekel (1834–1919) in 1866. Haeckel was inspired by the chapters in Darwin's *Origin of the Species* on the Struggle for Existence and Natural Selection to propose that a new science was needed to investigate what regulates population sizes of organisms and allows them to co-exist in nature's economy. Haeckel defined the proposed new science of ecology thus (as translated in Stauffer [1957]): "By ecology, we mean the whole science of the relationship of organism to environment including, in the broad sense, all the 'conditions for existence.'" In reality, the term ecology did not begin to be used until nearly 30 years later after its spelling was Anglicized to ecology at the 1893 meeting of the AAAS in Madison, WI. Initially, the term "oecology" was introduced to distinguish field studies in plant physiology

from laboratory studies, only the field studies were designated ecological. Rapidly other types of related field studies, such as studies of community composition and succession, became recognized as ecological studies. Thus the most important common denominator among early ecologists was their field orientation. Ecology was to be the study of nature in nature, *i.e.*, in the field, not the laboratory.

Although Darwin, Haeckel, and even Clements viewed humans as part of nature, Clements and Shelford [1939] pointed out that early ecologists were trained almost exclusively in botany and zoology departments and thus they concentrated on studies of plant and animal species. As consequence, ecology was "generally hostile or indifferent" to the study of man. The lack of interest by ecologists in human societies was also due in large part because sociology and economics were already established academic disciplines when ecology began to "crystallize" [McIntosh, 1985] in the late nineteenth and early twentieth centuries. Thus initially the community of ecologists was a small group primarily of botanists and zoologists with an interest in plant and animal distribution, animal population regulation, native plant and animal community composition, and succession. It was not till the first couple of decades of the twentieth century that there were enough people who viewed themselves as ecologists that they could form their own societies and establish their own journals. The first such society was the British Ecological Society (BES) which was established in 1913. Its inaugural meeting was attended by fewer than 50 people and by 1917 its total membership was only around 100 people [Sheail 1987]. The Ecological Society of America (ESA) was founded in 1917 and had about 300 inaugural members. A decade after its establishment, the Ecological Society of America had around 600 members and the British Ecological Society in 1930 had about 450 members [McIntosh, 1985, p. 161]. Early ecologists were finding it increasingly difficult to get their ecological studies published in existing journals. Consequently, one of the major motivations for establishing (and later for joining) these new societies was that they would publish a journal. The first ecological journal, *Journal of Ecology* (BES), began publication in 1913 and the second, *Ecology* (ESA), in 1920.

In spite of their small numbers, from the beginning ecologists were splintered into many subgroups (plant ecologists, animal ecologists, limnologists, marine ecologists, etc.) and the ecological community overlapped with many already existing scientific communities like foresters, fisheries biologists, geographers, soil scientists, etc. This is well illustrated in a survey of the disciplinary interests of the inaugural members of the Ecological Society of America [Burgess, no date]. Although plant and animal ecology were, not surprisingly, the most common disciplinary areas (57% of its members), nearly 40% of the ESA's inaugural members indicated that their primary disciplinary interest was not ecology (Table 1). Forestry and entomology were fairly common disciplinary interests of non-ecologists, and geology, climatology, soil physics and animal parasitology were the major interest of a few inaugural members. Over time, the number of subgroups in ecology has actually increased dramatically with the proliferation of national ecological societies and increasingly more specialized groups of ecologists focusing on some kind of vegeta-

tion (*e.g.*, tropical forest ecology), ecosystem (*e.g.*, wetland ecology) or application (*e.g.*, restoration ecology). Different groups of ecologists often emphasize different hypotheses. In the early twentieth century, for example, plant ecologists tended to focus on studies of plant distribution and succession while animal ecologists focused more on population regulation.

Table 1. The primary disciplinary interests of the inaugural members of the Ecological Society of America, adapted from Burgess [no date].

Discipline	Members	Percent
Plant Ecology	88	29%
Animal Ecology	86	28%
Forestry	43	14%
Entomology	39	13%
Marine Ecology	14	5%
Agriculture	12	4%
Plant Physiology	7	2%
Plant Pathology	4	1%
Climatology	4	1%
Geology	4	1%
Animal Parasitology	3	1%
Soil Physics	3	1%
TOTAL	307	100%

5   HOW MUCH CONVERGENCE TOWARDS A CONSISTENT SET OF HYPOTHESES HAS OCCURRED?

Peirce's philosophy of science relies on a community of scientists to judge how compellingly hypotheses have been confirmed. As has been noted by many authors (*e.g.*, [Peters, 1991]), there has not been in ecology the convergence toward a universally accepted and integrated set of hypotheses along the lines suggested by Peirce. Allen and Hoekstra [1992] made an attempt to unify ecology using hierarchy theory, but they did so by expressly not dealing with the reductionistic and holistic dichotomy among ecological hypotheses: "We will not rely on assertions that any ecological entity is real in an ultimate sense" [Allen and Hoekstra, 1992, p. 14]. There are many possible reasons for the lack of unity in contemporary ecology, including the relatively young age of the field, the historical and geographical contingencies of most aspects of ecology, and the multiple levels of

organization (organisms, populations, communities, landscapes, etc.) at which ecologists work. It seems to me, however, that two important and overlooked factors are (1) problems with the formulation of some defining hypotheses and (2) the lack of a uniform community of ecologists.

Peirce stressed the importance of avoiding ambiguous terms in hypotheses. Of the three defining hypotheses, the first, the adaptation-distribution hypothesis, was not ambiguously formulated, but its importance was overstated by pioneer ecologists. The Möbius-Forbes hypothesis of community equilibrium is ambiguous because neither Möbius nor Forbes defined precisely what they meant by "equilibrium" and they were vague about the ontological status of their biocenoses and microcosms. They both suggested, however, that underlying mechanistic interactions among species would result in the development of a community in which all the species would be mutually limited in abundance. They also overstated the importance of their hypothesis because they failed to take into account the importance of ubiquitous disturbances, both abiotic and biotic, on community composition and species abundances that were subsequently documented [Botkin, 1990; Glenn-Lewin *et al.*, 1992; Johnson and Miyanishi, 2007]. Even Clements was somewhat ambiguous about the true nature of plant formations. His detailed accounts in his *magnum opus*, *Plant Succession* [Clements, 1916], of various factors controlling the dispersal, establishment, and growth of plant species during succession are very mechanistic [Tobey, 1981; Eliot 2007]. Clements' main hypothesis is the succession/super-organism hypothesis and he defended it repeatedly [Clements, 1916; 1936].

Because Clements' claim that succession represents the ontogeny of climax formation is based on an organic analogy, it is necessary to examine the logic of analogies in order to evaluate it. An analogy is a proposed correspondence between two things in some respect [*e.g.*, structure, function] that are otherwise dissimilar. All analogies are of the general form: **A** is like **B**; **A** has property **P**; Therefore, **B** has property **P**. A hypothesis derived by analogy is only as reliable as the assigned property (P) on which it is based [Juthe, 2005]. The organic analogy, in which a climax formation (target subject) is said to be comparable in some respect (assigned property) to an individual organism of some kind (analogue) is an example of a different-domain-analogy [Juthe 2005]. For such cases, assigned properties can only be validly projected from the analogue to the target subject if each of the elements of the analogue which determine the assigned property corresponds one-to-one with counterpart elements in the target subject. Assigned properties that meet this requirement are called projectible. When analogies are based on non-projectible assigned properties, *i.e.*, the assigned property of the analogue has no exact counterpart in the target subject; the analogy is false. For example, birds and bats are both group of vertebrates that fly; birds lay eggs; therefore, by analogy bats must also lay eggs. This obviously false analogy is based on a non-projectible property, in this case egg laying. Unlike birds, bats do not have the morphological and physiological means to produce eggs. Hence egg laying is not a projectible property.

Organisms are complex entities whose constituent cells, tissues and organs interact to produce identifiable, self-replicating units. Clements believed that climax formations are also highly complex assemblages in which the constituent species interact in a variety of ways to produce identifiable, self-replicating units (climax formations or communities). Organisms (the analogue) undergo development (ontogeny); they develop in a predictable sequence from fertilized eggs to mature individuals. It is development, defined as ontogeny, a known characteristic of organism, which is the assigned property in the analogy. The climax formation, the target subject, by analogy must also undergo ontogenic development, *i.e.*, succession is an ontogenic process with a defined endpoint. The features of the analogue, however, that are responsible for its development, *i.e.*, primarily its genes, have no exact counterparts in a climax formation. According to Clements the overarching controls of succession are macro-climatic conditions. In other words, the organic analogy is false because development (ontogeny) is not a trait that is projectible from organisms to plant formations. Plant formations can change significantly over time for a variety of internal and external reasons, including disturbances and inter-annual fluctuations in environmental conditions [van der Valk, 1985; 1992], but the responses to these changes are not controlled or limited by some internal feature of the climax formation analogous to genes. Their lack of truly ontogenic development suggests that Clements made a category mistake when he hypothesized that formations are some kind of organism as was first suggested by Gleason [Gleason, 1917].

Meaningless, ambiguous and false hypotheses, however, are expected to occur in any science and according to Peirce will eventually be rejected or modified by the scientific community when these hypotheses fail to be confirmed by observations. This assumes that there is a unified community of ecologists who will determine whether a hypothesis has been confirmed or not. As noted, hypotheses such as Clements' succession/super-organism hypotheses have been investigated and rejected by twentieth-century plant community ecologists because their field observations did not confirm its predictions [Whittaker, 1975; Simberloff, 1980; McIntosh, 1985; Botkin, 1990]. The existence of many subgroups in ecology, however, allows hypotheses like Clements' succession/super-organism hypothesis to persist in other subgroups. For example, Davis and Slobotkin [2004] criticized the Society for Ecological Restoration for their outmoded (read Clementsian) ecological concepts about communities and ecosystem development (succession) in the Society's "Primer for Ecological Restoration". These "outmoded" concepts, however, were immediately defended as valid by leading members of the Society [Winterhalder *et al.*, 2004]. Quine and Ullian [1970, p. 6] point out that "Evidence for belief must be distinguished from causes of belief. Often we gather evidence to defend a belief that we already hold, while the cause of our already having held the belief is forgotten or undiscovered." This unfortunately seems to reflect to some extent the state of ecology today. Ecologists often are more concerned with collecting data to support their hypotheses (beliefs) than with critically evaluating and reconciling their hypotheses with their observations. Consequently, in the

short term, the development of a unified ecology with consistent hypotheses has not yet happened as Peirce believed that it would.

6 SUMMARY AND CONCLUSIONS

In the nineteenth and early twentieth century, abduction as defined by C. S. Peirce, produced a number of novel hypotheses that did not fall within the perceived boundaries of existing biological sciences. Some of these novel hypotheses resulted in the development of the new science of ecology. These are called its initial defining hypotheses: (1) adaptations to various environmental conditions are responsible for the distribution of organisms; (2) communities tend toward equilibrium; and (3) communities are a type of organism that develops along predictable lines (succession). Investigating the implications of these hypotheses initiated lines of field research that were different from those in established sciences like botany and zoology. Two other novel hypotheses (Liebig's law of the minimum, Semper's hypothesis about inefficiencies of energy transfer along food chains) that were proposed in the nineteenth century failed to have much impact on ecology until the mid-twentieth century. Many other hypotheses were also assimilated more or less unchanged into ecology from other disciplines.

The stimulus for the development of these defining hypotheses varied. The adaptation-distribution hypothesis developed from the realization by nineteenth-century German botanists that the physiological implications of anatomical and morphological features of plants could be used to explain the distribution of these plants that had been previously documented by plant geographers. Both the community equilibrium and succession hypotheses seem to have been inspired, at least in part, by the evolutionary theories of the influential, nineteenth-century British philosopher, Herbert Spencer.

All three defining hypotheses, but especially the adaptation-distribution and succession hypotheses, resulted in the development of major ecological research agendas in the late nineteenth and early twentieth centuries. These three defining hypotheses, however, are not logically consistent with each other. The adaptation-distribution hypothesis provides a mechanistic/reductionist explanation of the distribution of species and hence implicitly a mechanistic/reductionist explanation of the current composition and future composition of communities. The community equilibrium hypothesis and succession/super-organism hypotheses are more holistic formulations of community composition and community change. The succession/super-organism hypothesis seems to be based on a false analogy that equates the ontogeny of organisms with succession.

Peirce believed that false, ambiguous and inconsistent hypotheses would eventually be eliminated or reformulated when the scientific community compared observations made to test a hypothesis to the predictions made by it. In ecology, hypotheses have been tested and in some instances rejected by some ecological subgroups. Ecology, however, has always been composed of many subgroups and the research programs of these subgroups are focused on different hypotheses and

hence have different beliefs. Because subgroups are often intellectually isolated from each other, hypotheses rejected by one subgroup can continue to be held by other subgroups. Peirce predicted that a unified community of scientists would eventually eliminate inconsistent hypotheses by comparing predictions to observations. This elimination or reformulation has not occurred as predicted in ecology because, in large part, ecologists are still not a unified community.

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