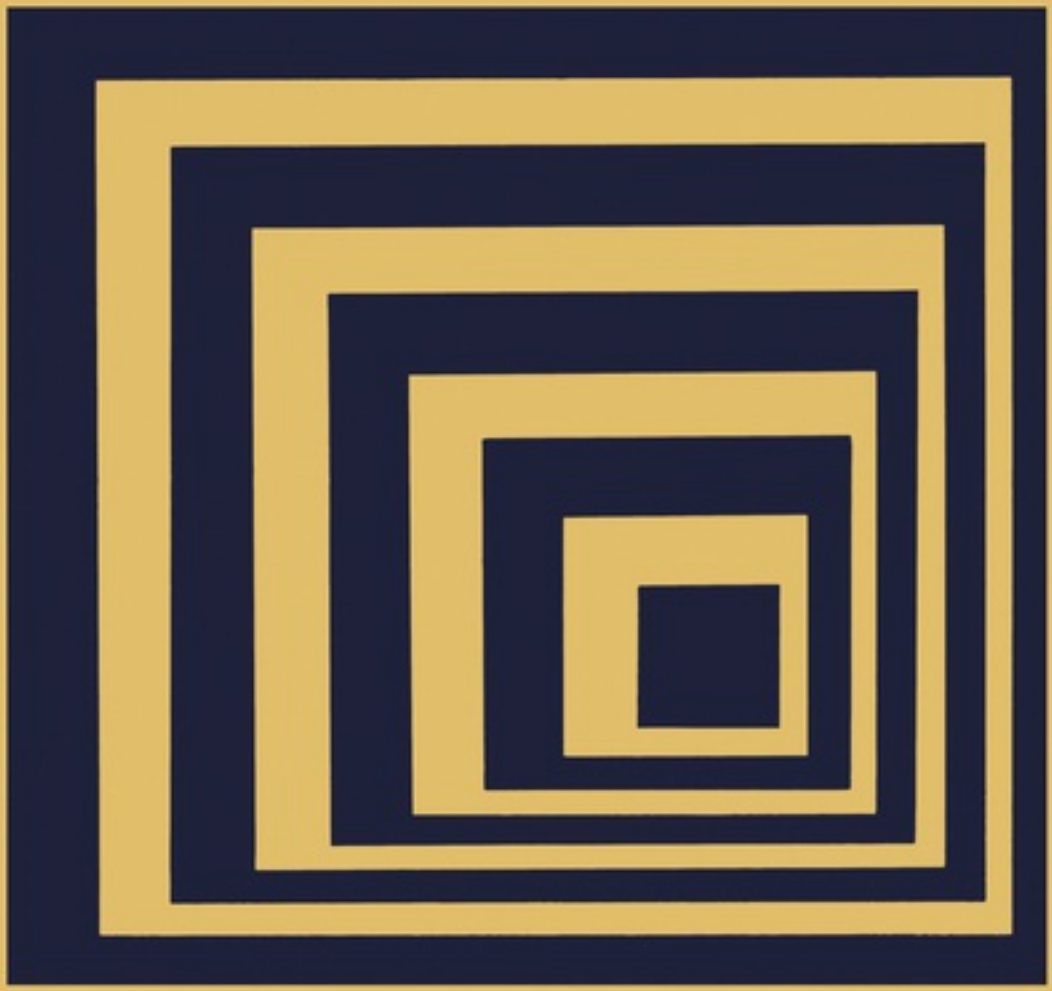
CAMBRIDGE STUDIES IN ECOLOGY

THE BACKGROUND OF ECOLOGY

CONCEPT AND THEORY

ROBERT P. McINTOSH



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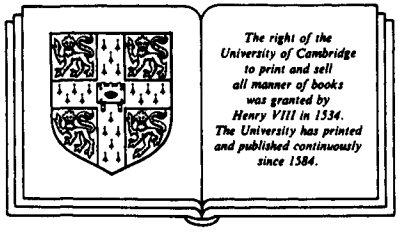

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For Joan

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Preface

An attempt to write a general account of the origins, development and current problems of ecology, even within the constraints noted below, might well be thought foolhardy. Ecology built upon traditions of natural history beginning in classical antiquity but developed as a science in the context of late 19th-century biology, natural history surveys, and conservation. It became widely known to the general public, often in distorted forms, only in the 1960s. It has been called polymorphic because it appeared and continues in numerous and different forms appropriate to the enormous variability and complexity of the things studied by ecologists. Until recently, ecology has not excited the interest of historians of science, and detailed historical studies of ecology or biographical works about ecologists are few. This volume was not, however written to fill the need for careful historical analyses of ecology and its relation to biology and to environmental concerns, although it leans heavily on those now available. It is an attempt to provide an account of the background of ecology and suggest its relevance to current problems of ecology as a science. It has an underlying assumption that some of the difficulties and conflicts now manifest in ecology can be better resolved if ecologists, particularly younger ecologists, become familiar with what went before them and their mentors and outside their immediate interests. Ecologists should be free of what one ecologist described as the "tyranny of the present," not simply because knowledge of past events is interesting but because ignorance of the past makes for redundance at best and confusion at worst. It is likely that the hope of enhancing understanding of current ecology influenced my selection of materials and contributes to the shortcomings of this book from a historian's viewpoint.

Because of limitations of space, sources, and the author, the present account of ecology is largely that which has been called Anglo-American ecology. Continental sources, influences, and parallels are noted, particularly where they were cited by British and American ecologists. However, it would be vainglorious to attempt an overview of ecology

at large. At best, it may be hoped that the present volume will achieve a beginning of a general account of ecology and its sources. It does not pretend to be definitive even within its geographical boundaries. Because ecology developed from rather separate traditions of plant, animal, freshwater, and marine ecology, the organization of the book is, in some degree, comparative. It attempts to follow developments in each of these somewhat isolated areas and, where possible, to identify parallels or convergences. The aim is to consider methodological, conceptual, and theoretical attributes developed in, or shared by, the several disparate sources of ecology, and no effort is made to review the enormous body of empirical ecological work.

The several chapters have a rough chronology, although strict chronology is not consistently followed. In the hope of suggesting the connectedness of ideas and different times, reference may be made, on occasion, to earlier or later events and comments. Chapter 1 is essentially a review of ideas expressed about the sources of ecology before it became a recognized science. Chapter 2 considers the emergence of ecology from the 1890s to 1915, ending with the creation of formal ecological societies. Chapters 3, 4, and 5 backtrack to the largely 19th-century beginnings of their respective topics and extend to the 1950s. Chapters 6 and 7 include more recent developments of ecology and extend from the 1920s and 1930s nearly to the present. Chapter 8 links ecology and the conservation movement of the early 1900s and ecology and the environmental movement of the 1960s and 1970s. Because the subject matters of the chapters overlap, some redundancy is unavoidable.

The scope of the book required that it be based almost entirely on published material. An effort has been made to cite and quote references where ecologists, and others, comment about ecology and their views of ecology as a science and its methodological and epistemological problems rather than the empirical substance of ecology. Unfortunately, it was not generally possible to provide extensive biographical data or the fascinating personal and anecdotal material which normally enlivens or disgraces scientific discourse. It may be hoped that ecologists will find in the book, and in the literature cited, materials useful in gaining an understanding of the sources and nature of ecology and its relation to other aspects of biology and environmental concerns. If the book also leads ecologists to identification with their predecessors and to their contemporaries in other aspects

of ecology, so much the better. It will be sheer lagniappe if historians, sociologists, and philosophers of science find in it some points of departure which encourage them to extend their own investigations to include ecology.

Notre Dame, Indiana Robert P. McIntosh

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R. P. McI.

1

Antecedents of ecology

Ecology in its early years was sometimes decried as not a science at all but merely a point of view. After nearly a century of trying to erect a conceptual, methodological, and theoretical framework for the most complex phenomena encountered in nature, ecology was familiar only to a relatively small number of academic biologists and applied biologists, range managers, foresters, and fishery and game managers. These shared an overlapping, but not coincident, network of concepts, methodologies, professional associations, publications, funding sources, and concerns about the relations of organisms as populations and communities to their environment. In the wake of widespread recognition, in the 1960s, of the "environmental crisis," ecology was abruptly thrust into the public arena and widely hailed as an appropriate guide to the relation of humans, as well as other forms of life, to their environment. Strikingly, ecology became a watchword, even in high political circles, just when Paul B. Sears, one of its most articulate practitioners and expositors, described ecology as "a subversive subject" (Sears 1964). Sears's point was that the view of nature derived from ecological studies called into question some of the cultural and economic premises widely accepted by Western societies. Chief among these premises was that human civilizations, particularly of advanced technological cultures, were above or outside the limitations, or "laws," of nature (Dunlap 1980b).

Although ecologists had long asserted that ecological science was significant in offering insight about, and to, human societies, they were ill prepared to cope with the abrupt seizure of the name and its extension to include all aspects of environmental concern, often leaving behind ecological concepts and canons of evidence which had been developed over the decades. Ecology was, and is, a science which does not fit readily into the familiar mold of science erected on the model of classical physics, and it deals with phenomena which frequently touch very close to the quick of human sensibilities, including aesthetics, morality, ethics, and, even worse in some minds, economics. Ecology

suffered more from some of its admirers and friends who sometimes misinterpreted or overextended its competence than from its critics. The concepts and methods of ecology, at best a polymorphic science, were often lost in the extension of the term to incorporate almost any idea, or ideal, concerning the environment taken as meritorious by some group. The large body of hard-won knowledge gained by ecologists which afforded some of the best evidence of the environmental crisis and promising guides for dealing with it was often bypassed, or even distorted, to support ill-founded "ecological" panaceas. Ecology was not, and is not, a predictive science, but ecologists knew a lot more than they were able to bring to the attention of those who made major decisions affecting the environment of humans and other organisms. One of the continuing difficulties of ecology is that its sources and boundaries are difficult to specify and this problem has been exacerbated in recent years. One ecologist, perhaps in desperation, wrote that ecology is what ecologists do. Examination of what ecologists do, or even what "protoecologists" (Voorhees 1983) did and thought, before there was a name for them, may lead to a better understanding of what ecology is, whence it came, and what it may become.

The term *ecology* shares with the word *biology* the distinction of first appearing obscurely in a 19th-century treatise and only gradually becoming accepted as a name for a distinct and respectable science. Ecology, like biology, came to include a wide range of phenomena which had been pursued since antiquity under different rubrics and philosophies of nature. The coinage of *biology* is variously attributed, Karl Friedrich Burdach apparently being the earliest to use it in 1800 (Baron 1966; Coleman 1977; Farber 1982). Lamarck, another of the earliest users of *biology* in 1802, believed that it was a new theory of living organisms (Farber 1982); and Treviranus, who used *biology* in 1802, described it as "the philosophy of living nature" (Burdon-Sanderson 1893). Ecology was similarly to be regarded as having portent for life and philosophy. Coleman (1977) wrote that it took a century for biology to progress from "a hopeful term" to a "vigorous and autonomous science by 1900." Ecology progressed slowly from the coining of the word by the eminent German zoologist Ernst Haeckel in 1866 to a recognized and vigorous science (ca. 1920), although it took a century for ecology to become widely familiar outside professional circles in the 1960s, and questions about its autonomy and maturity as a science persist today (McIntosh 1976, 1980a).

Some historians of science regarded 19th-century biology as dis-

tinctly different from, and more significant than, natural history or as even excluding it (Coleman 1977). Biology, in this view, concentrated on functional aspects of individual living organisms and became, according to Coleman, essentially synonymous with physiology in the 19th century. It may come as a surprise to many biologists that Farber (1982) believed it necessary to urge historians of science to recognize that natural history did not fade away in the 19th century. In fact, as Farber and most biologists know, natural history proliferated in the 19th century, fragmenting into separate disciplines to accommodate the deluge of new information about the kinds and properties of living organisms, their activities, and distribution. Darwinian evolutionary theory, largely a product of natural history, was the major intellectual achievement of 19th-century biology. Farber wisely urged parity in the significance of the developments of physiology and natural history in the 19th century and their continuance into 20th-century biology. This is certainly appropriate for ecology, which is an amalgam of both.

The terminological problems of biology and ecology are evident in the various interpretations given them. Biology had, late in the 19th century, acquired what Stauffer (1957) described as an "arbitrarily restricted" usage. Instead of being equivalent to physiology, as Coleman (1977) stated, biology had come to mean "what is now included under ecology," a usage commonly deplored by biologists (Boerker 1916). Haeckel, according to Stauffer, introduced the word *ecology* as a substitute for this limited meaning of biology, freeing *biology* for its more appropriate use as a general term including botany and zoology in all their forms. Ecology was described by Haeckel as a part of physiology (Smit 1967) and, as late as 1891, he felt it necessary to specify that "the terms biology and œcology are not interchangeable" (Haeckel 1891). J. S. Burdon-Sanderson (1893), in his presidential address to the British Association for the Advancement of Science, made ecological history by elevating "œcology" to one of three natural divisions of biology, equivalent in rank to physiology and morphology. He added that "œcology" represented, more than other branches of biology, Treviranus's "philosophy of living nature."

Ecology was seen by Haeckel and many 19th-century biologists as simply a branch of physiology; and two of the founders of American plant ecology, F. E. Clements and H. C. Cowles, perhaps for reasons of academic politics, described it as identical with physiology (Cittadino 1980; McIntosh 1983a). Other early animal ecologists described ecology as the "new natural history" (Adams 1917) or "scientific nat-

ural history" (Elton 1927). Many ecologists regarded their science as an extension of traditional natural history, which emphasized study of whole organisms in the field, in contrast to the emphasis on laboratory studies, which developed in 19th-century biology. Some of the newer breed of ecologist deplore the continuing blend of natural history in current ecology, which they believe makes it unnecessarily complex and necessarily unscientific (Peters 1980). Other ecologists assert that it is the very complexity of the natural phenomena it studies which is the essence of ecology and question the desirability, or feasibility, of molding ecology in the tradition of the mechanistic, reductionist science of the 19th century (Odum 1977).

A transformed natural history

Natural history in the 17th and early 18th centuries had been concerned with description of naturally occurring phenomena. It was defined by John Harris in *Lexicon Technicum,* a reference current in the early 1700s:

> Natural history is a Description of any of the Natural Products of the Earth, Water or Air, such as Beasts, Birds, Fishes, Metals, Minerals, Fossils, together with such Phenomena as at any time appear in the material world; such as Meteors etc. (Lyon and Sloan 1981:2)

Natural history in the Baconian and Aristotelian tradition consisted of describing individual facts of nature, forming a systematic classification of these facts, and from this generating empirical laws. Ecology, as it developed in the late 19th and early 20th centuries, was commonly criticized for adhering to observation, description, and an inductive approach to science. V. M. Spalding (1903), for example, stated an extreme inductionist position:

> At present it is really the main business of the ecological student to ascertain and record fully, definitely, perfectly and for all time the facts. He is not bound to tell us what they mean.

Other ecologists, such as W. F. Ganong (1904), acknowledged the criticisms of ecology as descriptive and emphasizing observation and facts. He called for a new method of experimental study and logical proof in place of "speculative yokings of conspicuous effects with prominent possible causes."

Some historians of science believe that descriptive natural history had already been transformed in the 18th century into "history of nature"

(Lyon and Sloan 1981). According to Lyon and Sloan, the initiation of a new scientific program by this transformation provided an alternative to the physical sciences, which had dominated 17th- and 18th-century science, and had "profound implications for the philosophical directions of 19th-century science." This transformed natural history, they argued, was the "historical root of modern evolutionary biology, biogeography, ecology." That root, they said, was imbedded in the attributes of "quality," "process," "historicity," and "concreteness" as opposed to "quantification," "mechanism," "rigorous deductive analysis," and "mathematical abstraction," the latter being the attributes which characterized the scientific revolution of the 17th century. Natural history was changed from "mere" description of facts into a set of scientific disciplines with their own methodology, ontology, and epistemology, distinct from the physical sciences, as the result of the work of natural scientists, such as Buffon, Hutton, and Lamarck, among a complex of other figures of 18th-century philosophy and science. Lyon and Sloan described this transformation as "in many respects as great an intellectual event as the scientific revolution of the seventeenth century." This assessment of the origin of a group of disciplines including ecology and its major associates evolutionary biology and biogeography as being "away from the physicist's paradigm" contrasts sharply with recent widespread assertions that ecology must move to conform to the 20th-century paradigm of science, erected on the "hard" physical sciences, if it is to attain "maturity" as a rigorous, deductive, mathematical, theoretical science (McIntosh 1976, 1980a; Cannon 1978; Rehbock 1983).

Lyon and Sloan (1981) asserted that the transformation from description of nature to a genuine historical understanding of nature as a temporal process, interpreting nature as a dynamic process rather than a static, nontemporal mechanism, was initiated by a radical change in natural history in the late 18th century, notably in the work of Buffon. Not all historians of science concur in this interpretation of the role of Buffon in the transformation. Oldroyd (1980) wrote of the work of Linnaeus and Buffon, "Although temporal change was envisaged, there was no historical inquiry into the earth's past, and its former organisms." It is striking that the qualities listed by Lyon and Sloan as distinguishing the new natural history of the late 18th century – quality vs. quantification, process vs. mechanism, concreteness vs. deductive abstract analysis, and historical vs. ahistorical explanation – are essentially those which are at the heart of much discussion about recent ecology in its own transformation following World War II.

Coleman (1977:160) said that 19th-century biologists lost interest in historical explanation:

> As biologists focused even more intently on problems of organic function they transferred their allegiance from the ideal of historical explanation . . . to the promise extended by the experimental investigation of vital processes.

The antipathy of some current ecologists to historical explanations and the reciprocal antipathy of others to a reductionist experimental approach in ecology is anticipated in the transfer Coleman suggests in 19th-century biologists, but the difference Coleman describes was more a separation of interest among biologists than a transfer (Mayr 1982). The distinction between historical and ahistorical explanation in ecology is still evident in current discussions of ecology. R. C. Lewontin (1969a), for example, recognized two groups of ecologists: (1) those who study ergodic[1] properties which are invariant and involve no historical considerations, and (2) those who study properties which are not invariant in time and which involve historical considerations. Some current theoretical ecologists introduced mathematical models, such as the Markov chain, which involve an assumption of time invariance and the absence of historical effects. Traditional ecologists generally assumed historical sequence to be the essence of ecology. Cowles (1901) wrote, "A plant society is not a product of present conditions alone, but the past is involved as well"; and Spalding (1903) urged Charles Darwin as the model for ecologists: "He would formulate a law not so much to express a present reaction as a habit and a history." *Ergodic* came into the ecological lexicon with the flush of theoretical ecology in the 1960s and even then was used sparingly. The question for ecologists is: Are there any ergodic properties in ecological phenomena?

What is ecology?

As ecology achieved high visibility and even notoriety in the mid-20th century, it was frequently confounded with any concern for, or ideology about, the environment. Diverse interpretations were offered for its origins or roots, often predicated on very different ideas of what ecology is. I have chosen the neutral term *antecedents* for the title of this chapter rather than *roots* (Worster 1977), *origins,* or even *history*

[1]Ergodic: having every sizable sample statistically the same; therefore, each sample is representative of the whole.

(Klaauw 1936; Brewer 1960; Kormondy 1969; Egerton 1977b), all of which may imply direct lineal connections which are rarely demonstrated. *Antecedent* in its familiar usage simply indicates what has gone before without intimating that what has gone before necessarily gave rise to what came later. Coleman (1977) warned of the pitfalls of the assumption that temporal sequence equals causal explanation, a problem familiar to students of ecological succession. The historical connections or, in biological parlance, phylogeny of ecology is seen very differently by ecologists past and present and recently by historians of science following different canons of historiography.

After decades of benign neglect by historians, philosophers (cf. Lindeman 1940, as a rare and transient exception), and commentators on intellectual history, detailed study of the history of ecology is limited. Histories of science, even histories of biology, give it passing mention at best. Allee et al. (1949) began their discussion in *The History of Ecology* by "giving warning" of the lack of knowledge of ecology among scholars and philosophers. The intrinsically polymorphic nature of ecology as a science, the widespread distortion of its content and competence which accompanied its meteoric rise in public awareness during the period of environmental concern, or crisis, of the 1960s and 1970s, and the lack of historical studies combined to allow diverse, even contradictory, opinions to persist about the roots or origins of ecology. Hence, what I call *retrospective* ecology encounters problems in identifying roots simply because ecology is, to continue the botanical metaphor, more a bush with multiple stems and a diffuse rootstock than a tree with a single, well-defined trunk and roots. Kuhn (1970) suggested that a developing scientific discipline may represent a fusion of several separate trunks lacking a common initial rootstock, and ecology fits that model.

Ecology shares with biology, in addition to its 19th-century origin, difficulty of concise definition, although definitions are myriad. Haeckel in 1870 elaborated on his brief mention of the word in 1866 and defined *ecology* as follows:

> By ecology we mean the body of knowledge concerning the economy of nature – the investigation of the total relations of the animal both to its inorganic and to its organic environment; including above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact – in a word, ecology is the study of all those complex interrelations referred to by Darwin as the con-

> ditions of the struggle for existence. (Trans. in Allee et al. 1949:frontispiece)

This definition illustrates the common and continuing tendency of zoologists and botanists to arrogate the whole of ecology to animals or plants, respectively. Haeckel's emphasis on the relation of ecology to Darwinian evolutionary theory was explicit in the title of the work (Haeckel 1866) in which the word first appeared, and he stated the connection in the mechanistic mode of 19th-century physiology:

> Thus, the theory of evolution explains the housekeeping relations of organisms mechanistically as the necessary consequences of effectual causes and so forms the monistic groundwork of ecology. (Trans. in Stauffer 1957)

Haeckel's definition is commonly abbreviated in ecology references and textbooks as the study of the interrelations of plants and animals with their environments. The modifiers *scientific study* or *under natural conditions* are sometimes added. These succinct definitions are generally satisfactory until one pursues the specific meaning of *environment, scientific,* or *natural* as applied by diverse ecologists. Some definitions are more elusive or even "strange and interesting" (Egler 1982). A leading textbook of general ecology stated, "What constitutes 'modern' ecology depends upon the ecologist or group of ecologists to whom the question is addressed" (Smith 1980). If definitions of ecology were confined to ecologists, this might be tractable, but ecology no longer can "develop outside the distorting influences often accompanying high popularity" (Allee et al. 1949), and it is difficult to confine its use to a professional group of ecologists. One of my favorite definitions, by a psychiatrist, is this:

> Ecology may be defined as that inter-intra confrontation of biological, social and historical factors that embrace one's family, school, neighborhood, and the many overlapping communities that teach values, defenses, and offenses, the meaning of oneself and one's existence. (Hedgpeth, 1969)

Cowles (1904) had commented, "No one at this time is . . . prepared to define or delimit ecology." The same difficulty was apparent to C. C. Adams (1913:16), who wrote:

> There are also so many degrees and kinds of work that go by the name ecological, which may or may not be, and so many also which are truly ecological but which do not go under that name, that it is necessary that the student shall be able to see through its diverse guises and recognize its essential character.

The "essential character" of ecology remained unclear. Definitions proliferated as its area of interest expanded. When animal populations became a focus, ecology was simply the study of the distribution and abundance of animals (Andrewartha and Birch 1954). Later, when ecosystems came to the fore, ecology became the study of the structure and function of ecosystems (E. P. Odum 1971). It seems that since the rise of ecology to high popularity in the 1960s, almost everyone is prepared to define or delimit ecology and, having done so, to say whence it came and to answer the question frequently raised in the early years of ecology, What good is ecology?

Sources of ecology seen by biologists

Some biologists and early ecologists looked to classical natural history for the beginnings of ecology even as they disputed the choice of a name. Lankester (1889) asserted that Buffon called attention to "bionomics" or the interrelations of organisms (Chapman 1931). Bionomics, like "ethology," lost out to ecology in the last decade of the 19th century in the choice of a name for the then rising young science. That several names were suggested for the unformed discipline having to do with organisms and their environment indicates that the time was ripe for a new science. W. M. Wheeler (1902) (later the first vice-president of the Ecological Society of America), although he preferred the word *ethology* to *œcology* for the nascent discipline, claimed that zoological *œcology* began with Aristotle. He included Pliny and a host of pre-19th-century figures up to Buffon among "œcologists." Cowles (1904) cited as ecology Theophrastus's recognition of mangroves, their salt-water habitat, and species relationships as well as his physiognomic conception of vegetation antedating such use by Alexander von Humboldt in the 19th century. H. S. Reed (1905), in what is probably the first history of ecological work, started with Andreas Caesalpino in the 17th century and continued with Linnaeus, C. K. Sprengel's work on flower structure and pollination, and Humboldt's geographical studies of vegetation. E. L. Greene (1909), the major American student of the history of classical botany, claimed expansively, "Even from primitive times every botanist was an ecologist." He specifically credited Theophrastus with beginning synecology, because he distinguished habitat groups or communities and he described Tragus as the first autecologist and phenologist because he recognized the ecological properties of plant populations. N. Taylor (1912) examined some modern trends in

ecology which, even then, he described as "that much used and sadly misunderstood word," but looked back only to the early 19th century, as he put it, "without unearthing the more-or-less apocryphal progenitors of the idea." C. E. Moss (1913) was critical of those who linked ecology with Lamarckian ideas of evolution and vigorously denied that A. P. DeCandolle was the first ecologist because this ignored Humboldt, Linnaeus, and Tournefort. He asserted, "It is hyperbolic" to describe Darwin as "the true premier ecologist." R. Ramaley (1940) wrote, contrary to Wheeler, that Aristotle "hardly takes a place in ecology," but Theophrastus "may well be called the first ecologist in history, for he wrote, and quite sensibly too, of the communities in which plants are associated, the relation of plants to each other and to their lifeless environment." Allee et al. (1949) commented that Aristotle's efforts are not yet ecology "but do constitute good natural history, . . . a part of the study from which ecology has developed." They saw the "modern" aspect of ecology taking form in the 18th century in the work of Linnaeus and Buffon. G. E. Du Reitz (1957) cited Linnaeus for recognizing succession and producing the first real vegetation profile in the botanical literature. E. P. Odum (1964) identified multiple roots of ecology, which, he said, remained largely divergent with little theory to connect them. Andrewartha and Birch (1973) wrote, "The laws governing communities and ecosystems were thoroughly discussed . . . and much was agreed on in the writings of Reamur, Buffon and Haeckel." This would have been a notable achievement indeed, since laws, if any, governing communities are not established even today.

Many early ecologists joined Haeckel in attributing ecology to evolution by natural selection and Charles Darwin. Spalding (1903) described Darwin as "the great exponent of ecology before it had a name." Cowles (1904) also voiced this belief: "If ecology has a place in modern biology, certainly one of its great tasks is to unravel the mysteries of adaptation." Concern with evolution and adaptation was a logical extension of the Darwinian emphasis on the environment, and many ecologists stressed the effect of the environment on the development, distribution, and morphology of organisms (McIntosh 1976, 1980a).

The essential relationship of evolution and ecology is evident in current ecology. Kiester (1982) suggested that a science of evolutionary ecology provides ecology "with needed theoretical help and would advance the unity of science." Orians (1980) similarly described eco-

system ecology as aided by "basic evolutionary principles," a proposition which was the basis of S. A. Forbes's (1880a) "a priori" approach to ecological systems. Bormann and Likens (1979a) commented on a reciprocal relation in which "theories of ecosystem development are beginning to play a major role in studies of evolution." A major aspect of current ecology hopes to develop ecological theory from the life history properties of species. The species is a critical entity of evolutionary concern, and speciation is central to most evolutionary theory. Some ecologists, however, suggest that the species is not necessarily the functional ecological unit, as is often assumed (Harper 1980). Other ecologists have sought properties of organisms other than specific distinctions, even using aggregate or "macro" variables of ecological entities on which to base ecological theory.

Ecology did not, however, converge with its very nearly twin science of genetics, and many years were to pass before a hybrid science of ecological genetics came into being. John Harper (1967) complained that ecology had abandoned evolution to genetics and that theoretical genetics developed with little concern for ecology. L. B. Slobodkin's (1961) hope that the resolution of many problems would be based on "amplifications of the existing theories of population dynamics, population genetics and interspecific competition" has yet to be realized. Although E. O. Wilson (1978) claimed that ecology had been transformed by natural selection "by stark reduction," the merger of ecology, with its concern with the environment, and genetics, with its concern with variation, into a unified science remains a prospect for the future.

Sources of ecology seen by historians

Historians who considered ecology at all were similarly divided in their views of its origins and orginators. One of the first historians to comment was R. C. Stauffer (1957), who wrote, "As a source for a vital stimulus to the continuing development of ecology we must look rather to the work of Charles Darwin." Vorzimmer (1965), however, stated, "It is even slightly ironical that most modern ecologists look back to Darwin as the Father of Ecology," because, he said, Darwin had ignored the significance of his contributions to ecology. Limoges (1971) argued that an ecological viewpoint was impossible before the Darwinian concept of nature and that ecology arose when Haeckel, stimulated by Darwin, coined the word in 1866. This attitude was recently stated

emphatically by Oldroyd (1980): "Ecology in the modern sense became possible only after the establishment of the Darwinian theory." Lynn White (1967) wrote, "The crystallization of the novel concept of ecology" (ca. 1850) was forced by "the emergence in widespread practice of the Baconian creed that scientific knowledge means technological power over nature" and that it was a "union of the theoretical and the empirical approaches to our natural environment." White, like many nonscientists discussing ecology, confounded it with general environmental impacts in his comment that the first cannon manufactured in the early 14th century "affected ecology" by precipitating cutting of forests. This linkage of ecology and technology is developed in detail by Tobey (1976, 1981) in his studies of the emergence of plant ecology.

Interest in the environment and the relation of humans to it permeates mythology, history, literature, and art. A continuing problem is discerning the relation of ecology to this ubiquitous interest. Glacken saw the end of the 18th century bringing in an entirely different concept of humans' relationship to nature influenced by incipient evolutionary thought. He wrote:

> It is no accident that ecological theory which is the basis of so much research in the study of plant and animal populations, conservation, preservation of nature, wildlife and land use management, and which has become the basic concept for a holistic view of nature has behind it the long preoccupation in Western civilization with interpreting the nature of earthly environments, trying to see them as wholes, as manifestations of order. (Glacken 1967:706)

Glacken identified three major questions of Western thought: (1) Is the earth purposefully made or designed? (2) Has the environment influenced humankind? (3) Has humankind changed the earth from its pristine condition? The search for answers to these questions was based on the yearning for order and purpose in nature which pervades much of Western religion and philosophy. Throughout the 18th century, order and purpose were linked in diverse religious and philosophical traditions having in common a belief that there is a Divine Creator and/or Manager who designed and operated the cosmic order after some eternal ideal. Evidence for design and purpose was commonly seen in natural history in the order observable in celestial events and natural phenomena, including relationships among organisms, humans among them, and between organisms and their environment

(Lovejoy 1936; McIntosh 1960). Caveats such as that of Theophrastus, who suggested there is disorder in the universe and that order must be proven, not assumed, or of Epicurean philosophers who wondered about inhospitable places such as desert or Arctic wastes, were not usually heeded in the widespread acceptance of a providential view of nature or in physico-theology, which saw evidence of design in nature (Glacken 1967). Glacken's (1967) book, *Traces on the Rhodian Shore,* is a mine of observations which are clearly antecedent to ecology and which strike a chord with any ecologist. These are attributed to persons from diverse times and cultures: Herodotus on predators, St. Basil on forest succession, Jose de Acosta on the biogeographical conundrums posed by the New World, and Benjamin Franklin on control of insect pests by birds. The balance of nature, described by Egerton (1976) as "the oldest ecological theory," was evident in the writing of St. Thomas Aquinas, who in an early comment on species diversity and stability wrote, "It is better to have a multiplicity of species than a multiplicity of individuals of one species." Such observations are not roots of ecology in the biological sense of that metaphor, for it is not clear that ecology grew from them in any direct way.

Glacken identified two pervasive views of nature which were evident in traditional natural history and persist in current discussions of ecological theory (McIntosh 1976, 1980a):

1. *Mechanical:* Actions of individual parts of a whole are explained by known laws, and the whole is the sum of the parts and their interaction.
2. *Organic:* The whole exists first and its design explains the action of the parts.

Glacken also reviewed post-Renaissance conceptions of nature and saw design concepts of nature as spawning ecological theory. He wrote:

> I am convinced that modern ecological theory, so important in our attitudes toward nature and man's interference with it, owes its origin to the design argument. The wisdom of the creator is self-evident, everything in the creation is interrelated, no living thing is useless, and all are related one to the other. (Glacken 1967:243)

It is this notion of interrelatedness that Stauffer (1960) described as "Darwin's fundamental ecological insight" which permeates ecology. What differs is the explanation for interrelatedness.

Naturalists, theologians, and philosophers before and well into the

19th century commonly concurred that there is order in nature based on a divinely created harmony. The differences were largely between those who were concerned with final causes and those who would allow the possibility of secondary causes of order in nature. Buffon, for example, rejected concern with final causes in the study of nature. Natural history, he said, was concerned with secondary causes – *how* nature acts, not *why* (Lyon and Sloan 1981). Burdon-Sanderson (1893) stated that the function of the physiologist was to investigate processes, not to inquire into final causes: "His question is ever How rather than Why." Current ecologists generally avoid anything described as final cause but not "how" and "why." Calow and Townsend (1981), for example, stated that the "physiological question is *how* organisms work and the ecological and evolutionary question is *why* they work in the way they do." W. D. Billings (1980), however, saw physiology considering *why* organisms grow where they do. Application of ideas of cause in ecology has proven extremely difficult, and the classic interpretations of cause-and-effect relationships are commonly questioned (Whittaker 1953). Some present-day ecologists speak, paradoxically, of "future" causes (Allen and Starr 1982).

Glacken's book is an admirable history of the views expressed in Western culture about the environment and "man's" relationship to it. But are these to be considered ecology, and can these philosophical and natural history observations be seen as giving rise in some continuous way to ecology qualified as "modern" or "self-conscious?" Clearly these traditions were antecedent to 20th-century ecology. In what way can it be said that ecology is rooted in them? If, as Glacken suggested, pre-19th century conceptions of humankind's relation to nature were of an entirely different order than those influenced by theories of evolution, what was the nature of the transformation in 19th-century science which gave rise to ecology as a distinctive aspect of biological science (Coleman 1977)? Identifying the origins of ecology is difficult in that all definitions specify that it has to do with the relation of organisms and their environment. Humans are clearly organisms. Glacken commented that the design argument explaining the nature of environments incorporated a number of ideas and added:

> In exploring the history of these ideas from the fifth century B.C. to the end of the eighteenth century, it is a striking fact that virtually every great thinker who lived within this 2300-year period had something to say about one of these ideas, and many had something to say about all of them. (Glacken 1967:713)

It is not surprising, then, that one frequently encounters assertions that ecology, or some aspect of it, began with diverse protoecologists from classical antiquity up to the Enlightenment (Liebetrau 1973; Egerton 1976; Worster 1977). The term *protoecologist* was coined in Voorhees (1983) to describe those who had ecological insights before a formal science of ecology was formulated.

The word *ecology* and the genesis of ecology as a recognized science are clearly products of the last third of the 19th century. Several ecologists and historians converged on ecology as a logical, even necessary, consequence of Darwinian evolutionary thought and on Darwin as the premier ecologist. But Donald Worster (1977), an intellectual historian seeking the "roots of ecology" in "nature's economy," described the idea of ecology as much older than the name, and he began "its modern history" in the 18th century, before it had a name. What he saw beginning was not, however, the field of science which is professional ecology but what he described as the "larger penumbra of ecological thought," which is very difficult to define, as shadows often are. The breadth of Worster's scope of ecology is indicated by his suggestion that John Wesley wrote a volume on ecology. This elastic view of ecology is also evident in Worster's assertion that "the Age of Ecology began on the desert outside of Alamogordo, New Mexico on July 16, 1945." Such an extended vision of who is an ecologist, whence ecology came, and when it began derives from Worster's definition of ecology and conception of historical scholarship.

Worster entitled the first section of his book "Ecology in the Eighteenth Century" and wrote, "Like a stranger who has just blown into town, ecology seems a presence without a past." Worster provided that past in the form of dual origins of ecology in the eighteenth century. One source he categorized as "arcadian": the holistic organismic views represented by Gilbert White's prescient observations in his parish at Selborne, which others, including myself (McIntosh 1958a), have seen as "anticipation of ecology." Worster described this tradition as continued in the 19th century by Henry David Thoreau and John Burroughs and linked in the 20th century to the philosophical views of Alfred North Whitehead and Ludwig von Bertalanffy, the last sometimes acclaimed as the intellectual source of current work in systems ecology. Worster's alternate source was "imperial," "anti-arcadian," mechanistic ecology, which he attributed to Francis Bacon but saw primarily exemplified by the "businesslike, ambitious and enterprising Swede" Linnaeus.

Worster's typology of ecology and ecologists is criticized adversely by some historians of science (Egerton 1979b; Tobey 1981), although reviews by ecologists are more favorable (Kormondy 1978; Smith 1978). Egerton regarded Worster's types as existing only in his mind and Worster's point of view as making a good story but not conveying objective history of ecology. R. Tobey (1981:1) wrote:

> Popular writers today assume that ecology sprang from the transcendental naturalism of Emerson and Thoreau or from the preservation movement represented by John Muir and John Burroughs. Historians know this is not true.

Since Thoreau and Burroughs are among those cited by Worster as typifying his "arcadian" ecology, Worster is a popular writer but not a historian by Tobey's classification, which Worster, no doubt, would dispute. Worster assigned apparently equal significance to his "arcadian" and "imperial" sources of ecology, but gives the nod to the "arcadian" root as dominant in current ecological thought. Tobey, conversely, described "key insights making possible the scientific paradigm of the first generation of ecological research" as deriving from "utilitarian and scientific problems," clearly meaning the "imperial," hard-nosed, scientific source described by Worster.

A more detailed analysis of Worster's case for the 18th-century roots of ecology is made by Nicolson (1982a pers. commun.) and serves as a review of the meanings given *ecology*. Nicolson's critique is directed at Worster's tripartite use of the meaning of ecology and his sliding from one meaning to the other. According to Nicolson, ecology can refer to (1) the professional science of ecology in a variety of guises – marine, terrestrial, etc.; (2) the political movement or philosophy broadly incorporating a variety of environmental concerns; or (3) the relation of any organism to the environment (i.e., "its ecology"). Nicolson asserted that Worster's analysis of the roots of ecology fails because of this semantic slipperiness. The other failing which Nicolson attributed to Worster, and to Egerton (1976), is that they ignored two opposing trends in historical scholarship. Although Worster asserted that "ideas grow out of specific cultural conditions," Nicolson claimed that he traced ideas independently of their context, as if ideas transcend the circumstances of their generation. This, Nicolson said, ignores a trend in history of science stemming from T. S. Kuhn's (1970) *The Structure of Scientific Revolutions,* which emphasizes "contextural historiography" or knowledge understood within its cultural context. Linking Linnaean ideas of economy of nature, founded on a static, nonhistorical, divinely

ordered system of nature, and "modern" post-Darwinian, ecological thought is unjustified in the view of Nicolson and of such other historians as Oldroyd (1980). Nicolson and Oldroyd argue that the Darwinian "revolution" places the complex of pre-Darwinian natural history observations in a completely different context than post-Darwinian ecology. S. A. Forbes (1880a, 1887), a major proponent of scientific ecology in its formative years, emphatically expressed a post-Darwinian, balance-of-nature concept; but it is not to be placed according to the views of Nicolson and Oldroyd, in the same class as Linnaeus's economy of nature even though some of the terminology is similar. Stauffer (1960), however, saw in Linnaeus's economy of nature "a crude but meaningful presentation of ecology in its eighteenth century guise." This primitive theme, he said, reappears in Lyell and was "transmuted by Darwin into vital elements of his theory of evolution." Nicolson's advice is, nevertheless: "Do not believe there was a science of ecology in the eighteenth century, even if a historian of ecology tells you so"–counsel which makes things difficult for ecologists.

It is perhaps unfair to marshal the several criticisms of Worster's account. It is, after all, a first effort to examine the intellectual tradition of which ecology may or may not be a lineal descendant. The point is not simply to criticize a notable effort which Egerton (1979b), in spite of his own assertion that Worster's thesis "seems simplistic and wrong headed," described as "clearly an important contribution to the history of ecology." Ecologists such as F. E. Smith (1978) derived "new perceptions about ecology and ecologists" from Worster's book, and Kormondy (1978) described it as a "very worthwhile guide" to ecologists. Ecologists sorely need a guide to understanding the background of their science, but it is unfortunate if the science of ecology is conflated with diverse historical concerns with the relation between humanity and the environment and if things that have simply "gone before" are linked as if they are in a direct line of development to ecology. Worster's "arcadian" and "imperial" categories, as different ways of looking at nature in the 18th century, are acceptable on their own grounds; his argument that the "arcadian," holistic natural history of Gilbert White is continuous with, and represented by, ecology in the present needs to be proven. Current ecology, even in its limited scientific context, is a battleground between those urging a "hard science," reductionist, "imperial" approach and those arguing a holistic, organismic, if not truly "arcadian," approach. The real modern counterpart of Worster's "arcadian" ecology lies outside scientific ecology, in that

"larger penumbra of ecological thought" which came to the fore with the surge of the environmental movement in the 1960s and subjected ecology to the distorting influence of high popularity of which Allee et al. (1949) warned.

The most diligent and productive historian of ecology is Frank Egerton. In addition to numerous publications on pre-Haeckelian ventures into ecological subjects, Egerton has edited or written several salient guides to the history of ecology which are essential to anyone entering that field. Egerton (1976) wrote the most detailed outline available on protoecological studies and observations before 1900, when ecology flowered as a science. He edited (Egerton 1977a) a collection of reprinted volumes and articles ranging from the 18th-century works of William Derham (*Physico-Theology,* 1716), John Ray (*The Wisdom of God Manifested in the Works of the Creation,* 1717), Linnaeus, including his essay *Economy of Nature,* (1762), and abridged selections from Buffon's *Natural History* (1780–85), to works of 20th-century ecology such as Victor Shelford's (1913) *Animal Communities in Temperate America,* Robert Whittaker's (1962) *Classification of Natural Communities,* and his own *History of American Ecology* (Egerton 1977a), a collection of articles about the history of ecology. He also wrote *A Bibliographical Guide to the History of General Ecology and Population Ecology* (1977b), and his *History of Ecology* (1983) expands the bibliographical coverage to include plant, marine, and animal ecology, limnology, and applied ecology. The more recent bibliography is restricted to the 19th and 20th centuries, whereas the earlier one begins with ancient times.

Egerton, like Worster, takes a comprehensive view of ecology, reaching back to antiquity in his reviews, bibliographies, and articles on demography and other ecological topics. He cited as ecologists included in the *Dictionary of Scientific Biography* Leeuwenhoek, Ray, Reamur, Linnaeus, Peter Kalm, and Gilbert White. Egerton (1976) construed ecology, before its formal period, as "similar to but not identical with the history of natural history." He interpreted the Hippocratic treatise *Airs, Waters, and Places* as "opening with an explicitly ecological program of correlations between environmental conditions and sickness." Egerton described naturalists in the 18th and 19th centuries as beginning "to grope toward the organization of an ecological science." He said phenology was an early, failed candidate for the framework of an ecological theory but that "in 1749, Linnaeus had outlined an ecological science based on the economy of nature." The

identification of pre-Darwinian observations of nature as ecology is disputed by such historians of ecology as Limoges (1971), Oldroyd (1980), and Nicolson (1982a pers. commun.), as we have seen. This makes it difficult for an ecologist, who is hardly in a position to ajudicate the scholarly dispute among historians. Clearly, there are substantial discontinuities and Kuhn-type paradigm changes in 19th-century biology, but just as clearly, many natural history traditions were transmitted from Linnaeus, Buffon, and Humboldt, reassembled by Darwin in his evolutionary thought, and later integrated into scientific ecology by recognized professional ecologists. Tracing the detailed links between 18th-century natural history and 19th-century biology, as well as those among 19th-century biologists, is manifestly beyond the scope of this volume.

Who founded ecology?

One by-product of the search for the origins or roots of ecology is the frequent designation of various individuals as the founder, father, or mother of ecology or some aspect of it. Sometimes this has had a nationalistic basis, particularly as ecology came to be a highly visible aspect of science, even suggesting a new ethical approach to the relations of humans with their environment (McIntosh 1976). As Worster (1977) put it, "In our time ecology has come to represent the arcadian mood that would return man to a garden of natural peace and piety." Many would claim parentage of such an ideal.

Credit for the origin of the word *ecology* was, erroneously as it turned out, transferred from the scientist Haeckel to the "arcadian" naturalist, poet, and philosopher Henry David Thoreau. The hold that such attributions have is seen in the resurrection of this reputed coinage in *Science* magazine after it had previously been reported to be an erroneous attribution in that journal (McIntosh 1975b). Even the *Oxford English Dictionary* contains the attribution to Thoreau. Thoreau was also credited with being the father of phenology, the aspect of ecology dealing with the chronology of biological events (Whitford and Whitford 1951), although Egerton (1976) disputed this parentage. E. S. Deevey (1942) described Thoreau as being an insightful and eloquent limnologist before the term was provided by Forel. V. Gendron (1961) claimed that Humboldt "single handed created the science of ecology." He attributed Humboldt's priority to his idea of vertical zonation of vegetation based on his ascent of the peak of Tenerife

"because these observations were the ones on which he founded the science of ecology." Daniel Drake, described as "a pioneer in modern ecology" by A. E. Waller (1947), was interested in phenology, but Waller's claim is bolstered largely by Drake's consideration of disease and environment in the 1830s. Titus Smith was described by Gorham (1955) as a "pioneer" of plant ecology based on his travels in Nova Scotia in 1801-2 and his recognition of different and changing forest types. J. C. Arthur (1895) wrote, "We may call Darwin the father of vegetable ecology." H. S. Conard (1950), in the foreword to his translation of Kerner von Marilaun's book *Plant Life of the Danube Basin,* said it was "the immediate and direct parent of all later works on plant ecology." Taylor (1980) identified Victor Hensen, a German physiologist and marine biologist, as the "father of quantitative plankton ecology." George Perkins Marsh was said to be the father of American ecology for recognizing the impact of human actions on the earth in his book *Man and Nature in America* (Marx 1970). An even broader claim was made by Robert Clarke (1973), who subtitled his book on Ellen Swallow *"The Woman Who Founded Ecology."*

Ellen Swallow (Mrs. Richards) recognized many problems of the environment in an era when industrialization and modern technology were just developing some of the basis of air and water pollution and rural and urban decay which are the bane of modern environmentalists. She was a crusader for establishing a scientific basis for bettering human life. According to Swallow:

> For this knowledge of right living we have sought a new name. . . . as theology is the science of religious life, and biology the science of life, . . . so let Œkology be hence the worthiest of all the applied sciences which teaches the principles on which to found healthy . . . and happy life. (Quoted in Clarke 1973:120)

The *Boston Globe* announced in November 1892, "Mrs. Richards names it Œkology," perhaps the first appearance in the public press of Haeckel's word (Clarke 1973). Despite this promising beginning, human ecology – or sociology, as it was alternately called – was not firmly incorporated in the young science.

Maycock (1967) described the Polish botanist Jozef Paczoski as the "founder of phytosociology," a distinctive branch of ecology. Morton (1981), following the lead of many plant ecologists, including H. C. Cowles and Arthur Tansley, wrote, "Plant ecology is usually considered to begin with the publication of E. Warming's *Plantesamfund*

in 1895." Warming's claim to paternity was reopened recently by Goodland (1975), who claimed that "his contribution remains unacknowledged." Actually, Warming's seminal contributions to plant ecology and the priority of his work *Plantesamfund* are probably the most widely asserted recognition of parentage for plant ecology by his contemporaries and subsequent commentators (cf. Waller 1947), and Warming needs no latter-day justification.

According to the ecologists Kormondy and McCormick (1981), "historians of science" mark the rise of "modern ecology" with the introduction of the ecosystem concept. They do not specify which historians do so. The difficulties of identifying ecology or its founders are compounded by the use of the modifier *modern* by ecologists and historians alike. Allee et al. (1949) in their encyclopedic work on animal ecology wrote that "modern aspects of ecology did not begin to take form until early in the 18th century," citing the work of Linnaeus and Buffon. The historian of science Oldroyd (1980), however, argued that ecology in the "modern" sense existed only after Darwinian theory, which eliminates Linnaeus and Buffon, at least, as "modern" ecologists. Taylor (1912) cited Warming as the father of "modern" plant ecology, whereas Boerker (1916) and Godwin (1977) preferred C. Schröter. Waller (1947) saw "modern" ecology arising in the medical sciences early in the 19th century, thus warranting his citation of the Cincinnati physician Daniel Drake as a pioneer of ecology. Egerton (1976) commented that phenology is not an important part of "modern" ecology, which he contrasted with that of the 18th and 19th centuries, implying that "modern" means 20th-century ecology. Ecologists recently are prone to restrict the realm of "modern" ecology to post-World War II developments in quantitative or theoretical ecology or, even further, to systems ecology.

Self-conscious ecology

Clearly, historians of science and ecologists who have commented on the history of ecology do not offer unequivocal guides to the origins of ecology, nor do they provide explicit criteria for determining when ecology came to be "modern" or "mature," who may be said to be founders of ecology, or what its lineage may be. One problem is that the roots of ecology are commonly sought using some perception of what it has become, and current perceptions of ecology differ greatly. One of the favorite lecture topics of ecologists through the years has been the na-

ture of ecology, or "What is ecology?" (Moore 1920; Taylor 1936; Dice 1955). If that question had ever been successfully answered, either by reference to the various definitions of ecology or by close analysis of what ecologists do, better consensus might have been achieved concerning the roots of ecology. The lack of consensus is due to the fact that seeking roots implies some idea of what it is you are seeking roots for. It is necessary to distinguish between retrospective ecology and what Allee et al. (1949) called "self-conscious" ecology. Retrospective ecology focuses on what I call the antecedents of ecology – that is, on seeing that someone was doing something similar to what later came to be recognized as an aspect of ecological science. It is looking backward rather than following the development of something, and unless it turns up hidden linkages it does not expose roots. Egerton (1976) commented, "The transmission of a man's work establishes his place in the history of science, but it should not be assumed that publication is automatic assurance of this transmission." What is lacking in many retrospective views of ecology before the 19th century is evidence that the work was connected with, or led to, that of later workers. That brilliant ideas have been amply studied, elegantly expressed, and even published without having influenced the work of contemporary scientists is familiar in the history of Gregor Mendel's lonely efforts.

F. E. Clements (1905, 1916) prefaced some of his early volumes on various aspects of ecology with historical summaries, but he gave little indication that these are anything but retrospective searches through the natural history literature for sharp insights which could be seen in hindsight as ecological. Ecologists looking retrospectively into the background of their science are generally innocent of the historiographic concerns which are of primary interest to historians of science. The crux of the present volume is the rise of self-conscious ecology and the establishment of ecology as a science, particularly its identification of distinctive concepts and questions and the various efforts to establish a theoretical framework. It is clear that ecology did not emerge fully formed from the head of Haeckel any more than biology emerged from Burdach, Treviranus, and Lamarck or genetics from Mendel. Haeckel's coinage of *ecology* in 1866 did not provoke a rash of ecological studies or prompt the identification of biologists as ecologists; in fact, hardly anyone noticed the new term for over two decades. Some have even accused Haeckel of neglecting his neologism and not pursuing ecology effectively himself (Egerton 1977b). Haeckel's biographer (Bolsche 1909) does not index *ecology*.

Ecology and genetics both surfaced as distinctive sciences around the turn of the century. Ecology, as early ecologists and later historians recognized, was stimulated by, and in some respects anticipated by, Darwin and his concept of evolution by natural selection (Stauffer 1957, 1960; Ghiselin 1969). Haeckel (1866) specifically attributed ecology to Darwinian evolution as early as 1866, but neither he nor anyone else developed the idea until the 1890s, when numerous biologists seized on the relationship and began to treat ecology as a formal discipline. Haeckel provided a name but little substance for the new science. Mendel, almost simultaneously (1865), supplied the substance of genetics without a name. His insights similarly lay fallow until their multiple rediscovery in 1900. Haeckel rose to worldwide notoriety and Mendel retired to scientific obscurity, yet both are acclaimed as the founders of major developments of 20th-century biology which, many assert, should combine to resolve the "great mystery" recognized by Darwin.

During the last decades of the 19th century, four quite independent aspects of biological science were developing – oceanography, its biological component; limnology, the freshwater analog of oceanography; plant ecology; and animal ecology (Egerton 1976). Oceanography (Deacon 1971; 1978; Schlee 1973; Sears and Merriam 1980) and, more recently, aspects of ecology (Cox 1979; Cittadino 1980, Tobey 1981; Kingsland 1981) have been the subjects of detailed historical studies. Their affinity as ecological sciences was not always recognized by their early practitioners. They developed with considerable redundancy and even today retain discrete institutional organization and publication outlets in spite of basically common ecological concerns.

The history of the emergence of ecology is relatively poorly known, in part, because historians of science have substantially ignored it in favor of following the dramatic development of physiology and genetics. Coleman (1977) asserted that late 19th-century biologists switched from historical explanation to experimental investigation. Mayr (1982) is critical of historians who do not understand there are two biologies – that of function (physiology) and that of evolutionary and historical causation (ecology, genetics, and evolution). Coleman was perfectly clear that there are two biologies, but denied that the transition from natural history to the history of nature, as suggested by Lyon and Sloan (1981), was a successful revolution in science. Specifically, he attacked the possibility that the history of nature constitutes an explanation or genuine understanding, an opinion shared by some current

ecologists. Coleman saw the historical ideal as occupying a lesser position, displaced by experimental physiology, which "offered little encouragement to the historian of life." Cravens (1978) similarly saw practitioners of experimental biology supplanting those he called "natural historians" and overshadowing them in terms of university and research institute appointments, journal space, prestige, "limelight," and glory. Some historians may understand that there are "two biologies" but commonly see experimental and functional biology as leading the pack, and their statements sometimes suggest that experimental-functional biology and biology are one. Coleman described "biologists" as "transferring their allegiance" to experimental biology. Allen (1979) described naturalists and experimentalists as being at war in the 19th century, the fray continuing into the 20th century as the ecologists entered the lists, not clearly knowing which side to join.

Ecology at the turn of the century was pursuing in some ways what Cannon (1978:105) characterized as "Humboldtian science," which was

> the great new thing in professional science in the first half of the 19th century, . . . the accurate measured study of widespread but interconnected real phenomena in order to find a definite law and a dynamical cause.

Cannon (1978:105) described the limited view held by some of 19th-century biology:

> It was only toward the end of the 19th century, after physics and laboratory physiology had risen to their position of dogmatic self-assurance, that this kind of activity was in its turn seen as old-fashioned, that Gauss's theory of terrestrial magnetism was judged not to be a theory at all, and Darwin not a professional biologist.

Cannon's "Humboldtian Science," in its biological aspects, exemplified the qualities Lyon and Sloan (1981) ascribed to the transformed natural history of the 18th century. Cannon identified the quality of "Humboldtian Science" which made it kin to ecology and distinct from experimental physiology as the presumed zenith of 19th-century biology – the concern of ecology for the complexity of "interconnected real phenomena." She wrote:

> Compared to this, the study of nature in the laboratory or the perfection of differential equations was old-fashioned, was simple science concerned with easy variables. (Cannon 1978:105)