

## ON THE EVOLUTION OF ECOLOGICAL IDEAS: PARADIGMS AND SCIENTIFIC PROGRESS

MICHAEL H. GRAHAM<sup>1</sup> AND PAUL K. DAYTON<sup>2</sup>

<sup>1</sup>Center for Population Biology, University of California, Davis, California 95616 USA

<sup>2</sup>Scripps Institution of Oceanography, University of California–San Diego, La Jolla, California 92093-0227 USA

**Abstract.** We introduce a heuristic model for studying the evolution of ecological ideas based on Thomas Kuhn's concept of the development of scientific paradigms. This model is useful for examining processes leading to ecological progress and the elaboration of ecological theories. Over time, ecological knowledge diverges and evolves as data are collected that either refute or support the current trajectories of accepted paradigms. As a result, the direction of ecological research continuously branches out into new domains leading to increased ecological understanding. Unfortunately, heightened ecological understanding also builds impediments to future progress. Increased specialization and the parallel evolution of seemingly independent subdisciplines generally compel researchers to become increasingly canalized. Specialization also accelerates the expansion of the ecological literature, making it difficult for researchers to track developments in their own subdisciplines, let alone the general field of ecology. Furthermore, specialization inherently focuses attention on contemporary research and hastens the erasure of memory of historical contributions to modern ecology. As a result, contemporary ecologists are in danger of losing touch with their historical roots and face a greater likelihood of recycling ideas and impeding real scientific momentum. Enhancing our historical perspective on the evolution of ecological ideas will be key in overcoming the negative consequences of progress and safeguarding the continued advancement of ecology.

**Key words:** ecological knowledge; ecology; evolution of ideas; evolution of theories; historical perspective; historical roots; modern ecology; paradigms; scientific progress; scientific revolution; specialization; theories.

### INTRODUCTION

*Is not Science a growth? Has not Science its embryology? And must not a neglect of its embryology lead to a misunderstanding of the principles of its evolution and of its existing organization?*

—Spencer (1887)

The accumulation of scientific knowledge is a dynamic process compelled both by contemporary and historical developments. It has been generally perceived that knowledge is compiled within a formal logical framework built upon direct observations that are tightly synthesized with various questions or hypotheses (Popper 1959, 1963). Ideally such hypotheses are tested empirically so that an increasingly broad understanding of natural patterns evolves in a stepwise fashion (Feynman 1965, Lakatos 1970, Loehle 1987). The tempo and direction of this evolution is guided largely by the present-day state of scientific understanding, public and private funding agendas, educational practices and objectives, and societal interest, all within the context of the contemporary culture. In practice, researchers also rely on the successes and failures of prior studies to provide clues to identify promising

future research directions. Characteristics of the most successful and encouraging scientific accomplishments are reinforced, while those perceived to be of little merit are abandoned.

Thomas Kuhn's publication *The Structure of Scientific Revolutions* (1962), and the series of discussions that followed (e.g., Kuhn 1970a, Lakatos and Musgrave 1970, Nelson 1974, Feyerabend 1975, Doppelt 1978, Gutting 1979, Barnes 1982, Restivo 1983, Cohen 1985, Reisch 1991, Cao 1993, Horwich 1993, Fuller 2000), provided a strikingly different view of the way that science progresses. Kuhn's book presented science as being much less unified than the Popperian model. Kuhn believed that the way in which humans acquire knowledge inevitably leads to a suite of methodological, philosophical, and even social constructs that guide scientists and their investigations, and he adopted the term "paradigm" to depict these constructs. He described the advancement of science as a process whereby extended periods of "normal science," during which scientists work comfortably within the confines of accepted paradigms, are isolated by brief episodes of "extraordinary science," or revolution. Kuhn argued that it was during these periods of extraordinary science that real progress is made. Revolution marked the point at which accepted paradigms suffered essential tensions and could no longer accommodate natural observations or data, forcing scientists to shed the constraints of the

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paradigms in search of new understanding. Although the Popperian and Kuhnian views of scientific progress were contemporary and not mutually exclusive (Kuhn 1970b), Kuhn's (1962) ideas proved to be contentious, as apparently few scientists were willing to be labeled as "normal" relative to "extraordinary."

We believe that Kuhn's concept of paradigms has utility for studying processes leading to scientific progress because it provides a tangible system for examining how scientific theories are rejected or accepted. Although young relative to other scientific disciplines, ecology has had a rich and exciting history of discovery and progress (see for example McIntosh 1985, Bramwell 1989, Real and Brown 1991, Bocking 1997). Our goal is to review the general evolution of ecological ideas in search of processes that stimulate ecological breakthroughs. We find two aspects of Kuhn's (1962) work particularly relevant to studying the evolution of ecological ideas: (1) the effect of paradigm development on the canalization of scientific progress; and (2) the notion that such canalization can only be broken through revolution and upheaval. Our focus here is primarily on the former as our goal is to describe the seemingly paradoxical manner in which established paradigms in ecology serve to both stimulate and constrain ecological breakthroughs. In the final paper of this Special Feature, Paine (2002) more thoroughly discusses the role of scientific revolutions in the advancement of ecology, ultimately questioning whether ecological revolutions actually occur. We do not intend to philosophize and explore the relevance of all aspects of Kuhn's (1962) book to ecology, nor to validate his beliefs, but rather we endeavor to use his idea of paradigms as a basis for studying the advancement of ecology.

#### POST-KUHNIAN PARADIGMS IN ECOLOGY

Kuhn's (1962) concept of paradigms has been contentious for a variety of reasons. Philosophers have argued over the utility of distinguishing between normal and extraordinary science (Feyerabend 1970, Toulmin 1970, Watkins 1970), whether revolution is indeed necessary for scientific progress (Popper 1970, Williams 1970), and even over the seemingly simple definition and identification of paradigms themselves (Masterman 1970, Shapere 1971). In fact, much of the dispute seems to revolve around the latter issue, stemming from Kuhn's vagueness in his original description of paradigms (Kuhn 1962) and his own subsequent difficulties in providing a precise definition (Kuhn 1970a, b, c, Westman 1978). If Kuhnian principles are to be useful in studying the evolution of ecological ideas, a more concise formalization of the paradigm concept is needed.

As with many issues in contemporary ecology, we believe that the problems surrounding the definition of the term paradigm are simply matters of scale. We have observed that, to many present-day ecologists who

were practicing at the time Kuhn's (1962) book was first published, paradigms represent the belief systems that dictate how ecological data are collected and analyzed, and the standards by which data are compared. An example would be Darwinian natural selection and its distinction from Lamarckian evolution. The primacy of natural selection leads presumably few biologists to spend time and money in search of the heritability of acquired traits, as Lamarck had proposed. Consequently, Darwin's ideas have determined much of the direction in which ecological and evolutionary research has progressed. Other examples are the theories of island biogeography, continental drift, or the biological species concept. Each of these constructs provide a broad set of rules, standards, and hypotheses that help guide future research. This is the typical representation of paradigm emphasized by Kuhn (1962). Yet, a younger student of ecology might give a different definition of paradigm, interpreted similarly to that of Webster's "a pattern or example" (Mish 1994). That is, paradigms may also be considered to have a more limited representation, focusing on specific and individual models or theories such as the intermediate disturbance hypothesis, keystone predation, metapopulations, or any of the numerous "rules" and "laws" that have been proposed in the biological sciences. Kuhn believed that this interpretation was also correct and useful, and that this more focused usage of the term may, in fact, be the most interesting (Kuhn 1970a).

We suggest that implied differences between these two definitions (i.e., broad and specific) might be reconciled by a more continuous concept of paradigm, and that paradigms are simply representations of the current state of scientific understanding. Whether paradigms reflect truths held by most practitioners within an entire discipline, or those few studying a more focused line of research, they are the essential and much sought after by-products of the scientific method. A paradigm might subsequently be described as any individual or set of concepts, standards, or ideas that are used to guide the accumulation of scientific knowledge at any of a variety of scales. A paradigm to one ecologist may be the single model that characterizes their specialized field of study, whereas to another it is the suite of practices that defines the general way that they collect and analyze their data. The commonality of all paradigms is thus their representation of the status quo, against which we gauge the success of our progress towards increased ecological understanding.

An important consequence inherent to the establishment of paradigms is the generation of dialectical "camps of thought" (Naeem 2002). As soon as one group of researchers proposes some generality in nature (destined to become paradigmatic), an opposite stance is often generated (Barber 1961, McIntosh 1987). As relevant data accumulate, evidence for or against the generality waxes and wanes, keeping the evolution of ecological ideas in a constant state of flux (Kingsolver

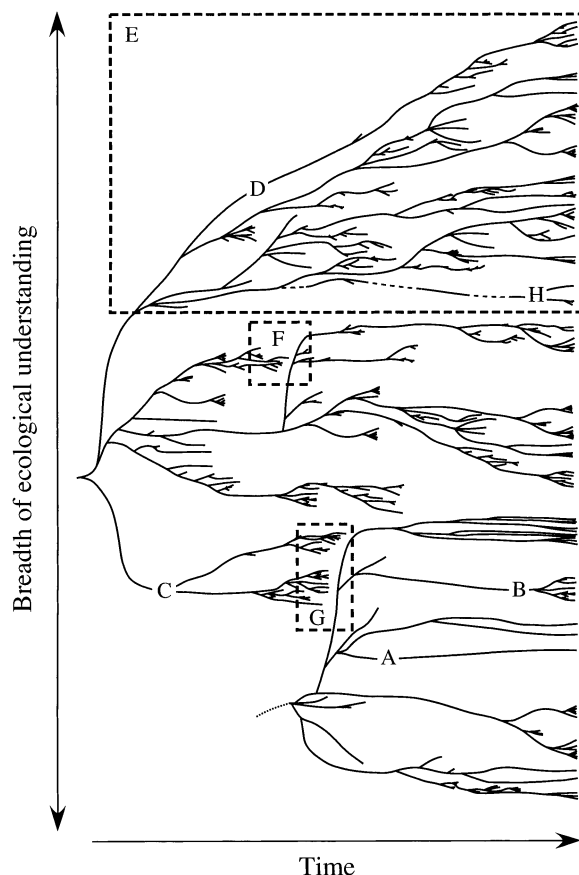


FIG. 1. A two-dimensional conceptual representation of the evolutionary history of ecological ideas. The horizontal axis represents increasing time from left to right; the vertical axis represents the range of ecological understanding. Solid lines symbolize accepted paradigms at any given time, whereas broken lines are paradigms with intermittent acceptance. Letters and dashed boxes represent concepts referred to in the text.

and Paine 1991). There may be cases in which data are collected that cannot refute the generalities of accepted paradigms, whereby the paradigms are reinforced and brought into closer agreement with fact (Loehle 1987, Mentis 1988). This process is in essence Kuhn's (1962) interpretation of normal science. In most cases, however, data do not support the absolute generality of accepted paradigms, requiring paradigms to be modified in order to better explain observed patterns in nature. Such data probe the applicability of the paradigms, often resulting in modifications to underlying models that can be minor. As a result, scientific knowledge can gradually diverge and evolve in new directions, without entirely shedding the old ideas. On the other hand, data may be so anomalous that subsequent research steps far away from established principles. The cumulative result of these different processes of paradigm evolution is a hierarchical network of scientific understanding (Fig. 1).

In this continuous model of paradigm development,

the advancement of science is driven largely by the occurrence and recognition of anomalous data (i.e., data outside the confines of existing paradigms). Kuhn (1962) reasoned that anomaly leads to crisis, crisis leads to extraordinary research, and extraordinary research leads to revolution. Yet one researcher's anomaly may be another's standard. As such, differences in the perceived severity of an anomaly will lead to different trajectories. If a datum is not viewed as anomalous then there is no need to modify existing paradigms. If, however, an anomaly is seen as real, existing paradigms will require refinement, with severe anomalies convincing more heavily indoctrinated researchers and spurring the beginning of extraordinary research and revolution.

#### ALTERNATE ROADS TO PROGRESS

We consider ecological progress to be simply the expansion of our understanding of how natural systems work. Whether this expansion occurs gradually along established lines of research or leaps dramatically into new areas, the goal is to fill the gaps in understanding (Fig. 1). The view of paradigm development as a continuous evolution of ideas helps to highlight numerous processes that can lead to or characterize ecological progress.

First, and most obvious, there are both good and bad ideas. Ecology is a theory-laden discipline (McIntosh 1987). In some cases, it can be demonstrated early during a particular line of reasoning that data do not match theoretical predictions, quickly ending further theory development along those lines. In other cases, empirical testing of theories can lag far behind theory development, with models gaining paradigm status based on very few empirical tests. As such, a limited amount of contradictory data can quickly topple even the most well articulated and beloved theories. The broken-stick model of MacArthur (1957) is one example of a concept that quickly gained followers (e.g., Hutchinson 1957), yet was just as quickly deposed as conflicting empirical data were accumulated (Preston 1962). The history of ecological progress is thus riddled with numerous dead-end ideas (Fig. 1).

On the other hand, significant amounts of data may be collected that fail to negate a given theory, strengthening the theory's importance in helping to explain nature (Loehle 1987). In this sense, repeated testing serves to reinforce the generality of a particular paradigm and selects for its current trajectory. In the absence of anomalous data there may be little alteration of the paradigm for long periods of time (A in Fig. 1). Continued support for Mendelian laws of heredity (Olby 1966) or Watson and Crick's (1953) double-helix model of DNA structure are good biological examples; note that we could not find clear ecological examples. Furthermore, if the current expression of an accepted paradigm is found to well represent natural patterns and modification is not necessary, then additional re-

search along those lines can occur through specialization. New theories develop as shallow offshoots of the main paradigm, gradually broadening in relevance as ecologists attempt to explain nature in greater and greater detail (B in Fig. 1). Depending on the realized breadth of new understanding, these offshoots can represent individual ideas or the creation of subdisciplines, as in the recent radiation of MacArthur and Pianka's (1966) model of animal foraging optimization into the diverse field of foraging ecology (Stephens and Krebs 1986).

Support for accepted paradigms, however, may be short-lived, and new data may suggest limited generality. Again, in these cases, paradigms must be refined to account for the anomalous data or abandoned for superior models (Loehle 1987, Mentis 1988). Refinement is represented in our hierarchy by the progression of paradigms tangential to their prior trajectory (C and D in Fig. 1). Refinement can occur in the presence (C in Fig. 1) or absence of paradigm fragmentation (D in Fig. 1), analogous respectively to the ideas of cladogenesis and anacladogenesis in organismal evolution (e.g., the splitting of the biogeographical theory of static population distributions into opposing dispersal vs. vicariance theories [Brown and Lomolino 1998], and the transition from Grinnellian to Eltonian to Hutchinsonian concepts of the niche [Real and Levin 1991], respectively). The stronger the anomaly the greater the degree of departure. The tempo of advances in ecological understanding can also vary greatly. Paradigm development may progress as a function of gradual model refinement (E in Fig. 1; Reznick et al. 2002 on *r*- and *K*-selection, Robles and Desharnais 2002 on the predation hypothesis), leading to an increasingly broad systematic increase in ecological understanding (termed conceptual evolution by Paine [2002]); note however that conceptual evolution is not a Kuhnian concept. In other cases, paradigm evolution can be extremely abrupt as a particular model is completely abandoned and usurped by another (F and G in Fig. 1). Such abrupt and catastrophic events are Kuhn's (1962) revolutions or paradigm shifts. In some cases, Kuhnian revolutions which originate internally as insights from one subdiscipline within a field become so broad that they better explain observed phenomena in some other subdiscipline than that discipline's own suite of paradigms, in which case the old paradigms are shed for the new ones (F in Fig. 1). In this case, the two paradigms share a common ancestral idea. An example is the sweeping impact throughout biology of Darwin's (1859) world-shattering publication *Origin of Species*, which, although influenced by scientists in other fields (e.g., Lyell and Malthus), was based on biological principles. In other cases, revolutionary ideas may come from completely unrelated fields or result from truly novel or ingenious ideas that have no precedent in the historical trajectories of paradigm development within the discipline (G in Fig. 1), such as Wegener's (1915)

geologically based theory of continental drift which revolutionized the field of biogeography (Brown and Lomolino 1998).

Finally, some theories may be premature (Stent 1972), represented by ideas for which there is currently little popular support. As such, paradigms can intermittently come in and out of favor (H in Fig. 1). Delayed acceptance of these theories might be due to (1) a lack of technological or analytical tools for critically testing them (e.g., McClintock's [1948] theory of transposable genetic elements), (2) insights gained from progress in other fields (e.g., eventual support for Hooker's [1867] vicariance model by the theory of continental drift [Wegener 1915]), or (3) a lag time required for the discipline to mature conceptually such that the relevance of the theories can be recognized (e.g., Lindeman's concept of trophic dynamics [Cook 1977]). Discouragingly, intermittent acceptance of paradigms can also be due simply to the recycling of ideas (see for example Jackson's [1981] account of J. Salisbury's [1929] neglected contributions to niche theory, or Pianka's [1999] reference to Diamond's [1975] reinvention of Clementsian and Gleasonian successional dynamics as "community assembly"). This situation can result from poor historical appreciation of the development of important ideas within a given discipline (Jackson 1981 on competition, Young 1990 on marine invertebrate recruitment, Hixon et al. 2002 on population regulation), or even social and methodological constraints (Barber 1961 on general science, Grosberg and Levitan 1992 on supply-side ecology), such as the publication of papers in seemingly obscure, or simply different, journals and languages.

There is also a sense of duality in the way that paradigms affect the advancement of ecology. A tug-of-war exists between the collection of observations (data) and the establishment of paradigms to which observations are compared (Brady 1982, McIntosh 1987). Paradigms provide ecologists with a starting point for their investigations, guiding future research by representing the success of past scientific explorations. They tell us where and how to begin looking for patterns in our observations, with the suggested generality of a paradigm helping to identify if data are anomalous. Paradigms, and their perceived inadequacy, can thus fuel ecological progress. We have a tendency, however, to appreciate and understand that with which we are most comfortable. In one sense, paradigms represent the extent of this comfort level, and as such, scientists may retreat to the safety of their paradigms and chose to ignore or reject anomalous data (Barber 1961). In some cases, this comfort level can be so attractive that researchers begin to design studies that are simply confirmatory (Dayton 1979, Brady 1982, Loehle 1987); that is, hypotheses are proposed to which the answers are already known or are at least expected. Fuller (2000:xi) also asserted that the collective response necessary for ideas to reach paradigm status represents

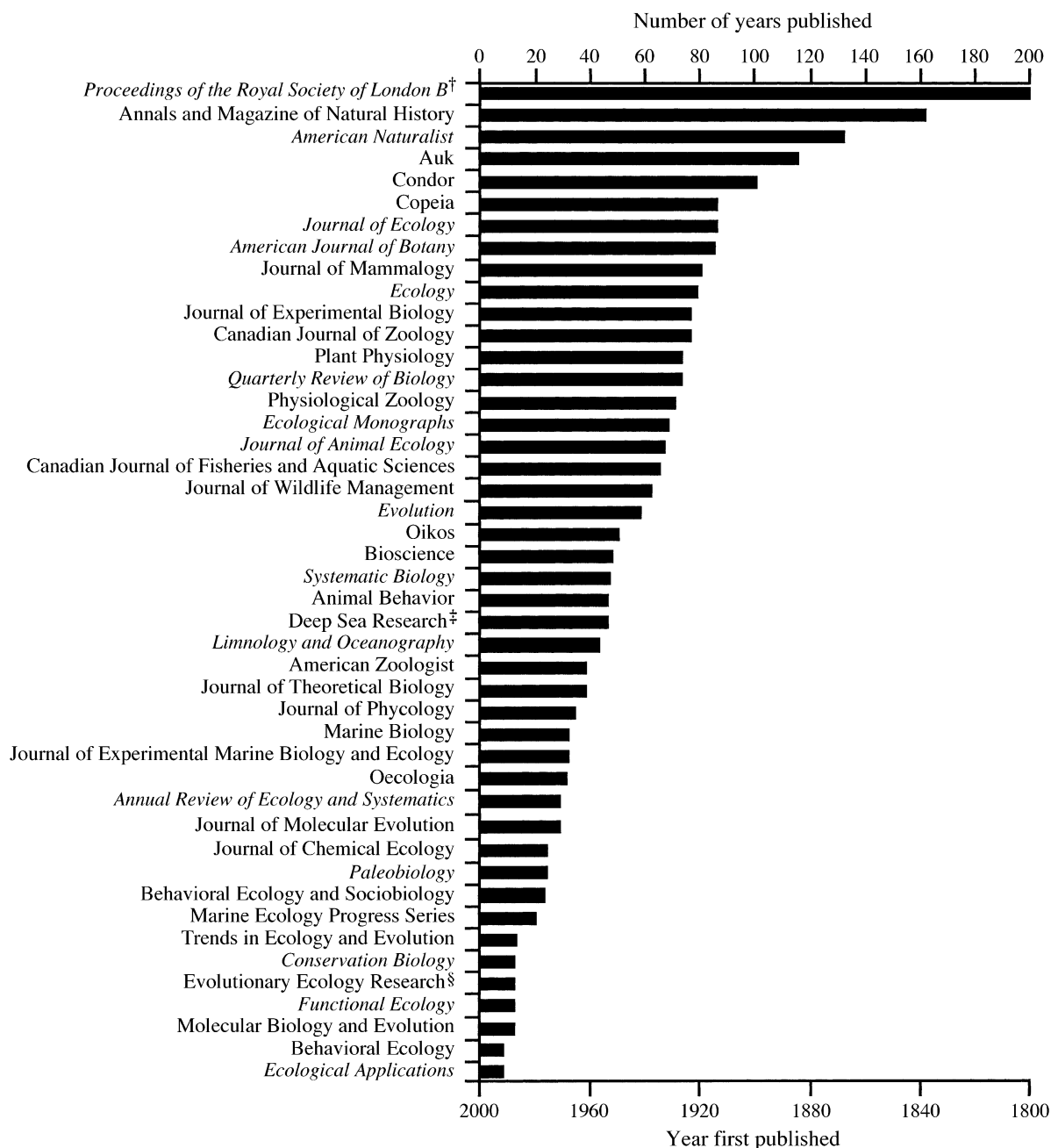


FIG. 2. Duration of publication for 45 top international ecology, evolution, and behavior journals. The list of journals is adapted from Brett et al. (1999). Papers are in order of the date of first publication. All published issues (up to 1996) of italicized journals can be "full-text" searched using JSTOR.

<sup>†</sup> Previously *Proceedings of the Royal Society of London*.

<sup>‡</sup> Includes *Deep Sea Research* Parts I and II.

<sup>§</sup> Including *Evolutionary Ecology*.

leadership from the middle, where "to think ahead of the pack is just as bad as to think behind it." Paradigms thereby also serve to constrain ecological progress. This perpetual tug-of-war results in the hierarchical network of ecological understanding depicted in Fig. 1. In the end, the temporal map of ecological progress

is marked by both liberating expansions into new areas of research and restrictive gravitation towards favored models and pet theories.

The creation of dialectical camps, the tug-of-war between data and the paradigms to which they are compared, and the never ending need to secure jobs, grants,



and publications, also creates the potential for social competition among researchers to strongly influence the establishment of paradigms. In addition to the accumulation of corroborative data, theories can gain inertia by amassing supportive ecologists (Dayton 1979, Brady 1982); the more influential the ecologist, the greater the inertia. The general dynamics that result from competition for the key ideas in science were well discussed by Kuhn (1962) and are not rehearsed here. We would like to note, however, that the influence of these social pressures on the advancement of science are not strictly negative. Kuhn's (1962) book suggested that "new paradigms can succeed by capitalizing on the anomalies that their more established competitors cannot explain" (as quoted by Fuller 2000:3). Thus, the battle over which theory best explains the available data can spur the advancement of ecology.

#### CONSEQUENCES OF PROGRESS

We believe that many consequences of ecological advancement will be obstacles to future progress. Here we briefly discuss just a few: (1) ecological specialization; (2) erasure of history; and (3) expansion of the literature. These problems are interconnected and have the potential to divert researchers and hinder ecological breakthroughs.

It is apparent that, during its short history, ecology has developed numerous specializations. Although increased specialization represents the articulation of scientific knowledge and can be considered a significant sign of progress, specialization also reflects the canalization of ideas and the loss of general approaches to ecology. The extent of specialization can be observed in dates of origin for the top 45 existing ecology, evolution, and behavior journals (Fig. 2). The early years of ecology were supported by relatively few journals, with a primary emphasis on broad natural patterns. From 1900 to 1940 the number of journals exploded as biologists began to align themselves according to both organism and function; that is, they became more specialized. The 1950s, 1970s, and 1990s saw the birth of habitat-oriented and conservation journals; many applied journals were not examined because of their own unique history of evolving issues and paradigms. As such, an ecologist working during the early 1900s utilized individual journals that were much more general than ecologists see today. Although the combined scope of present-day journals is exceedingly broad, each individual journal tends to be more specialized. Such specialization compels even the most scholarly researchers to become increasingly myopic, as it becomes harder to track general ecological developments in lieu of the specific, and often esoteric, advances made in their own subdisciplines (Barber 1961, Peters 1991).

This focus on specialized topics inherently forces emphasis on contemporary research as prior studies may be deemed too broad to be relevant to the spe-

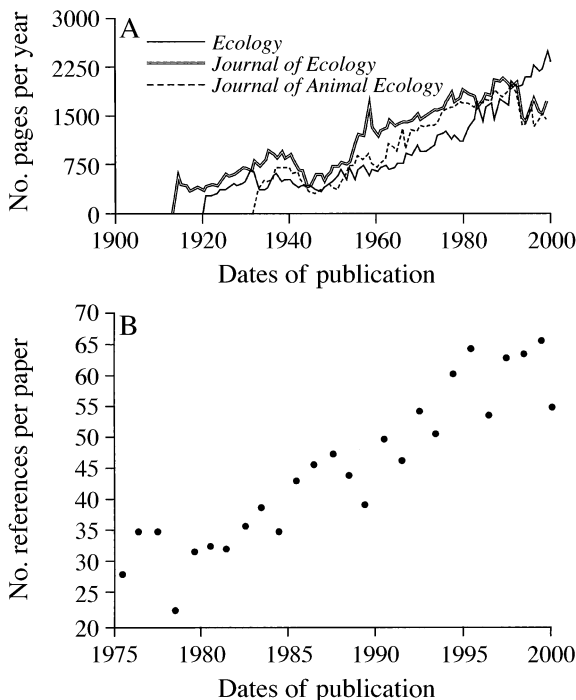


FIG. 3. (A) Number of pages published per year in *Ecology*, *Journal of Ecology*, and *Journal of Animal Ecology*. (B) Number of references in the *Literature Cited* of papers recently published in *Ecology*. Data in panel (B) represent mean number of references for 15–20 papers randomly selected from each volume between 1975 and 2000. Papers published as a *Note* or as part of a *Special Feature* were excluded.

cialized research efforts (Peters 1991). Consequently, specialization acts to erase traces of the historical development of ecology. Many general ecological textbooks are structured around the fragmented network of ecological subdisciplines (e.g., predator–prey interactions, life history strategies, food webs, and island biogeography), emphasizing new ideas and concepts that effectively (although maybe not purposefully) divert students from studying ecology's historical roots. There obviously are exceptions to this pattern, yet the problem remains that textbooks serve as the student's introduction to ecology, and teachers and students simply accept modern theories based on the text. This indoctrination may not seem problematic until data anomalous to these textbook theories are encountered. In such cases, without an historical appreciation for the development of ecological ideas, ecologists can neither easily relate theory to reality nor detect the recycling of historical debates and issues.

The problems with specialization and the erasure of history are exacerbated by, and correlated with, the inevitable expansion of the ecological literature that has occurred since the beginning of ecology's development as a scientific discipline (Tansley 1914). In addition to the increased number of relevant journals, the number of pages annually published per journal has

steadily increased (Fig. 3a). This expansion of the literature is also evident in the rapid increase in the number of references in the literature cited of recent *Ecology* papers (Fig. 3b). There are more specialized fields, more journals, and simply more papers and pages to read. Yet, while ecologists cite many recent references, they often lose track of the roots of their research (Jackson 1981, Young 1990). In some cases, the contributions of early ecologists can be vital to the advancement of modern ecology. In his 1886 presidential address to the Biological Society of Washington, G. Brown Goode (p. 102) declared:

Without the encyclopedists and explorers there could have been no Ray, no Klein, no Linnaeus. Without the systematists of the latter part of the eighteenth century the school of comparative anatomists would never have arisen. Had Cuvier and his disciples never lived there would have been no place for the philosophic biologists of today. There were then, it is certain, many men equal in capacity, in culture, in enthusiasm, to the naturalists of today, who were giving careful attention to the study of precisely the same phenomena of nature. The misfortune of men of science in the year 1785 was that they had three generations fewer of scientific predecessors than have we. Can it be doubted that the scientists of some period long distant will look back upon the work of our own times as archaic and crude, and catalogue our books among the "curiosities of scientific literature?"

As ecologists lose touch of their roots, they face a greater likelihood of recycling ideas and losing real scientific momentum. Obviously this situation is an impediment to progress and scholarship.

#### A ROLE FOR HISTORY

It is important to remember that these problems are reflections of ecological progress. Specialization and the expansion of the literature clearly are signs of increased understanding. Still, we believe that contemporary ecologists would benefit from the development of new tools and skills for maintaining a high level of scholarship in the presence of ecological progress. We offer some suggestions.

An important key to overcoming the negative consequences of progress is to enhance our historical understanding of the evolution of ecological ideas (see for example Goode 1886, Kingsland 1985, Golley 1993, Egerton 2001a, b). As a first step, we recommend that ecologists trace the developmental history of their own specialized fields; here "full-text" searching of all issues of selected journals using JSTOR (some journals identified in Fig. 2) is clearly a valuable yet underutilized resource.<sup>3</sup> Understanding the lines of paradigm ascent or descent clarifies hierarchical nodes

linking concepts that served as the origins of various ecological subdisciplines. In addition to better appreciating advances in other subdisciplines, studying these linkages will facilitate a better understanding of broad ecological developments in the face of specialization. It may also expose areas of redundancy and idea recycling (Hixon et al. 2002), providing researchers with an impetus to step away from these cycles and towards more productive lines of research. Furthermore, these "genealogical" exercises put students in direct contact with the contributions of even their most ancient predecessors (Hixon et al. 2002, Naeem 2002), helping to thwart the erasure of history. The next four papers of this Special Feature are a testament to the benefits of maintaining proper historical perspective.

But ecologists can do much more. We applaud those who have endeavored to bring researchers into contact with old, yet important, ecological literature contributions (e.g., Real and Brown 1991, Egerton 2001a, b). Some ecology programs also incorporate history of ecology courses into their curricula, and more and more ecologists are making concerted efforts to blend both contemporary and historical contributions into their course syllabi. However, there is a real need for novel pedagogical techniques for helping students to better utilize literature resources and reference tools to tackle the unique characteristics of the ever-expanding ecological literature. Most web-based literature search engines are limited to only the last 20–30 yr (e.g., Current Contents, BIOSIS) and tend to exacerbate the erasure of history. Ecologists need to develop, or find and adopt, tools to help them manage the expansiveness of the growing literature that results from our push for progress. Ultimately, the burden is on individual ecologists to continue, and step up, their support for the virtues of good historical perspectives. This perspective was our goal in developing the symposium that led to this Special Feature.

#### ACKNOWLEDGMENTS

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<sup>3</sup> URL: (<http://www.jstor.org>)

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