CONTRIBUTIONS

Commentary

Biological Invasions: Politics and the Discontinuity of Ecological Terminology

Each scientific discipline has its lexicon of terms. Ecology is not different. As far as we know, terminologies of individual disciplines have never been changed in response to governmental policy statements. A recent attempt to make the long-established ecological term "invasion" concordant with the definition in an Executive Order of one country's president (Davis and Thompson 2001) probably has no precedent. According to these authors, invasion always implies some kind of impact, and all "invasive" taxa are harmful. There are several problems with their proposal. (Others were already addressed by Daehler [2001].)

The term "invasion" was first used in an ecological context by Goeze (1882:109) in his book "Pflanzengeographie," in connection with the spread of non-native species. On the same page, he presented the invasion of mango in Jamaica as an example of a beneficial invasion. Therefore, the term "invasion" by itself was used without any necessary connection with negative or positive impacts. This is also how "invasion" was understood by Clements (1904 et seq.) and other ecologists in the first half of the last century.

Elton's (1958) book on invasions is a clear starting point for invasion ecology as a new discipline. Unfortunately, Elton never defined the terms "invasion" or "invader." Most of the examples used by Elton were introduced species that had profound economic and/or environmental impacts, because the best data were available for such taxa. However, Elton (1958) also discussed the spread of some alien species that had no obvious impacts (e.g., *Lamium album* and several freshwater shrimps). He also used the term "invaders" with reference to the intermixing of faunas during the Pliocene. Therefore, it seems that he applied the terms "invasion" and "invader" rather broadly, without obligatory connotations of impact.

Contemporary use of this term is often inconsistent, but, in general, converges to a biogeographical definition ("invaders are species coming from elsewhere") and distinguishes invasion from colonization and weediness (Williamson 1996:58). "A biological invader is a species of plant, animal or micro-organism which, most usually transported inadvertently or intentionally by man, colonizes and spreads into new territories some distance from its home territory" (di Castri 1990). "'Invasion' occurs when a species colonizes and persists in an area which it previously had not inhabited" (Shigesada and Kawasaki 1997). "[An] invasive species [is] a non-indigenous species that spreads from the point of introduction and becomes abundant" (Kolar and Lodge 2001). In ecological dictionaries, invasions are defined as "the mass movement or encroachment of organisms from one area into another" (Lincoln et al. 1998), or "expansion in the distribution of certain species of plants, animals and microorganisms which are transported by humans and often competitively favored by the disturbance around human settlements" (Calow 1998). There is no impact connotation attached to these definitions! Use of the term "invasion" in other biological disciplines is usually associated with some kind of effect, but not necessarily negative, e.g., "invasions" of plant roots by mycorrhizal fungi or nitrogen-fixing rhizobia (see Marks 1991, Reed and Walker 1991, Gianinazzi et al. 1996). Also, is there anything negative about evolutionary "terrestrial invasions" (Gensel and Edwards 2001, Little 1990) or "post-glacial plant invasions" (Macdonald 1993)?

There has been some historical continuity in ecological terminology. However, there is much confusion, especially in the recent literature, particularly because many newcomers to the burgeoning field of invasion ecology ignore existing terminology and instead rely on the highly emotional negative connotations of the word "invasion" in relation to war and other aggressive human activities. This is especially true for the popular literature on invasions (e.g., Bright 1998, Devine 1998). Unfortunately, such sloppy terminology has permeated what should be authoritative documents on this topic, including the IUCN's (1999) "Guidelines for the prevention of biodiversity loss due to biological invasion," and the Global Invasive Species Programme's "Global Strategy on Invasive Alien Species" (McNeely et al. 2001). Because of such frequent misunderstandings, some of us participated in a kind of international "terminological consensus" in plant invasion biology (Richardson et al. 2000). This was based on a broad literature search and discussions with many ecologists. Our intention was to provide operational definitions that could be used to define, on ecological and objective grounds, terms such as "casual," "naturalized," and "invasive" with reference to introduced plant taxa. The terms "invasion" and "invasive" have clear operational meanings in ecology. To change these to match inappropriately worded policy statements would, in our view, do nothing to help anybody.

To be sure, many invaders do have a strong negative impact, and terms like "weeds," "environmental weeds," "aquatic nuisance species," "exotic pests," "transformers," or "non-native edificators" are used for such invaders (e.g., Schenikov 1964, Reed 1977, Wells et al. 1986, Center et al. 1991, Pyers et al. 1995, Richardson et al. 2000, Worboys et al. 2001). In the United States, for example, many states have "Exotic Pest Plant Councils" to deal with harmful invaders in natural and seminatural areas. Also, it is important to note that perhaps the most important "policy" document of all relating to biological invasions, the Convention on Biological Diversity, is crystal clear with respect to which alien species need to be the target of control actions. Article 8(h) of the Convention reads: "Prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species" <http://www.biodiv.org/convention/articles.asp>. The U.S. Congress Office of Technology Assessment (1993: 52—53), in a landmark assessment of the status of harmful alien species in the USA, also does not equate "invasive" with "harmful," and clearly defines key concepts with respect to ecology rather than human perception.

We believe that the definition of invasive proposed by Davis and Thompson (2001) would be more hindrance than help to conservation efforts. Some in the general public, and particularly those involved in commercial interests that use non-native species (e.g., the nursery trade, cattle and sheep ranchers in the New World, and foresters), have the mistaken impression that conservation practitioners oppose the introduction and use of all non-native species. The cooperation of many of these people will be necessary, however, to bring about changes in public policy and to assure approval of funding for large-scale efforts to prevent and control harmful invaders. It is therefore incumbent upon conservation practitioners to clearly articulate that they are concerned only with those species that have negative impacts on the native populations, species, communities, ecosystems, and natural processes that they seek to protect. Use of terms such as "environmental weeds," "harmful invaders," "exotic pest species," or "transformer species" better convey this important point.

In summary, broad, inclusive definitions are more productive in situations where special terms for particular subsets of included phenomena already exist. Hammering a generally accepted broad term into something narrower causes much more confusion than clarification. Ecological terms like succession, ecosystem, or diversity are illustrative examples.

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H.A. Gleason and the Individualistic Hypothesis Revisited

Summary

Henry A. Gleason's individualistic concept has commonly been misconstrued as asserting that the community is a random collection of species, and the species are responding solely to the physical or abiotic envi-

ronment. Neither of these is true, but both persist in the ecological literature as part of a false dichotomy of the nature of community, impeding understanding of ecological communities. This essay reviews some of the misunderstandings of Gleason's concept by ecologists and historians in the context of his ecological work.

In his essay, "Ecological fragmentation in the Fifties," Michael Barbour (1995) described something "profoundly important" in ecology that took place in the 1950s. This "revolution" was a major event in the then long-running, and still very much with us, debate between proponents of the "holistic ecology" of Frederic Clements and the "reductionist," Henry Allan Gleason. According to Barbour, by 1960, the majority of ecologists had changed their concept of community from the "organismic," even "superorganismic," concept of Clements to the "individualistic" concept of Gleason. This revolution was not accomplished without breaking a few eggs, if not hearts or heads. It is certainly true that Gleason's individualistic concept, generally ignored before the 1950s, was resurrected and widely accepted during and after the 1950s, and Gleason's reputation as an ecologist was secured (McIntosh 1967, 1975, 1995, Nicolson 1984, 1990, 2000). The revolution, like many revolutions, was not complete. Adherents of Clementsian-like organismic conceptions persist in ecology, and a preference for holism over reductionism is widely evident, often independently of any direct influence from Clements's writings. Loucks (1998) noted the need to seek an equilibrium between the two, "thus the challenge for ecosystem studies is to balance a desire to explain outcomes by looking at parts of complex systems (reductionist view) against the desire to understand how the parts work together in a fully functioning system (holistic view)."

As is not uncommon in debates about a well-established idea or paradigm and a contrary paradigm, there has been a tendency to polarize the viewpoints (Underwood 1986) and, in some cases, to misinterpret them. The term "paradigm," derived from the work of Thomas Kuhn (1970), has been commonly used to refer to the major positions in this debate, indicating that they are not merely competing scientific theories, but differing conceptions of the nature of the underlying natural reality and the form of scientific practice best suited to reveal it. A persistent theme in the discourse about Clementsian vs. Gleasonian views has been the interpretation of Gleason's individualistic concept in ways that neither Gleason, nor subsequent proponents, ever intended. This has the advantage of simplifying efforts to discredit a position, but does not further the attempt to clarify the differences or advance the argument. The purpose of this essay is to examine ways in which Gleason's individualistic concept has been misconstrued. Some scientific critics of the individualistic concept have said that it held that the ecological community was a random aggregation of species from the available species pool. Other ecologists have asserted that Gleason's concept entailed that the relations among species were due solely to the conditions of the physical (abiotic) environment, and that the interactions (biotic) between and among organisms were not important.

Gleason's work has attracted the interest not only of ecological scientists but also of historians of ecology. It might be supposed that careful historical scholarship would have produced a clear and balanced account of Gleason's views on the nature of vegetation. This has, however, not always been the case. Like their scientific colleagues, historians of ecology have often worked with partial or partisan characterizations. We will comment upon several historian's versions of Gleason's ideas. We will also argue, however, that knowledge of the historical context of Gleason's arguments can help us to interpret his meaning more accurately.

In his earliest expression of his individualistic concept, Gleason (1917*a*) described it as the "Individualistic Concept of Ecology." In both later expositions (1926, 1939), he described it as "The Individualistic Concept of the Plant Association." The latter description limited the sweep of his ideas, and their implications for animal ecology, and ecology in general, were not widely recognized until later (Nicolson 1990, McIntosh 1995). Gleason (1909*a*) was himself quite clear, however, as to the close interrelation between the concepts of plant and animal ecology.

It is likely that the imputation of random combinations of species to Gleason's individualistic concept resulted from readings of his pioneer studies of the distribution of individual plant species within associations (Gleason 1920, 1922*a*, 1925, 1929). In these articles, Gleason seems to indicate that the distribution of species within stands of natural vegetation ("associations" in Gleason's usage) is usually random (Goodall 1952). If this were true, the work of future generations of ecologists would have been greatly simplified. Colwell (1985) noted the shift toward Gleason's individualistic species concept and wrote, "At the very least, the individualistic concept is currently regarded as a kind of null model for community organization . . . ." Other disputes in ecology about assembly rules had posited null models of random combinations of species. Some ecologists have mixed up the null models with Gleason's individualistic concept. Becking (1957) had thought it necessary to caution ecologists against reading the individualistic distribution of species as implying random combinations of species: "However from this the conclusion may not be drawn that tree species are independent of that gradient in the sense that they combine at random." Becking's caution was not always heeded. Many later commentators continued to identify Gleason's individualistic concept with the imputation of random combinations of species within the association, or the primacy of abiotic factors.

Daubenmire (1968), in his well-known textbook on plant communities, denied the individualistic concept, asserting that "no organism lives in a biological vacuum, as implied by the 'individualistic concept.'" He added that accepting it "is to repudiate the thoroughly documented principle of competitive exclusion." Price (1984) wrote, "In ecological time species colonize a patch simply because the conditions are adequate for survival, uninfluenced by the presence of other species on the same trophic level, or by those on levels above," attributing this to the "individualistic response paradigm" proposed by Gleason.

Liss et al. (1986) provided both misunderstandings of Gleason's thought and wrote that, according to the individualistic view, distinct kinds of communities were not evident. "Communities to the extent that they exist at all are little more than random assemblages of populations that colonize and occupy a particular site because of similar habitat requirements." They also commented, "Knowledge of how individual species populations react to the habitat and the physical conditions is of primary importance in understanding a community." The latter point was emphasized by Pound (1988), who wrote, "Simberloff, echoing the writings of phytosociologists (e.g., Gleason 1926), argued that individualistic responses of organisms to physical features of the environment are, along with chance and history, enough to explain community patterns."

Shipley and Keddy (1987) asserted that "The debate concerning pattern (of vegetation) has usually been structured as a dichotomous choice between the predicted patterns of the community-unit and individualistic concepts . . . ." They provided an analysis of numerous articles which, they said, constitute "a large body of evidence which falsifies the causal assumptions of the individualistic concept . . . ." The burden of this evidence, they wrote, is "the importance of both biotic factors as well as interactions between biotic and abiotic factors in determining the structure of such communities." It is clear in Gleason's writings on communities that he recognized the importance of biotic factors and of the interaction of biotic and abiotic factors in community structure, so it is not clear just what was falsified by this evidence.

Noy-Meir and Van der Maarel (1987) took a somewhat intermediate stance on Gleason's individualistic approach. They said he denied the importance of facilitation between species, but "recognized that competition had a role in structuring vegetation." Brown and Kurzius (1987) noted the difficulty of assigning Gleason's concept to the random pole of the debate. "It might seem logical to associate the Gleasonian concept with random assemblages, but as we shall see, species that exhibit a great deal of independence in their distribution can nevertheless show highly non-random patterns of co-existence." Southwood (1987), however, in an essay on community concept, wrote, "The Clementsian view was rejected by their contemporary H. A. Gleason who considered the association to be largely a random assemblage . . . ."

This conflation of the individualistic concept with "random assemblages" ignores the careful observation of vegetational dynamics and structure that is to be found throughout Gleason's ecological writing. It may be based upon a misreading, albeit an understandable one, of his early quantitative work.

Gleason's statistical articles on the distribution of species within plant associations are now upwards of 70 years old, and some historical contextualization is required if we are to interpret them correctly. In several of his papers (1929, 1936, for instance), Gleason stated that, within any given stand of vegetation, species are distributed more or less "at random." He assumed random distribution in order to derive his statistical expressions. However, only on a single occasion (as far as the present authors are aware) did Gleason seek explicitly to justify the conclusion that randomness was the real condition of vegetation rather than merely a heuristic assumption that aided statistical analysis:

> *But are plants distributed within an association merely by the laws of probability and chance rather than by environmental control? The fact that species and area are correlated according to a mathematical formula indicates that the former is the case.*
> (Gleason 1925)

This argument is obviously erroneous. That a distribution may be described mathematically does not prove randomness, since many other forms of distribution may be equally well mathematically described.

Gleason also implied, on occasion, that distribution was random because dispersal was accidental (1925). However, in his key 1926 paper on the individualistic concept, Gleason provided several telling exemplifications of the problematic relationship between dispersal and ecesis. Thus, he was evidently fully aware that the (partial) randomness of dispersal need not necessarily be reproduced in ecesis, the establishment of the plant. These apparent lapses in the consistency of Gleason's argument are odd, given that his writing is generally distinguished by logical rigor and meticulous accuracy of expression. To elucidate this conundrum, we must examine precisely what Gleason meant when he used the term "random."

Gleason's quantitative papers were remarkable pioneering achievements. However, their author was not well educated in mathematics or statistics (Nicolson 1990). This lack of statistical training reveals itself in the fact that, in contrast to the clarity of his prose, Gleason's mathematical exposition is occasionally difficult to follow. He is also imprecise in his use of the term "random." Gleason's technique of "random" sampling, for instance, involved the first quadrat being "located anywhere" and the others being "located successively in a pre-determined relation to the first," in a straight line or at the corners of a square, a method sometimes called stratified random sampling. This may be an effective and practical way of surveying vegetation, but it is not random sampling as a statistician would recognize it. It should be noted, however, that professional statisticians were themselves divided about the merits and the mechanics of random sampling at this time (Nicolson 1990).

Throughout his many publications on the structure of the association, Gleason failed to make a clear or consistent distinction between the notion of randomness and that of uniformity. Thus, in the same paper (1936), he argued both that:

> *It has long been known that natural vegetation is generally divided into definite areas, each of them uniform, or essentially so, in appearance and structure throughout its entire extent . . .*

And that:

> *Many carefully planned series of observations have shown that, within the extent of a single plant society, the individual plants are distributed at random, or in other words, by chance.*

Statistically speaking, these statements are formally incompatible.

A random distribution is not the same as a uniform one. When applied to the distribution of plant species within an association, the statistical definition of randomness would entail that the probability distribution of the numbers of different species occurring in any given quadrat is the same as that in any other quadrat, *and* that the number of different species in any quadrat is completely independent of the number of species in any other quadrat. In practice, a random distribution of plants in space would not be wholly uniform in appearance. Gaps and clumps would occur. But even if a quadrat could be found with, say, only one species, the probability of finding only one species in an adjacent quadrat would be exactly the same as if one had observed 20 or 30 species in the first quadrat. On the other hand, a uniform distribution, statistically speaking, is one that gives every possible value equal probability. Suppose every quadrat had between 20 and 30 species, and that the probability of those numbers of species occurring in any quadrat throughout the association was the same, then that association would display a nonrandom uniform distribution. Thus, uniformity entails a degree of spatial evenness and homogeneity.

Our statistician colleagues tell us that undergraduate students often find the difference between random and uniform distribution hard to grasp. It is hardly to his discredit that Gleason, who had no formal statistical training, also appears to be somewhat unclear on this matter. With the benefit of historical retrospection, however, we can express Gleason's meaning more precisely than he was able to do. In fact, not much reinterpretation of his writing is required. For example, it is abundantly clear that, in his groundbreaking paper of 1920, Gleason's principal working hypothesis—his null hypothesis—was not randomness within the plant community, but uniformity:

> *The use of a chosen quadrat in representing this structure [of the association] depends absolutely on the theory of the homogeneity of the association . . . . If the association were absolutely homogeneous . . . any quadrat could be chosen to represent the vegetation. Since no association is perfectly uniform, any one quadrat may by its structure accentuate the variability instead of concealing it.*

But in the same paper, Gleason's conflation of uniformity and randomness is also apparent:

> *If plants were distributed absolutely at random over the association, that is if the association were absolutely uniform throughout, separated quadrats would never be necessary.*

The confusion would seem to have sprung from Gleason's failure to appreciate that his biological null hypothesis, that is, uniformity, was different in character from the probabilistic first principles from which he derived, perfectly properly, his statistical indices.

As will be seen most clearly from Gleason (1925), the research question to which Gleason applied his statistical tests was, "Do different species grow together, on a recurring basis, within the association?" Thus, in his actual field practice, Gleason was primarily concerned quantitatively to assess not departures from randomness, but departures from uniformity. On the basis of these observations, Gleason concluded that, within the confines of any given association, species did not grow together in recurring groups:

> *In other words, environmental differences in the aspen association . . . are not of sufficient magnitude to affect the distribution of the species, unless these differences exist within the limits of a single square meter.*

As Gleason pointed out, on several occasions, it is the uniformity of an association that allows it to be visually recognized and described:

> *Homogeneity of structure, over a considerable extent, terminated by definite limits, are the three fundamental features on which the community is based. Without these three features, Grisebach would never have published his statement of a century ago; without them, all our studies of synecology would never have developed . . . Uniformity, area, boundary and duration are the essentials of a plant community.* (Gleason 1939)

It was the distinctive uniformity of the plant community that justified the use of the quadrat method to characterize it.

It should be borne in mind that one of the matters that most occupied Gleason in the formative years of his development as an ecologist was the problem of the interaction between prairie and forest in his native region, the Midwest (Gleason 1909*b*, 1912, 1913, 1917*b*). Here one could see two quite different associations in close proximity, divided by a narrow transitional area. When the ecologist passed from one association to the other, he went from one relatively uniform

form of vegetation, through a zone of very marked discontinuity, to another area of different but equally uniform vegetation. It was under these circumstances that Gleason conceived of relative uniformity as a distinguishing characteristic of the association. As explained above, Gleason's statistical investigations were predicated upon the impulse to characterize and measure this uniformity.

What, according to Gleason, were the causes of this relative uniformity within the association? First, the physical environment of any given association must itself be relatively uniform. However, his experience of the prairie/forest problem had taught Gleason that physical uniformity alone could not be a sufficient cause of vegetational uniformity. In the Midwest, prairie might grow upon soil that had previously supported forest, and forest might encroach upon prairie without any intervening change in the physical environment. Gleason was absolutely clear that what maintained the uniformity of the different forest and prairie vegetations were biotic factors, especially the influence of the dominant upon the subordinate species of each association. The shade cast by the dominant trees excluded the prairie species from the forest floor: the thick sod formed by the roots of the grasses prevented forest species from establishing themselves in the open prairie (Gleason 1927).

Hence the recognition that, when Gleason wrote "random" he often meant "uniform," leads us also to a recognition of the falsity of the assertion, frequently made as we have seen above, that Gleason's individualistic hypothesis ignores biotic factors. On the contrary, Gleason's conception of the association accorded crucial importance to interactions between and among organisms. It was such biotic interactions that imposed and maintained the distinctive uniformity of the association. Thus, he wrote in 1910:

> *The plant itself is in many cases the controlling agent in the environment; the differentiation of definite associations is mainly due to the interrelation of the component plants; and the physical environment is as often the result as the cause of the vegetation.*

And reiterated in 1939,

> *. . . the dominant plants, which are distributed over the whole area of the community, exert such a uniform effect on the other species that discrepancies in the physical environment are more or less smoothed out or obliterated.*

Gleason was, of course, well aware that the uniformity of any association was relative, imperfect, and local.

> *We all readily grant that there are areas of vegetation, having a measurable extent, in each of which there is a high degree of structural uniformity throughout, so that any two small portions of one of them look reasonably alike . . . More careful examination of one of these areas, especially when conducted by some statistical method, will show that the uniformity is only a matter of degree, and that two sample quadrats with precisely the same structure can scarcely be discovered.* (Gleason 1926)

Even within a single locality, variation was continuous:

> *. . . it became evident, from actual field observation, that two separate patches of the same association were never exactly alike, either in component species or in the relative numbers of individuals of any species and that the degree of likeness was roughly inversely proportional to their distance apart.* (Gleason 1953)

Over longer distances, association composition changed steadily, reflecting gradual environmental change. Along the floodplain of the Mississippi, for example, the forest might seem constant in composition for mile upon mile. But:

> *As the observer continues his studies further down stream, additional species very gradually appear, and many of the original ones likewise very gradually disappear. In any short distance these differences are so minute as to be negligible, but they are cumulative and result in an almost complete change in flora after several hundred miles. No ecologist would refer the alluvial forests of the upper and lower Mississippi to the same associations, yet there is no place along their whole range where one can logically mark a boundary between them. One association merges gradually into the next without any apparent transition zone.* (Gleason 1926)

Wiegleb (1989) went beyond the common bipolar representation of the dispute concerning the individualistic hypothesis in posing three hypotheses: H_0, the random assemblage hypothesis; H_1, the individualistic (Gleasonian) habitat response hypothesis; and H_2, the competitive hierarchy response hypothesis with competition an important factor among species. He clearly separated the individualistic hypothesis (H_1) from the random hypothesis (H_0), but its relation to H_2 is less clear. Gleason did not regard interspecies competition as the sole mechanism controlling community competition, as did some later animal community theorists, but he did allow it a place in influencing entrance of individuals of a species into a community and in the composition and structure of the resulting community. He did not believe that the species were responding solely to habitat.

The imputations of random combinations of species and sole response to physical environment for Gleason's concept persist in more recent references. Goldsmith (1993) extended the misinterpretation of Gleason to his successors, and asserted that John Curtis and Robert Whittaker resurrected Gleason's individualistic hypotheses, and that they, and by implication, Gleason, believed that the "biosphere is atomistic and random." He illustrated this by an analogy of ecological entities behaving "like billiard balls." Fortin (1994) posited an extreme null hypothesis of species independent of one another with no interactions between them, attributing this to Gleason's individualistic concept. Brown (1995) reviewed Gleason's individualistic concept, deeming it to be a logical consequence of G. E. Hutchinson's niche concept, although the reverse would be chronologically true. In noting a tension between community, as seen by Gleason and by Robert MacArthur, whose work was influenced by Hutchinson, Brown commented, correctly, that "it is incorrect to equate Gleasonian individualism with the influence of abiotic conditions and MacArthurian structure with the effect of biotic interactions." However, commenting later on similarities among plants inhabiting mediterranean climates, he noted that "MacArthurian structure is caused largely by biotic conditions," whereas "the Gleasonian individualism can be attributed to adaptations to abiotic interactions," which is clearly incorrect. A slightly different misinterpretation of Gleason's thought appeared in Pulliam's (1997) recollections of his own ecological education. He wrote "A Gleasonian view of the world predominated in which all niches were assumed to be full and all species were thought to be in their proper places." This may have described the view of the animal community theory of Pulliam's graduate days, but it bears little relation to Gleason's thought which had species often not in their "proper place."

Keddy and Weiher (1999) posed the dichotomous approach to communities, noting that "the theme of whether plant communities are discrete communities or random assemblages can be traced back through writings by Tansley, Clements, Gleason, Ellenberg and Whittaker," no doubt putting Gleason at the random pole. More specifically, they commented "that the rejection of Pielou's null model constitutes the first demonstration that communities occur in discrete clusters rather than random (individualistic) associations," erroneously specifying Gleason's concept.

As we have noted, when describing community composition, Gleason may sometimes have used the term "random" when he might more accurately have written "uniform." But it is important to recognize that, in other contexts, he accurately characterized processes that are genuinely stochastic in nature. Clements and his followers tended to view successional changes as proceeding in systematic, ordered series toward a predetermined endpoint. To Gleason, by contrast, succession was the product of the behavior of individual plants and, as such, was highly dependent on accidents of timing and dispersal. As he put it, "the early stages of dune communities are due to chance alone" (Gleason 1926). Succession is, thus, an area in which it is accurate to identify the individualistic concept with random processes of dispersal (Gleason 1927).

Maurer (1999) noted the confusion among ecologists about Gleason's views "Gleason's individualistic concept of community structure is often associated with the idea that interactions among species are not important in establishing the composition of a plant or animal association." Maurer recognized that negative interactions among species did not conflict with Gleason's ideas, although positive interactions did not fit as easily. However, according to Maurer, "regardless of the kinds of interactions among species in a given community, seed dispersal was sufficiently probabilistic that there must always be some degree of chance involved in which a particular set of species was able to establish persistent populations in a given community." This is a fair statement of Gleason's concept, but is, as we have seen, all too frequently extended to an assumption of random combinations of species. In some instances, negation of Gleason's concept took the form of derision. One critic commented "It is not always necessary to destroy old theories in the erection of new ones, as in the current trend to expunge Clements and climax from ecological thought in favor of Gleasonian individualism and perpetual motion" (Johnson 1999).

Many ecologists read Gleason quite clearly, "The significance of the biotic and ecological factors in the environment is acknowledged by Gleason," (Ponyatovskaya 1961). Moore (1990) wrote, "The alternative view (to Clements) pioneered by Gleason, perceives vegetation as an assemblage of individual plants belonging to different species with each species distributed according to its own physiological requirements as constrained by competitive interactions." Taper et al. (1993) reported individualistic responses of bird species, but asserted, "The fact that species respond individualistically does not imply that species do not respond deterministically to abiotic conditions and to other species."

Historians' Gleason

The first writer to write about Gleason from a purely historical viewpoint rather than a scientific one was probably Donald Worster (1977). Unfortunately, Worster rechristened Henry Allan Gleason as "Herbert" and located him at the University of Michigan in 1926, which was seven years after he had left to join the staff of the New York Botanical Garden. Worster's characterization of Gleason's views on vegetation was very concise. The climax community was, according to Worster's account of Gleason's theory, "a haphazard, imperfect and shifting organization," which is at least two-thirds accurate. Oddly, however, Worster suggested that the individualistic concept of vegetation carried the implication that "man need not worry overly much about disturbing" the natural environment. Thus, Worster represented Gleason as an apologist for technology—intensive, exploitative farming. There is nothing in Gleason's published work, nor in the several unpublished sources that are available to historians (Gleason 1944, 1961), nor in what we know of his character as a man who loved plants and the places where they grow, which sustains this view. Worster was unable to present a sympathetic, or even a balanced, assessment of Gleason because he was, as he made abundantly clear throughout his book, avowedly on Clements' side in the holism vs. reductionism debate. As one of us has argued elsewhere (Nicolson 1988), Worster based his view of the history of ecology upon an oversimplified and unsatisfactory dichotomy between good guys and bad guys.

Ronald Tobey's more detailed study of Clements and his school appeared in 1981. Much of what Tobey wrote about Clements's organicism is of considerable interest, but his account of the views of scientists opposed to Clements leaves something to be desired. Tobey's interpretation of Gleason would seem to be that he held the individualistic hypothesis because he "did not understand" the rich complexity of the Clementsian system:

> *In Gleason's universe . . . there were only individual organisms . . . This position was philosophically untenable, as any nineteenth century idealistic philosopher would quickly have shown, but Gleason . . . whistled his tune oblivious to the cemetery of buried doctrines similar to his . . . [Gleason] did not recognize the ontological problem with his concept of the species.*

As is exemplified in several of our quotations from Gleason's writings, he did not, in fact, hold that only individual organisms exist in nature. He regularly stressed that plant communities existed, and that their structure was the product of interaction between and among species. He repeatedly acknowledged that plant communities could be studied and mapped in the field. What he did maintain was that associations were not fundamental organic entities. How they were named and classified was entirely a matter of convenience. All the classificatory categories into which vegetation is arranged are human constructs:

> *Different mills produce different qualities of flour from the same wheat. The association concept is a product of our mental mills.*
> (Gleason 1931)

Far from being overly simplistic, as Tobey implies, Gleason's theory of classification was sophisticated and forward-looking, as Whittaker acknowledged in 1962. It is a tenet of most modern classification theory that whether or not any particular classification should be regarded as valid can only be judged in terms of the practical context within which that classification is deployed (Bloor 1982). This is certainly close to, if not identical with, Gleason's views on the classification of vegetation.

Hagen (1992) provided a more balanced picture of the Clements/Gleason debate than his predecessors. However, he characterized Gleason as an armchair theoretician who "never collected data to support his claims." This is unjustly to ignore Gleason's several very substantial contributions to American field ecology (for instance Gleason 1907, 1909*a*, 1910, 1912, 1918, 1924), all of which are relevant to an understanding of his ideas. The foundations of Gleason's theory lay in his considerable experience of vegetation, both within and outside of the United States (Gleason 1915). The point we wish to emphasize here is that Gleason's papers on the individualistic concept must be understood, and assessed, in the context of the totality of his work in ecology. If this is done, there will be no doubt that his theoretical arguments had a substantial empirical base.

Hagen makes a stronger point when he cautions against making too complete an identification between the individualistic concept and more modern views on vegetational structure. Certainly it would be unrealistic wholly to equate the individualistic concept with advanced niche theory, sensitive as Gleason undoubtedly was to the importance of competitive interactions between species, and the fact that no two species had identical environmental requirements (Gleason 1917*a*). On the other hand, Hagen's assertion that "Gleason did not use natural selection to justify his claim that ecology could be reduced to the activities of independent individuals," would seem to be unfounded. Again, if one considers the individualistic concept against the background of Gleason's work in ecology as a whole, it will be seen that he regarded floristic evolution, adaptation, and migration as among the principal factors that determined the character of long-term vegetational change (Gleason 1922*b*, 1923)

Both Tobey and Hagen criticized Gleason for arguing that the association was not an organism because it did not have definite boundaries. But, in fact, Gleason did not advance any such opinion. He certainly pointed to the importance of recognizing that continuous variation in vegetational composition occurred, such as along the floodplain of the Mississippi. In his view, the absence, in this context, of a definite boundary between very different forms of vegetation was indeed suggestive of the lack of a definite structure to the association. But Gleason knew very well that, under different circumstances, associations might have clear-cut boundaries, as exemplified by the prairie and forest communities of the Midwest. He argued, however, that the existence of these definite boundaries was equally explicable in terms of the individualistic phenomena of plants. The boundary between forest and prairie was not produced by any emergent function of those two associations. Contra Clements, Gleason's consistent thesis was that, whether or not they have definite boundaries, associations have no functional properties beyond the sum of the functions and interactions of their constituent plants.

Gleason's understanding of the relation of plant to environment and other organisms was clear as early as 1910, when he noted that establishment of a plant is conditioned as much by other plants as by the physical environment (Gleason 1910). In the 1917 exposition of the individualistic concept, he wrote, "One of the most important features of the environment is the control of the original physical features by the plant population itself." In the same version, he asserted, "As soon as the ground is occupied competition restricts it (the plant) to its proper proportion." In 1926 Gleason repeated, "it is also a fact that plants are themselves a part of the environment," and commented that dominants smooth out the physical environment. In each of his three expositions, Gleason was explicit about the effect of, even control of, the physical environment by organisms and of the competitive interactions among the plant species.

Persistence of implications of communities formed as random groups of species without interactions among themselves does not help to resolve the difficult problems of communities and succession facing ecologists. Although Gleason explicitly denied that the plant community, or association, as he called it, was an integrated unit in any sense comparable to an organism, he should not be read as suggesting that it was a random collection of species. He used terms such as "coincidence" and "kaleidoscope" in describing the plant association, and attributed an important component of chance to the arrival of propagules. Vegetation, he wrote, "varies constantly in time and continuously in space," and degree of difference increased with distance. Gleason (1939) wrote, "Into this favorable environment other species also immigrate and from all of the arrivals the environment selects the species which may live and dooms the others."

Typical of the period, Gleason focused his attention on plants. In 1939 he returned to his initial version of the individualistic concept of ecology and briefly included animals. He allowed the different capacities of animal migration, but reiterated the point that only "organisms which have reached a favorable environment are able to continue to live." Thus, species combinations are restricted and by no means a random collection of species. Nor does the individualistic concept preclude pattern in communities. Gleason recognized that differences in a series of communities cumulate with distance "so that the ends of the series may be strikingly different although connected by apparently negligible differences." The search for pattern and rules for its formation in communities was pursued by ecologists, with increasingly involved sampling and analytic technique, and was perpetuated in the work of John Curtis and Robert Whittaker (Barbour 1996). Michael Austin (1985, 1989) has added new insights. Curtis (1959) stated the essence of Gleason's concept, still sometimes misread.

> *It must not be assumed, however, that the vegetation of Wisconsin is a chaotic mixture of communities, each composed of a random assortment of species, each independently adapted to a particular set of external environmental factors. Rather there is a certain pattern to the vegetation with more or less similar groups of species recurring from place to place.*

Or even more succinctly, Curtis wrote of the individualistic hypothesis, "not all things are possible only some."

The belated recognition in the 1950s of Gleason's contributions to ecology by ecologists and, later, by historians, produced extended analysis about the nature of community. Some of the comments by ecologists and historians turned on the debate about the Clementsian organismic concept of the community unit and Gleason's individualistic concept. Austin (1999) lamented the lack of communication between the supporters of different paradigms in community ecology, which, he said, "has led to inconsistencies and lack of progress in ecology." The lack of communication is compounded by misleading communication in the case of Gleason's concept.

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A History of the Ecological Sciences, Part 6: Arabic Language Science—Origins and Zoological Writings

Arabic Civilization, like the Byzantine, was a synthesis; in this case, primarily of Arabic, Byzantine, and Persian cultures (von Grunebaum 1970). Because Arabic and Persian cultures did not emphasize science, and because Byzantine science barely rose above the mediocre level of Roman science, one might guess that Arabic language science would be no better than Byzantine science. Much of it certainly was not better, but a significant portion of it was. The greatest achievements were in mathematics, astronomy, alchemy, physics, and geography. Almost all surveys of Arabic language science have neglected zoology (Anawati 1970, Huff 1993, 2000, Turner 1995, Rashed 1996, Dallal 1999) and sometimes botany; the notable exceptions are by Nasr (1968, 1976) and Sezgin (1970:357–380). Zoology was disseminated mainly through interesting animal stories, but was also pursued through medicine, veterinary medicine, hunting, and pest control (Bodenheimer 1928:128–167, Petit and Théodoridès 1962:171–180, Pellat et al. 1966). Professor Remke Kruk's studies provide the basis for a new synthesis on the history of Arabic language zoology, which we hope he will someday provide.

Alexander the Great had wanted to conquer Arabia, but died in Babylon before he made the attempt. What was there to conquer? Excepting Yemen in the far south, it consisted of oases, camel caravan trails, and desert—not an environment favorable for the flowering of complex civilization. No one had ever united the tribal Arabs, and around the year 600, there was no awareness that anyone ever would. Yet only a decade before, the charismatic Muhammad of Mecca began retreating into a cave to meditate and listen to a voice telling him to lead his people away from paganism to worship the one god, Allah. Muhammad would be Allah's prophet, and the religion he preached would unite the Arabs in religion and would also provide a means for uniting them politically. Although intolerant of paganism (which much later included Hinduism), Muhammad saw himself as the last of the Hebrew prophets (including Jesus), and therefore he tolerated Judaism and Christianity, even though adherents to those faiths paid more taxes and had fewer rights than Muslims.

The Arabs lacked science in their indigenous traditions, but the cultural, political, and military momentum that Muhammad set in motion continued after his death in 632, and Arabs were willing to learn from those they conquered. Within a century, a vast empire stretched from the Atlantic across North Africa, Syria, Mesopotamia, and Persia to the Indus Valley in India. Arabic was the language of Islamic religion, and it also became the language of most of the conquered lands, excepting mainly Iran and, later (after they became Muslims), the Ottoman Empire, although many Iranians and Turks read Arabic. It was too vast an area to govern for long using medieval communications and transportation, and gradually it separated into various states. Not only the Arabic language, but also commerce and culture, persisted over vast regions after the large empire began to break down.

The Umayyad dynasty established the first Muslim Caliphate at Damascus in 661. From the start, they were Hellenized and they encouraged scientific studies. However, they lacked the religious fervor of the Abbasids, who overthrew them in 750 and moved their Caliphate to Baghdad. The second Abbasid Caliph brought men of science to Baghdad, the third ordered the collection of Greek treatises, and the fourth established, about 828, a House of Wisdom to sponsor translations from Greek into Arabic, although many of them were first translated into Syriac, then from Syriac into Arabic. Much care went into the translations, but some confusion was inevitable, as when the same Arabic word, qunfudh, was used for hedgehogs and sea urchins (Kruk 1985). Later on, the House of Wisdom inspired other scientific institutions in Cairo, Cordova, and elsewhere in the Islamic civilization (Rosenthal 1975). Arabic language science was studied and advanced over a very much larger territory than were Greek and Roman civilizations. Libraries were valued, and many were created. Acquisition of paper-making techniques from the Chinese during the 700s made this practicable. Institutions of higher learning, called madrasas, also developed, but they focused on religion and Islamic law and lacked courses in science. Some professors taught science in their homes (Huff 1993:74–75). Muslims followed the Byzantine example of supporting hospitals and teaching medicine at them (Savage-Smith 1996:930–936).

Two early writers on animals were from Basra, Iraq. ‘Abd al-Malik al-Asma’i (739/740–c.831), wrote works on wild animals, horses, camels, and sheep (Sarton 1927–1931:I, 534–535) and influenced his younger, more famous contemporary, Abu ‘Uthman ‘Amr ibn Bahr (*c.*776–868/869), who is known to history by an unflattering nickname, al-Jahiz (goggle-eyed). He was a highly esteemed author in the tradition of Aelianus and Timotheos, and had access to an Arabic translation or paraphrase of the Aristotelian *Historia Animalium*, possibly Ibn al-Bitriq’s, completed about the year 815 (Kruk 2001*a*). Al-Jahiz’s stories of about 350 kinds of animals contain some original observations (Kopf 1952, Lewin 1952, Bodenheimer 1958:194–195, Pellat 1969, Plessner 1973). Bayrakdar’s case for al-Jahiz being an evolutionist is unconvincing, but his narrower claim that he “recognized the effect of environmental factors on animal life” (1983:151) seems valid. Apparently, al-Jahiz was the first to discuss food chains, although his details are not always accurate. He claimed that “the lizard is clever in hunting the snake and fox.” Perhaps his source was translated into Arabic from a book claiming that the snake and fox are clever in hunting the lizard. He continued (VI, 133: see Asin Palacios 1930:38–39 [in Spanish], and Zirkle 1941:84–85):

> *The mosquitoes go out to look for their food as they know instinctively that blood is the thing which makes them live. As soon as they see the elephant, hippopotamus or any other animal, they know that the skin has been fashioned to serve them as food; and falling on it, they pierce it with their proboscises, certain that their thrusts are piercing deep enough and are capable of reaching down to draw the blood. Flies in their turn, although they feed on many and various things, principally hunt the mosquito. . . . All animals, in short, can not exist without food, neither can the hunting animal escape being hunted in his turn.*

This is the earliest known description of a food chain. Al-Jahiz’s animal stories remained immensely popular and influenced later writers.

‘Abd al-Latif (1162–1231) was born in Baghdad and became an outstanding physician (Sarton 1927–1931:II, 599–600). He lived in Cairo (1191–1204) and collected information on Nile crocodiles and different kinds of lizards. His accounts of their natural history were based upon both his own observations and previous descriptions. He assumed that crocodile eggs would produce either crocodiles or skinks, depending on whether the hatchlings took to water or to the sand (Provençal 1992). This became part of the traditional folklore.

The only Arabic language rival to al-Jahiz’s animal book was one by Muhammad al-Damiri (1341–1405), a professor at Cairo’s Al-Azar University. Al-Damiri’s *The Life of Animals* is a scholarly encyclopedia that summarizes a vast amount of information (Al-Damiri 1906–1908), although it lacks original observations and includes imaginary beings such as the mount on which the Prophet rode to heaven: it had a human face, horse’s mane, and camel’s feet (Somogyi 1950, Vernet 1971:549). Clearly, there was an increase in information about animals during almost six centuries separating al-Jahiz and al-Damiri, but there was no one to separate the gold of science from the dross of folklore.

“Books of useful knowledge” often contained chapters or sections on animals. Ibn Qutayba (828–884/889), from Baghdad, was a younger contemporary of al-Jahiz who served as a judge in Dinawar, Iran, before returning home to teach (Huseini 1950, Lecomte 1965, Kunitzsch 1975). Possibly he had access to the same Arabic version of Aristotle’s *Historia Animalium* as al-Jahiz used (Bodenheimer and Kopf 1949), and he had access to some unknown Arabic language work on agriculture, perhaps a translation of Kassianos Bassos’ *Geoponika* that no longer exists. Ibn Quayba also drew upon Arabic folklore, which could be quite unreliable. His *The Choice of Transmitted Information* has 22 chapters on animals, one on plants, and one on stones. Examples of his folklore are: horses have no spleen, camels no bile, and male ostriches no marrow in their bones (IV.11); giraffes are produced from hybrids between female camels and male hyenas, and males from that mating mate, in turn, with wild cows (IV.12). Some of his information seems based on observation, but often accompanied by hasty generalizations. In a chapter on “Animals hostile to each other,” he plausibly reports (IV.13) that there are hostile relations between owls and all other birds, and therefore other birds will attack an owl during the day when its poor eyesight renders it harmless, “but when the night comes, nothing can withstand it.” More problematic, however, is his claim in the same chapter that "Hostility exists between the ass and the crow and between the serpent and the pig; whereas the crow maintains friendly relations with the fox and the latter with the serpent." His unknown authority on agriculture reported that "Between the cabbage and the vine there is enmity; if cabbage be planted in the vicinity of a vine, one of the two will wither and shrivel" (IV.33).

Abu Hayyan al-Tauhidi (d. 1009?), who may have been Iranian, was an intellectual who earned a meager living in Baghdad by copying books. He compiled a book of knowledge meant to entertain and to inspire wonder at the wisdom of creation. Its discussion of animals contains some material not known from other Arabic-language sources, but it also drew heavily from a version of Aristotle's *Historia Animalium* and a version of *Physiologos* (Kopf 1956:398).

Two scholars from Qazwin, Iran, who wrote on science are named al-Qazwini for their home town; they may or may not be related. Zakariya al-Qazwini (c.1203–1283) went to Damascus for an education and then served as a jurist in Iraq (Ahmad 1975). The first of his two works, *Wonders of the Creation*, is on cosmography. Drawing upon both Greek and Arabic-language sources, this work showed vast knowledge, but little originality or critical thinking. He discussed, for example, not only plants and animals, but also angels, without making clear that knowledge of the former comes from observations, whereas knowledge of the latter comes from religious writings. (Some of his accounts were translated into German by E. Wiedemann [1916], and extracts from that were translated into English by Bodenheimer [1958:216].) His other work, on geography, was entitled *Wonders of the Lands* in the first version (1262) and *Monuments of the Lands and Histories of the Peoples* in the second version (1275). It is a dictionary of towns and countries that gave some indication of latitude and longitude, and also discussed the influence of locations on the people, plants, and animals. Hamdullah al-Qazwini (b. 1281/1282) was a financial officer for Abu Sa'id, the Mongol Il-Khan. He wrote three works: a universal history, a rhymed Persian history, and *Hearts' Delight*, a science encyclopedia, of which two parts are available in English: geography (discussed in Part 7) and zoology (Stephenson 1928). He divided animals into domesticated (a sampler is in Nasr 1968:118–125) and wild. The most important section of each discussion contained the "properties" of a species—what each part could be used for, according to folklore.

Hunting was a sport for many upper-class Muslim men, and there are manuals on falconry and other kinds of hunting, written by an Arab, Moamin, an Iranian, Ghatrif, and others (Tjerneld 1945, Viré 1960), and a memoir by a Syrian hunter, Usamah (1095–1188), who observed or participated in hunting by both falconry and other means (Hitti 1929). However, these writings added little to natural history beyond what was known from other sources. Arabic language authors also wrote on horse medicine (Viré 1965, Karasszon 1988:116–129).

Several aspects of zoology were widely discussed in Arabic-language medical literature. The common assumption that Islamic civilization forbade dissection of human cadavers or even animals is incorrect (Savage-Smith 1995), although there were few significant discoveries made during such investigations. There are several indications that Arabic-language medical authors enriched the understanding of parasites, gained when the medical encyclopedia by Paul of Aegina (died after 642) had been translated into Arabic (Théodoridès 1957, 1966:136–137, Hoeppli 1959, Part I). Al-Razi (c.854–925) was a leading medical author (Pines 1975) who discovered that a skin disease previously ascribed to an injured nerve was actually due to parasitic Guinea worms (Stewart 1950, 350), although the source of the worm was unclear. Generally, physicians followed the Greco-Byzantine tradition in accepting the spontaneous generation of parasites (Kruk 1990, 1999*a, b*). Two leading medical authors, Ibn Sina (Latinized as Avicenna, 980–1037) and Ibn Rushd (Latinized as Averroës, 1126–1198; Arnaldez and Iskandar 1975), wrote commentaries on Aristotelian zoological works, and a section of Ibn Sina's *Shifa* on animals was translated into Latin during the early 1200s by Michael Scot. As a medical reference, Ibn Sina's *Canon of Medicine* was second in importance only to Al-Razi's *Comprehensive Book of Medicine* (Anawati and Iskandar 1978). The *Canon*'s chapter on intestinal worms (which Ibn Sina believed arose from fermentation) was translated into English by Khalil (1922), who also discussed the identification of four kinds of worms described. Ibn Zuhr (c.1091–1162) was a physician from Seville, Spain, whose two important medical texts indicate some progress in knowledge of parasites. For example, he described the itch mite (Théodoridès 1955, Hamarneh 1976).

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The Ecosystemic Life Hypothesis III: The Hypothesis and its Implications

In the first article in this series (Fiscus 2001), I introduced the ecosystemic life hypothesis as a potential solution to conceptual roadblocks that I encountered when trying to define ecological health. In the second article (Fiscus 2002), I presented four concepts that, when connected together, suggest life and ecosystem are inextricably linked. In this final article, I present the ecosystemic life hypothesis proper and discuss its far-reaching implications.

The ecosystemic life hypothesis melds the ideas of coupled transformers (Lotka 1925), ecological origin of life (Odum 1970), ascendancy (Ulanowicz 1997), closure to efficient cause (Rosen 1991), and others mentioned in the previous two articles into four propositions. I preface the hypothesis using additional concepts of emergence, phase transition, and bifurcation, but do not define these here; for these I follow the work of Holland (1995), Kauffman (1993), and Prigogine (1996), respectively.

Preface concepts

A) Life is an *emergent property* of physical and chemical dynamics. Thus it requires physical and chemical dynamics, but is also *independent* of those dynamics to a degree described within the concept of emergence.

B) The original emergence of life from nonliving dynamics was a *bifurcation* into two alternate system states. This bifurcation was also a *phase transition* in which dynamics began qualitatively new behavior.

The hypothesis:

1) The bifurcation at the origin of life resulted in *two functional pro-*

cesses: a molecular string *composer* (proto-autotroph) and a molecular string *decomposer* (proto-heterotroph). The composer function is to harness energy (solar, chemical, or thermal) to form chemical bonds and build molecular strings. The decomposer function is to harness energy in chemical bonds made by the composer, and to break molecular strings into component parts. The composer also stores energy in molecules, and the decomposer also dissipates some of this stored energy.

2) The bifurcation into composer and decomposer had the special property that the two system states (or functional subsystems) were *interdependent.* The composer–decomposer system thus had whole-system capacities that neither subsystem possessed in isolation. These capacities provided a greater ability to survive or persist as a dynamic process in a changing environment—a greater capacity for sustained production.

3) The *coupled complementary processes* inherent in the composer–decomposer system are necessary for life to persist (to sustain physical–chemical dynamical operation) because they counter the two most fundamental threats to life simultaneously. These threats are disorganization (as in dilution) and over-organization (as in crystallization).

4) The ecosystemic organization of life from its origin onward is more fundamental than the cellular or organismic forms of organization. The composer–decomposer system is the common ancestor of both metabolic and genetic processes, both of which are processes of molecular string composition and decomposition integrated with energy storage and release. Thus cells were generated later via a process of "encapsulation and miniaturization" (Odum 1970). The ecosystem (autotroph integrated with heterotroph) is the general, self-perpetuating form of life, and cells and organisms are special-case subunits of life that cannot persist in isolation.

This hypothesis provides insight into life's capacity for open-ended evolution. The simple functional forms of composer and decomposer operate as a team and, in doing so, are mutually causal; each helps to create and recreate the other (see Macy 1991 on mutual causality). As their operations in concert are iterated many times, varied combinations of molecular building blocks generate the novelty necessary for evolution. The composer–decomposer split is also the genotype–phenotype split, as the composer and decomposer functions (phenotypes) both also involve molecular strings (genotypes). This is not to say that the molecular strings themselves embody all necessary capacities of life, as I think the cycling first provided by "circulating seas" (Odum 1970: Fig. 1) must have been internalized as well.

Cross-coupling of positive and negative feedbacks in the composer–decomposer system enables life to navigate a window in which entropic (dissipative, disordering) and syntropic (concentrating, ordering; from Fuller 1979) forces are played one against the other, and neither dominates. The fact that all known ecosystems depend upon autotrophs and heterotrophs then becomes not an emergent result of interaction or coevolution, but a unique integration of component part and systemic whole that is the signature basis of life. The hypothesis may be paraphrased thus: life achieves its independence through interdependence. It also suggests that the kernel of the part-to-whole organizational innovation that is the key characteristic of life is the ecosystemic organization of energy flow coupled to nutrient cycling, two topics usually covered in Ecology 101.

Discussion

Because ecosystems have always been conceptualized as fluid in their boundaries with the physical environment, even mutually influential, they provide a better bridge between nonlife and life than do the much more clearly bounded units of cell or organism. The ecosystem is thus a plausible intermediate dynamical realm between physics/chemistry and cellular/organismic life. The congruence of Odum's (1970) ecological origin of life scenario—in the functional coupling between the production and consumption processes—with the concepts of Lotka, Ulanowicz, and Rosen, enables integration of their views in a constructive conceptual framework of life as ecosystemic in origin and in fundamental nature.

Kauffman (1993) and others have developed the importance of autocatalysis for understanding life and pre-life, but only recently has this concept been extended to highlight the ecosystemic life paradigm. Lee et al. (1997*b*) talk of "molecular symbiosis" and also "molecular ecosystems" (Lee et al. 1997*a*) arising from autocatalysis and self-replication.

One way to falsify this hypothesis would be to find a system with only one functional type, either composer or decomposer. As a "thought experiment," the prospect of finding a system with only autotrophs or only heterotrophs seems absurd, but this does not alter the fact that it would refute the claims presented. This gut feeling does show how the idea of ecosystemic life appears at once trivial and profound. Another potential challenge to the hypothesis may be the Archaea: ancient microbes, some of which inhabit hot springs, thermal ocean vents, and other such forbidding environments. I admit scant knowledge of the ecological and biological dynamics of this group, and they may well prove the views here wrong.

However, if I were to redo my master's degree research—to start over in my search for an indicator of soil ecological health—I would be much aided by the ecosystemic life hypothesis. In fact, I would approach the problem in a fundamentally different way. First, with the help of Ulanowicz' focus on autocatalysis and loops of causality, and Lotka's emphasis on whole systems, I would seek initially to sketch a larger, "full-circle" picture of the dynamics in which soils are embedded. As Ulanowicz (1997) shows, the choice of system boundary can make all the difference between seeing dynamics as mechanical vs. nonmechanical. From an enlarged view including all major energy and material flows, it becomes clear that nematodes cannot be significant to production or sustainability in conventional agriculture (an assumption mentioned in Fiscus 2001: Part one); the subsidies of nutrients provided via fertilizer make their role in mineralization irrelevant. Second, I would seek as benchmark a reference set of dynamics or a reference part-to-whole relationship, rather than indices measured at some reference site. In other words, I would not seek to map quantitative measures such as diversity or functional group abundance ratios between reference and study sites, but would compare qualitative, systemic relationships between the two.

Based on this revised approach, I would assess ecological health by the degree to which a system possesses the intact kernel of composer and decomposer subsystems operating in concert. This organizational integrity enables natural systems to operate using renewable energy while also achieving a high degree of materials recycling. Thus, all three properties—composer–decomposer integration, renewable energy, and recycling materials processes—are the systemic keys to life's capacities for sustained production and open-ended evolution. This approach instigates a shift in perspective away from assessing health by monitoring nematode communities in soil systems (or any such specific ecological indicators). Ironically, it is the functional irrelevance of nematodes in the enlarged context of agriculture that helps to elucidate the conceptual problems with ecological health.

Using a qualitative, systemic criterion for ecological health, the systems with poor health are immediately apparent. Only the human-driven aspects of agricultural systems fail to keep composer and decomposer functions integrated. From this unhealthy systemic organization arise two negative symptoms and a dire prognosis. Conventional agricultural systems decouple composer and decomposer processes and are highly dependent on nonrenewable energy and nonrecycling materials processes. From the conceptual framework of ecosystemic life, such systems lose the capacity for open-ended evolution, and system trajectories are therefore predicted to move toward an evolutionary dead end. This approach also reveals why I sensed infinite regress in trying to hem in soil ecological health initially. Human disturbance may knock soil systems back in developmental status, complexity, diversity or maturity, but it does not alter the inner source of health. No matter how disturbed by agricultural practices, the life in soils possesses the capacity to restore itself.

Ecosystemic life (as an integrative or "connectionist" concept) may also help resolve recurring conceptual problems within ecology. Three examples of major concepts with which ecosystemic life is consistent simultaneously are: (1) The diversity–stability debate (diversity sometimes helps, sometimes hinders stability); (2) The bottom-up vs. top-down ecosystem control debate (ecosystem dynamics are sometimes driven by primary producers, sometimes by higher trophic levels such as keystone species); (3) the unit vs. assemblage debate about succession (communities and ecosystems sometimes appear to act like superorganisms, sometimes like assemblies of nearly independent individuals and species). When viewing life as a unified whole requiring two complementary functional units, and thus two intertwined dynamical aspects (ebbs and flows between diversity and stability) bottom-up and top-down control and unit vs. assemblage behavior are to be expected. Ecosystemic life provides a framework by which two seemingly contradictory ecological principles can be true at once, much as the dual or complementarity theory of light does in physics.

I did not cover here all concepts and workers who have contributed to these discussions. I mention Pattee (1973), Maturana and Varela (1980), Root-Bernstein and Dillon (1997), Lovelock (1993), and Margulis et al. (2000) as contributors whose works necessarily must be included in a comprehensive study of these topics.

Summary

The ecosystemic life hypothesis inverts the current working assumption that life originated and developed from the cell or organism in general to the ecosystem in the specific. It also alters the assumption that ecological dynamics are strictly emergent properties arising, from the bottom up, from interactions of many independent organisms or agents. Instead, organisms are seen as emergent properties of ecological, network dynamics of energy flow coupled to nutrient cycling. The irreducible or nonfractionable kernel of complexity is the interoperating composer–decomposer system of energy capture and materials cycling. Depew and Weber (1995) state this inversion as the position of a school of thought within systems ecology: "From their perspective, ecosystems are not perspicuously viewed as loosely integrated superorganisms. . . . On the contrary, reformed systems ecologists tend to view organisms as very tightly integrated ecological systems." If this systems ecological approach turns out to be better than an organism-centric approach to understanding life, it could have great implications for how we conduct ecological and life science.

Whole-part integration—focus on whole-to-part and part-to-whole relationships in living systems—which I attempt to employ and develop here, is a synthesis of reductionism and holism. This hybrid paradigm promises meaningful development of the concept of ecological health, as well as other benefits perhaps imaginable. For example, could the ecosystemic life and whole-part approach enable design of human systems such that emergent properties, while not fully controllable or predictable, could be steered toward the beneficial? The ultimate benchmark for system health and quality, as well as the ultimate role model, mentor, and design guide for human policy and development realms, may well be life itself.

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Gray Matters in Ecology: Dynamics of Pattern, Process, and Scientific Progress

Introduction

Has ecology stagnated as a scientific discipline? More specifically, does ecology lag behind other areas of scientific inquiry in terms of progress toward achieving greater understanding, and if so, why? In a provocative essay, O'Connor (2000) criticized the pace of progress in ecology, arguing that other life sciences, especially areas such as molecular biology, have progressed at a far more rapid rate. He contended that a central problem is a focus by ecologists on "what" questions rather than "how" or "why" questions. Questions of the former type result in description of patterns, whether observational or statistical, whereas questions of the latter type result in examination of processes hypothesized to generate these patterns. O'Connor (2000) asserted that the most important distinction between ecological–environmental sciences and "successful" life sciences is that the latter "has developed ideas about how things work whilst ecology has retained a focus on what is." Most ecologists, including O'Connor, recognize that progress in ecology depends on both pattern recognition *and* process evaluation. At issue is whether pattern-based studies have dominated ecological research programs to the detriment of the process-based studies. Rather than attempt to address whether ecology lags behind other disciplines, we ask why ecology does not progress at a more rapid rate. Specifically, our purposes are to (1) test the hypothesis that ecology is fixated on "what" questions, (2) identify alternative mechanisms that might impede the rate of scientific progress in ecology, and (3) suggest actions required to alleviate these impediments.

Historical perspective

The views of O'Connor (2000) present an interesting and timely contrast to those of Robert MacArthur, who opined in his book *Geographical Ecology* (1972:1) that "To do science is to search for repeated patterns, not simply to accumulate facts, and to do the science of geographical ecology is to search for patterns of plant and animal life that can be put on a map." Of course, MacArthur and his academic descendants did more than identify patterns; they proposed mechanistic hypotheses to explain the causal processes underlying the observed patterns (Morris et al. 1999). Nonetheless, a major emphasis of MacArthur's ecological paradigm undeniably involved the characterization of pattern, and the threads of this paradigm are woven throughout much of modern ecology (Brown 1999, Morris 1999).

Our thesis is that science, including ecology, has as an ultimate goal: the understanding of processes underlying observed patterns. In simplified form, then, scientists proceed by recognizing a pattern and subsequently devising studies to evaluate competing hypotheses regarding the causes of the pattern's existence. Within this context, progress in science may be estimated by the rate of process-based discovery. O'Connor (2000) claimed that ecology lags behind successful life sciences because ecologists have remained fixated on descriptions of patterns. Regardless of whether ecology lags behind other biological disciplines (and we believe that it does in some instances), it is instructive to assess the validity of the mechanism proposed by O'Connor (2000). We have written this paper with three objectives in mind. First, we provide an empirical test of the "fixation" hypothesis by asking whether the relative frequencies of pattern- vs. process-oriented investigations in ecology have shifted over time. Second, we introduce a simple, ecologically motivated conceptual model of the dynamics underlying rates of scientific change. We use the model to generate predictions explaining variation in rates of scientific change, and we test the validity of the predictions with respect to ecological studies and the terminology of ecology. Finally, we return to the issue raised by O'Connor (2000), namely, why ecology lags behind other life sciences, and identify shortcomings that must be overcome if the rate of process-based discovery in ecology is to keep pace with other disciplines in biology.

Are ecologists fixated on patterns?

To test whether the discipline of ecology has experienced an increase in the frequency of process-based studies over time, we reviewed 180 articles published in *Ecology* during the 80-year interval 1920–2000. Starting with Volume 1 (1920), 20 articles were examined from each volume published at 10-year intervals. Within a volume, articles were selected randomly and without replacement. Notes, editorials, and reviews were omitted from consideration, as were articles that dealt strictly with methods or theoretical modeling.

Central to our analysis was an ability to score articles along a continuum ranging from pure pattern recognition to pure process-based studies. We developed a scoring system that was modeled after attributes identified by O'Connor (2000) in his discussion of process-oriented research. Our scoring continuum (Table 1) ranged from 0 to 5. A score of 0 was assigned to studies that were purely descriptive, whereas a 5 was assigned to studies that reported tests of quantitative hypotheses based on a process-based body of theory. We agree with Johnson (1999) and O'Connor (2000) on the trivial nature of many null hypotheses in ecology. Thus, articles featuring statistical tests of randomness without a corresponding process-based hypothesis were assigned a score of 0 or 1. We assigned more weight to studies such as meta-analyses that synthesize patterns and suggest processes that might underlie them, irrespective of their validity (e.g., Bergmann's Rule). In keeping with O'Connor (2000), we ascribed progressively more significance to competing vs. single process-based hypotheses and to quantitative vs. qualitative hypotheses in terms of their potential contributions to process-based science (Table 1).

Spearman rank correlations revealed a significant relation between pattern–process scores and year of publication ($r_S = 0.46$, $P < 0.001$; Fig. 1). After relatively modest increases in process-based studies during 1920–1950, recent articles in *Ecology* have become progressively more process-based (Fig. 1). On the whole, then, it would appear that ecologists are not fixated on pattern-based studies. Some

Table 1. Scoring system used to quantify levels of pattern- vs. process-oriented investigations in *Ecology*, 1920–2000. We selected 20 feature articles randomly for each year and assigned a score of 0–5 based on criteria described in the table.

Score	Description of scoring criteria
0	Purely descriptive study: no prior claims of knowledge; explicit goal was a description of the system's current state
1	Pattern confirmation study: principal objective was to determine whether a previously described pattern also occurred in the current system
2	Pattern synthesis study: objectives included determination of the existence or strength of a general pattern from several previous reports, and suggestion of an underlying process
3	Simple process-based study: test of a single qualitative hypothesis based on a process-based body of theory
4	Study of competing, process-based hypotheses: test of several alternative qualitative hypotheses generated by a process-based body of theory
5	Purely deductive, process-based study: test of one or more quantitative hypotheses based on a process-based body of theory

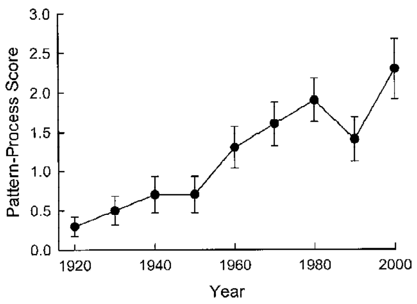

Fig. 1. Mean (±1 SE) pattern–process scores for articles published in *Ecology*, 1920-2000, based on a random sample of 20 articles from each year in 10-year increments. Pattern–process scores increased by 7.5-fold over the period, or about 2.5% per year. Definitions of scores are given in Table 1.

ecologists might even argue that traditional publication outlets for descriptive studies, such as *Ecology*, are increasingly becoming fixated on process-based studies. Recent editorial criteria for *Ecology* support the notion that process-based studies are the preferred fare. Although publication in *Ecology* originally was "open to all who have material of ecological interest from whatever field of biology" (Foreword to Volume 1, 1920), in *Ecology* today, "preference is given to research and synthesis that leads to generalizations potentially applicable to other [systems]"; moreover, the current emphasis is on "papers that develop new concepts in ecology, that test ecological theory, or that lead to an increased appreciation for the diversity of ecological phenomena" <http://esa.sdsc.edu/esapubs/Ecology.htm>.

Despite an increased emphasis on process-based studies, it is sobering to realize that the average article in *Ecology* has not progressed much beyond pattern synthesis, as evidenced by the mean score of 2.3 for publications in 2000 (Fig. 1). This value presumably is biased high for ecological studies generally, because by selecting *Ecology,* we subsampled only from studies regarded as being of high quality and because of the editorial preference for process-based studies. Why has our attainment of a balance between pattern and process not been more rapid? Stated slightly differently, what mechanisms might explain variation in progress within ecology?

A model of scientific progress

Conceptually, science can be viewed as a population of ideas. Individual ideas are "born" from the minds of researchers who recognize patterns and posit mechanistic explanations for their existence. Likewise, an idea "dies" as a consequence of critical studies that lead to rejection of the idea's correctness. The instantaneous per capita birth rate of ideas (b_i) ultimately is determined by the ingenuity of the scientists involved and by their ability to identify patterns in the phenomena being observed. Similarly, the instantaneous per capita death rate of ideas (d_i) is determined by the rate at which crucial experiments are conducted, which in turn is a function of the rate at which scientists can envision such experiments and overcome logistical barriers to conducting them. In general, greater birth *and* death rates should exemplify more productive scientific disciplines, because they combine to yield a bountiful harvest of ideas and an efficient means of separating wheat from chaff.

Rates of change of ecological terminology

The dynamics of a discipline's vocabulary represent one possible measure of the rate of birth and death of ideas. We propose that the use of new terms within ecology is a measure of b_i, the birth rate of ecological ideas, regardless of whether these terms are coined uniquely (e.g., metapopulation) or are appropriated from other fields (e.g., fractal dimension). Moreover, the disappearance of terms from the ecological literature is a measure of the death rate (d_i) of ideas. O'Connor (2000) felt that the development of distinct terminology signified that a discipline was moving toward more complex, process-driven exploration. In contrast, he felt that the vocabulary of ecologists was "imported from every day" and suggested that an ecologist from the 1930s would be comfortable reading today's issues of *Ecology*. Here, we do not consider whether papers filled with technical jargon necessarily reflect better science. Rather, we ask whether the terminology of ecology has stagnated. Are we still using the same pool of terms familiar to Elton and his contemporaries?

We addressed this question by searching the online issues of *Ecology* archived in JSTOR (Volumes 1–77, 1920–1996). The search capability of the archive allows one to search for terms used in the full text. We randomly selected 10 articles published in each 10th volume of the journal, beginning with 1944 and continuing through 1994, plus the year 2000. For each of the 10 articles, we selected a series of key words to be analyzed. We used the key words provided by the authors in all selected papers published during 1974–2000, excluding names of study sites and organisms and terms with no specific ecological meaning (e.g., "description"). For earlier decades, in which no key words were available, we selected terms from the title, abstract, or first page of the paper. We attempted to pick terms that were used to define the research—the "key" words in the presentation—and made an effort to avoid selecting only the terms with which we were or were not familiar. Our selection procedure yielded 33–61 key words per decade, with individual articles providing 2–10 words. We then searched the JSTOR archive for articles that used each term, noting the earliest use of the term, the latest citation to include the term, and the total number of citations within the database.

If O'Connor's description of ecological terminology is correct, then articles written recently should draw from the same pool of terms as articles written in the 1940s and 1950s. Thus, the average date of first citation and the average date of the latest citation of key words should be the same for each set of papers drawn from different decades. Note that we searched the same pool of articles for the terms selected in each decadal sample, so a term used in a paper in

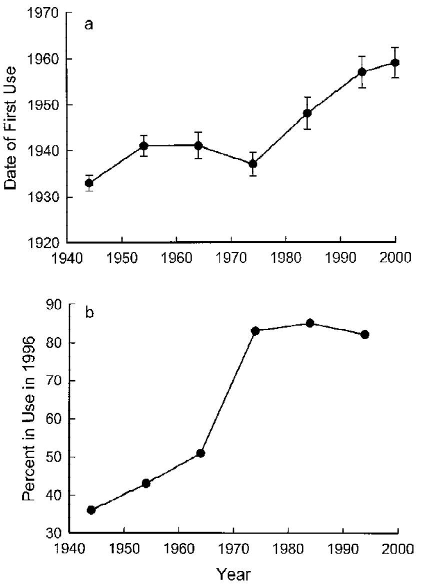

Fig. 2. Terminological "births" (a) in ecology, expressed as the mean (±1 SE) year in which a key word was first used in *Ecology*, plotted against the year in which the key word appeared in our sample. Terminological "deaths" (b) were calculated from the same sample and were expressed as the percentage of key words from a given year that still were in use in *Ecology* in 1996.

1994 would not necessarily have a later "first citation" date than a term used in 1944. In fact, if O'Connor is correct, both sets of terms (1994 and 1944) will have equal probabilities of early citation origins. In contrast, if ecological terminology is dynamic and changing, then the average year of first citation should be become progressively more recent, and a substantial death rate should occur for terms with early birth dates.

The average date when a term was first used became more recent during 1944–2000 (Fig. 2a). Each decadal sample included terms that were used in papers published in 1920, so the trend must result from new terms added in later decades. The pattern shown by the "death rates," the years in which terms disappear from the ecological literature, is simpler (Fig. 2b). We found higher rates of jargon death for terms used in early decades of our survey.

Our results partially support O'Connor's characterization of the ecological literature. Many papers, even in the latest issues of *Ecology*, use key words that have been present in the field from its inception, and terms become extinct slowly. However, our results also indicate a significant addition of new terms (Fig. 2a).

Scale dependence and scientific progress

What factors might influence the rate of scientific progress? Assume for a moment that levels of ingenuity are comparable among ecologists and other life scientists. Then r_i ultimately is determined by the rate at which empirical patterns are documented and the rate at which critical tests of ideas are conducted. We suggest that fundamental, scale-dependent attributes of biological systems can explain much of the variation in process-based science that is evident among disciplines. Specifically, we predict that the temporal scale, level of biological complexity, and spatial scale of a biological system constrain the rates of pattern documentation and process-based hypothesis testing, and thus, r_i.

If we are correct, then rates of growth in the science of ecology should vary in a predictable manner. Specifically, rates of process-based discovery should vary inversely with: (1) the generation times of the taxa studied (from monerans to sequoias); (2) the level of complexity of biological organization examined (from molecules to ecosystems); and (3) the spatial scale examined (from microscopic to global). We tested the validity of the population model of scientific progress by expanding our analysis of published studies in *Ecology* .

To test predictions 1–3, we categorized each of the 180 articles according to the focal organism's generation time, the level of biological organization examined, and the spatial scale of the study (Table 2). If a study involved more than one focal organism, the longer generation time was used, whereas average scores were computed for articles spanning more than one level of biological organization or spatial scale.

Spearman rank correlations indicated that the year of publication was related negatively to spatial scale ($r_S = -0.30$, $P < 0.001$), but was un-

Table 2. Categories used for generation time, level of biological organization, and spatial scale.

Attribute	Category	Score
Generation time	Hours–weeks	1
	Months–1 year	2
	Years	3
	Decades–centuries	4
Biological organization	Physiological–morphological	1
	Individual	2
	Population	3
	Community	4
	Ecosystem	5
Spatial scale	Microsite[†]	1
	Local habitat	2
	Landscape	3
	Regional	4
	Continental–global	5

[†] Includes experimental mesocosms and laboratory settings as well as microhabitats.

related to generation time ($r_S = -0.04$, $P > 0.25$) or level of biological organization ($r_S = -0.06$, $P = 0.18$). As predicted, pattern–process scores were negatively correlated with generation time, level of biological organization, and spatial scale (Table 3), although collinearity among the three explanatory variables makes it impossible to disentangle the relative contributions of these three variables.

To assess our model of scientific progress more carefully, we conducted multinomial logistic regression. For this regression, we rescaled the pattern–process scores to correspond to three categories: pattern only (0–1); simple process (>1–3); and complex process (>3–5). In addition, because of the high level of correlation of biological organization and spatial scale ($r_S = 0.55$), we used the sum of the two variables (hereafter termed "complexity") as an explanatory variable in the multinomial regression. Finally, to reduce the number of cross-classified categories, we recoded the generation time from four categories to three: hours–weeks, months–year, and years–centuries.

Because of the temporal trend in pattern–process scores (Fig. 1), we incorporated year of publication into our base multinomial model. Year of publication was a significant predictor of pattern–process score ($\chi^2 = 30.6$, df = 2, $P < 0.001$). Adding complexity to the base model roughly doubled the amount of variation explained ($\chi^2 = 28.5$, df = 2, $P < 0.001$), whereas adding generation time to the base model provided a smaller improvement in fit ($\chi^2 = 8.3$, df = 4, $P = 0.04$). The model containing all three main effects indicated that year of publication and complexity served as good ($P < 0.001$) predictors of the pattern–process score, but generation time did not ($P = 0.19$), due to its collinearity with complexity.

Our results indicate that process-based studies have been generated at a higher rate by ecologists studying systems at simpler levels of biological organization (e.g., ecophysiology), smaller spatial scales (e.g., laboratory or microcosm), and perhaps shorter generation times (e.g., hours or weeks).

Table 3. Spearman rank correlations (upper right triangle) and *P* values (lower left triangle) between pattern–process scores, generation time, level of biological organization, and spatial scale for 180 articles published in *Ecology*, 1920–2000.

	Pattern–process score	Generation time	Biological organization	Spatial scale
Pattern–process score	-----	-0.19	-0.39	-0.46
Generation time	0.004	-----	0.20	0.28
Biological organization	<0.0005	0.002	-----	0.55
Spatial scale	<0.0005	<0.0005	<0.0005	-----

Thus, to the extent that our underlying assumptions are correct and our definition of scientific progress is appropriate, rates of progress in ecology can be expected to vary among subdisciplines in response to these parameters. In a broader context, we suspect that these parameters collectively reflect the ease with which stochastic events can be controlled experimentally and the rate at which information regarding the system can be acquired. Disciplinary differences within the life sciences in relative rates of process-based research may thus be explained, in part, by underlying differences among systems in terms of their characteristic "life-span" and the importance of stochasticity (Bouzat 2001). Identifying and understanding the web of processes shaping the structure and dynamics of complex ecological systems (i.e., systems characterized by large spatial scales and high levels of biological organization) may pose the biggest challenge to modern ecology (J. H. Brown, *personal communication*).

Gray matters in the science of ecology

O'Connor (2000) has done ecology a favor by admonishing ecologists for our collective lack of progress in process-oriented discovery and our unhealthy appetite for trivial hypotheses. We agree that ecologists should emphasize research on questions of "how?" and "why?" and we view as a positive sign the recent developments on information-theoretic approaches to data analysis that have been emphasized in ecology (Burnham and Anderson 1998, Maurer 1998, Anderson et al. 2000). If there is a danger in a paradigm shift toward process-based research, it rests in the temptation to contrast in bold strokes of black or white the relative merits of descriptive pattern recognition and hypothesis-driven tests of processes that generate patterns. Just as theoretical developments of high quality are tied closely to their empirical inspirations (Begon 1998, Stenseth 1998), so too are pattern and process inextricably linked in science. For instance, the mapping of the human genome constitutes an eloquent example of descriptive natural history, i.e., the raw material for a geographical ecology of DNA (Shurin et al. 2001, but see O'Connor 2000). Will the flood of studies devoted to molecular-level patterns lead to subsequent conceptual breakthroughs that spawn process-based research programs? Undoubtedly. But these breakthroughs will depend upon the process-based research that becomes possible because of the enormous amount of descriptive information now available on patterns of base pair sequences that are the end-products of evolution.

Recognition of patterns provides the fuel for developing and testing hypotheses about underlying processes. Used properly, theory can lay bare the processes shared in common by a diverse array of seemingly singular ecological systems (Begon 1998). O'Connor appreciates the complementary nature of pattern- and process-based research (R. J. O'Connor, *personal communication*), but his essay

(O'Connor 2000) failed to convey the importance of the former (Bouzat 2001). Although an emphasis on contrasts is a useful pedagogical tool, it behooves us to remember that, in the real world, phenomena are seldom either black or white. In science, and especially in ecology, gray matters.

Obstacles to scientific progress in ecology

We focus on two potential obstacles to improved progress in ecology: information exchange and ingenuity. Certainly other obstacles, such as funding (Shurin et al. 2001) exist, but we have chosen two obstacles that are largely dependent upon ecologists rather than external factors.

Information systems and pattern synthesis

O'Connor (2000) argued against the notion that stochasticity and a restricted ability to conduct experiments were valid explanations for the putatively slower rates of progress in ecology, citing advances in astronomy in the absence of experimentation. Astronomy indeed serves as a model for the evolution of ecology as a science, for astronomers have successfully conducted theory-driven, process-based studies of systems spanning enormous scales and levels of complexity. Similar advances in our understanding of the complexity in ecological systems will require a merger of the reductionist approach with the synthetic power of a macroecological approach (Maurer 2000).

A synthetic approach necessitates large-scale, coordinated efforts to collect data derived from diverse ecological systems, to manage these data responsibly, and to make them readily accessible to ecologists. Descriptive natural history studies, and quantitative studies that represent a search for patterns, form the basis for these metadata. A major obstacle for ecological synthesis stems from the lack of central data repositories. Molecular biologists overcame a similar obstacle by requiring the deposition of DNA sequence databases in a common archive as a condition for publication. Once established, this database grew exponentially, from 600 sequences in 1982 to more than 10 million in 2000. This database, which became Genbank, spawned not only the human genome project but also the entire field of bioinformatics. Because of the heterogeneous nature of ecological data, ecologists have only just begun to address issues related to systematic data archiving (e.g., Baker et al. 2000, National Center for Ecological Analysis and Synthesis <www.nceas.ucsb.edu>.

The ingenuity issue: confronting the fairy tale

In Jacob and Wilhelm Grimms' classic, "Little Snow-White," a magical mirror could, at a moment's notice, canvass an entire kingdom in search of the most beautiful inhabitant. The mirror's owner, Snow-White's proud, haughty stepmother, routinely consulted the mirror, inquiring: "Looking-glass, looking-glass, on the wall, who in this land is the fairest of all?" Each time, the mirror would reassure her that her beauty was unparalleled. When, inevitably, little Snow-White matured, the mirror unceremoniously informed her stepmother that she was second best; predictably, the queen was apoplectic.

Compared to ecology, are successful life sciences and biomedical research peopled by individuals who are more ingenious, intelligent, and capable of identifying the "keystone" bricks vital to conceptual advance and thus progress? Romesburg (1991) believed so. Such blasphemous pronouncements tend to bring howls of self-righteous protest from full-blooded ecologists, or at least make hairs rise on the necks of ecologists-in-training (Knight 1993, Romesburg 1993). Surely any lack of progress in ecology must be attributable to the yokes of disciplinary complexity, insufficient funding, and other burdens borne by ingenious ecologists.

Or do we, like the queen, protest too much? Perhaps it is time to quit pouting, look into the mirror, and recognize that "the difficulty of a problem depends not only on the problem, but on the qualities of the problem solvers" (Romesburg 1991: 747). And although we wholeheartedly support efforts at professional development, we submit that heightened levels of ingenuity ultimately must come primarily from new generations of ecologists possessing keener intellects than their predecessors. If we truly are dedicated to advancing the science of ecology, then our goal should be to effect a directional selection of intellect and critical inquiry among new recruits to the discipline. We raise this issue not to offend, but because we believe that our ultimate legacy will be determined largely by two factors: the intellectual quality of our professional descendants, and the manner in which we train them to do science.

Improving the quality of scientific minds in ecology will require a commitment by practicing ecologists to market the discipline of ecology to potential recruits. Aggressive "hawking" of our professional wares will strike some as anathema and will produce angst in others. Yet if we fail to proclaim the virtues of ecology to students, if we fail to convey to the brightest young minds the intellectual challenges and opportunities afforded by our field, who will? Secondary school science classes and college-level introductory or service courses provide excellent venues for spreading the good word about ecology (Slingsby 2001). Effective marketing can take many forms, but a common denominator should be imaginative deliveries that bring ecology to life and demonstrate its relevance and complexity.

Ecologists also should examine critically the manner in which we train students to do science. Too often we "lower the bar" in introductory courses, watering down ecology to a level comfortably accessible to the majority of students, yet staid or trivial to the brightest of them. By doing so, we run the dual risk of rewarding mediocrity and losing outstanding students to other disciplines that are viewed as more challenging. Blame for diluting course content often is aimed at administrators who place a premium on student-contact-hours per faculty

FTE. But decisions on curriculum reside with faculty, so blaming administrators is passing the buck. And even if the content of introductory courses were administratively mandated, the courses provide ecologists with an opportunity to identify bright, aspiring ecologists. Instilling in these talented undergraduates the challenges presented by ecology perhaps is more effective in nontraditional educational settings, e.g., by providing research opportunities, interactions with graduate students, and individual mentoring. Progress in ecology, which deals with gray matters, will depend on our current and future investment in gray matter.

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