

ECOSYSTEM CONSEQUENCES OF BIODIVERSITY LOSS: THE EVOLUTION OF A PARADIGM

SHAHID NAEEM

Department of Zoology, University of Washington, 24 Kincaid Hall, Seattle, Washington 98195 USA

Abstract. The ecosystem consequences of dramatic declines or changes in biodiversity have spurred considerable research and tremendous debate that has rekindled most of the major conflicts in ecology, creating a sense of déjà vu. These conflicts include whether ecosystem or community ecology provides better insights into the workings of nature, the relative importance of biotic vs. abiotic factors in governing community composition and structure, the virtues of phenomenological vs. mechanistic research, the relationship between biodiversity and stability, the relative importance of taxonomic vs. functional diversity, and the relative strengths of observation vs. experimental approaches.

Although the tone of the debate has been regrettable, its magnitude signifies the emergence of a new paradigm, one in a series of debates associated with the dialectic that has structured ecological inquiry over two millennia of Western science. This dialectic concerns the tension between those who seek to explain nature by studying its parts and those who seek to explain nature by studying whole-system behavior. Philosophers and historians argue that such a dialectic generates cycles in which a central tenet is challenged by an emerging paradigm, generating new theories and new data to test the emerging paradigm. The scientific community evaluates the accumulating evidence (and it is here that the debates arise), and if subscription to the emerging paradigm increases sufficiently, the emerging paradigm evolves into a new central tenet. Fractionation within the sciences exacerbates this cycle because subdisciplines often focus on either the parts or the whole. Such splintering can be traced to the abandonment of the holistic approach of Aristotelian science during the Scientific Revolution. While such holism may have lessened debate, some have argued that it stagnated Western science. The dialectic, the cycles of emerging paradigms it generates, and the debates that surround each emergence represent the vehicle by which ecology moves forward. Emerging paradigms force scientists to revisit central tenets, pitting old ideas against new theories and new data, and this revisiting is what generates the sense of déjà vu and the cycles of vigorous debate, but ultimately each cycle leads to synthesis and progress.

The emerging paradigm that biodiversity governs ecosystem function is rapidly evolving. In the words of Thomas Kuhn, its controversial experiments have successfully articulated the paradigm. It has successfully challenged ecology's central tenet that biodiversity is primarily an epiphenomenon of ecosystem function secondarily structured by community processes. In its most extreme form, it claims that the reverse is true. Of course, neither the central tenet of ecology nor the emerging paradigm is correct in an absolute sense, but the dialectic that promoted the emergence of biodiversity and ecosystem function as a paradigm redirected ecology to focus on the feedback between ecosystem function and biodiversity rather than studying them independently. The final stage in the evolution of this emerging paradigm will be explicit tests of synthetic mechanisms that have been proposed. Familiarity with the ecological dialectic provides a framework by which ecologists can understand the origin and utility of paradigms in ecology, provides a proper context for the debate that surrounds paradigms as they emerge, promotes synthesis, and deters intellectual chauvinism that may inadvertently accompany specialization within ecology.

Key words: biodiversity; community ecology; ecosystem ecology; ecosystem function; paradigm.

INTRODUCTION

No single feature of the earth's biota is more captivating than its extraordinary taxonomic diversity. Like most captivating features, however, this diversity has been a distraction in ecological research, causing

ecologists to focus on patterns in the distribution and abundance of species while drawing attention away from a more powerful and more inclusive perspective on nature. An emerging paradigm, one that synthesizes community and ecosystem ecology while concentrating on functional rather than taxonomic diversity, promises to refocus attention on the broader significance of the earth's biota.

Exploring the implications of this paradigm for eco-

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logical research provides an example of the importance and utility of scientific paradigms. Note that paradigms are described in a variety of ways, even by Kuhn himself (Graham and Dayton 2002). Here, I have reserved “paradigm” to describe an unprecedented scientific achievement that is compelling enough to convince adherents from traditional perspectives to shift their allegiance, regroup around the new paradigm, and tackle problems anew, following Kuhn’s (1962) initial definition (p. 10). In this instance, the “compelling achievement” (Kuhn 1962:10) is the synthesis of ecosystem and community ecology in the form of a body of recent theoretical and experimental work that suggest ecosystem function is governed, in part, by biodiversity. I claim that this achievement is “compelling” because the explosion of research in this area clearly indicates either ecologists shifting their allegiance from traditional nonsynthetic views to embrace this approach or recruitment of younger ecologists to this perspective. The problem, understanding the environmental consequences of biodiversity loss, is now being addressed in a new way.

The central thesis that currently guides community ecology in ecologists’ explorations of diversity sees patterns in the distribution and abundance of species as a function of abiotic (physical and chemical conditions) and biotic factors (interactions among species such as competition, facilitation, disease, and predation). Abiotic factors set regional patterns in distribution and abundance while biotic factors secondarily modify regional patterns. Several volumes document the power of this paradigm to constructively guide ecologists towards a predictive understanding of distribution and abundance (Cody and Diamond 1975, Price et al. 1984, Strong et al. 1984, Diamond and Case 1986, Kikkawa and Anderson 1986, Gee and Giller 1987, Ricklefs and Schluter 1994, Weiher et al. 1998). For the purposes of illustration, the central thesis can be described using a heuristic model in which biotic diversity, here taken to be a vector of abundances (\mathbf{d}) for the number of species at equilibrium (\hat{S}), is a function of biotic and abiotic factors. Written as an equation

$$\hat{S} = f(\mathbf{d}, \mathbf{B}, \mathbf{e}, \mathbf{A}, \varepsilon) \quad (1)$$

where \mathbf{d} is a vector of densities of each species, \mathbf{B} is the matrix of biotic interactions among species (Levins 1968, May 1974), \mathbf{e} is the vector of abiotic environmental conditions, and \mathbf{A} is a variance–covariance matrix of abiotic conditions. I use a variance–covariance matrix for abiotic factors because abiotic conditions, such as temperature, precipitation, and potential evapotranspiration, often covary with one another. The parameter ε represents error, a complex term that accounts for those stochastic processes, chance events, phenomena that cannot be measured, and nonlinear processes that limit ecologists’ ability to predict distribution and abundance with full precision.

This heuristic model (Eq. 1) represents the Central

Thesis of Community Ecology (henceforth, the CTCE), but its emphasis on abiotic and biotic regulation of distribution and abundance excludes, or at least does not admit to a strong role for, ecosystem processes in understanding nature. By such exclusion, it does not provide a holistic framework for understanding nature and therefore limits its own power, scope, and utility. Note that Eq. 1 is constructed to reflect the tendency of the CTCE to emphasize biotic interactions, but synthetic work in community ecology has long acknowledged that ecosystem-level processes, such as environmental stress (Menge and Sutherland 1987), energy input (Currie and Paquin 1987, Currie 1991, Currie and Fritz 1993), and productivity (Hairston et al. 1960, Oksanen et al. 1981, Rosenzweig and Abramsky 1994, Naeem and Li 1998), modify the way biotic interactions structure communities.

The major limitation of the CTCE is that it portrays the earth’s biodiversity as a passive consequence of intrinsic structure (i.e., number, type, and arrangement of interspecific interactions) and extrinsic factors (i.e., climate, geology, and chance events). To be sure, a rich variety of productive explorations of biotic diversity have been possible using the framework of the CTCE. Ecologists have explored how \hat{S} is a function of resource use (MacArthur 1960, 1972, Sugihara 1980, Tilman 1982), energy inputs (Wright 1983, Currie 1991), environmental productivity (Rosenzweig and Abramsky 1994), island properties (MacArthur and Wilson 1967), stability properties of communities (May 1974) or food webs (Pimm and Lawton 1977), stoichiometry (Reiners 1986, Sterner et al. 1992, Elser et al. 1996), the presence or absence of keystone species (Paine 1966), disturbance (Connell 1978), or synthetic combinations of these (McNaughton 1977, Grime 1979, Huston 1979, De Angelis 1992).

At the end of all these explorations, however, biodiversity appears to be largely a slave of the environment. Changes in environmental conditions that affect \mathbf{e} (e.g., acidification, eutrophication, increased ultraviolet radiation, or global warming), \mathbf{d} (e.g., changes in rates of local extinction or biological invasions), or ε (e.g., increase in frequency of disturbance) are seen as threats to biodiversity or \hat{S} . Efforts are directed towards predicting biodiversity’s response to environmental change as if biodiversity were some sort of hapless, passive victim of such change.

The emerging paradigm, which is the subject of this paper, offers to radically alter this perception and approach to studying the earth’s biota, and to usher in an era of a more synthetic ecology. This paradigm is one in which the environment is seen primarily as a function of diversity. The emerging paradigm, at least in spirit, turns the CTCE on its head, transforming Eq. 1 into

$$\mathbf{e} = f(\mathbf{d}, \mathbf{B}, \varepsilon). \quad (2)$$

(Note that in Eq. 2, diversity is represented by \mathbf{d} and

B not by \hat{S} .) This perspective explicitly prescribes an active role for the biota in governing environmental conditions. Such a paradigm seems patently absurd and quite contrary to conventional thinking, but two recent developments in the evolution of contemporary thinking in ecology encourage adopting this alternative view of nature. First, ecologists now focus less on diversity as conceptualized through taxonomy or equilibrium notions of community diversity (i.e., \hat{S}) in favor of a more inclusive concept of “biodiversity” (Harper and Hawksworth 1995). Second, physical and chemical conditions of the environment are increasingly recognized as driven, at least in part, by ecosystem function (e.g., nutrient cycling and energy flow). That is, rates of ecosystem or biogeochemical processes affect state (physical and chemical) conditions. I will call this emerging paradigm the Biodiversity–Ecosystem Function Paradigm (henceforth, BEFP). I will provide a brief overview of biodiversity–ecosystem function studies, but several papers provide more extensive reviews of the issues and research surrounding this paradigm (Schulze and Mooney 1993, Johnson et al. 1996, Chapin et al. 1997, 2000).

Although there is tremendous excitement over this new direction in ecological research, there is also a tremendous debate and a disturbing sense of *déjà vu* as explorations of this new paradigm continue. Both the first formal assessment of the issues and the first experimental assessment occurred only in the past decade (Schulze and Mooney 1993, Naeem et al. 1994). Though very recent, these studies have fed an explosion of research on the relationship between ecosystem function and biodiversity (Naeem et al. 1994, 1995, 1996, 2000, Tilman et al. 1996, 1997a, b, Hooper and Vitousek 1997, 1998, McGrady-Steed et al. 1997, Naeem and Li 1997, Wardle et al. 1997a, 2000a, Doak et al. 1998, Hooper 1998, Hughes and Roughgarden 1998, Loreau 1998a, Mikola and Setälä 1998, Naeem 1998, Symstad et al. 1998, Van der Heijden et al. 1998, Allison 1999, Hector et al. 1999, Mulder et al. 1999, Yachi and Loreau 1999, Norberg 2000, Symstad 2000). Considerable debate, however, surrounds the interpretations of these studies (André et al. 1994, Givnish 1994, Aarssen 1997, Garnier et al. 1997, Grime 1997, Huston 1997, Wardle et al. 1997b, 2000b, Hector 1998, Hodgson et al. 1998, Lawton et al. 1998, Loreau 1998b, Wardle 1998, 1999, Naeem 1999, 2000, Hulot et al. 2000, Tilman 2000) and it is here where the sense of *déjà vu* arises. Consider the following questions being addressed in these debates. Are diversity and production related (Johnson et al. 1996, Hector et al. 1999)? Are diversity and stability related (Doak et al. 1998, Tilman et al. 1998)? Are species unique or redundant in their contributions to ecosystem processes (Lawton and Brown 1993, Gitay et al. 1996, Mooney et al. 1996, Naeem 1998)? Does niche complementarity lead to greater efficiency of resource use (Huston 1997, Hector 1998, Loreau 1998b)? Which are more informative,

descriptive or experimental studies (Tilman et al. 1997c, Wardle et al. 1997b)? Should species be grouped by their ecological properties rather than their taxonomic affiliations (Hooper and Vitousek 1997, Tilman et al. 1997a, Hulot et al. 2000)? Given the familiarity of these debates to community ecology, is anything really new to this emerging paradigm?

I argue that the emerging paradigm is indeed a new and profoundly different view of biotic diversity. I also argue that the debate is the hallmark of an emerging paradigm, and that any new paradigm requires revisiting central debates within a discipline that in turn invariably creates a sense of *déjà vu*. Emerging paradigms conflict with central theses that were once paradigms themselves. The debates that arise from these conflicts between central theses and emerging paradigms may seem a waste of time, but they are critical to the evolution of scientific ideas. To support these arguments, I provide a historical and philosophical context for the BEFP and provide an example of how emerging paradigms generate novel approaches to scientific problems.

I am handicapped, however, by being neither a historian nor a philosopher, so I tread lightly on such unfamiliar terrain and borrow heavily from the works of others. Yet I believe that even a relatively elementary exploration can provide useful insights concerning ecological paradigms. I argue that the BEFP is one phase in the evolution of ecological thinking whose roots trace back over 2300 yr to Aristotle. I propose that the conflict between central theses and emerging paradigms represents a dialectic critical to the continued development of ecology. It is through this dialectic that synthesis emerges and it is through these syntheses that novel approaches to problems in the ecological sciences are forthcoming. This discussion shows that the history and philosophy of ecology are as important to its development and progress as advances in natural history, technology, mathematics, modeling, experiments, and statistics.

A BRIEF OVERVIEW OF BIODIVERSITY AND ECOSYSTEM FUNCTION

The concepts of biodiversity and ecosystem function are not new to ecology even though the study of the relationship between them is relatively recent. The concept of biodiversity emerged in the early 1980s (Harper and Hawksworth 1995) to refocus attention on the earth's biota from a more inclusive perspective. Unlike taxonomic diversity, biodiversity includes genetic and ecological diversity across all scales (spatial, temporal, and biotic scales of organization ranging from cells to ecosystems; Harper and Hawksworth 1995). Ecosystem function is an older concept associated with the idea that the collective metabolic activities of organisms within a habitat consume energy and move matter between organic (dead or living) and inorganic pools. Tansley (1935) coined the term “ecosystem” partly

because he felt that “natural human prejudices” tend to focus attention on organisms rather than on the system as a whole (Aber and Melillo 1991). Ironically, though he coined the term to foster a more holistic vision of nature, community ecology, with its emphasis on diversity, and ecosystem ecology, with its emphasis on material cycling and energy, grew into relatively separate disciplines (McIntosh 1985, Likens 1992, Grimm 1995).

The BEFP concerns two issues, one less questionable than the other. First—and few would argue with this claim—the biota plays an essential role in ecosystem processes. The second, more contentious claim is that diversity plays a significant role in such processes. Put simply, the existence of life alters the environment and the diversity of life determines the manner in which life alters the environment, much as if diversity were a catalyst to life’s biogeochemical activities. Even if only a single prokaryotic cell were to be found in an ecosystem, biogeochemical processes would occur and the environment would change, albeit on a minute scale. Organisms, however, often grow exponentially in mass and number, multiplying from minute, undetectable levels to enormous levels capable of reconfiguring flows of energy and the cycling of matter. Thus, while studying the dynamics of a subset of the species in an ecosystem’s community can be, and has been, a powerful method for understanding nature, not considering biogeochemical processes (or from a local perspective, ecosystem processes such as decomposition, nutrient mineralization, assimilation, production, or other biotically driven changes in the distribution and abundance of materials between pools of inorganic and organic matter) limits the scope of such investigations. Organisms move hundreds of gigatons (1×10^{15} g) of matter between organic and inorganic pools annually through these processes (Butcher et al. 1992, Schlesinger 1997) and these activities play significant roles in environmental factors such as pH, temperature, humidity, soil and water fertility, and much more. When examined as processes which affect human welfare, or “ecosystem services,” their importance, culturally and economically, prove to be extraordinarily varied and invaluable (Ehrlich and Mooney 1983, de Groot 1992, Costanza et al. 1997, Daily et al. 1997).

Ecosystems are, of course, more than just embodiments of organic–inorganic matter cycling and energy flow. All told, anywhere from 1×10^7 to 1×10^8 species are found among the earth’s ecosystems, but it is largely unknown whether such phenomenal diversity is essential to ecosystem processes. For example, 1 g of soil can contain 1×10^4 species of microorganisms (Klug and Tiedge 1994), a prairie grassland can contain nearly 200 species of herbaceous plants (Leach and Givnish 1996), a Peruvian tropical canopy can contain 3429 species of beetles (Erwin 1997), and temperate soils can contain ~ 150 microarthropod species (Usher et al.

1979). Is such diversity necessary for ecosystem processes to occur?

Why has the BEFP emerged now? Quite possibly, questioning the ecosystem significance of the earth’s diversity may simply have been considered uninteresting or irrelevant until global change drew attention to the problem. Instead of asking what the significance of biodiversity is, biologists have focused on its origin (e.g., evolution, phylogeny, and paleobiology) and its distribution and abundance over space (e.g., population, community, and landscape ecology) and time (e.g., paleoecology and biogeography). The relatively recent and dramatic declines or changes in biodiversity due to the activities of rapidly expanding human population (Wilson 1988, Soulé 1991, Ehrlich and Ehrlich 1992, Jenkins 1992, Pimm et al. 1995, Stork 1997, Eldredge 1998) have generated tremendous national and international interest in understanding the potential consequences of such loss (Groombridge 1992, Heywood 1995, Kunin and Lawton 1996). Coupled with concerns for human impacts on biogeochemical cycles (Vitousek et al. 1986, 1997, Vitousek 1994, Jordan and Weller 1996, Houghton 1997), it is not surprising that the relationship between declining biodiversity and ecosystem function has emerged as a modern topic of ecological research.

THE BIODIVERSITY–ECOSYSTEM FUNCTION PARADIGM: FROM NOTION TO MECHANISM

An ecological paradigm begins with a notion which, via theory, observation, and experiment, evolves through a phenomenological stage to a final mechanistic phase. The BEFP is based on the notion that the earth’s diversity is integral to the function of ecosystems, and the BEFP has evolved rapidly to its mechanistic phase. Such rapid scientific evolution, however, has yielded a thin science, one in which observational, theoretical, and mechanistic studies do not, as yet, represent robust knowledge. This pattern of scientific evolution, however, is typical of paradigms. Here, I sketch the history of the BEFP from notion to mechanism.

Beginning

There is a tendency to simply adapt existing practices to emerging concepts, but such an approach does not work for the BEFP. One could begin by exploring whether or not diversity is a function of ecosystem function; the inverse of the BEFP. That is, one could begin by simply rewriting the CTCE (Eq. 1) as

$$\hat{S} = f(F) \quad (3)$$

where F represents a specific ecosystem function (e.g., CO_2 sequestration, N mineralization, rates of decomposition). One can then test this model by examining whether \hat{S} and F are correlated. This correlational approach has revealed that regional gradients in biodiversity either show negative or no relationship with

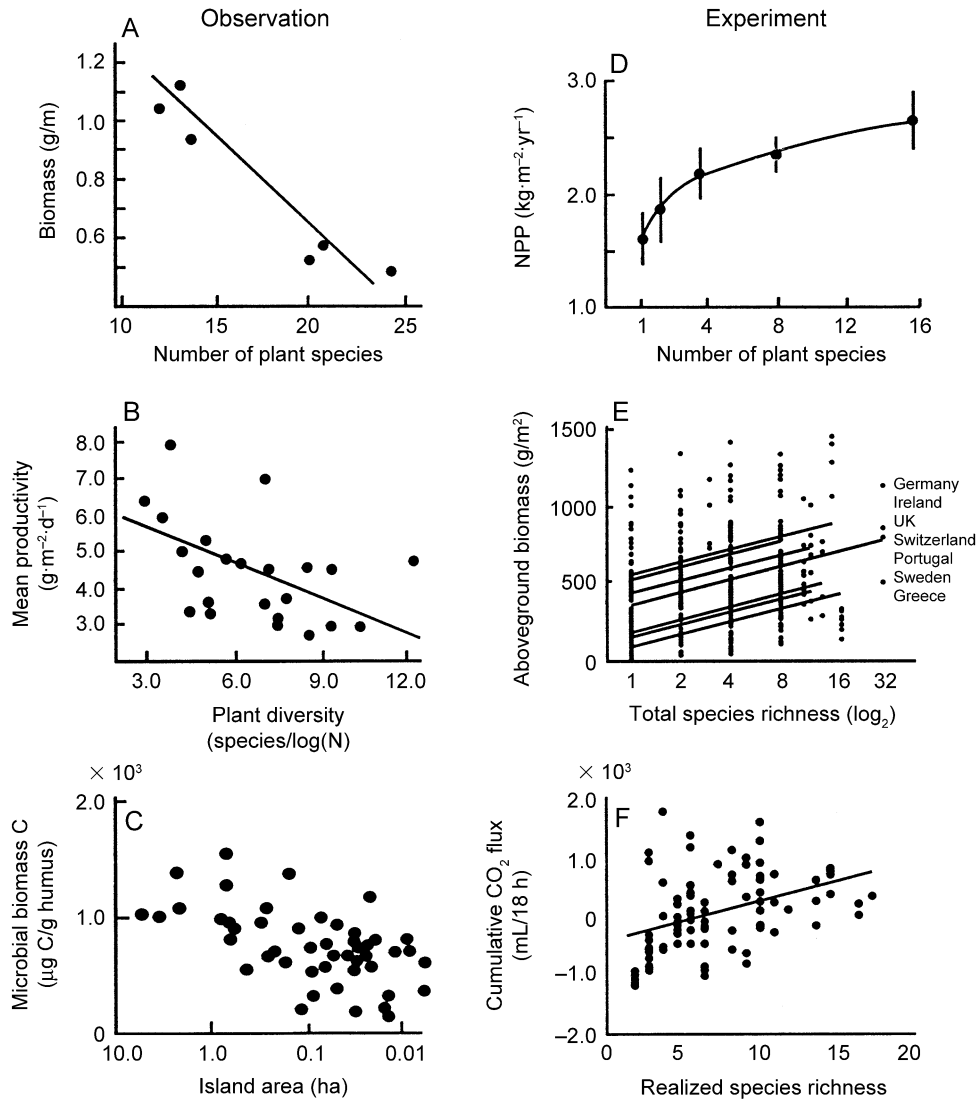


FIG. 1. Empirical evaluations of the relationship between biodiversity and ecosystem function. Observational studies (A–C) on the left appear to contradict results from experimental studies on the right (D–E), but this apparent contradiction occurs because observational studies examine biodiversity and ecosystem function across sites, while experimental studies examine the relationship within a study site. (A) Plant biomass compared with plant species richness across several sites in a savanna (after Bulla 1996). (B) Plant productivity compared with plant diversity plotted as species over the log of plant density (N) at different grassland sites in New York State, USA (after McNaughton 1993). (C) Microbial biomass compared with island size from different islands in a Scandinavian archipelago where, due to higher fire frequencies on larger islands, plant diversity is lower on larger islands. Note that island size is plotted from right to left to reflect increasing plant diversity from left to right. (D) Net primary production of plants in a greenhouse experiment compared with plant species richness in pots (mean \pm 1 SE; after Naem et al. 1996). (E) Aboveground plant biomass in experimental grassland plots from seven European countries compared with the number of plant species plotted on a \log_2 scale (from the BIODEPTH experiments; after Hector et al. 1999). Note that across sites (pooled data from all countries) there is no relationship, but lines indicate positive log-linear associations between diversity and ecosystem function (slopes and intercepts derived from analysis of covariance), on average, within sites. (F) CO_2 flux measured in microbial microcosms compared with the actual or realized species richness after some local extinction occurred in bottles (after McGrady-Steed et al. 1997).

biodiversity (Moss 1973, McNaughton 1993, Bulla 1996, Wardle et al. 1997c, Waide et al. 1999; Fig. 1).

Although such studies provide valuable insights into the correlates of ecosystem function, they cannot readily separate effects due to biodiversity from effects due to covarying factors such as temperature, soil fertility,

rainfall, area, or fire frequency (Tilman et al. 1997c, Wardle et al. 1997b, Naem 2001). Similarly, lack of an observed correlation between \hat{S} and F may be due to factors, such as environmental heterogeneity, that mask the relationship. Ecologists should not forget that history has shown on numerous occasions that causa-

tion and correlation are not necessarily the same. That is, while $\hat{S} \propto F$ can reflect causation, documenting its existence by observational studies does not necessarily confirm that $\hat{S} = f(F)$ because of some direct causal linkage between \hat{S} and F .

The appropriate construction of the paradigm

Testing whether increased biodiversity enhances ecosystem function requires breaking from the CTCE (Eqs. 1 and 3) and placing diversity on the right hand side of the equation and including biogeochemical or ecosystem factors. The heuristic equation would be

$$F = f(\mathbf{d}, \mathbf{B}, \mathbf{f}, \mathbf{P}, \mathbf{e}, \mathbf{A}, \varepsilon) \quad (4)$$

where \mathbf{f} is a vector of abundances of carbon and nutrients (C, N, P, K, S) that cycle between inorganic and organic forms and \mathbf{P} is a transition matrix for these same elements from organic to inorganic forms. In words, a specific ecosystem function (F) is a function of biodiversity (\mathbf{d}, \mathbf{B}), associated biogeochemical processes (\mathbf{f}, \mathbf{P}), and the abiotic environment (\mathbf{e}, \mathbf{A}). For example, in a very simplified fashion, primary productivity is a function of the densities of photosynthetic species (\mathbf{d}), the matrix of interactions among them (\mathbf{B}), soil nutrient content (\mathbf{f}), the rates of transition of these nutrients between available inorganic forms and unavailable (immobilized) organic forms (\mathbf{P}), and the co-varying factors of precipitation, insolation, and temperature (\mathbf{e}, \mathbf{A}). As this example illustrates, when the BEFP is stated in a more appropriate form such as Eq. 4, it is not as mysterious or absurd as its naive formulation (Eq. 2).

The thinking represented by Eq. 3 motivated the Bayreuth conference in 1992 that sparked an explosion of hypotheses concerning the relationship between biodiversity and ecosystem function. Though simple, Eq. 3 represents a framework from which hypotheses can be readily generated because it entails only imagining what a plot through a bivariate space, defined by ecosystem function and biodiversity, might look like. At the conference, three different hypotheses were posed that summarized much of the thinking at the time (Vitousek and Hooper 1993): diversity shows (1) no relationship (null) with ecosystem function, (2) a linear relationship, or (3) an asymptotic relationship in which a small amount of diversity was responsible for the bulk of an ecosystem's function. Since then, Schläpfer and Schmid (1999) have uncovered 51 published biodiversity–ecosystem function hypotheses. This large number of hypotheses reflects the fact that a bivariate space is inadequate for understanding the relationship between biodiversity and ecosystem function, as clearly shown by the more detailed and appropriate Eq. 4.

Building a unifying phenomenological framework

Such a profusion of hypotheses on biodiversity appears to represent confusion, but this wealth of ideas provides the material with which ecologists can con-

struct a unifying framework. There are three central ideas to the majority of hypotheses postulated thus far. First, there is the general perception that local ecosystem function exhibits a maximum (F_{\max}) most likely set by the physical and chemical, or abiotic conditions of the region. Second, there is the perception that a small amount of diversity (D_{\min}) can provide a fair amount of function. Corn–soybean rotations on farms, for example, are depauperate, yet may exhibit much of the function of a species-rich grassland they most likely replaced. Third, there is the perception that species range from being equivalent to one another (redundant) in their contributions to ecosystem function to the idea that they are quite unique (singular; Walker 1992, Lawton and Brown 1993, Gitay et al. 1996, Naeem 1998). In particular, because species interact with one another, their effects on ecosystem function may be multiplied through impacts on other species with which they interact (Power et al. 1996). Stated another way, increments in biodiversity are viewed as affecting ecosystem function either additively or multiplicatively (Sala et al. 2000).

Resorting to the well-known device in ecology of employing a simple phenomenological model to formalize an ecological concept and explore its implications, the following equation can be used:

$$F(D) = \frac{F_{\max} D^c}{D_{\min} + D^c} \quad (5)$$

where c is a coefficient of species multiplicativity and $c \geq 1$. This is a modified Michaelis-Menton model that treats the activity of a system as a saturating function of local conditions. The motivation for such a construct is that the biota drive ecosystem processes and biodiversity regulates these processes somewhat like a catalyst. Many of the postulated hypothetical relationships between biodiversity and ecosystem function can be obtained from this equation by simply varying the terms that represent species equivalency (D_{\min}) and species multiplicativity (c). The parameter c captures this concept by allowing increments in biodiversity to have additive effects when $c = 1$ or multiplicative effects when $c > 1$. Depending on the value of c or the degree of equivalency (redundancy) among species, a range of possible relationships occurs, from ecosystem function as a saturating function of biodiversity, to a sigmoidal function, and on to a near exponential function when c is high (Fig. 2).

Phenomenology to mechanism

Phenomenological models in ecology, such as Eq. 5, have been, and continue to be, important first steps in the evolution of ecological ideas. F. W. Preston's canonical lognormal (Preston 1962, May 1975, Sugihara 1980) and the models of P. F. Verhulst, R. Pearl, J. A. Lotka, V. Volterra, R. H. MacArthur, and G. E. Hutchinson (Kingsland 1985) provided little clue concerning the mechanisms for such concepts as intrinsic rate of

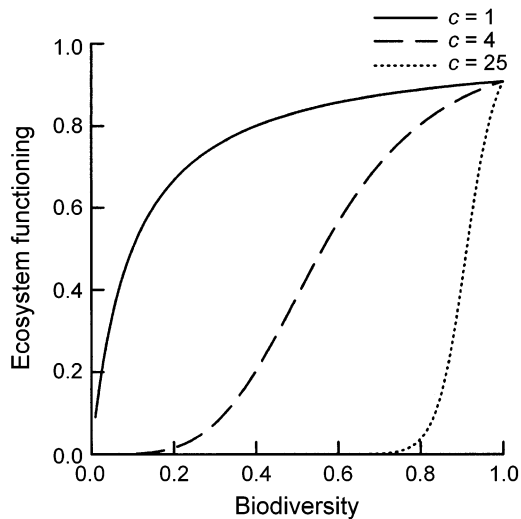


FIG. 2. Hypothetical relationships between biodiversity and ecosystem function derived from a phenomenological model. This model treats ecosystem function as if it were catalyzed by biodiversity where 0 = no biota and 1.0 = maximum possible biodiversity. The variable c is the coefficient of interaction where high values indicate that species have strong effects on each other.

population increase (r), carrying capacity (K), and biotic interactions such as interspecific competition (α_{ij}). Yet, the ideas of these ecologists revolutionized ecological thinking, transforming it into the predictive, experimental discipline it is today.

Phenomenological constructs guide ecologists towards identifying mechanisms. In the same spirit as r , K , and α_{ij} , the model represented by Eq. 5 provides B_{\min} , F_{\max} , and c as phenomenological terms. These concepts also provide a quantitative means for exploring data, such as those shown in Fig. 1. More importantly, they motivate a search for mechanism.

Biodiversity–ecosystem–function research has clearly followed this pathway from phenomenological theory to hypotheses to experiments to mechanism. In the first test of the hypotheses outlined by Vitousek and Hooper (1993), Naeem et al. (1994, 1995) proposed niche complementarity as the mechanistic basis for our findings. We argued that greater biodiversity led to greater efficiency of local resource exploitation in our model ecosystems. For example, having different growth forms of plants in our experimental communities led to greater filling of limited space compared to lower diversity communities. Greater spatial filling by plants meant greater light interception, leading to greater production. Tilman et al. (1996) argued similarly that increased efficiency of nitrogen use explained a positive asymptotic relationship they observed between plant species richness and production in their prairie grassland assemblages. These proposed niche complementarity mechanisms have led to the development of mechanistic models (Tilman et al. 1997b,

Loreau 1998a), but empirical confirmation has yet to be done.

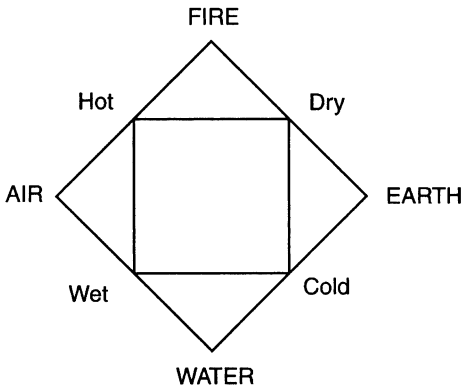
Huston (1997) argued that an alternative explanation concerns the higher probabilities of species with strong impacts on ecosystem function being found in higher diversity communities. This second mechanism, known as the sampling effect (Aarssen 1997, Hector 1998, Loreau 1998b, Hector et al. 1999, Wardle 1999), is difficult to separate from niche complementarity, and one or both mechanisms are likely to be responsible for observed patterns of association between diversity and ecosystem function. Loreau and Hector (2001) have developed a mathematical means for testing the relative likelihood that experimental results are due to either niche complementarity or sampling, but direct experimental tests that specifically examine how these two factors contribute to ecosystem function remain to be done. The niche complementarity and sampling effect mechanisms should therefore not be mistaken as opposing explanations, but rather as co-occurring processes by which depauperate replicate ecosystems derived from a once extensive, highly diverse system can function differently in predictable ways.

In spite of the increasingly mechanistic approaches now dominating biodiversity–ecosystem function theory, it is worth noting that to date no experiments have explicitly tested either mechanism. It is also important to note that studies so far have been short-term, small in size, often focusing exclusively on plants, and done on highly manipulated or completely artificial ecosystems (Naeem 2001). They were designed to “articulate” the BEFP, not to provide information that could be used for precisely predicting the ecosystem consequences of declining biodiversity. As such, this research does not constitute a comprehensive or robust body of work, but it has proven valuable for provoking further inquiry as tests of the phenomenological predictions of the BEFP (Fig. 2) and by attracting adherents of the CTCE to consider this alternative perspective.

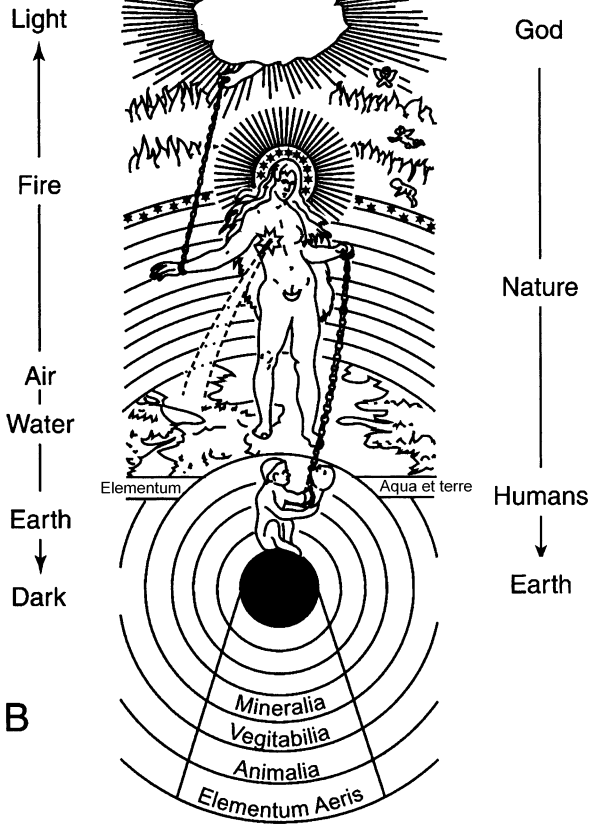
THE ECOLOGICAL DIALECTIC

Contemporary ecology is the result of progress made over two millennia of scientific thinking that has ranged from the use of natural magic to the use of biologically based mechanisms in developing an understanding of nature (Henry 1997). This progress, however, has not been a smooth process like some grand march through time as it is often presented in textbooks (Hellman 1998). Rather, contemporary knowledge is one point along a zigzagging pathway that bounces among opposing ideas. This irregular course is driven by the ecological dialectic, a process in which seemingly diametric views of nature force ecologists to explore how nature works. The process is one in which periodic discord arises when debate between subscribers to opposing schools challenge each other with novel theoretical and empirical findings. The outcome is generally

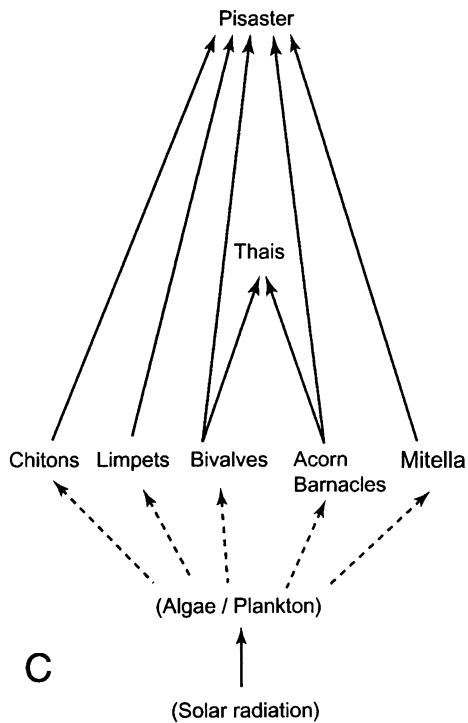
FOUR QUALITIES AND FOUR ELEMENTS



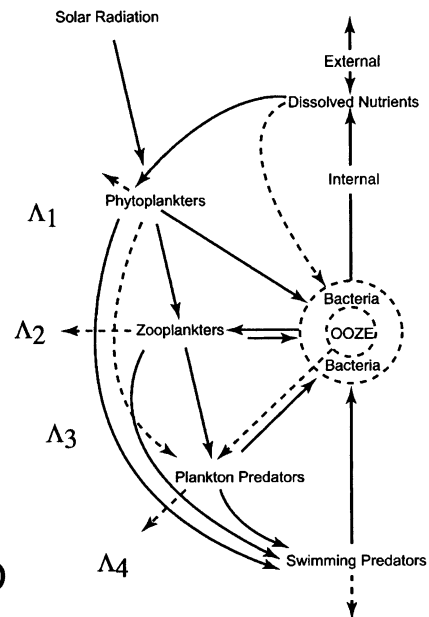
A



B



C



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FIG. 3. The evolving paradigm of nature. (A) The Aristotelian perspective in which all entities are related by their composition of four fundamental elements (earth, air, fire and water) and the properties (hot, cold, dry, or wet) with which these elements endow all entities. (B) A Paracelsian perspective from the work of Robert Fludd. All of nature is organized along a gradient from dark to light in which air is condensed fire, water is condensed air, and earth is condensed water. Processes are regulated by God (fist in heavenly cloud) who symbolically controls nature (chain linking nature with God) which is seen as a nurturing force over the earth, and nature controls humans (chain linking woman with ape-like man), shown

a synthesis of the opposing views. The BEFP provides a contemporary example of this process. Recognizing that the debate surrounding the BEFP is just another iteration of the cycle of debate and syntheses that shape intellectual history is the first step in deciphering the message behind the discord.

The ecological dialectic

The epistemological method of contrasting an idea with its opposite as a mechanism for understanding nature constitutes the dialectical approach that has been central to the philosophies of Aristotle, Plato, Kant, Hegel, and many others. G. W. F. Hegel's (1770–1831) dialectic roughly argues that the evolution of understanding (and history itself) is a cycle of thesis followed by antithesis followed by synthesis which in turn can become thesis again, and so on until some absolute, irrefutable thesis emerges. Kingsolver and Paine (1991) recognize that such cycles of theses, antitheses, and syntheses are a fundamental part of ecology's history, though, unlike Hegel, they see no end in sight.

In *The Dialectical Biologist*, Levins and Lewontin (1985) defined the biological dialectic as the inseparability of one part and another, arguing that the whole evolves based on properties derived from its parts and the interactions ("interpenetration") among its parts. Their application of this philosophical framework to ecology led them to conclude that ecology suffers from a tendency to identify and assign importance to the various parts and processes of nature rather than embracing its internal contradictions (Levins and Lewontin 1985). That is, ecology refuses to acknowledge the dialectic. I refer to this recurring tension among ecologists created by assigning more importance of one class of processes over other processes in governing ecological phenomena as the "ecological dialectic."

The origin of the ecological dialectic

The debate surrounding the BEFP did not arise spontaneously upon the publication of a handful of high-profile publications in the 1990s. Rather, it is a manifestation of the ecological dialectic. The ecological dialectic began historically with the abandonment of the Aristotelian perspective during the Scientific Revolution of 17th century Europe in which Western science lost its unifying framework. Aristotle (384–322

BC) considered all entities, living or nonliving, earthly or spiritual, to be made up of only five elements; earth, fire, water, air, and a distinct fifth element known as the ether or the "quinta essencia" or quintessence (Fig. 3A). Depending on elemental composition, all entities also manifested only four essential properties: hot, cold, wet, and dry (Fig. 3A). The Aristotelian perspective therefore held that organisms were intimately linked to everything, be they minerals, heavenly bodies, and even numbers and artifacts, unified by their composition from a small set of elements and sharing a small set of properties (Henry 1997).

During the Scientific Revolution, scientists found it increasingly difficult to reconcile traditional or Aristotelian-based perspectives with rapidly emerging ideas and observations of the period. Paracelsus (P. T. A. B. von Hohenheim, 1493–1541) was a key figure who influenced many natural philosophers to break away from the Aristotelian perspective (Nordenskiöld 1928, Read 1957, Debus 1965, Henry 1997). Robert Fludd (1574–1637), an English Paracelsian, broke away from the Aristotelian perspective by treating fire, air, water, and earth as points along a gradient from the pure light of the heavens to the darkness of earth below ground (Fig. 3B). Similarly, Johannes Baptista Van Helmont (1579–1644), a prominent Belgian Paracelsian, argued that air was a mixture of gasses and that life was made of water, not earth (Henry 1997). Thus, Paracelsus and the Paracelsians, while retaining the foundations of Aristotelian thinking including its inherent mysticism, shattered the holism of the Aristotelian perspective. This is seen in Fig. 3B where Fludd's anti-Aristotelian construct (Fig. 3B) retains the notion of four principle Aristotelian elements (Fig. 3A) while adding a biblical God as a force regulating Nature.

Also critical to reshaping science was the abandonment of the practice of invoking mystical processes to explain nature. Empirical mysticism, based on the premise that entities had occult or hidden abilities to affect other entities, was a common part of scientific inquiry prior to the 19th century. Processes such as gravity, magnetism, electricity, optics, astronomical movement, biological reproduction, microbes, fermentation, and animal physiology were understandably mysterious and were more amenable to hypotheses based on natural magic, numerology, and Biblical reasoning than

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as an earthly creature lower in stature than nature but capable of thought (pondering a human skull). Note that this perspective recognizes the connection between the equivalent of a biosphere divided into autotrophs (Vegetabilia) and heterotrophs (Animalia), lithosphere (Mineralia), and atmosphere (Aeris). Although holistic, the universe is distinctly divided (after copy of Fludd's original in Debus [1965]). (C) A community perspective derived from R. T. Paine's influential paper on keystone species (Paine 1966), which, by some measures, is seen as an ecological paradigm (much to Paine's chagrin) for how nature works. Biotic interactions govern patterns in the distribution and abundance of species. I have added the basal trophic levels of algae and plankton (and accompanying dashed arrows indicating trophic interactions) implicit in Paine's study but not illustrated. (D) An ecosystem perspective derived from R. Lindeman's influential paper on the trophic–dynamic concept (Lindeman 1942) which, by some measures, is also seen as a paradigm. Note that only the left side of Lindeman's original symmetrical drawing is reproduced here in the interest of preserving space.

what is now considered acceptable. Natural history in particular made abundant use of empirical mysticism. As J. Henry (1997:53) notes, "With the rapid expansion of the lore of flora and fauna which was a feature of the burgeoning of observational natural history . . . a whole new area of occult qualities was opened up." As empirical mysticism fell into disfavor, however, "rational" mechanisms based on known processes were used to replace natural magic and mystical processes.

Cycles of thesis–antithesis–synthesis could only begin with the abandonment of the unifying umbrella of Aristotelian thinking. That process has continued unabated into recent sciences, resulting in considerable fragmentation. In ecology the largest and most recent fragmentation has been the separation of community and ecosystem ecology (Worster 1977, Kingsland 1985, McIntosh 1985, Likens 1992, Golley 1993, Grimm 1995). Comparing R. T. Paine's (a leading community ecologist) illustration of an intertidal community (Fig. 3C) and R. L. Lindeman's (1915–1942, ecosystem ecology) illustration of a pond (Fig. 3D) with Aristotle's (Fig. 3A) and Fludd's (Fig. 3B) illustrations of nature, it is clear how the connection has been lost between organisms and their larger universe.

The BEFP and the ecological dialectic

The 1992 conference in Bayreuth, Germany, called upon the ecological community to evaluate the larger question of the consequences of biodiversity loss for the biosphere. The conference essentially called for synthesis which, following the ecological dialectic, was for ecologists to employ theory, observation, and experiment to challenge the CTCE. But addressing the problem required expanding the domain of community ecology to encompass ecosystem ecology. Likewise, ecosystem ecology was required to expand its domain of natural phenomena to encompass community ecology.

At one level, the BEFP is simply another iteration of the thesis–antithesis–synthesis cycle, but its synthetic nature means that its implications touch upon issues most of the subdisciplines of ecology contend with. Each subdiscipline in ecology has its theses and paradigms. Debates surrounding such issues as density-dependent vs. density-independent population regulation (Andrewartha and Birch 1984, Hixon et al. 2002), the role of biotic vs. abiotic factors in structuring communities (Strong et al. 1984), intrinsic vs. extrinsic processes in succession (Clements 1916, Gleason 1926), the relative merits of experimental vs. observational studies (Roush 1995, Morin 1998), the relationship between community complexity and stability (MacArthur 1955, May 1974, Goodman 1975, Haydon 1994), and many other debates are structured by the ecological dialectic.

The central thesis in each debate concerns the relative importance of different processes in governing

natural phenomena. In each case, however, the issues concern either inter- or intraspecific interactions (i.e., species multiplicativity), ecosystem functions (F), diversity (D), or, in the case of observation vs. experiment, the appropriate methods for demonstrating cause and effect (i.e., identifying mechanisms) in ecology. All of these are parts of the hypotheses that have arisen from the BEFP (i.e., Eq. 5). Not surprisingly, a sense of déjà vu arises as one reads the literature associated with the BEFP.

CONCLUSIONS

The utility of ecological paradigms and the BEFP

Each iteration of the thesis–antithesis–synthesis cycle in the evolution of ecological thinking is signaled by the appearance of a new paradigm. The emergence of each paradigm is typically surrounded by debate, which, so long as it remains constructive, challenges ecologists to reevaluate their science. By promoting synthesis, encouraging the modification of traditional perspectives to accommodate new information and new ideas, and strengthening the linkages among disciplines that become increasingly fragmented, paradigms serve vital functions in the intellectual growth of ecology. Paradigms are ephemeral, each to be replaced by another in the continuing cycle driven by the ecological dialectic.

An example of the utility of the BEFP

Part of the definition of a paradigm shift is that its subscribers approach existing problems in novel ways. An example of how the BEFP has done this concerns climate change. In studies of global climate change, the biota is still largely seen as a slave to the environment, very much as outlined in Eq. 1. The biota are imagined to shift their geographical distributions and ranges, species composition, ecosystem function, and dynamics in direct response to climate change (Peters et al. 1992, Woodward 1992, Gates 1993, Kareiva et al. 1993, Mooney et al. 1993, Solomon and Shugart 1993, Walker and Steffen 1996). In spite of the fact that the biogeochemistry of global change would inherently suggest that there might be feedbacks between global change and ecosystems, this is still relatively unexplored terrain (Woodwell 1995). As D. M. Gates (1993:26) notes, "Global warming may also produce a large biological positive feedback through the release of carbon dioxide and methane from vegetation, soils, and clathrates. This is a wild card in the deck, and one that is not well understood."

The BEFP encourages examining this "wild card," arguing that biodiversity may be an important component to carbon dioxide flux (Naeem et al. 1994, McGrady-Steed et al. 1997). If CO_2 flux is affected by biodiversity (the BEFP) and climate affects biodiversity (the CTCE), there is reason to suspect a biodiversity–climate feedback (climate \rightarrow biodiversity \rightarrow cli-

mate). Again, while there is little doubt that there are biotic feedbacks in climate processes (e.g., climate → biota → climate; Lovelock 1979, Woodwell 1995), this biodiversity-based hypothesis seems patently absurd and contrary to conventional thinking (e.g., Eq. 2), and taken out of context or misunderstood, it can inadvertently have policy or environmental implications that are not at all supported by current research. Nevertheless, the major contribution of the BEFP and the controversial experiments that have articulated the paradigm is that they have provoked a different line of reasoning. By simply bringing biodiversity into the global climate change arena, the BEFP has stimulated new thinking.

Why the acrimony?

New research that is in conflict with traditional perspectives is often surrounded by scientific debates (Dunwoody 1999). If the BEFP and its surrounding debates are typical of paradigms in the history of ecology, why the acrimonious tone? The acrimonious tone includes questioning the ethics of scientific publishing houses that have published BEFP papers, questioning peer review, and questioning the integrity and motivation of the scientists promoting the BEFP (Guterman 2000, Kaiser 2000). Perhaps what Levins and Lewontin (1985) note about ecology is true: some of the participants in the debate might be unaware of the dialectic as an essential part of intellectual evolution. Participants should recognize that the CTCE is essentially correct, that biodiversity is a product of its environment, and the antithesis, that the environment is, in part, a product of the organisms within it, is also correct. This is an inherent contradiction that should be embraced as Levins and Lewontin (1985) suggest. Ecosystem processes provide the key to understanding this part-whole (or species-environment) relationship. The BEFP seeks unity, not one concept over another.

New research that is in conflict with or the antithesis of traditional perspectives often generates debate (Hellman 1998, Dunwoody 1999) and the BEFP is no exception. Without the framework provided by history and the ecological dialectic, antitheses are likely to be misinterpreted as either challenges to the efficacy of established research or possibly bad science. Such misinterpretations are more than likely to engender acrimony.

As synthesis (in the Hegelian scheme of the evolution of scientific ideas), the BEFP brings together the disparate disciplines of ecosystem and community ecology and in so doing, represents a synthesis of the CTCE and the antithesis of ecosystem ecology. An ecosystem involves biotic cycles of organic-inorganic matter transformation, flows of energy, and material exchange among other systems driven by autotrophic and heterotrophic processes while a community consists of these species and the interactions among them (Fig. 4). The BEFP merges these two perspectives by

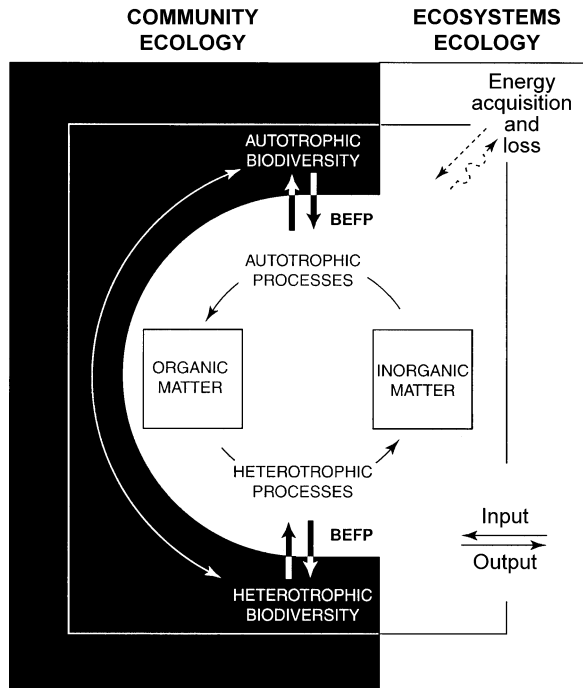


FIG. 4. Synthesizing community and ecosystem ecology through the biodiversity-ecosystem function paradigm (BEFP). The traditionally separate disciplines of community ecology (black portion on left, representing biotic interactions within and among trophic groups) and ecosystem ecology (white portion on right, representing material pools, ecosystem processes that move materials among these pools, and energy and material inputs and outputs) are shown as two interlocking parts joined together by the BEFP. That is, biodiversity, whether it be genetic, individual, taxonomic, or functional, governs the magnitude, variability, and stability of ecosystem processes.

pairing them as if one were a hand and the other a glove (Fig. 4). There are two points of contact. First, autotrophic biodiversity (e.g., plants, algae) is coupled with autotrophic processes (e.g., nutrient uptake, primary productivity) or with inorganic-organic matter conversion. Second, heterotrophic biodiversity (e.g., consumers, decomposers) is coupled with heterotrophic processes (e.g., herbivory, decomposition) or organic-inorganic matter conversion. Of course, the real world is more complex than Fig. 4 portrays. For example, I have left out the physical and chemical environment and ignore the fact that some organisms exhibit properties somewhere between autotrophs and heterotrophs, such as mixotrophs (Porter et al. 1985, Jørgensen 1989, Rothaupt 1996a, b).

A sign that the BEFP may now have evolved to the stage of synthesis in the cycle of paradigms may be the conference held in Paris, France, in December 2000. This workshop was entitled, *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*, and the report from this conference outlines scientific certainties, uncertainties, conflicts, possible resolutions to these conflicts, and syntheses (Loreau et al. 2001). This

conference, like the one in Bayreuth, is an important hallmark, one in which many of the researchers who have been critical of one another worked together to achieve consensus and synthesis.

True synthesis, however, will require the BEFP to mature and expand its currently limited scope. The CTCE is a mature and powerful perspective, one that has long considered the role of extrinsic factors in regulating local diversity (e.g., productivity, climate, disturbance, history), feedbacks between the biota and ecosystem function, multiple trophic levels, and ecological scale (e.g., spatial and temporal heterogeneity). This expansion of scope is beginning. Recent studies have expanded to include wetlands (Engelhardt and Ritchie 2001), heterotrophs such as insects (Mulder et al. 1999), mycorrhizal fungi (Van der Heijden et al. 1998), stream arthropods (Johnsson and Malmqvist 2000), zooplankton (Norberg 2000), soil invertebrates (Mikola and Setälä 1998), soil microbes (Griffiths et al. 2000), and extrinsic determinants such as disturbance and herbivory (Sankaran and McNaughton 1999). Much more work, however, is needed before the CTCE and BEFP can be joined (Naeem 2001).

Concluding remarks

The CTCE or the BEFP are steps in the evolution of understanding nature, not accurate representations of the true workings of nature. Kuhn (1962) began his deliberations on paradigms with a consideration of alternative perspectives of the history of science. One perspective is that science progresses by the accretion of scientific truths, discarding outmoded ideas as "errors," "myths," or "superstitious beliefs." This perspective, however, requires considering the science of today as little more than tomorrow's discredited ideas. The second, more appropriate perspective is that outmoded scientific principles are simply incompatible with today's principles (Kuhn 1962). To dismiss the visions of nature provided by Aristotle, Paracelsus, Fludd, Lotka, Elton, Clements, Hutchinson, or MacArthur as myths is both shortsighted and counterproductive. It is difficult to know what ecologists centuries from now might consider peculiar or quaint in today's ecological theories.

My decision to focus on the Scientific Revolution, in particular the Paracelsians, rather than more contemporary history stems from my concern that, because of ecologists' disdain for natural magic, mysticism, and most recently phenomenology, ecologists have lost their once expansive vision of nature. This situation is unfortunate because global change research requires expansive thinking. One gets the sense, when looking at library bookshelves and textbooks, that other scientific disciplines embrace their history whereas ecologists are embarrassed by their history much before Darwin. That is, whereas the American Medical Association uses the magic wand of Hermes entwined by a snake (the Caduceus), chemists proudly trace their

roots in alchemy and the Philosopher's Stone, and astronomers are intrigued by the heavenly crystalline spheres of Eudoxus of Cnidos, ecologists are embarrassed by the Ouroboros (a serpent eating its tail that symbolized the Aristotelian unity of everything), Larmarkian selection, Hutchinsonian ratios, equilibrium based Lotka-Volterra models of nature, and the near-mystical notions of scale invariant food web patterns. This dismissal is unfortunate because ecologists should keep in mind that today's truths are very likely to be incompatible with tomorrow's truths. Students of ecology should embrace the history of the discipline and the many lessons it has to offer.

In the end, the BEFP, like all paradigms, is likely to run a predictable course (if it even survives this decade!). The BEFP may evolve from antithesis to synthesis to thesis. History predicts, however, that a new antithesis will emerge and a new synthesis will follow, and so on. This cycle, in essence, is the way science works.

As biologists continue to explore nature, no matter how familiar it may seem to them, new observations, new theories, and new experiments will provide continuing challenges, and explorations will have to begin anew. Although Kingsolver and Paine (1991) may be right that there is no end to the ecological dialectic, keeping the nature of ecological inquiry in mind provides a balanced, productive perspective from which ecologists can interpret the reports of their colleagues' ecological explorations. T. S. Eliot describes this process of inquiry most succinctly in *Four Quartets* (1943):

*We shall not cease from exploration
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time*

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