Complementary Models for Ecosystems

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COMPLEMENTARY MODELS FOR ECOSYSTEMS

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Ecosystems were first defined in western literature by Tansley (1935) as the functional combination of the "organism-complex" plus environmental factors. This level of organization was conceived in response to philosophical agonies over the "superorganismic" concept of community, a historical background that signaled inherent difficulties with the concept from its beginning. The ecosystem was thought by Tansley to be part of a hierarchical series of biological entities of increasing scale and complexity, a notion very much embraced today (E. Odum 1971; Ricklefs 1983). Through time, ecology at the ecosystem level has become a vigorous, well-funded, and practical aspect of the discipline of ecology.

Still, in many ways the ecosystem remains the least coherent of the organizational levels of ecology. It lacks a logical system of interconnected principles and a well-understood and widely accepted focus. Some of this incoherence may be inherited from the community origins of the concept; some may result from the multiple approaches that are inevitable in addressing a concept of such scope. McIntosh (1985) illustrated the confusion resulting from the introduction of "systems ecology" and "ecosystem analysis" to the field. Jordan (1981) betrayed a disciplinary identity crisis when he asked, "Do ecosystems exist?" From whatever source, this incoherence confuses students and investigators alike. I suggest that it underlies the lack of useful, theoretical development since approximately 1960 and the present digression of ecosystem research into a largely reductionist mode. These are contestable assertions. Rather than defending them, I address special congenital difficulties with the ecosystem concept that hinder the development of interconnected principles, and then suggest ways of addressing ecosystems that may alleviate some of these problems and stimulate theoretical development.

CONCEPTUAL PROBLEMS

The ecosystem concept is dimensionless. Ecosystems can range from a rotting acorn to the biosphere. For the most part this characteristic is a positive attribute, lending generality to the properties of ecosystems at all size scales. The enormous range of possible scales can lead to ambiguity and confusion, however, if scales

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are not clearly recognized and defined in designing research and relating the results to systems of other scales (Allen and Starr 1982). Characteristic lengths or times (in the mathematical sense) representing the scales at which binding interactions take place are rarely defined in ecosystems unless they happen to have convenient boundaries for several functions, as do lakes and watersheds. For an example of characteristic length on a system without physical bounds—an algal bloom—see Kierstead and Slobodkin (1953).

The second difficulty is related to the first: the relative intangibility of ecosystems as compared with organelles, cells, and individual organisms. Ecosystems, along with populations or communities, rarely have the boundary integrity or behavioral cohesion that are associated with levels of organization bounded by membranes or integuments. Space capsules and the biosphere are notable exceptions. This is, of course, an old problem with community ecology as well. To move from the consideration of ecosystems in a conceptual way to observation and experimentation in the field, ecosystems have to be bounded on the landscape or in the seascape. We usually attempt to make boundaries across zones of minimal interaction or exchange. Unfortunately, not all processes or functions may map over the same space or volume in nature. For example, although watershed divides are superb boundaries for water budgets, they usually do not demarcate natural units for soil-moisture regimes, insect outbreaks, or fire tracks. Because there are different kinds of interactions, different boundaries must be set for different questions and foci.

This phenomenon leads to the third difficulty with the ecosystem concept, the confusion concerning ecological properties that fall into the ecosystem domain. Perhaps because textbooks subdivide ecology into population, community, and ecosystem sections, ecosystem ecologists have perceived a subdisciplinary limit to the kinds of interactions that pertain to ecosystems. Typically, these interactions are limited to fluxes of energy or matter. This has established an artificial barrier to the properties that constitute the domain of ecosystem ecology, omitting, for example, regulatory processes at the population level. Ironically, such restriction contradicts Tansley's original argument (Webster 1979). If we return to Tansley's original point of view, then every aspect of ecology falls within the domain of the ecosystem level of abstraction.

Three conclusions emerge from the foregoing. The first is the necessity for careful scaling when defining a particular ecosystem. The second is that scaling will be different for different attributes, even on the same landscape or seascape. The third is that, by definition, interactions that may define an ecosystem must include population and community-level attributes not normally incorporated in ecosystem analysis. Collectively, these conclusions lead to the position that there are many kinds of interactions that may define particular ecosystems. Some of these interactions may not be usefully definable only in terms of material or energy. Each of these ways is legitimate, and quite probably, each would define different ecosystems at different scales on the same piece of terrain. For example, in the landscape of a golf course, questions about soil microbial processes would have to be studied at the scale of each of the green, fairway, trap, and "rough" patch-mosaic units; questions about grass herbivory might be studied at the scale of the entire managed portion of the course; questions about the roles played by robins would have to involve the entire course and the adjacent "rough" vegetation complex. Each of these defines the scale of the ecosystem in terms of the ecosystem process addressed.

This reasoning suggests that an effective approach to developing ecosystem theory should be explicitly dualistic or multiple in nature. The concept of multiple explanations was addressed by Botkin et al. (1979), Levins and Lewontin (1980), and Allen and Starr (1982). Botkin et al. stated, "Once a question is specified for a particular ecosystem, one can generate a model designed to answer that question. . . . We cannot pretend to construct a general theory for ecosystems, but we can construct a general syntax in which to develop specific theories." (1979, p. 29.) Levins and Lewontin asserted, "The problem for science is to understand the proper domain of each abstraction rather than becoming its prisoner" (1980, p. 67).

A second suggestion for evolving a more effective ecosystem theory is to define the logical relationships between evidence, axioms, theorems, and conceptual models. We have many constructs in ecology representing different degrees of empirical confidence and theoretical meaning (e.g., niche, succession, second law of thermodynamics, competition). Rarely, however, are these defined in terms of their status in the context of logic, and even more rarely are they interconnected in a logical scheme. This leaves us with a confusing plethora of disparate "facts," working concepts, and complex models.

I propose that we should deliberately seek multiple, but complementary, characterizations, or models, for ecosystems. Each of these should be based on fundamental laws or axioms. These then can be elaborated into a series of increasingly incisive deductions through a logical interconnection with further laws, axioms, or evidence. Resulting deductions can then be framed as testable hypotheses when possible. Interactions between complementary deductive models should yield higher-order hypotheses. Two examples of such complementary characterizations, or models, of ecosystems follow, one based on energy, the other based on matter. I suggest that using these two, and developing other interacting models, will implement the development of theory for ecosystem ecology. If successful, such an approach will extend the utility of the ecosystem level of organization for understanding nature.

DESCRIPTION 1: ENERGETICS

The pattern of energy flow in ecosystems is unquestionably the best-developed aspect of ecology at the ecosystem level. Since its introduction by Lindeman (1942), this has been a theoretically based, pleasingly coherent body of knowledge and avenue of inquiry. Especially with the formal incorporation of thermodynamics into ecological energetics (Morowitz 1968), this approach has become rich in predictive power (e.g., Odum and Pinkerton 1955; H. Odum 1956; Engelmann 1966) and has provided a strong organizational basis for ecosystems. In fact, some might say it is *the* organizational theory for ecosystems.

The central core of ecological energetics is the second law of thermodynamics;

that all systems tend toward maximum entropy and that open systems can be maintained by negentropy are the first steps toward explaining bioenergetics. The concept of coupling open systems to the energy flux of larger open systems is the basis of the practice of biophysics, physical biochemistry, and metabolism at all levels, from organelles to the biosphere. From this coupling concept flows recognition of trophic levels, food chains, food webs, productivities, and efficiencies. We have recognized how evolution has resulted in patterns of energy acquisition, storage, and flow that on one hand have led to radiational differentiation in life history attributes of species within an environment, and on the other hand have led to a convergence in patterns by unrelated taxonomic groups in geographically removed but analogous environments.

With the conceptual structure of energetics we have become equipped to understand the limits to trophic levels; the relationship of size to metabolic rate; the energetic adaptiveness of size, shape, and locomotion; the relationships between trophic levels, organism size, and trophic-level biomass; and the biomass of trophic levels along food chains. This material is so well developed that a detailed exposition is not needed here. (For a more complete example of a deduced set of "corollaries" based on three axioms of energy flow, see H. Odum 1975.)

Yet energetics alone does not help us to understand or predict many ecological phenomena. For example, pure energetics does not explain the size per individual of organisms within a trophic level of a particular system. By itself it does not explain why or how much energy flows through detritivorous rather than herbivorous food chains, or how matter can be limiting to life, or why the biosphere has its particular chemical composition. Although energetics is a rich and productive means of describing ecosystems, energetics is not sufficient to explain all aspects of ecosystems. In fact, it is only one complementary description for ecosystems.

DESCRIPTION 2: MATTER

Whereas the first complementary model for ecosystems is based on energy and finds its initial axiom in the second law of thermodynamics, I propose that the second complementary model is based on matter and finds its initial axiom in the chemical stoichiometry of organisms. The functional relations between microbial chemistry and soil processes were realized early in this century (e.g., Waksman and Starkey 1931), but Redfield (1958) was the first to recognize the full implications of such a stoichiometry. He noted that plankton are composed of carbon, nitrogen, and phosphorus in a characteristic atomic ratio. From this simple relationship and observations of the geochemistry of oceans, Redfield deduced patterns of abundance of these and other elements in the sea and the atmosphere. Because Redfield was considering planktonic organisms and only carbon, oxygen, nitrogen, and phosphorus, he was dealing with a relatively simple, cellular stoichiometry. Many marine plankton, especially nanoplankton, do not have structures other than protoplasm and thin cell walls composed of carbon, nitrogen, and phosphorus so that these ratios represent a "core" stoichiometry from which other organisms and biospheric components are derivatives.

In recognition of the power of Redfield's analysis, others have examined the stoichiometry of various biospheric components in terms of "Redfield ratios." At first the results have seemed disappointing, but at second examination we can see that variations are at once meaningful and predictable (Bolin et al. 1983). Because the immense understanding of biogeochemistry is not integrated into ecological theory as well as is energetics, I develop a systematic set of deductions that originate from the core stoichiometry of protoplasm, proceed to the operating of biogeochemical cycles, and ultimately explain the singular physical and chemical nature of the biosphere. This series of ideas composes the second complementary model of ecosystems.

Basic Axiom of Stoichiometry

This axiom can be stated in its most general form: organisms have a regularly ordered chemical composition (axiom 1; fig. 1). This means that the relative proportions of elements are highly regular within kinds of organisms and that there is much similarity in chemical composition between kinds of organisms. Both the similarities and the departures from similarity in composition are important in evolutionary and ecosystem terms. To develop the important relationships between this axiom and the deductions to follow, it is useful to divide the world's biota into two functional groups, which I term "protoplasmic life" and "mechanical structures." Protoplasmic life embraces the contents of all cells including vacuoles (which are nonprotoplasmic), from microorganisms to multicellular plants and animals. By mechanical structures, I mean the stiff structures that compose simple and massive cell walls, tests, shells, endoskeletons and exoskeletons, and specialized products such as hair and nails. This simple dichotomy is not ideal. Protoplasm and mechanical structures do exchange materials from storage locations to sites of active metabolism (e.g., nitrogen storage in woody tissues of plants, Pate 1980; calcium and phosphate storage in bones of vertebrates, Pautard 1978). Nevertheless, it serves as a useful organizational device that adequately characterizes the statistically different chemistries of these artificial units.

The chemical elements of greatest interest for protoplasmic life are for the most part the essential elements. This is not, in fact, very definitive because elemental essentiality varies widely between biological groups and it has not even been defined in all cases (Bowen 1979). Furthermore, nonessential elements frequently become involved in biological processes through their chemical analogy with essential elements. The important distinction to be made for this argument is that there is a small group of light elements essential to all life and composing most of the mass of protoplasmic life: carbon (C), hydrogen (H), nitrogen (N), oxygen (O), phosphorus (P), and sulfur (S). All other elements are used in considerably smaller amounts in protoplasm and with great variability.

Water is a special case of a form of biologically critical matter. Water is required in large amounts by living organisms, but its main role is as an internal medium. Thus, its role in biosynthesis, while still great, is small compared with its flux through organisms. The importance of water in stoichiometric comparisons is also diminished by the fact that chemical compositions are calculated on a dry-mass basis.

Table 1 contains stoichiometric data for major groups of organisms in terms of

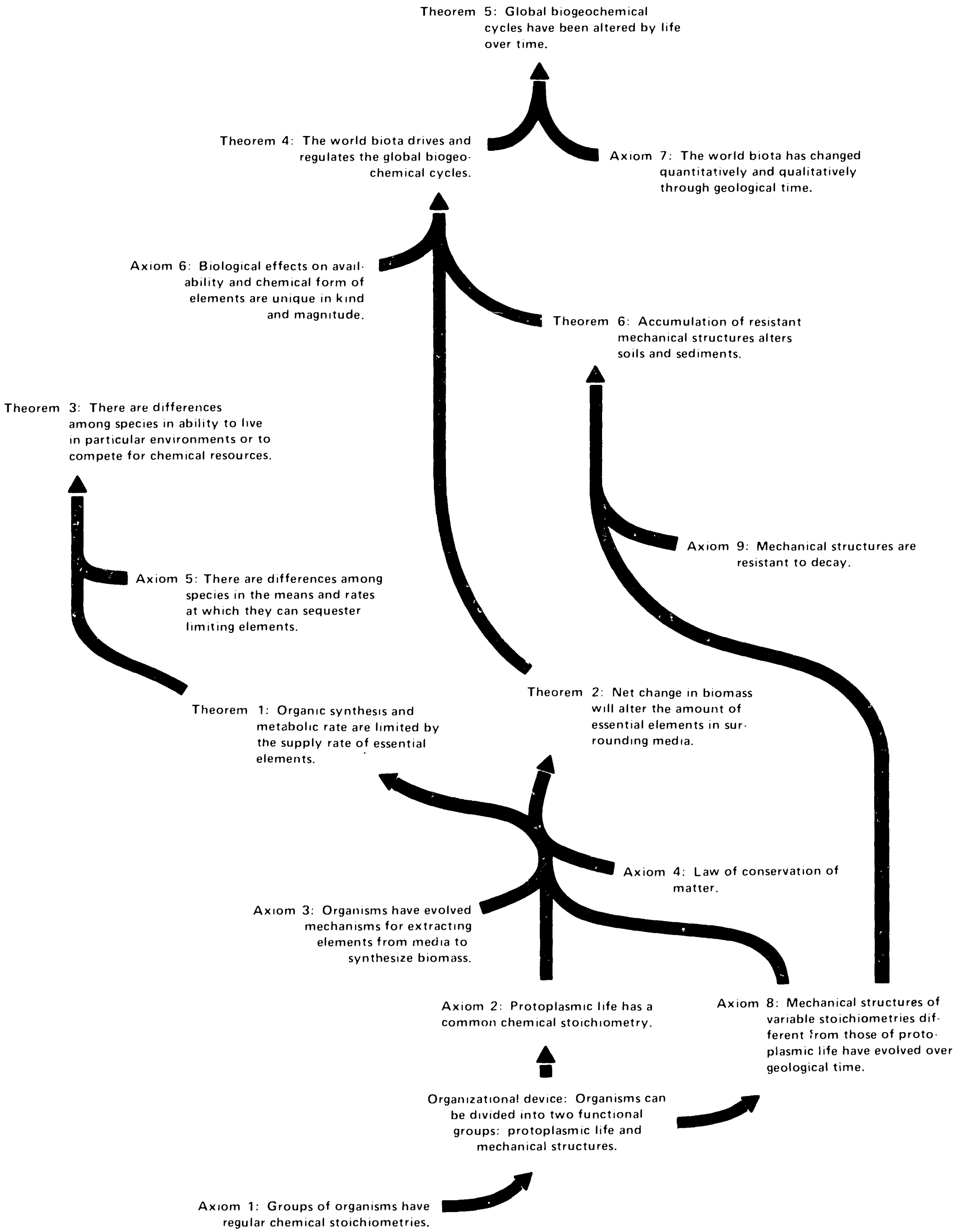

FIG. 1.—A logic flowchart for axioms and theorems concerning the relationship of organismal chemical stoichiometry and biospheric biogeochemistry.

TABLE 1

ATOMIC RATIOS OF MAJOR BIOGENIC ELEMENTS TO PHOSPHORUS FOR GROUPS OF ORGANISMS

BIOLOGICAL GROUP	ELEMENT:PHOSPHORUS ATOMIC RATIO								
	C	H	O	N	S	Ca	Mg	K	Si
Bacteria	46	76	15	7	<1	<1	<1	3	<.01
Fungi	—	342	132	15	<1	<1	<1	4	<.01
Phytoplankton									
Marine	53	130	77	11	<.1	<1	2	<1	11
Angiosperms									
Herbaceous	230	337	157	23	<1	4	<1	5	<1
Woody	1103	1618	754	53	5	6	6	7	<1
Zooplankton									
Marine	143	207	74	26	—	3	2	1	—
Crustaceans									
Marine	115	207	86	21	<1	2	<1	1	<.1
Mollusks									
Marine	789	2278	19	136	5	741	6	<1	2
Insects	68	133	37	16	<1	<.1	<.1	<1	<1
Fish									
Marine	68	117	31	14	<1	<1	<.1	<1	<.01
Mammals	29	48	8	4	<1	2	<.01	<1	<.01

NOTE.—Data for insects, fish, and mammals from Bowen 1966; remaining data from Bowen 1979. Where Bowen gave data as ranges, a simple average of the range is used. Concentrations made on a dry-mass basis. Ratios shown as <1 are >.1, <.1 are >.01, and <.01 are >.001. Values for mollusks were estimated from hard-part and soft-part data in a ratio of 3:1.

ratios of all the major elements and four minor elements with P on an atomic basis. The ratio in terms of P follows the precedent of Redfield, which in turn is based on the central position played by P as the major element most likely to be rate-limiting in the long term in aquatic and marine systems. The argument for a complementary model follows the simple case for protoplasmic life, represented best in the table by bacteria, and then is expanded to include mechanical structures.

Protoplasmic Life

Protoplasmic life has a common stoichiometry of chemical elements in particular proportions (axiom 2; fig. 1). The bulk of simple cells and of the protoplasm of specialized cells and organisms is, in fact, C, H, O, and N, which are the four lightest elements of the periodic table that can make covalently bonded compounds (Chapman and Schopf 1983). It is these, together with P and S, that are usually found in the most regular proportions. The absolute amounts and, to a lesser degree, the stoichiometry of cells may vary through changes in the storage of critical compounds (e.g., vacuolar storage in plant cells), but these differences are small in comparison with the differences between protoplasm and mechanical structures.

The law of material conservation dictates that organisms must extract mass from their environment to make additional organic mass. Operationally, organisms have evolved mechanisms, usually energy-demanding, for extracting elements from their surrounding media and chemically reorganizing these elements into new organic matter (axiom 3; fig. 1). From this first axiom and the material-conservation law we can deduce theorem 1 (fig. 1; and it can be observed) that organic synthesis, and thus metabolic rate, can be limited by the supply rate of essential elements. Because in nature the major elements are often in shorter supply compared with demand than are the minor elements, the major elements are more often limiting to synthesis.

Referring to the second axiom on the chemical composition of protoplasmic life and again using the law of conservation of matter (axiom 4), we can also deduce that with net growth, organisms and their accumulated products reduce the amount of essential elements in the surrounding media. Conversely, with a net decrease in organic mass, the amount of essential elements in the media increases (theorem 2; fig. 1). Theorem 2 is a statement that the amount of elements in a finite medium are, in part, a function of the amount of elements removed by biotic uptake. This is merely a formal way of stating the mass-balance principle, which is a major tool in biogeochemistry (e.g., Vitousek and Reiners 1975). In more-descriptive terms, as individual organisms grow, develop, and die, they acquire, sequester, and release major (and sometimes chemically analogous) elements. Elements can be recycled within organisms and certainly recycle between them and the media of air, water, soil, or sediments. As populations grow, the net effects of these processes lead to characteristic withdrawals of elements from, and returns to, the abiotic environment. These processes may be diurnally or seasonally rhythmic, irregular, or steady depending on the magnitudes of the populations and their associated detritus. These processes are part of the characteristic exchange and turnover rates within and between biotic and abiotic pools and of the local and global components of biogeochemical cycles.

Again referring to theorem 2 (net change in biomass affects nutrient-pool size) and introducing axiom 5, that there are differences between species in the ways and rates at which they can extract and sequester elements, we can deduce theorem 3: these differences lead to ecological differences in the ability to compete for nutrients (assuming competitive conditions) or to survive in a particular environment even without competition. This is part of the basis for niche differentiation, which leads in turn to predictable outcomes of competition, geographical distribution, and succession (Tilman 1982). This is a "spin-off" deduction from the usual domain of ecosystem ecology, but it points up the actual intimacy of interactions from all levels of biological and ecological thought.

Theorem 2 states that the increase or decrease in the mass of organisms (or their accumulated products) can control the amount of constituent elements in the abiotic environment. To theorem 2 can be introduced axiom 6, that the uniquely biological processes that drive the uptake and release of C, H, O, N, P, and S, in particular, are large enough (over cumulative time) to control the levels of these elements in at least some of their major abiotic pools. The basis of this axiom lies in an enormous body of evidence from geology and paleontology that is summed up by Lovelock (1979) and Rich (1984). Axiom 6 (biological activities uniquely influence elemental distribution and fluxes) leads to another deduction, also expressed previously on empirical grounds by Redfield (1958) and others, that the world's biota drives and regulates the global geochemical cycles of the major elements (theorem 4). Theorem 4 is deduced strictly on mass-balance grounds for the major elements as defined here, but the presence of two biological products—reduced carbon and free oxygen—also leads to fundamental changes other than mass-balance effects on the geochemical cycles of biologically minor and even nonessential elements (Lovelock 1979). Some of these affected elements, such as iron (Cloud and Gibor 1970), are quite major elements of the lithosphere and among the critical mineral resources required by industrialized societies (Meyer 1985). With the biological influence, if not control, of geochemical cycles, chemical cycles are more properly referred to as "biogeochemical cycles."

Accepting theorem 4 (the world's biota drives and regulates biogeochemical cycles) and taking into account the fact that the earth's biota has changed quantitatively and qualitatively through earth's history (axiom 7), simultaneously causing similar changes in the influence of the biota on biogeochemical cycles, then we can deduce theorem 5: the global biogeochemical cycles of earth have been altered by life over time. Again, the evidence supporting axiom 7 comes from the geological record (e.g., Schopf 1982).

Mechanical Structures

The paleontological record demonstrates that stiff, non-protoplasmic structures have developed through time along with specialized cells, multicellular organisms, and larger size. Axiom 8 states that these structures have developed with various chemical compositions, all differing from that of protoplasm. Thus, the stoichiometry of life has been altered in various ways with the evolution of multicellular life and larger size.

The evolution of mechanical structures is associated with adaptations for slow sinking (planktonic diatoms), for defense, for anchoring organisms, or for rigidifying large body masses in order to maintain body form against the pull of gravity. Such adaptations have been accomplished in various ways, all of biogeochemical significance. Diatoms and other unicellular eucaryotes construct elaborate tests of silica dioxide or calcium carbonate. Although the stoichiometry of the core protoplasm of these organisms is probably similar to that of bacteria, the whole-body stoichiometry is drastically altered in certain respects (see Si:P for marine phytoplankton, and the C:P, O:P, and Ca:P ratios for zooplankton in the table).

With the evolution of larger organisms, cell specialization and even more massive supporting structures appeared. In some groups like mollusks, sponges, and coralline coelenterates and algae, calcium carbonate and sometimes calcium phosphate is used to form exoskeletons (Pautard 1978), thus altering the proportions of carbon and calcium to phosphorus (see mollusks in the table). The other basic form of exoskeleton found in fungi and arthropods is formed of chitin, a nitrogenous polysaccharide. This elevates the C:P, H:P, O:P, and N:P ratios of fungi, crustaceans, and insects compared with bacteria.

The rise of vertebrates introduced cartilaginous and bony endoskeletons. About 60% of bone by dry weight is primarily hydroxyapatite, $Ca_{10}(PO_4)_6(OH)_2$ (Pautard

1978; LeGeros and LeGeros 1984). The addition of bone to soft tissues of vertebrates depresses the ratios of most elements with respect to P except Ca. This is particularly true of the heavier-boned tetrapods (represented by mammals in the table), whose skeletons must bear body weight in the low-bouyancy medium of air (except for pelagic mammals).

Sessile organisms such as reef or marine littoral animals and especially land plants tend to have more-massive supporting structures than do mobile organisms. Plant life on land favored a sessile growth form, which in turn led to adaptations for securing resources from a specific volume of soil and air and from space open to solar flux. Where resources were less limiting, these adaptations accompanied increases in size and, in the broadest sense, longevity. Supporting tissues necessary for an increase in size were fabricated into polysaccharides (especially cellulose) and aromatics of thickened and lignified cell walls, largely from C, O, and H, locally inexhaustible elements extracted from fluid resources of the atmosphere (carbon dioxide and water) that flowed through the volume occupied by individual plants. Consequently, the stoichiometry of land plants, especially woody plants, is vastly different from that of planktonic algae (table 1). As expected, the C:P, H:P, and O:P ratios of woody angiosperms are much higher than the ratios for bacteria or marine phytoplankton. Curiously, the other element-to-P ratios are higher as well, suggesting a generally greater economy in the use of P in both herbaceous and woody plants. The wholesale incorporation of lignins and tannins into the cell walls and cytoplasm of land plants represents an amplification of stoichiometric change. These aromatics are known in marine plants (Fenical 1982), but their development in land plants is unparalleled, possibly as protective chemicals for perennial structures against pathogenic attack (Swain 1979) as well as for mechanical stiffening.

The alteration of organismal stoichiometries through the variable elaborations of mechanical structures has two biogeochemical effects. The first is parallel to that described by theorem 2 for protoplasmic life: the requirement for elements to synthesize mechanical structures leads to a biological influence on the quantities removed from and returned to the surrounding media.

The second effect is quite different in degree from protoplasmic life. Mechanical structures are characteristically resistant to decay and mineralization (axiom 9). This is especially true of carbonates, chitin, bone, and cellulose accompanied by lignins and tannins. Consequently, we deduce theorem 6, that these mechanical structures alter the composition of soils and sediments by their slower decay rate. Thus, we have humus-bearing soils, sediments of reduced carbon (coal, carbon-rich shales, petroleum, and gas), and organically produced apatite of economic significance as phosphate fertilizer (Brinck 1979). Even the rain of silica and carbonate tests of planktonic organisms produce massive oceanic deposits (Broecker 1974) of geological and economic importance.

To theorem 6 can be added axiom 6: uniquely resistant biological materials affect geochemical cycles in a kind and/or to a degree different from what would be found in a nonbiotic world. This leads to a broadened meaning and support for theorem 4, that the world's biota drives and regulates the global geochemical cycles of major (and in this case, some minor) elements. Biotic influences on these cycles can be surprisingly strong in particular times and places, even for elements of marginal concentrations in the biota: aluminum (Mackenzie et al. 1978; Stoffyn 1979), silica (Lund et al. 1963; Broecker 1974), calcium (Deuser et al. 1983), barium (Chow and Goldberg 1960), various metals (Bruland et al. 1979), and others (Trudinger and Swaine 1979; Lowenstam 1981; Wollast 1981). Determining the degree to which the cycle of an element is biologically controlled is difficult given the circular causal-loop patterns of these cycles. This determination rests in large part on the ratio of biological demand to environmental supply. The higher this ratio, the more the biological control and the less the geochemical control.

To complete the linkage of deductions regarding mechanical structures with the final theorems developed for protoplasmic life, we can recognize that mechanical structures contribute to theorem 5, that biogeochemical cycles of the earth have been altered by life over geological time to the present environment we now take for granted.

The role of the biota in driving and regulating biogeochemical cycles is so powerful in its cumulative effects that the biota has transformed the chemical and physical nature of the globe. In his classic book *The fitness of the environment* (1913), Henderson marveled at the unique fitness of the earth's environment for life as we know it. He concluded that the universe was somehow "biocentric." By the 1940s, it started to become clear that such fitness was no accident, but resulted from aeons of carbon fixation, organic-matter burial, net oxygen liberation, nitrogen transformations, and mineral oxidation (e.g., Lovelock 1979). The most profound result of the stoichiometry of life has been the wholesale reorganization of the biosphere to a chemical state we now regard as normal. The maintenance of a stable climate and chemical environment in the biosphere by the world's biota is perhaps the most unifying and significant phenomenon of ecology.

INTERACTIONS BETWEEN COMPLEMENTARY MODELS

The second complementary model of ecosystem structure and function is useful for raising certain classes of hypotheses and understanding a range of ecological problems. But like the first, energy-based, complementary model, by itself it is limited. More fruitful insights may accrue when we examine the cross-linkages between branches of the two complementary models. For example, theorem 3, regarding differences in modes of nutrient uptake (fig. 1), is a distinct branch of the second model. The inverse size–metabolic rate law could be a branch of a formalization of the first, energy-based model. These branches can be linked as follows.

Autotrophs growing in oligotrophic, deep-water environments must derive nutrients from the water medium rather than a more concentrated and stable substrate. This mode of mineral nutrition is best achieved with a high ratio of surface area to volume for individuals. Such a ratio is achieved by small individual size. Thus, pelagic systems would be expected to have a producer trophic level dominated by simple colonial or single-celled phytoplankton. This line of reasoning is merely an elaboration from theorem 3 via simple physiological principles.

The interface of this chemically based deduction with energetics is through the inverse size–metabolic rate law (H. Odum 1956). According to that law, small organisms metabolize at a high rate per unit mass. Small cells thus have a high productivity-to-biomass ratio and, as a population, turn over rapidly. Such cells are typically unprotected by noxious or toxic chemicals, and for demographic reasons, they can tolerate a high grazing rate. Thus, heterotrophs are likely to be larger than autotrophs, and energy flow is likely to be more important through the grazing pathway than the detritus pathway. This simple set of familiar deductions (see Wiegert and Owen 1971) illustrates a higher set of deductions through the interfacing of two complementary models for ecosystems.

A THIRD COMPLEMENT?

The two complementary foci described here contribute to the development of an ecosystem theory through logical connections between increasingly subtle and complex hypotheses. The interaction between these holds even more promise. It is clear, though, that these complementary approaches are not sufficient to explain or explore all pertinent issues of ecosystem ecology. For example, neither of these models, either alone or in concert, answers questions about the number of species an ecosystem comprises, the apportionment of energy flow between populations, the biological basis for regulation and homeostasis, or how ecosystems respond to disturbances.

It could be argued that such questions are not a proper part of the ecosystem level of organization, that they belong at a lower level of organization, the community level. Such an argument would simplify matters, but it is unacceptable if ecosystems are to be treated in the way originally conceived of by Tansley. Furthermore, descriptions of energy flow and chemical flux are mere bookkeeping exercises if they are only applied to steady-state (or assumed steady-state) systems. The real power of the ecosystem approach comes when it is applied to systems undergoing some dynamics, whether engendered by intrinsic change or natural or human-imposed disturbances. Biologically driven dynamic processes are ultimately based on population and community properties.

An analysis of ecosystem behavior in this sense is incomplete and, in fact, illogical if the biotic-community component is not included. The ecosystem hierarchical level encloses or subsumes the biotic community, and without an incorporation of the biotic community the scientific understanding of ecosystems will never be complete (see also Webster 1979). From this point of view, it seems that a third complementary approach to ecosystems must be recognized, possibly one that is built on population interactions, causal networks, or the "connectedness" properties of the whole ecosystem (Allen and Starr 1982). Developing such a third complementary model is well beyond the scope of this paper. Such a model is badly needed, however, to develop the theoretical framework for the ecosystem in order to clarify the discipline and promote conceptual advances at this difficult level of organization.

SUMMARY

The ecosystem level of ecological research is fraught with conceptual difficulties that have contributed to faltering progress in theoretical development.

An acceptance of multiple models for different aspects of ecosystems may assist in reducing this confusion. Two complementary models of ecosystems are suggested: the first based on energy, the second based on matter. Whereas the first follows from the second law of thermodynamics, the second complementary model derives from the chemical stoichiometry of the biota. These models can be developed independently but have many points of interaction. These points yield another series of predictions and hypotheses. While these complementary models serve as theoretical structures for much of the body of ecosystem concepts, they are not adequate by themselves. Other complementary models, perhaps centered on explicit linkages at the population and community levels, are necessary.

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