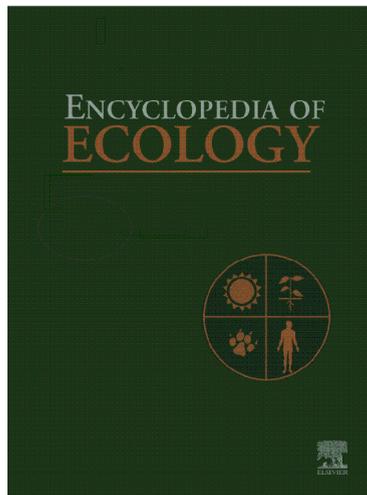


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## Summary

Evolutionary algorithms provide robust, relatively easy-to-use methods for a wide range of parameter estimation problems. Recent developments have led to more reliable and/or faster algorithms, and these methods may be considered along with the early generation evolutionary algorithms currently used in ecological modeling.

Evolutionary algorithms provide one of the few available methods to automatically generate models – rather than parameters – from data, their main competition being artificial neural networks (see Artificial Neural Networks) and relational learning systems. Their inherent white-box nature and robustness provide important advantages in automatic model generation, though much still remains to be done in these areas. They may be particularly appropriate where the underlying mechanisms of the process being modeled are evolution-like. In these cases, the application of coevolutionary techniques in ecological modeling merges seamlessly with the wider field of evolutionary simulation.

See also: Artificial Neural Networks; Ecological Models, Optimization; Spatial Models and Geographic Information Systems.

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## Evolutionary and Biochemical Aspects

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### Introduction

#### Diversity of Organismal Stoichiometry

#### Elemental Composition and Biological Function

### Stoichiometry and Phenotypic Evolution

#### Further Reading

## Introduction

Darwin's theory of evolution by natural selection provides a general explanation for the diversity of life. If organisms differ in traits that are heritable, then differences in reproductive success among individuals will result in changes in the relative prevalence of traits in subsequent generations; over time, this process of natural selection leads to adaptation, an improved fit between the features of organisms and the demands of the environment.

Adaptations may often be manifested in the biochemical makeup of organisms. This is because an organism's biochemistry has functional and economic consequences

that influence reproductive success. From a functional perspective, an organism's makeup affects its ability to meet environmental challenges because compositionally distinct biomolecules, cellular structures, and tissues have different chemical properties that determine their biological roles. From an economic perspective, an organism's makeup reflects its demand for structural resources, and environmental scarcity of particular substances may constrain the evolution of reliance on those substances. The composition favored by natural selection should reflect the optimal compromise between these functional and economical considerations.

Ecological stoichiometry, the study of the balance of energy and chemical elements in living systems, provides

a general structure for examining how the composition of life has evolved. Clearly, organisms are not bags of independently functioning atoms, and a focus on elements will often miss the consequences of how elements are arranged in biochemicals. However, this focus has significant advantages because it provides a currency that facilitates comparisons across diverse taxonomic groups and levels of biological organization.

Consider the following examples that illustrate some of the ways in which elemental composition can have adaptive significance.

The water flea, *Daphnia*, is a common herbaceous crustacean found in lakes, ponds, and quiet streams. There is now ample evidence that the rate at which a *Daphnia* can grow is functionally related to the concentration of phosphorus (P) in its tissue when P is scarce in the environment. The connection between body P levels and growth rate exists because growth rate depends on the concentration of RNA in *Daphnia* tissue, and RNA is an abundant cellular component that contains more P than other major biomolecules. This linkage among whole-body P concentration, RNA levels, and growth rate is the central prediction of the growth rate hypothesis (GRH), which is described more thoroughly in Organismal Ecophysiology.

Aquatic mollusks depend on calcium (Ca)-rich shells for protection against fish and crustacean predators. The protective benefit of a shell for mollusks depends on its thickness, form, and Ca content, which affects hardness and other physical properties that help shells maintain structural integrity in the face of attack. Because Ca influences shell function, it is not surprising that Ca availability is thought to have played an important role in the evolution of molluscan shell morphology. Ca availability can also induce short-term changes in shell investment, which has been demonstrated in the freshwater snail *Lymnaea stagnalis*. The relationship between Ca availability and shell investment suggests that the evolutionary significance of predation pressure will be mediated by the types of resources available in the environment.

Aphids are insect herbivores that tap into a plant's phloem and feed on sap. Solutes in sap tend to be rich in carbon (C) but contain few nitrogen (N)-rich amino acids, P-containing molecules, or other important minerals and vitamins. Sap thus creates a significant dietary challenge for an insect because its elemental composition (high C:N and C:P ratios) differs substantially from the balance of these elements in insect tissue. Adaptations to this imbalance include phenotypes that promote mutualistic interactions with bacteria and ants. For example, aphids such as the greenbug aphid, *Schizaphis graminum*, house intracellular bacteria which supply essential amino acids to their hosts after receiving C and nonlimiting amino acids. Aphids have also evolved the ability to produce a

carbon-rich exudate called 'honeydew', which some species present to ants in exchange for protection from aphid predators and parasites. Thus, the compositional disparity between aphids and their food may have been a key factor promoting the evolution of mutualistic interactions.

These examples illustrate how elemental composition can play a role in a wide range of phenomena that ultimately affect an organism's reproductive success. It follows that conditions favoring particularly strategies for maximizing reproductive success will also have resulted in evolutionary changes in elemental composition. If so, organisms should differ in elemental composition, and these differences should be associated with biochemical differences that affect functional capabilities. Let us review some of the available evidence for evaluating these predictions.

## Diversity of Organismal Stoichiometry

All organisms contain the same major elements (e.g., C, N, P, Ca, hydrogen (H), oxygen (O), S (sulfur)), but existing information indicates that the concentrations of these elements in organisms can differ substantially among and within taxonomic groups. Patterns of elemental abundance are best described for C, N, and P (Table 1), which have received most of the attention in ecological stoichiometry because of their importance in biological structures and because N and P commonly limit production in nature.

First, let us examine the relative amounts of C, N, and P in plants and other autotrophic organisms. The C:N:P composition of individual autotrophs is generally quite variable because molecules containing these elements can be stored in large quantities in vacuoles or in the cytoplasm. Despite this variability, there are still clear differences in C:N:P composition among species. One way to categorize this variation is by making comparisons among major habitats, such as oceanic, freshwater, and terrestrial systems. In oceans, particulate matter (which provides a measure of phytoplankton biomass) tends to be rich in N and P relative to autotrophic biomass in freshwater and terrestrial systems. Seminal work in the mid-1900s by Alfred Redfield showed that the relative amount of C, N, and P in marine particulate matter was 106:16:1 (molar ratio). This description is referred to as the Redfield ratio. More recent findings have shown that although the average C:N:P composition of marine particulate matter tends to be relatively homogeneous across sampling locations, there is more than threefold variation in C:P and N:P ratios across different phytoplankton phyla and superfamilies. In lakes, particulate matter tends to contain much less P than it does in oceans. On average, C:P ratios in freshwater particulates are about 300, and N:P ratios are about 30; these values are

**Table 1** Approximate ranges for C, N, and P concentrations across species in select taxa

Taxon	% C	% N	% P
Terrestrial plants (leaves)	36–64 <sup>a</sup>	0.25–6.4 <sup>b</sup>	0.02–1.0 <sup>b</sup>
Benthic invertebrates	35–57 <sup>c</sup>	6–12.0 <sup>c</sup>	<0.2–1.8 <sup>c</sup>
Zooplankton		7–12.5 <sup>a</sup>	0.5–2.5 <sup>a</sup>
Terrestrial insects	36–61 <sup>a</sup>	6–12.0 <sup>d</sup>	0.35–1.5 <sup>e</sup>
Freshwater fish	~40–50 <sup>f</sup>	8–12.0 <sup>f</sup>	1.5–4.5 <sup>f</sup>
Birds and mammals			0.7–3.7 <sup>g</sup>

<sup>a</sup>Elser JJ, Fagan WF, Denno R F, *et al.* (2000) Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408: 578–580.

<sup>b</sup>Güsewell S (2004) N:P ratios in terrestrial plants: Variation and functional significance. *New Phytologist* 164: 243–266.

<sup>c</sup>Cross WF, Benstead JP, Rosemond AD, and Wallace JB (2003) Consumer-resource stoichiometry in detritus-based streams. *Ecology Letters* 6: 721–732.

<sup>d</sup>Fagan WF, Siemann E, Mittler C, *et al.* (2002) Nitrogen in insects: Implications for trophic complexity and species diversification. *American Naturalist* 160: 784–802.

<sup>e</sup>Woods HA, Fagan WF, Elser JJ, Harrison JF (2004) Allometric and phylogenetic variation in insect phosphorus content. *Functional Ecology* 18: 103–109.

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<sup>g</sup>Gillooly JF, Allen AP, Brown JH, *et al.* (2005) The metabolic basis of whole-organism RNA and phosphorus content. *Proceedings of the National Academy of Sciences of the United States of America* 102: 11923–11927.

Element concentrations are reported as % dry mass. Data are for whole organisms unless otherwise noted.

substantially higher than the Redfield values of 106 and 16. Phosphorus content in lake particulates is also highly variable: N:P ratios in one survey ranged from 6.5 to 125 across sites. Mean C:N ratio in lake particulates is about 10, similar to values for ocean particulate matter. Terrestrial autotrophs tend to have much higher C:N and C:P ratios than oceanic and freshwater autotrophs: the mean C:N ratio in leaves is around 36, and the mean C:P ratio is near 1000. C:nutrient ratios in whole plants are likely even higher than ratios in leaves because wood, bark, and other secondary growth generally contain low concentrations of N and P. Concentrations of N and P in leaves also differ substantially among plant species (Table 1), showing 25- and 50-fold ranges of variation, respectively.

Next, consider the elemental composition of animals. Because animals have limited capacity for nutrient storage and possess mechanisms for selectively acquiring and retaining particular substances, individual animals tend to maintain their elemental composition within limited bounds. However, there are often significant differences in whole-body stoichiometry among animal species.

Patterns of elemental abundances in invertebrates have been most thoroughly cataloged for two groups: zooplankton and insects. Zooplankton species, which consist mostly of rotifers, cladocerans, copepods, and other small crustaceans, vary considerably in P content, but are less variable in terms of N and C (Table 1). For example, P concentration (% dry mass) in zooplankton varies five-fold across species, whereas zooplankton N content varies less than twofold. Terrestrial insect species also vary considerably in P concentration, which can range from ~0.35% to ~1.5% dry mass in adults (Table 1). As in zooplankton, N concentration in insect species is more tightly constrained, varying only about twofold (~6–12% dry mass) among adults across species. Zooplankton and

insects contain similar concentrations of C, N, and P, but both groups contain considerably more N and P than autotrophs (Table 1). The compositional disparity between invertebrate animals and autotrophs is particularly striking in terrestrial systems.

Less information is available about whole-body C:N:P stoichiometry for vertebrates, although descriptions are available for some fish, birds, and mammals (Table 1). In fish, P content can range from 1.5% to 4.5%. The N content in fish is again less variable (8–12%) than P content, and mean values are similar to levels found in invertebrates. P content appears also to be high and variable in terrestrial vertebrates. For example, reported levels for P content range from 0.67% in pigs to 3.67% in humans. P concentrations in vertebrates are considerably higher than in invertebrates due in large part to the high P content of bone.

These comparisons illustrate that there are clear compositional differences among major taxonomic groups: the low N and P concentrations in terrestrial plants and the high P content in vertebrates are particularly distinctive. Perhaps more importantly, there is also considerable variation in C:N:P stoichiometry within groups such as zooplankton, insects, and fish, whose members have many morphological and ecological similarities. It is thus likely that the adaptations distinguishing species are reflected in the elemental composition of organisms. If so, the chemical composition of organisms may be a key factor guiding the evolutionary dynamics of populations. To get a better understanding of the evolutionary relevance of stoichiometric variation, we must first explore how elemental composition is connected to functional capabilities that ultimately affect an organism's reproductive success. Useful information for making this connection comes from a multilevel analysis of organismal biochemistry.

## Elemental Composition and Biological Function

The elements themselves have distinct properties that influence their roles in biological systems. For example, the ability of a C atom to form strong, stable covalent bonds with C itself and with other major elements (e.g., H, N, O, S, and P) explains why C forms the backbone of a variety of kinetically stable polymers that serve as membranes and other structural biomolecules. In addition, C–C bonds have the highest bond energy of all solid nontransitional elements, which makes C atoms well-suited for their prominent role in energy storage molecules. These biochemical features help to explain why C is often the most abundant element in the dry mass of organisms. Nitrogen is typically the fourth most abundant component of organism dry mass (after C, H, and O). Biological N tends to occur in a reduced state bound to C and H; the resulting amine group (R–NH<sub>2</sub>) is basic. The combination of this basic amine group with an acid carboxyl group is the peptide bond that links amino acids in proteins. At neutral pH, the amine group is protonated, providing one of the few sources of positive charge in biomolecules. In addition, N–H bonds are polar and readily form H bonds to other polar groups; these bonds are critical for determining the structure of proteins and nucleic acids. Phosphorus is typically the fifth or sixth most abundant element in organisms. It occurs almost exclusively in the oxidized phosphate form (HPO<sub>4</sub><sup>2-</sup>) in biological systems. As bound phosphate, it can

function in several important ways, including (1) as a link between subunits in large molecular assemblies (e.g., DNA, RNA, and phospholipids), (2) as a carrier of chemical energy (e.g., adenosine 5'-triphosphate, ATP) and substrates (e.g., glucose phosphate), (3) as a signaling mechanism (e.g., cyclic-adenosine monophosphate, c-AMP), and (4) as a component of biominerals (e.g., calcium phosphate). Phosphate serves as an effective link in nucleic acids and a center of mobility in lipids because it readily reacts with attacking reagents. This flexibility is essential to RNA, which must have the capacity to turn over quickly in order to be effective in carrying rapidly reproducible information.

The distinctive chemical properties of C, N, and P suggest major differences in elemental composition among organisms which will be associated with differences in capacities for meeting environmental challenges. However, the connection between elemental composition and biological function becomes much more tangible with a general description of how elements are distributed among biomolecules, cellular components, and tissues.

## Elemental Composition of Biomolecules

Variation in elemental composition among organisms can be driven by stoichiometric differences at many levels of internal organization. As outlined below, major classes of biomolecules such as lipids, carbohydrates, protein, and nucleic acids contain different concentrations of C, N, P, and other major elements such as H, O, and S (**Table 2**).

**Table 2** Approximate C:N:P:H:O:S stoichiometry (% of mass) of selected macromolecules and other organic compounds

	%C	%N	%P	%H	%O	%S
<i>Lipids</i>						
Glycerol (triacylglyceride) <sup>a</sup>	75	0	0	14	12	0
Cholesterol	84	0	0	12	4	0
Phosphatidylcholine (phosphoglyceride) <sup>a</sup>	67	2	4	11	16	0
<i>Carbohydrates</i>						
Starch and cellulose	46	0	0	3	51	0
Lignin	63	0	0	6	31	0
Chitin	44	7	0	7	42	0
Peptidoglycan <sup>b</sup>	49	12	0	7	30	1.5
<i>Proteins</i>						
Protein <sup>c</sup>	54	17	0	7	20	2.7
Rubisco (large subunit)	54	17	0	7	21	1.2
Myosin (heavy chain)	53	17	0	7	22	0.8
Collagen	54	18	0	7	21	0.5
<i>Nucleic acids</i>						
DNA <sup>d</sup>	38	17	10	4	31	0
RNA <sup>d</sup>	36	16	10	3	35	0
<i>Other organic compounds</i>						
ATP	24	14	18	2	41	0
Chlorophyll	74	6	0	8	9	0

<sup>a</sup>Fatty acid chains consisting of stearic acid (saturated fatty acid with 18 C atoms).

<sup>b</sup>Oligopeptide side chain with five amino acids, 5% each of all 20 amino acids.

<sup>c</sup>Hypothetical nonphosphorylated protein consisting of 5% each of all 20 amino acids.

<sup>d</sup>Assuming 50% G–C base pairs.

As a result, differences in biomolecular mixtures result in stoichiometric variation at higher levels of organization, such as among cellular structures or tissues. Variation in elemental composition among organisms can potentially be explained by stoichiometric differences at any level of organization, provided components at that level (1) have distinctive elemental signatures, (2) vary significantly in concentration among organisms, and (3) contain a sizable fraction of the whole-organism pool of some element. Determining which components explain the variation in whole-organism stoichiometry is a key step in relating elemental composition to biological functions that affect fitness.

What then is known about variation in elemental composition among major biomolecules, and how might this variation be related to biological function?

### Lipids

Lipids are a diverse group of chemicals with a variety of biological functions. Triacylglycerols, waxes, and other fats and oils are the principal mechanism for storing energy in most organisms; sterols and phospholipids serve as structural elements in membranes; and other less-abundant lipids act as electron carriers, pigments, and enzyme cofactors. Triacylglycerols, waxes, and phospholipids are the primary components of lipid biomass in organisms, and are thus more likely than other lipids to contribute to a distinctive whole-body elemental composition.

Triacylglycerols and waxes consist of only C, H, and O; they contain neither N nor P. Carbon content in these molecules is generally high. For example, a triacylglycerol with three 16-carbon unsaturated fatty acids will contain 76% C; myricyl palmitate, the primary component of beeswax, contains about 82% C. The C content of triacylglycerols is substantially higher than levels in other major biomolecules (Table 2) and in animal bodies as a whole (see Table 1).

Phospholipids contain a glycerol molecule attached to two fatty acids and a functional group. Phospholipids consist almost entirely of C, H, O, and P, which is contained in a phosphodiester linkage between the functional group and the glycerol molecule. The functional group in some phospholipids does contain N, although the N content in phospholipids is generally low. For example, phosphatidylcholine, a common phospholipid, contains 67% C, 1.9% N, and 4.2% P.

Storage lipids are likely the only form of lipids that will contribute significantly to whole-organism stoichiometry. Storage lipids can make up a substantial fraction of organism biomass. For example, mean lipid concentration in insects has been measured to be about 25%; similar levels have been measured in marine calanoid copepods and albacore tuna. Similarly, triacylglycerols in adipose tissue make up about 21% of the mass of a nonobese 70 kg man. Storage lipid levels can also vary substantially among taxa and among individuals within taxa. In whole tuna, lipid content can vary from 1% to 43% dry mass.

Lipid stores are known to vary with fluctuations in activity demands and resource availability. Because storage lipids are rich in C but contain no N or P, increases in storage lipid levels will increase C:N and C:P ratios in whole organisms, but will have no effect on body N:P ratios. Directional selection on energy storage could thus result in evolutionary increases in whole-body C:N and C:P ratios. Unlike triacylglycerols, phospholipids contribute little to the total biomass of most organisms. For example, in crustacean zooplankton phospholipids make up only about 6% of total body mass; in the mussel *Mytilus edulis*, phospholipid content ranged from only 0.36% to 0.64% in soft tissue.

### Carbohydrates

Carbohydrates generally serve as fuel, energy stores, and building materials, although specific carbohydrate-containing molecules also act in cell-cell recognition and information transmission. Sugars and starches are carbohydrates involved in energy transport and storage; they have a general chemical formula of  $(\text{CH}_2\text{O})_n$ . Thus, like storage lipids, carbohydrates with this basic formula contain neither N nor P. However, they contain less C than lipids. For example, glucose contains 40% C and glycogen contains 52% C, while triacylglycerols typically contain more than 70% C. Carbohydrate fuels generally make up only a small fraction of organism biomass: in humans, glycogen is only about 225 g of the mass of a nonobese 70 kg man. They are thus unlikely to contribute substantially to variation in whole-body C:N:P stoichiometry.

Structural carbohydrates are more significant contributors to organismal stoichiometry, especially in plants. Insoluble carbohydrate polymers serve structural and protective roles in the cell walls of plants and bacteria and in animal connective tissue. Examples of common structural polysaccharides include cellulose and lignin, which are tough, fibrous polymers in plant cell walls; chitin, which strengthens insect exoskeleton; and hyaluronate, which provides viscosity and lubrication in vertebrate joints. Cellulose  $(\text{C}_6\text{H}_{10}\text{O}_5)_n$  contains 46% C and no N or P. It makes up most of the mass of wood, and will thus largely determine the elemental composition of large terrestrial plants with extensive support structure. Selection favoring investment in cellulose will increase C:N and C:P ratios in whole plants but will not affect plant N:P ratios. Some other structural polysaccharides do contain N. For example, chitin has an acetylated amino group ( $-\text{NH}$ ) in place of the hydroxyl group ( $-\text{OH}$ ) in cellulose. As a result, it contains 6.9% N, which is within the range (6–12% N) found in the bodies of insects. Chitin generally makes up <10% of insect biomass, but chitin investment can differ among species. Because chitin itself contains no P, variation in chitin investment could explain some of the variation in insect C:P and N:P ratios.

### Protein

Proteins are versatile nitrogenous biomolecules that serve structural, signaling, and catalytic roles in cells. They occur in thousands of varieties ranging in size from small peptides to large polymers with molecular weights in the millions. The 20 amino acids that are the monomers or building blocks of proteins all have a carboxyl group and an amino group bonded to a carbon atom, but they have different side chains which determine their distinct chemical properties. Differences in side-chain composition are also what determine differences in the elemental composition among amino acids. On average, the 20 common amino acids contain 53% C, 17% N, and no P; greater investment in protein will thus increase levels of N and reduce P content in organisms. Proteins constitute the largest fraction of the biomass in most cells. For example, proteins make up 50% of the dry mass in the bacteria *Escherichia coli*, 30–50% of the dry mass in crustacean zooplankton, 30% of plant leaf biomass, and about 40% of the dry mass in a nonobese human male. Protein investment thus is a major determinant of whole-body elemental composition.

There is also considerable variability in elemental composition among amino acids. C content ranges from less than 30% in cysteine to 65.5% in phenylalanine, and N content ranges from 7.7% in tyrosine to 32.1% in arginine. This variation has some relationship to amino acid function. For example, amino acids with aromatic side chains (phenylalanine, tyrosine, tryptophan) are relatively nonpolar and participate in hydrophobic interactions; they also have high C (mean = 63.2%) and low N (mean = 10%). In contrast, amino acids classified by their positively charged side chains (lysine, arginine, histidine) contain low C (mean = 45.7%) and high N (mean = 26.2%). These amino acids are important for enzyme catalysis and are often involved in weak electrostatic interactions with negatively charged biomolecules like nucleic acids. Selection on traits biasing the overall amino acid composition of protein could thus be manifested in the elemental composition of whole organisms.

Sulfur is not present in most macromolecules in organisms, but does occur in protein (Table 2). It is present in two amino acids: methionine and cysteine. The average S content of the 20 commonly occurring amino acids is 2.7%, but protein S content is generally lower (on average 1.3%). This can at least partly be explained by the relatively low S content in some of the most commonly occurring proteins, that is, rubisco (ribulose biphosphate carboxylase, the enzyme catalyzing C fixation in plants, and thus probably the most common protein in the world), myosin (a major protein in muscle tissue), and collagen (a major protein in the extracellular matrix of metazoan animals).

Proteins not only make up a substantial fraction of intracellular mass, they are also key components of important extracellular excretions such as hair, nails, skin, feathers, horns, spider webs, poisons, and venoms. Most of the dry mass of hair, claws, hooves, tortoise shells, and horns consists of  $\alpha$ -keratin, a strong fibrous protein. Fibroin, the protein of silk, is a polypeptide rich in N-rich alanine and glycine. These excretions clearly have important functional consequences, and thus provide a rich set of opportunities for determining how elemental composition relates to the evolution of traits.

### Nucleotides

Nucleotides are the constituents of nucleic acids (DNA, RNA), which store and transmit genetic information. They also act as carriers of chemical energy in cells, as enzyme cofactors, and as secondary messengers. Nucleotides consist of a nitrogenous base, a five-carbon sugar, and a phosphate group. In DNA and RNA, nucleotides are covalently linked by the phosphate group; the negative charge of the phosphate group at neutral pH is essential for stabilizing nucleotides against hydrolysis and for retaining them within a lipid membrane. Differences in the nitrogenous base determine the elemental and functional variation among nucleotides. Nucleotides, as they appear in RNA, contain on average 36.2% C, 16% N, and 9.6% P; the elemental composition of nucleotides in DNA is very similar. Thus, nucleotides in nucleic acids have N levels that are similar to those found in protein (16% vs. 17%), which are in turn much higher than levels in most organisms. Most notably however, nucleotides contain very high levels of P and low C:P and N:P ratios relative to other major biomolecules. The P content of an average nucleotide is also an order of magnitude higher than the P content of most insects, marine invertebrates, and plants.

RNA can comprise a large, but variable fraction of organism biomass. For example, RNA content can range from 12% to 30% of cell dry mass in *E. coli*, from 0.1% to 14% dry mass in invertebrates, and from 0.02% to 9% dry mass in birds, mammals, and fish. This substantial variation coupled with the high-P, low-N content of RNA make this molecule a major source of variation in organismal C:N:P ratios.

DNA levels are known to be much lower than RNA levels in most organisms. Genome size varies by up to five orders of magnitude among taxa, but this variation is accompanied by corresponding changes in cell size. As a result, DNA levels as a fraction of cellular biomass appear to be quite consistent across organisms and thus likely explain very little of the variation in C:N:P stoichiometry among taxa.

ATP is a nucleoside that is widely used for transporting energy in cells. An ATP molecule contains 24% C,

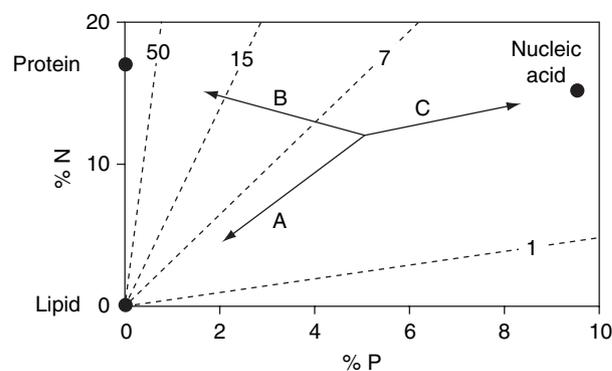
14% N, and 18% P; it is thus even more P-rich than the nucleotides in nucleic acid. However, ATP generally makes up only a small fraction of the total biomass of most organisms. For example, ATP levels range from 0.3% to 1.8% dry mass in marine copepods, and from only 0.02% to 2% dry mass in insects. As a result, variation in ATP content is unlikely to explain much of the variation among organisms in C:N:P stoichiometry.

### Biominerals

Biominerals are inorganic solids produced by a wide variety of organisms to harden and stiffen tissues. Hard tissues containing biominerals are used for support, protection, and resource acquisition. The physical properties of these tissues depend on the identity of biominerals and the degree of biomineralization; thus, there is often a clear link between tissue elemental composition and function. Biominerals also make up a large fraction of the biomass in some organisms.

The three principal classes of skeletal biominerals are calcium carbonates, silica, and calcium phosphates. Calcium carbonate is the most abundant and widespread biogenic mineral. It makes up a large component of mollusk shells. Bird egg shells also consist mainly of calcium carbonate; hen egg shells contain about 95% calcium carbonate. Investment in thick, calcium carbonate-rich egg shells is thought to be an adaptation to hard nesting substrates or other conditions where egg damage is likely. Silica-based scales and skeletons are common in several ameba groups, but are found in only a few animals (sponges, a few copepods, some brachiopod larvae). Diatoms contain uniquely high concentrations of silica (Si:N ratios in diatoms are typically about 1), which serves as a main constituent of diatom cell walls. Silica is also an important component of some grasses and sedges. For example, plants in the genus *Equisetum* (horsetails) use silicic acid to maintain stem erectness; levels of silica in *Equisetum palustre* have been reported to be as high as 7.4% of dry mass. Calcium phosphates serve as skeletal material in vertebrates and a few brachiopods. Bone consists mainly of a calcium phosphate known as hydroxyapatite  $[\text{Ca}_{10}(\text{PO}_4)_6]$ , which is also prominent in teeth and antlers. Although calcium-, silica-, and phosphorus-containing molecules are the most common biominerals, other elements such as iron and zinc form the basis of structural molecules in some organisms. For example, the marine bloodworm *Glycera dibranchiate* contains a copper-based biomineral (atacamite,  $\text{Cu}_2(\text{OH})_3\text{Cl}$ ) in their jaws, which are extremely resistant to abrasion.

In summary, storage lipids, structural carbohydrates, protein, RNA, and biominerals are the biomolecular constituents of organisms that will likely account for most of the variation in elemental composition among organisms. Greater investment in lipids, for instance, will increase



**Figure 1** Stoichiometric diagram illustrating how altering storage lipid allocation proportionally affects %N and %P, leaving N:P constant but changing C:P and C:N (arrow A); how altering protein allocation increases %N while lowering %P, increasing N:P (arrow B); and how altering nucleic acid allocation disproportionately affects %P, lowering N:P (arrow C). Dashed lines indicate particular N:P ratios. Sterner RW and Elser JJ; *Ecological Stoichiometry*. © 2002 Princeton University Press. Reprinted by permission of Princeton University Press.

body C but lower N and P contents, higher protein levels will increase body N but lower body P content, and greater investment in RNA will substantially increase body P levels (Figure 1). These differences show how selection for functions met by particular biomolecular mixtures can influence the evolution of body composition. Conversely, an organism's elemental composition should reflect its ability to respond to specific adaptive challenges.

### Elemental Composition at Higher Levels of Organization

Stoichiometric variation also occurs at higher levels of internal organization because organisms have different allocations to cellular structures and tissues having distinct biomolecular mixtures. A description of this variation is valuable because it helps to link elemental composition more directly to phenotypes.

A focal point in ecological stoichiometry has been the compositional difference between ribosomes and other cellular components. Ribosomes are the centers of protein synthesis; they catalyze peptide bond formation between amino acids in sequences determined by genetic information received from messenger RNA. The rate of protein synthesis often depends more on the number of ribosomes in cells than on the efficiency of individual ribosome molecules. As a result, ribosome concentration may largely determine protein synthesis rate, a trait with important evolutionary consequences (see below).

Ribosomes have the highest P concentration of any organelle. Ribosomes consist almost entirely of RNA

and protein, with RNA making up a sizable fraction of ribosome mass (the RNA:protein ratio in eukaryotic ribosomes is about 1.2; in prokaryotes, it is 1.8). Because RNA is P rich (~10%), the biomolecular makeup of ribosomes results in a particularly P-rich structure (eukaryotes: 41.8% C, 16.3% N, 5% P; prokaryotes: 40% C, 16.1% N, 5.6% P).

Other cellular components likely also influence whole-organism stoichiometry. For example, the mammalian nucleus contains about 12.8% N and 2.3% P, which reflects an abundance of high-N nuclear proteins and the high P content of DNA. Mitochondria and chloroplast are also high-N organelles, as each contain about 11% N. They also contain very little P (0.31% and 0.32% P, respectively). Animal cell membranes have a fairly high amount of phospholipids relative to protein, and as a result have moderately high P content (59.5% C, 9.5% N, 1.5% P). Finally, plant cell walls consist mostly of N- and P-free cellulose and lignin, although they do contain small amounts of proteins and lipids. The estimated composition of plant cell walls is 35–38% C, <0.5% N, and ~0% P. These calculations suggest that adaptive allocation to particular cellular components will create a link between elemental composition and biological function.

Clear compositional differences also exist among different tissues. For instance, the N content in the leaves of apple trees (~1.2% dry mass) is considerably higher than N levels in stems and roots, which contain higher concentrations of cellulose and lignin (Table 3a). N content is particularly low in a tree's older woody tissue. In the crayfish, *Astacus astacus*, there are substantial differences in C:P and N:P ratios among the hepatopancreas (a digestive organ) and other major tissues (Figure 2). Finally, N and P levels differ among human tissues, and similar differences are likely in most other mammals (Table 3b). P content is particularly high in bone and other bony tissues such as teeth. Bone makes up roughly 10% of the biomass in mammals, and the skeleton may contain as much as 85% of a mammal's P content.

**Table 3a** N concentrations in different components of apple trees<sup>a</sup>

Tissue	Age (year)	% N
Leaves		1.23
Spurs		1.04
Wood	1	0.93
	11–18	0.16
Roots	1–6	1.24
	14–18	0.32

<sup>a</sup>Data from Murneek AE (1942) Quantitative distribution of nitrogen and carbohydrates in apple trees. *Missouri Agricultural Experimental Station Research Bulletin* 348, as reported in Sterner RW and Elser JJ (2002) *Ecological Stoichiometry*. Princeton, NJ: Princeton University Press.

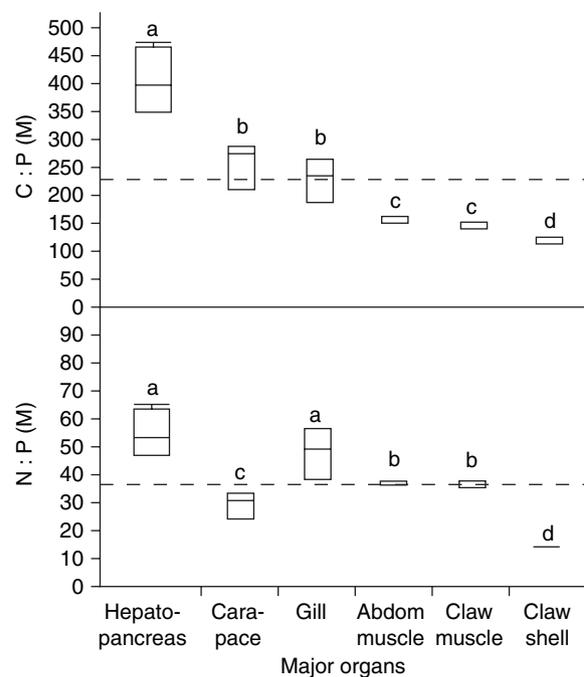
**Table 3b** N and P concentrations (% dry mass) in human tissues

Tissue	%N	%P
Kidney	7.2 <sup>a</sup>	0.70 <sup>a</sup>
Liver	7.2 <sup>a</sup>	0.94 <sup>a</sup>
Muscle	7.2 <sup>a</sup>	0.3–0.85 <sup>a</sup>
Bone	4.3 <sup>a</sup>	~12.00 <sup>a</sup>
Skin	16.0 <sup>a</sup>	~0.10 <sup>a</sup>
Hair	15.7 <sup>b</sup>	0.01 <sup>b</sup>
Nails	14.0 <sup>c</sup>	0.01 <sup>c</sup>

<sup>a</sup>Bowen HJM (1979) *Environmental Chemistry of the Elements*. London: Academic Press.

<sup>b</sup>Johnston FA, Debrock L, and Diao EK (1958) The loss of calcium, phosphorus, iron, and nitrogen in hair from the scalp of women. *American Journal of Clinical Nutrition* 6: 136–141.

<sup>c</sup>Iyengar GV (1978) *The Elemental Composition of Human Tissues and Body Fluids*. New York: Verlag Chemie.



**Figure 2** C:P and N:P ratios for major tissue of adult *Astacus astacus* crayfish. Extensions of boxes represent the 25th and 75th quartiles. Different characters on top of each box indicate statistically significant difference. From Faerovig PJ and Hessen DO (2003) Allocation strategies in crustacean stoichiometry: The potential role of phosphorus in the limitation of reproduction. *Freshwater Biology* 48: 1782–1792.

## Stoichiometry and Phenotypic Evolution

The previous section illustrated some of the compositional differences among structures that serve different biological roles. Ecological stoichiometry has also explored the evolutionary implications of these differences from both functional and economic perspectives.

### A Functional Perspective: The GRH

Establishing the relationship between elemental composition, phenotypes, and functional performance is a key step toward understanding the role of stoichiometry in adaptive evolution. The clearest example of such a relationship is the positive association among P content, RNA content, and growth rate described by the GRH (see Organismal Ecophysiology). The GRH has obvious evolutionary implications because growth rate influences an organism's age and size at maturity, traits that often affect survivorship and fecundity.

A test of the GRH in an evolutionary context comes from a comparison between *Daphnia* species from different geographic regions. This comparison found that *Daphnia* from the arctic have higher P content and faster growth rates than *Daphnia* species from temperate lakes. These results suggest that the short arctic growing season selects for rapid growth, which is reflected in whole-body stoichiometry. Indirect support for the GRH comes from studies on zooplankton that show positive associations between body P concentration and growth rate across ontogenetic stages.

### An Economic Perspective: Stoichiometrically Explicit Tradeoffs

Growth rate and other life-history attributes have been a focal area of theoretical and empirical research in evolutionary biology for more than 30 years. This work has shown that the evolution of life histories is guided by tradeoffs, in that costs associated with the expression of one trait limit the expression of another. Examples of life-history tradeoffs include those between current reproduction and future reproduction, reproduction and growth, or growth and defense.

Evolutionary tradeoffs will often be mediated by the availability of resources that must be allocated between traits. Life-history theory has often been based on the assumption that a single substance underlies such resource-based tradeoffs. For example, a model might be based on the assumption that a consumer has access to a pool of food energy that can be used equally well to meet its demands for growth or defense. Under this assumption, an increase in one trait (e.g., growth) leads to a proportional decrease in the expression of the other (defense). However, as outlined above, there are key elemental differences among biomolecules that should lead to differences in resource requirements between traits. In fact, resource requirements of traits such as growth, reproduction, and defense may be similar to the elemental composition of those traits because most of the substrate is used for structure rather than the metabolic requirements of trait assembly.

The existence of stoichiometrically distinct demands leads to an important prediction for the evolution of life histories: an optimal investment strategy will depend on the stoichiometry of each trait and the relative supply of different elements in the environment. Investment in a trait that requires an element that is difficult to acquire will be more costly than a trait requiring the same amount of another element that is relatively available. As a result, selection may favor traits (e.g., rapid growth) that rely heavily on particular substances (e.g., P) only when those substances are readily available in the environment.

Several empirical patterns suggest that economic considerations have influenced the evolution of organismal stoichiometry. For example, leaf nutrient concentrations are generally lower in plant species that dominate nutrient-poor sites than they are in species from fertile areas. Similarly, insect herbivores tend to contain less N than insect predators; one explanation for this pattern is that N scarcity in plant tissue has selected for lower N dependence in herbivores. Economic constraints may also have influenced the evolution of stoichiometry at finer scales. For example, enzymes used by the bacterium *E. coli* and the eukaryote *Sacharomyces cerevisiae* to assimilate C contain significantly less C than do typical proteins in these organisms. This result is intriguing because C assimilatory enzymes are probably most valuable to the organisms when C is scarce in the environment. The low C content in these enzymes may thus reflect selection for higher enzyme production in the face of a particular scarcity. Similar patterns have also been documented for the S content of S-assimilating enzymes of *E. coli* and *S. cerevisiae*.

Economic constraints can also be integrated with functional considerations to predict the evolution of organismal composition. Consider the evolutionary tradeoff between growth rate and competitive ability in marine phytoplankton. Such a tradeoff is likely in many organisms because the high resource demands associated with rapid growth will often put an organism at a competitive disadvantage when resources are scarce. Ecological stoichiometry provides a basis for determining the mechanisms underlying this tradeoff. In phytoplankton, response to this tradeoff can be characterized by investments in assembly machinery for biosynthesis and in resource-acquisition machinery. Assembly machinery consists of P- and N-rich ribosomes, while resource-acquisition machinery consists of chloroplasts and nutrient-uptake proteins that are rich in N but contain little P. When resources are abundant, selection favors greater investment in ribosomes for supporting rapid growth, leading to lower optimal N:P ratios. In resource-poor environments, phytoplankton with low N:P ratios are less successful because of their limited investment in resource acquisition and their high P demands for

assembly. The N:P ratio in phytoplankton that is predicted to evolve by natural selection will thus depend on the availability of resources in the environment because of the different functions of P- and N-rich structures.

See also: Animal Physiology; Biogeochemical Models; Ecological Stoichiometry: Overview; Ecophysiology; Ecosystem Patterns and Processes; Fish Growth; Grassland Models; Lake Models; Optimal Foraging Theory; Organismal Ecophysiology; Plant Competition; Plant Physiology; Population and Community Interactions; Predation; Trace Elements.

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## Evolutionary Ecology: Overview

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## Further Reading

Evolution and ecology are inexorably intertwined, neither existing in isolation, both are dependent on each other. Each is concerned with living organisms (i.e., any thing capable of replicating itself) and their environments. Evolution is the gradual genetic change of living organisms over time due to ecological pressures they experience. Ecology is the study of the interactions between these organisms and their environments. 'Environment' includes all the physical (things like temperatures, soil conditions, rainfall, wind, hours of sunlight, etc.) and biotic (things like natural material produced by living organisms, prey

species, competitors, parasites, predators, etc.) factors directly influencing them as well as anything affected by them. Ecology focuses on target organisms at several different levels: individuals, populations, assemblages, or entire communities (see Autecology and Synecology). Since environments include all physical and biotic factors, those of most organisms are exceedingly complex and multidimensional. With ecology so broadly defined, one might well ask, "What isn't ecology?" Because ecology is an essential building block for all organisms and the nature of their existence, it encompasses many other disciplines,