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Perspective

Atomic ecology: coupling atoms and ecology

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The functional roles of molecules in organisms and ecosystems are driven by the atoms that form them, including their three-dimensional form, bond polarity, size, and conformation. Recent advances in environmental and ecological sciences, such as ecological stoichiometry, ionomics, biochemistry, biogeochemical-niche studies, and omic ecological approaches, have provided substantial data and results that support the associations of the elements/atoms in organisms and ecosystems with their fundamental functioning and structure in nature. With the availability of big data, artificial intelligence, and powerful analytical tools, we now have the opportunity to understand basic ecological questions from the perspective of atomic composition. By studying the continuous interchanges and feedbacks of atoms between organisms and their environmental media, we both understand the present ecosystem shifts and project future shifts due to global change. We thus advocate the advancement of "atomic ecology" as an approach for studying ecosystems and organisms based on their atomic composition and use. This approach of leveraging the atomic compositions of organisms and ecosystems offers a practical and consistent tool to increase our knowledge of essential and fundamental questions about the functioning and traits of the biosphere.

The atoms of life. Living beings consist of atoms of various elements that we will call bio-elements. The most abundant bio-elements include hydrogen (H) at 59%, oxygen (O) at 24%, carbon (C) at 11%, nitrogen (N) at 4%, phosphorus (P) at 1%, and sulphur (S) at 0.1%–1% (percentages are based on the total number of atoms in organisms) [1]. C, H, and O form the foundation of organismal structure, including water and the primary structure, because they are the building blocks of organic molecules and the sources of energy for all types of living organisms. N, P, and S are components of various biomolecules, enabling biochemical reactions that confer unique functionalities to the basic organic molecules involved in organismal function, ranging from storing fundamental life information (DNA, RNA) to controlling the machinery responsible for all cellular and organismal functions. For example, molecular structures such as Rubisco and chlorophyll, which regulate life processes, and molecules that carry information such as DNA and RNA, and those involved in the storage and release of energy such as ATP and NAD all incorporate N, P, and to a lesser extent, S.

Due to its atomic characteristics, C is uniquely capable of forming a large number of molecules in the biosphere, in gaseous, liquid, and solid states. The specific traits that make C versatile include its natural abundance, the tendency of its electrons to form four covalent bonds, and its ability to form single, double, and triple bonds with other atoms, achieving electronic stability [2]. These properties position C as the most suitable element to form the foundational molecular and material structures of life. N, O, and H possess some traits, such as abundance, that could make them potential contenders for the primary element of life and the basic skeleton of organic molecules, but C outcompetes them [2]. N is an essential element that plays a crucial role in the formation of proteins and genetic molecules such as DNA and RNA. N requires three additional electrons to achieve a total of ten electrons and fill its second electron shell. By sharing three electrons, N can complete its outermost electron shell and attain a more favourable electron arrangement. This configuration is important for providing atomic stability to the N atom but also leads to N engaging in highly energetic chemical reactions and forming rigid bonds, which can limit its flexibility [3]. O, despite being abundant in Earth's crust and mantle, lacks the capacity for forming the complex geometries required for life's intricate architecture. The limited ability of H to form strong bonds with other atoms restricts its versatility in connecting multiple atoms and serving as the scaffold for complex chemical structures.

From an environmental and ecological perspective, the base of the matter/energy of life is sustained by four fundamental components: water, atmospheric gases, minerals from the lithosphere, and energy (light). The six basic elements—C, O, H, N, P, and S—play crucial roles in providing these fundamental components. Their presence in the hydrosphere, soil, and atmosphere frequently governs ecological processes and directly influences ecosystem structure and function. O, for example, is toxic to anaerobic organisms but essential for aerobic organisms, determining the composition and structure of ecosystems. Water, consisting of O and H, is indispensable for all forms of active life [1]. N exists in various compounds, and its transformations drive the N cycle, influencing the presence of taxonomic groups and thus overall ecosystem structure [4]. P availability determines community structure and productivity in aquatic and terrestrial ecosystems [5]. The N:P ratio also plays a crucial role in determining ecosystem structure and function [5,6]. The use of "phosphates" as essential compounds in biological systems has been extensively discussed in the litera-

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ture, with arguments highlighting their ability to link nucleotides while retaining a negative charge, preventing the free diffusion of DNA and RNA polymers, and reducing the rate of hydrolysis [7]. S, another important element, is vital for the biosynthesis of cofactors and for the active sites and tertiary structures of proteins [8].

These six bio-elements, however, are not the only bio-elements with important roles in organisms [1]. Other bio-elements present in lower concentrations, such as potassium, magnesium, iron, sodium, nickel, copper, silicon, calcium, molybdenum, manganese, and zinc, have more-specific functions. They act as cofactors in catalytic reactions in various biochemical and physiological processes. These bio-elements are involved in multiple biological processes such as photosynthesis, metabolite transport, enzymatic control (coenzymes), respiration, water flow and balance, internal cellular homeostasis and reproduction, neuronal electrical transmission, regulation of ion balance in chloroplasts and vacuoles, sugar transport in the phloem, secondary metabolism, maintenance of internal cellular osmotic or pH equilibria and balances, and strategies for stomatal control and avoidance of water stress [9]. All these bio-elements thus strongly contribute to organismal functions, although to varying degrees. They must be considered in addition to the six elements involved in the construction of families of organic molecules (sugars, lipids, amino acids, and nucleotides) when studying biological function [9] (Fig. 1). Some of these additional elements play crucial roles in supporting life by contributing to the functions of primary elements such as N or specific forms of C. For example, molybdenum and iron are essential for processes such as N_2 fixation and nitrate assimilation, enabling the availability and use of N by organisms.

Atoms, evolution, and ecology. The presence and availability of all these elements influence the overall functionality and stability of living systems, contributing to the intricate web of interactions that sustain life on the Earth. The cycling and status of elements in the biosphere-hydrosphere-atmosphere continuum have become increasingly linked to life throughout its evolution on our planet. In fact, the evolution of life has gone hand in hand with increasing control and influence over the cycling of these elements, operating at various scales, from small ecosystems such as ponds and forests to the global biosphere. The species-specific elemental composition can be related to each species-specific phylogeny and evolutionary history [10]. This particular species-specific use of the distinct bio-elements aligns with the significant biological control of the element's cycle on a global scale (Fig. 1). Recent studies that utilize extensive species databases have shown that the phylogenetic and legacy effects of elements like C, N, and P account for most of the variability observed between species. Conversely, for elements with lesser or marginal roles in organismal functions and structures, such as aluminum, manganese, and zinc, phylogenetic and legacy effects become less significant. This observation was made in a recent study that examined 83 distinct plant species across the climate gradient of the Iberian Peninsula [10]. In fact, research has demonstrated that in the upper soil layers of various soils along environmental gradients, the content and concentration of key soil elements, such as C, N, and P, tend to exhibit greater homogeneity. Furthermore, their pairwise ratios are more similar, underscoring the substantial influence of biological control on their cycles [9,10]. In addition to the well-established relationship between elemental composition and the ecological niche, several aspects of an organism's elemental composition are associated with fundamental ecological processes. These factors include production, growth, defense, anti-stress mechanisms, and litter decomposition [6,9]. Some elements that are extensively used by ecosystems due to their performance and function therefore possess an ecological dimension. The evolution of organisms has been affected by their differential use of these elements, providing a new approach to understanding ecological reality (Fig. 1). By studying how each bio-element contributes to and affects ecosystems at different levels, from individual organisms to entire ecosystems, we can identify the mechanisms that connect the various levels of ecological complexity. Indeed, the use of different elements to account for the diverse functionalities of organisms and to address ecological questions such as trophic web structure has gained momentum in the last few decades, emerging as a subdiscipline of ecology (Fig. 1).

Understanding ecosystems from their atoms. A brilliant group of ecologists led by JJ Elser and RW Sterner introduced a new dimension in ecology during the 1990s with several seminal articles on ecological stoichiometry. One pivotal aspect of this field is the growth rate hypothesis (GRH), introduced by Sterner and Elser [5]. GRH proposes that elevated rates of growth are associated with increased demands for P due to the synthesis of P-rich ribosomal RNA (rRNA) [6]. The principle behind this hypothesis is that organisms need to allocate more resources to P-rich rRNA to meet the higher demand for synthesizing proteins required for rapid growth. The N:P ratio and growth rate are thus interconnected by the close relationship between allocating P to ribosomes and allocating N to protein synthesis [5]. Greater allocation to P-rich rRNA becomes possible under low N:P environmental ratios. Both N and P limit the capacity of protein synthesis, but beyond a threshold of availability, only a further increase in P can further increase the rate of synthesis. When growth rates are high, N:P ratios decrease due to the importance of P-rich RNA in accelerating protein synthesis [5]. The metabolic basis of GRH can therefore be analogous to the construction of a house, where both bricks (amino acids and proteins) and bricklayers (P-rich RNA) are required to build the walls. Even when ample bricks are available, the walls cannot be built without bricklayers, and the rate of growth of the walls can be accelerated only by increasing the number of bricklayers.

These studies, initially conducted primarily in lakes, were subsequently expanded to other ecosystems and found correlations with various ecosystem traits, including the structure of trophic webs [5,6,9]. Relationships between lower N:P stoichiometries and higher growth rates have also been identified in other studies in the bodies of terrestrial plants [5,6,9] and terrestrial animals [7,9]. Lakes with four dominant trophic levels (phytoplankton, zooplankton, planktivorous fish, and piscivorous fish) were generally dominated by large-bodied zooplankton and the P-rich (low N:P ratio) crustacean *Daphnia* [5]. In contrast, lakes with three dominant trophic levels (lacking piscivores) were dominated by low-P (high N:P ratios) zooplankton [5]. A lower N:P ratio at the base of trophic webs stimulates the rate of growth and production of biomass in the lower trophic levels, facilitating the transfer of energy and matter throughout the trophic webs and promoting their expansion. In fact, the imbalances of N and P in various ecosystems in recent decades, primarily due to anthropogenic activity, have had important consequences for species composition and fundamental functional traits within ecosystems [5,6]. These imbalances have had repercussions on important ecological aspects such as production rates and trophic relationships, altering the overall structure and functioning of ecosystems [5,6]. These findings highlight the critical role of maintaining appropriate N and P ratios for the stability and sustainability of ecological systems. Some studies have not clearly observed the occurrence of GRH [11], but a recent study has identified several potential causes for this lack of detection [11]. These factors include the accumulation of P in non-RNA pools, inactivated ribosomes, altered rates of translation elongation and protein turnover, and limitations imposed by resources other than P [11]. These findings, however, do not undermine the fundamental association between the substantial allocation of P-rich RNA and the capacity for enhanced growth rates, which are the key mechanisms underlying GRH [11].

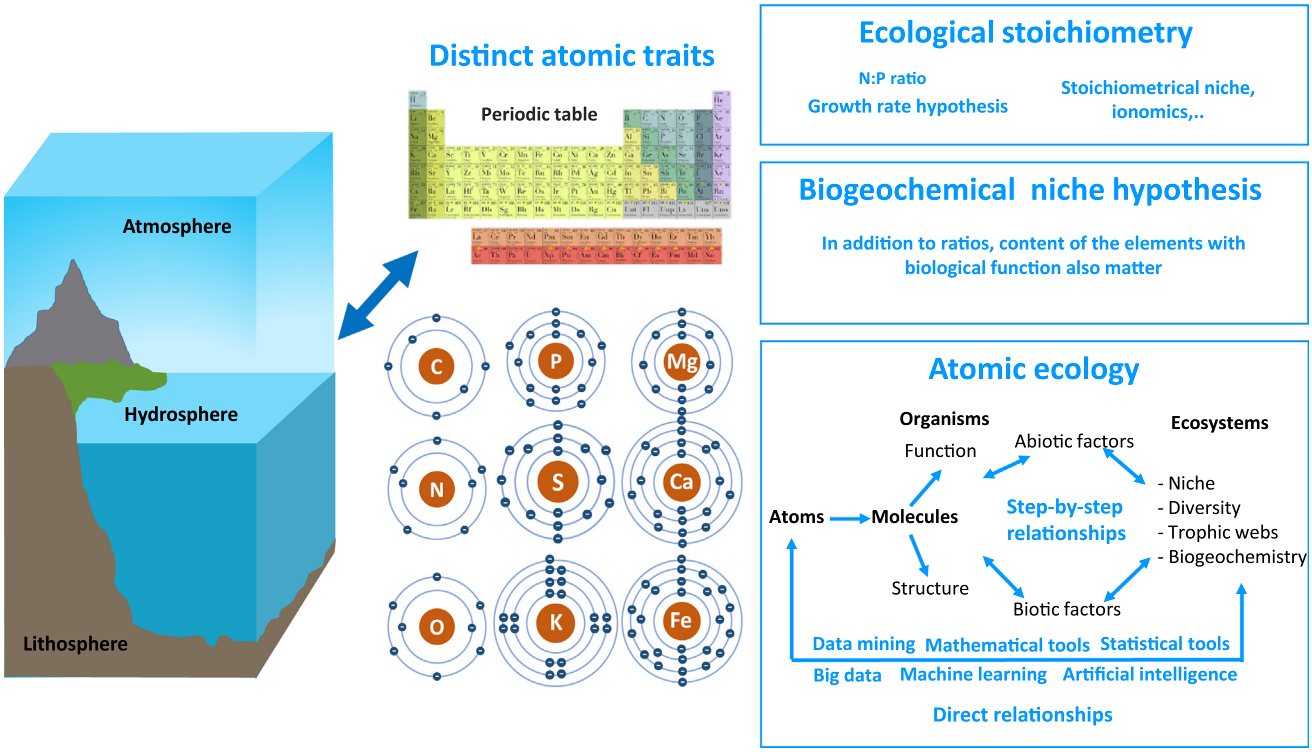

Fig. 1. Schematic of "atomic ecology": identifying the role of atoms in organisms and ecosystems. The intricate functioning of organisms and ecosystems depends on the unique properties of the atoms that compose them. These properties include their three-dimensional structure, bond polarity, size, and conformational arrangement. Recent breakthroughs in the environmental and ecological sciences, encompassing ecological stoichiometry, ionomics, biochemistry, biogeochemical-niche studies, and omic ecological approaches, have generated a wealth of data supporting the correlation between the elements/atoms in organisms and ecosystems and their fundamental structures and functions in nature. Capitalizing on the availability of vast amounts of data, artificial intelligence, and robust analytical tools, we now possess the means to comprehend ecological inquiries through the lens of atomic composition. By investigating the continual exchange and feedback of diverse atoms between organisms and their environments, we can both gain insight into the present state and anticipate ecosystem transformations under global change. We thus advocate for the advancement of "atomic ecology" as a framework for examining ecosystems and organisms based on their atomic compositions and uses. Leveraging the atomic compositions of organisms and ecosystems provides a practical and cohesive approach to increase our understanding of essential questions about the functionality and characteristics of the biosphere.

Several new studies in the last two decades have provided further evidence that elements other than C, N, and P can contribute to a better understanding of organismal and ecosystem functioning under field conditions. These elements may be limiting factors in some terrestrial and aquatic ecosystems and can have community-level effects [6,9,10]. These additional bio-elements have therefore more recently been incorporated into ecological stoichiometric studies to establish links between the elemental compositions of individuals and species and their ecological traits, such as drought resistance (related to potassium), the light environment (related to magnesium), and levels of N and S deposition [6,9]. Other studies have similarly observed that phylogenetic fingerprinting can characterize plants, animals, and microbes based on their elemental compositions [6,9].

Beyond one of the fundamental concepts in ecology, the ecological niche concept, recent studies have provided consistent evidence supporting the biogeochemical niche hypothesis (BNH) [6], which considers all bio-elements, or at least as many as possible. BNH is based on three complementary rules. First, each taxonomic group or genotype has a distinct elemental composition, with differences increasing with taxonomic distance and evolutionary time. Second, sympatric species tend to have distinct elemental compositions to minimize competitive pressure when in equilibrium. Third, trade-offs between adaptation to stable environments and success in fluctuating environments lead to differences in homeostasis and plasticity amongst species, in turn leading to a continuum of strategies. The distances between species in the BN framework thus depend on taxonomic differences, sympatry (coexistence), and homeostasis/plasticity due to long-term evolutionary divergence and recent convergent or divergent evolutionary processes (Fig. 1). Several studies have provided evidence that supports this BNH across organisms and ecosystems, including plants, animals, and microbial communities [6]. These studies have found that elemental composition and stoichiometry were more similar in phylogenetically close species than in distantly related species [6]. These studies have also reported the dependence of plant and animal taxonomy or phylogeny on the stoichiometries of organs or bodies [6]. Coexisting species tend to have distinct elemental compositions that minimize competitive pressure, as observed in recent studies [6]. This finding further demonstrates that fundamental ecological questions, such as direct competition for resources, are linked to modifications in the use of elements by competing species, leading to greater differences and singularities in elemental composition amongst species [6].

Similar approaches that link elemental composition to ecological issues have been published in recent years. Gonzalez et al. (2018) [12] introduced the "multidimensional stoichiometric niche" hypothesis, which defines the position of taxonomic/trophic groups in a three-dimensional space determined by C, N, and P, demonstrating its applicability to animals. This hypothesis attempts to incorporate rates of nutrient cycling, although quantifying these rates is more challenging compared to determining elemental concentrations and ratios. This hypothesis has also interestingly opened the possibility to incorporate more elements, and element fluxes and transformation rates as additional axes, although quantifying these rates is more challenging compared to determining elemental concentrations and ratios. Instead, the BN multidimensional space should allow the establishment and quantification of the links between the species BN distances and their taxonomic/phylogenetic distances and between homeostatic capacities and sympatries, and thus provide information on species/taxa evolutionary processes with only information of elemental composition.

Another approach that uses elemental composition, similar to the BNH, is ionomics. Ionomics primarily focuses on the genetics of plant mineral nutrition and aims to determine the profiles of mineral elements in plants. It is commonly used to study the contents of electrically charged bio-elements, which are mostly absorbed from soils. Ionomics research often involves investigating the impact on plant health, food quality, and the identification of hyper-accumulation species. Ionomics emerged from the convergence of metabolomics and plant nutrition [9] and with the incorporation of modern analytical platforms such as inductively coupled plasma (ICP) techniques, allowing for the simultaneous determination of most elements. Ionomics aims to determine the elemental compositions of organisms relative to soil concentrations of nutrients and trace elements and to plant functional traits [9]. By integrating this information with bioinformatics and genetic tools, such as genomic sequencing, identifying the genes that control the uptake, storage, and use of soil nutrients and trace elements in plants becomes possible [9]. This identification further enables the analysis of the effects of genes and environments on plant nutrition and of the physiological status of plants [9]. Ionomics has aimed to explain shifts in ionic composition by identifying specific genes and their control in changing environmental conditions, thus providing knowledge and information to improve the nutrition of crop species and it is primarily focused on the study of the composition of the medium (soil) to describe the ionic niches in the abiotic dimension of an ecosystem. BN is instead mainly focused on organisms and their total elemental compositions and stoichiometries as proxies for optimal functioning and morphology. This is based on the idea that the entire genome of each genotype/species determines species-specific functionality and morphology (more distinct as genomic differences increase) and thus a distinct use of different bio-elements, which in turn contribute asymmetrically to different functions and morphological structures. BN can thus be used without knowing about the control of gene expression or about gene function. Moreover, whereas ionomic approach has been developed for plants, BN is developed to be equally applicable to all types of taxa.

Atomic ecology. The presence and availability of essential atoms in diverse ecosystems are intricately linked to fundamental ecological traits, including production capacity, species composition, and trophic structure. This complex interplay among these elements is crucial for sustaining life and shaping the unique characteristics of each ecosystem within the biosphere. We propose a novel approach that we name "atomic ecology" to study and comprehend ecology and its core concepts, such as niches, competition, production, trophic webs, and diversity. Our approach involves investigating the use and composition of elements with biological functions, their total content/concentration, and the key stoichiometric relationships with functional implications. This approach connects all these factors to enhance our understanding and assessment of ecosystem structure and functioning at various scales.

Evolution is driven by the selection of genotypes that better adapt their functionality and morphology to environmental conditions. This adaptation involves continuous changes and the optimization of function, resulting in the differential use of bio-elements that alter the elemental compositions of organisms. Examining the atomic/elemental composition to identify niches in ecosystems offers practical advantages. Large amounts of field data can be used to identify biogeochemical niches, and all ecosystem components (including microbes, soil, water, fungi, animals, and plants) can be connected through elements common to all of them (Fig. 1).

To develop this novel approach, we require comprehensive information on the elemental composition of organisms and their environments, such as soil and water. This data should provide solid information about the content/concentration of as many elements with biological functions as possible, as well as key pairwise ratios like the N:P ratio. However, it is essential to acknowledge that the relationships between atomic/elemental composition of organisms and their environments are more complex than only considering stoichiometric relationships, such as the N:P ratio. These complexities cannot be fully captured by elemental ratios alone. Recent studies have highlighted the critical importance of the content/concentration of specific microelements in algae species, particularly in response to specific niche traits like temperature conditions. Several recent studies have also shown the determinant importance of the content/concentrations of some microelements in microbe species, linked to very specific singular functions and responses to particular niche traits, in some cases include the active presence of elements like lanthanides, which serve vital catalytic functions. Recent research has even suggested that actinides can functionally replace lanthanides [13]. Moreover, recent studies have observed that minor actinides can even functionally replace some essential lanthanides [14]. Additionally, for macro-nutrients and general micronutrients, many examples in the literature emphasize the importance of elemental content/concentration in explaining organism functions with ecological relevance. For instance, molybdenum content is linked to specific biological functions like N fixation, observed only in specific plant and microbial taxa [15]. Iron, essential for nearly all life forms, has diverse functions across taxa and even within similar taxa, making it challenging to establish clear elemental ratios with other elements associated with general organism functions. Iron also shares roles with copper in oxygen transport in different animal taxa, illustrating the complexity of these relationships [16,17]. Even when using the N:P ratio as a scaling factor for a particular organism's entire body, N and P can impact distinct functional/biological variables, such as varying P storage capacity among plant species or differential P use for solid structural/protective structures, distorting the relationship between N:P ratio and growth rate [11]. Furthermore, the established relationships between cell/organism growth rate intensity and N:P ratio depend on the separate concentrations/content of N and P. An inverse relationship between N:P ratio and growth rate is significant only when both N and P reach a certain individual content/concentration and are not limiting [5,11].

The direct relationships between the environment (water and soil), elemental composition, and element use by organisms occur through continuous feedback mechanisms along spatial and temporal gradients. These interactions adhere to the fundamental principles of life, encompassing matter, energy, information, and evolution [18]. We propose to focus ecological and biogeochemical research on the atomic composition of life's molecules, such as proteins, enzymes, co-enzymes (e.g., ATP or NAD), and large structural chemical formations (e.g., animal bones or plant lignin). This "atomic ecology" research will thus serve as a practical tool to identify theoretical issues and gain insights into fundamental aspects of ecosystem structure and function. It could also provide valuable insights into how organisms and ecosystems respond and adapt to global change drivers.

Certainly, the transition from atomic composition to the main ecological topics involves several steps, from atoms to molecules, from molecules to organism functions and structures, from organisms to communities and their relationships with the environment and element cycles, and finally to concepts such as diversity, ecological niches, trophic web structure, and biotic and abiotic relationships. We have two clear approximations to this challenge (Fig. 1). First, we can observe the links between the two extremes by using meta-data of organisms and/or media elemental composition with data mining, creating big data sources, and using statistical/mathematical tools to assess the links between elemental composition of organisms and basic ecosystem traits. This first approach is already in our hands given the continuous increase of databases and the increasing tools for data mining and statistical analyses, such as artificial intelligence and machine learning approaches (Fig. 1). The other approach is to understand the overall mechanisms and generalities from atoms to ecological traits step-by-step (Fig. 1). This second approach is even farther from being completely assessed and understood at this moment, and it opens a wide field for future research. The first step, however, has a completely logical fundament because the functional biological role of bio-molecules is determined by their three-dimensional structure, polarities of their bonds, and electrical charge distribution. These traits are determined and specific for each molecule due mainly to its atomic composition and the disposition of its atoms in the covalent structure. The atomic components and unique three-dimensional shape of a particular molecule determine its function [19]. This logic of the first step has been observed in some seminal studies, for example, observing that under environmental changes, there exists a coordinated change between elemental composition and molecular structure in the same organism [20]. Thus, some preliminary studies coupling elemental composition analyses with metabolite composition analyses have produced encouraging results. However, despite the logical nature of its scaling relationships scaling up relationships until ecosystem structure and function is a big challenge. In this regard, we can go step-by-step and even skip one or more steps. For example, the coordinated study along environmental gradients of ecological traits, such as trophic relationships, together with atomic and molecular analyses, can help determine how an organism's elemental composition determines and is related to biotic relationships and the niche community structure in different abiotic conditions. All these coordinated studies can provide evidence of changes in organisms' elemental composition underlying shifts in species niche structure and changes in biotic relationships. Furthermore, this can allow us to obtain information about how changes and differences in elemental composition are related to variations in ecological topics such as community diversity and trophic web structural changes (Fig. 1).

Building on these insights, our aim is to continue global research that connects the general composition of organisms and their environments with all elements serving biological functions across a broad spectrum. This research will encompass fundamental ecological topics, including the structure and function of trophic webs, biotic and abiotic relationships, ecosystem balances, ecological niche studies, ecosystem/community diversity, and responses to global changes and human-driven interactions with the biosphere. Advances in technology favor this endeavor, as elemental analyses of organisms, soil, and water are becoming increasingly accessible, and vast amounts of data and databases are available to scientists.

While inherent limitations exist due to random and stochastic effects in the atomic composition of life's molecules and macromolecules, we observe parallel evolution between the divergence of functional traits, morphological structures, and changes in the use and composition of elements during genotypic and phylogenetic diversification. This parallel evolution results from a continuous trade-off and feedback loop involving the interchange of elements between organisms and their environments. Additionally, the properties of stable atoms involved in life, such as C, Fe, and P, remain constant regardless of the situation. The function of bio-elements in biological systems primarily depends on their physicochemical traits, and biological and ecological evolution selects each bio-element for specific uses aligned with their fundamental characteristics. The stability and unique physicochemical properties of bio-elements enable us to construct and understand ecological processes by examining the use of different atoms within the atomic dimension of ecology. This approach enhances our comprehension of ecosystem functioning and potential shifts/responses to environmental changes (Fig. 1).

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

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Jordi Sardans conducts research on biogeochemistry, ecological stoichiometry, ecometabolomics and the research in the field of the effects of global change drivers on some ecological and economic sources such as water, fertilizers, energy and at the end on human wellness and health. He is also interested in the ecological problems in arid lands and in its carbon and nutrient cycles. Finally, he is also working on the links between ecosystem and organism atomic and molecular composition with key ecological topics such as ecological niche, biodiversity, and production.

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