Perspective

Application of ionomics and ecological stoichiometry in conservation biology: Nutrient demand and supply in a changing environment

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1. Introduction

The increasing pressure of anthropogenic activities on organisms and environments constitutes a significant challenge in biological conservation. Multiple disturbances on both local and global scales require conservation biologists to compile data originating from various sources and consider the studied organisms as components of the whole Earth system (Sodhi et al., 2011). Due to ongoing anthropogenic pressure, ecosystems and populations are threatened with various risks, including species extinction, habitat loss and transformation, environmental overexploitation, biodiversity loss and spread of invasive species. It is time to bridge the gaps between organismal biology, ecosystem ecology and global environmental factors to gain the knowledge needed to understand how ongoing global changes will impact the biosphere and our lives. The functioning of organisms is shaped by biogeochemical interactions between organisms and their environment and among individuals (Bianchi, 2021; Huang and Salt, 2016; Jeyasingh et al., 2014; Kaspari, 2021); therefore, to understand how organisms function in real-life environments, we should consider the studied organisms as components of biogeochemical cycles (Schlesinger and Bernhardt, 2020; Smil, 2000; Vitousek, 2004). In particular, it is more important than ever to obtain an adequate understanding of the nutritional limitations imposed on organisms by various combinations of local- and global-level biogeochemical phenomena. These limitations could be an underlying mechanism of biodiversity loss in both aquatic and terrestrial ecosystems (Aréón et al., 2021; Nessel et al., 2021). Conservation efforts should employ diversified tools and frameworks to protect species, their habitats, and human wellbeing, and we argue that considering biogeochemical phenomena could help conservationists provide complementary views to those generated in other disciplines, supporting decision-
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we then present two examples of conservation biology problems that may be addressed using ionomics and ecological stoichiometry: (1) describe how biogeochemistry is linked to biological conservation, and could serve as complementary tools in use-inspired research to gain such another, and we emphasize that ecological stoichiometry and ionomics tool for the assessment of the optimal direction of nature protection underlying biodiversity, as well as how these approaches can serve as a part of the immune system.

ecological stoichiometry – a research framework (part of the ionomics approach) generating questions concerning organismal nutritional needs for basic body-building that shape organismal ecology and ecosystem ecology. It considers how the nutritional demands of organisms and the supply of nutrients in their environments affect organismal growth, their interactions with biotic and abiotic factors and nutrient cycling throughout the entire ecosystem.

ionomics – an approach to organismal biology linking physiological, ecological and evolutionary phenomena with the nutritional needs of organisms, considering all of the approximately 25 vital chemical elements, including heavy metals. It acknowledges the most basic rules of life—i.e., the law of the conservation of matter and common biochemistry of all living entities originating in their shared evolutionary history. It considers (1) that the proportions of all atoms forming organismal bodies are critical in driving phenotypic fitness-related traits, (2) that they may be adjusted within the limits of stoichiometric homeostasis and (3) that they may evolve in response to environmental stressors (for more, see (Kaspari, 2021)).

juvenile food – food sources eaten by juveniles to produce new tissues and organs. Juvenile food is used for the growth, development and maturation of fully functioning adult bodies; therefore, it must provide specific nutrients in necessary proportions, in addition to energy.

life history evolution – evolution of fitness-related components of organisms, or life history traits, such as patterns of growth and development, age and size at maturity, size at birth, offspring size/number/sex, lifespan, and life cycle characteristics. These traits are optimized under specific environmental stressors to ensure fitness.

macromolecules – here, proteins, lipids and carbohydrates.

stoichiometric mismatch – incompatibility between the proportions of atoms in food and those in the body of the consumer that consumed the food.

stoichiometric phenotype – also called the ‘ionome’, ‘organisomal stoichiometry’, and ‘elementome’; the proportions of all atoms in the body of a considered organism. For more details, see (Jeyasingh et al., 2014; Kaspari, 2021; Peñuelas et al., 2019).

stoichiometry – balancing reactions. In every chemical, biochemical, biogeochemical, and physiological reaction, the amounts of each element forming reactants and products must be the same.

making in conservation practices.

A lack of understanding of general natural laws underlying nutritionally driven interactions between organisms and their environments and between food web compartments may result in poor conservation strategies that are unsuccessful or even have negative effects on targeted organisms and environments, as suggested by several researchers (Elser et al., 2020; Filipiak et al., 2022; Parreño et al., 2022; for a broader perspective, compare with Fernández-Martínez, 2022; Kaspari, 2021). We propose the use of ionomics and ecological stoichiometry in conservation biology studies to gain the required knowledge and to prevent the design of poor conservation strategies. In the following sections, we briefly present how biogeochemical approaches to ecology (Bianchi, 2021), namely, ionomics and ecological stoichiometry, can be applied in conservation biology studies to better understand the ecological processes connecting organisms with environments and the underlying biodiversity, as well as how these approaches can serve as a tool for the assessment of the optimal direction of nature protection activities (note: the text in bold is explained in Box 1 (glossary)). We highlight that to protect species, communities and ecosystems, we need to know how they are functioning and how they are connected to one another, and we emphasize that ecological stoichiometry and ionomics could serve as complementary tools in use-inspired research to gain such knowledge. Below, after providing a theoretical background, we describe how biogeochemistry is linked to biological conservation, and we then present two examples of conservation biology problems that may be addressed using ionomics and ecological stoichiometry: (1) conservation of insect pollinators and (2) CO2-driven nutrient dilution.

2. Biogeochemistry applies to individuals, populations and communities: theoretical background

Every organism is a component of Earth’s biogeochemical system (Vernadskii, 1924; Kaspari, 2021; Schlesinger and Bernhardt, 2020) and can be considered a small cog in a large wheel, in which atoms flow from one sink to another in a never-ending circuit (Fig. 1; Vernadskii, 1924; Schlesinger and Bernhardt, 2020; Sterner and Elser, 2002). The biogeochemical origin of life and most basic natural laws driving the functioning of all living organisms result in one of the most remarkable features of life on Earth: all living organisms, from bacteria to whales, are composed of atoms comprising the same approximately 25 chemical elements but in different proportions (Kaspari, 2021; Kaspari and Powers, 2016; Williams and Rickaby, 2012). Therefore, all of the diversity of life and all interactions between lifeforms that we are able to comprehend have their mechanical origin in 25 chemical elements endlessly cycling in food webs. In applying a biogeochemical approach to organismal ecology and conservation biology, we focus on (1) ionomics, recognizing that the chemical composition of an organism shapes its functioning and fitness (Frausto da Silva and Williams, 2001; Kaspari, 2021; Fernández-Martínez, 2022), and on (2) stoichiometry, that is, we consider that the production of a molecule is possible when and only when the chemical reaction leading to the production of this molecule is stoichiometrically balanced. Similarly, all the chemical reactions
leading to the production of fully functional cells, tissues, organs, and organisms must be stoichiometrically balanced (Sterner and Elser, 2008). When focusing on organismal ionomics and stoichiometry, we summarize the chemical balance of the entire metabolism and whole body-building process of developing organisms (Salt et al., 2008; Kaspari, 2021). Thus, we acknowledge that a fully functional body of any organism must not be constructed under arbitrary proportions of chemical elements (Fig. 2). Importantly, there are connections between

Fig. 1. Organisms as entities embedded within an ecosystem. Interactions between the components of this food web are shown in black (for clarity, only the most important components and interactions are shown). The bars under the ecosystem component images depict the proportion of atoms constituting these components. The discrepancy between the bars representing the two components shows stoichiometric matching/mismatching, which is further explained in Fig. 2. Inanimate natural components supply atoms in specific proportions, which vary over time and in space. Vital atoms are incorporated into organic molecules in molecule-specific proportions, contributing to the living portion of the food web. This process is shown with black arrows. Because this process shapes organismal functioning, health, and fitness, it also influences interactions undertaken by organisms to balance their nutritional requirements (i.e., to cope with mismatches between the demand for and supply of materials for body-building and maintenance). These interactions are depicted with red arrows. The proportions of elements in various compartments of an ecosystem were estimated based on previous studies (Filipiak, 2016, 2018a; Merian et al., 2004; Pokarzhevskii, 1985; Schlesinger and Bernhardt, 2020; Sterner and Elser, 2002). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
the genes, proportions of elements constituting an organism, and overall chemical composition of this organism (Lahner et al., 2003; Salt et al., 2008; Huang and Salt, 2016; Kaspari, 2021). Ultimately, organismal functioning and fitness are shaped by these connections (Frausto da Silva and Williams, 2001; Williams and Rickaby, 2012).

Organisms are comprised of organic molecules. Accordingly, we acknowledge that the production of every molecule, and consequently, of the whole organism, is limited by the stoichiometry of each molecule. Therefore, any molecule vital for the functioning of a given organism is available to this organism only if the proportion of atoms currently available in the environment allows molecule construction. This means that molecule production must not be limited by stoichiometric balancing of a certain reaction, where a limited number of specific reactants prevents formulation of the needed product. This key rule of

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**Fig. 2.** Interactions between components of the food web are driven by nutritional mismatches. Although organisms require organic molecules, the formation of their bodies is limited by the stoichiometric balancing of physiological reactions leading to the generation of muscles, nerves, wings, bones, blood, and all the other organic machinery produced based on the food that is consumed. This situation results in limitations and costs that must be overcome by implementing specific strategies. These strategies may include adjusting organismal physiology and morphology, changing their behavior, extending development or altering the size and quantity of progeny. Implementing such a strategy is costly for an organism—i.e., it negatively affects its health and fitness. As an example, the lower diagram shows that pollinators experience various stoichiometric mismatches, driven by the nutritional quality of their juvenile food. In this way, the health, development and functioning of pollinators are limited by the nutritional quality of their juvenile food.
Sterner and Elser (2008). Regarding photosynthesis, they explained how CO₂ chemistry, imposing constraints on biology, was well described by M. Filipiak and Z.M. Filipiak.

The stoichiometric phenotype among organisms, the life histories of individuals, and, ultimately, the environmental supply shape the ensuing ecological interactions. Therefore, prolonged development time or a decreased body size (Filipiak, 2018a).

To build a fully functioning, healthy adult body with optimally developed organs and morphological structures needed to maximize fitness, growing organisms undergo an incomprehensibly large number of chemical reactions, each of which must be stoichiometrically balanced (Fig. 3). Thus, the entire complicated process of growth and development leading to the formation of a fully functional adult body is stoichiometrically limited (Fig. 3).

Currently, in a rapidly changing environment, understanding mismatches between organismal demand and environmental supply is crucial for successful conservation efforts (e.g., Parreño et al., 2022). This topic is largely unexplored, as studies have focused on the energy budgets of organisms and on macromolecules to generate hypotheses in the fields of ecology and evolutionary theory (Birnie-Gauvin et al., 2021; Kozłowski, 2006; Stearns, 1996; Wright et al., 2018). Life history studies often assume that organisms ingest, assimilate and allocate homogeneous “resources” that may be divided into blocks and allocated to needed organismal compartments. In reality, the characteristics of ingested, assimilated and allocated matter differ substantially. Digested matter is processed by organisms, and the molecules constituting this matter are subjected to a series of physiologically driven chemical reactions (Richard and de Roos, 2018; Sterner and Elser, 2002). During organismal growth and development, specific biomass is produced because of the construction of necessary molecules into tissues, organs and structures. This body-building process is not driven by homogeneous “resources”. Rather, it is the effect of the assimilation of specific proportions of various nutrients from ingested matter, further decomposition of such matter and allocation of its components to various fitness-related functions (Richard and de Roos, 2018; Sterner and Elser, 2002).

In the context of organismal demands for matter with specific qualities, both autotrophs and heterotrophs are consumers (autotrophs do not produce matter independently). Their demand for body-building blocks that are essential for healthy growth, optimal development and maximal fitness is among the most important factors affecting their physiology, behavior, ecology and evolution.

3. Linking biogeochemistry and conservation biology

The goals of biological conservation are to protect and maintain biological diversity, ecological integrity, and their ability to endure over time (Trombulak et al., 2004). For conservation efforts to be successful, the first step is to identify threats to biodiversity and ecological integrity, and the second step is to understand how those key factors affect ecosystems along a spatial and temporal continuum (e.g., Cardoso et al., 2020). However, the second step is often overlooked in conservation efforts (e.g., Ludwig et al., 2001; Komenen and Müller, 2018; Stevenson et al., 2022; Stout and Dicks, 2022). Consequently, although directed conservation practices are being incorporated on both a local and global scale to mitigate habitat loss and transformation, environmental pollution, overexploitation, invasive species or climate change, the goals are not always achieved (e.g., Reyné et al., 2021; Tscharrnkte et al., 2016). The lack of identification of direct drivers and mechanisms underlying the abovementioned negative phenomena and processes was noted as an important factor responsible for the inefficiency and failure of the conservation practices (e.g., Filipiak, 2019; Jones and Rader, 2022).
Furthermore, most biogeochemical studies, with a focus on basic ecology, have adopted exclusively ecological perspectives, presenting empirical or theoretical examples rarely or not at all linked to conservation strategies. Unsurprisingly, the mismatch between basic and applied science has been recognized as an important gap between science and conservation practices (Hulme, 2014).

A biogeochemically oriented ionomic approach (Huang and Salt, 2016; Salt et al., 2008) and ecological stoichiometry-based framework (Sterner and Elser, 2002) offer tools to bridge gaps in our knowledge and support conservation applications (Elser et al., 2020; Filipiak, 2018b; Kaspari, 2021). For example, ionomics and ecological stoichiometry may be considered to predict and suppress harmful algal blooms (Ipek and Jeyasingh, 2021), to improve the predictive powers of ecotoxicology and better understand the impacts of pollution on organisms (Coffin et al., 2022; Peace et al., 2021), to support wild bee conservation (Filipiak et al., 2022; Parreño et al., 2022), and to elucidate the mechanisms underlying biological invasions (González et al., 2010). Below, and in the following sections, we briefly present how the biogeochemical approach to conservation biology can serve as a tool for determining the mechanisms and drivers of biodiversity decline and some other issues. Moreover, we present how it can serve as a tool for the assessment of the optimal direction of nature protection activities.

For illustrative purposes, let us apply the biogeochemical perspective to soil–plant–herbivore interactions in biological conservation. Soil chemistry determines plant stoichiometry (Kleijn et al., 2008), whereas herbivore fitness depends on the nutritional value of its host plants (Simpson and Raubenheimer, 2012; Sterner and Elser, 2002).

Knowledge of the biochemical properties of the considered ecosystem can contribute to conservation practices related to habitat restoration and plant reintroduction (Kleijn et al., 2008), safeguarding plant diversity (Staade et al., 2021; Vogels et al., 2017), and protecting vulnerable herbivore species (Martin et al., 2020). An interesting example is the feeding behavior of folivore koalas inhabiting environments with a low soil Na concentration, resulting in Na scarcity in eucalyptus leaves (Au et al., 2017). These koalas exhibit unusual feeding behavior: they consume the Na-rich bark. Biogeochemistry contributes to koala conservation in the following way: (1) Na scarcity decreases animal health, survivability and fitness (Kaspari, 2020, 2021); (2) at the same time, Na deficiency in the environment increases with latitude, resulting in Na-scarce leaves (Martin et al., 2020); and (3) trees having Na-rich bark exhibit their own habitat preferences (Martin et al., 2020). Considering the above aspects, Martin et al. (2020) stated that Na deficiency in the environment could constitute a significant barrier precluding koalas from global change-induced migration to high elevations. Thus, a better understanding of nutritional landscapes is needed for successful koala conservation; to obtain crucial information, a biogeochemical approach may be needed.

Kleijn et al. (2008) reported that the biogeochemical properties of target sites, rather than standard conservation measurements, must be considered when restoring heathlands and acidic grasslands. A study on heathland habitats revealed that rare plant species were significantly more sensitive to changes in the amplitude of soil biogeochemical parameters, especially to high NH$_4$ concentrations and NH$_4$/NO$_3$ ratios, than common species. The authors emphasized that upon prolonged...
Box 3
TSR – a useful tool with which to measure the stoichiometric limitation of organisms.

The trophic stoichiometric ratio (TSR) uses the ratio of carbon (C) to multiple other chemical elements as a proxy for the nutritional mismatch between a consumer and its food:

\[ \text{TSR}_x = \frac{(C : X)_{\text{food}}}{(C : X)_{\text{consumer}}} \]

where C is the carbon concentration and X is the concentration of element x. The TSR may be considered an indicator of the highest possible concentration (threshold point) of the considered element in food that is too low according to consumer needs, limiting the growth and development of the consumer.

The TSR is based on the following (for a detailed rationale, see Appendix S1 in (Filipiak, 2019)):

- the scarcity of element x in food limits consumer growth and development when
  \[ (C : X)_{\text{food}} / (C : X)_{\text{consumer}} \geq \text{GGE}_x / \text{GGE}_c \]

where C is the carbon concentration, X is the concentration of element x, GGE\(_x\) is the gross growth efficiency of element x, and GGE\(_c\) is the gross growth efficiency of carbon.

The above equations may be understood as follows:

\[ \text{TSR}_x \geq \frac{\text{GGE}_x}{\text{GGE}_c} \]

The minimum balanced ratio of (GGE\(_x\)/GGE\(_c\)) can be conservatively estimated as 1/0.25 = 4 because on average, 75 % of the consumed carbon is released as CO\(_2\), and the other consumed elements may be incorporated at a 100 % maximal rate. Hence, it is conservatively assumed that for (C:X)\(_{\text{food}}\)/(C:X)\(_{\text{consumer}}\) ≥ 4.0, element x may impose a constraint on growth and development. Accordingly, a TSR ≥ 4 indicates stoichiometric limitation of the consumer due to imbalanced food. Various elements may be differentially acquired, assimilated, reused, and excreted, but the TSR conservatively assumes that noncarbon elements in food are assimilated by the body at a maximal rate (100 %) to avoid the indication of false stoichiometric mismatches.

The TSR index compares the elemental compositions of an animal’s body and food consumed (not the food assimilated). The matter assimilated into the body has a different elemental composition than the ingested matter. The limitation imposed on growth and development is rooted in the physiological effort required to assimilate necessary atoms into the body and avoid surplus atoms—i.e., it is costly. This effort and its associated cost are proportional to the difference between the stoichiometry of the food consumed and stoichiometry of the assimilated matter. The stoichiometric mismatch represented by the TSR index is a mathematical illustration of this physiological effort and its cost.

The TSR might be used in studies working with whole food webs and nutritional flows within and between ecosystems that are driven by consumers facing specific nutritional limitations. Likewise, the TSR might be applied to the study of multidimensional stoichiometric niches of coexisting species that theoretically occupy similar ecological niches but might use food resources with different stoichiometries. Studies concerning life history evolution and optimization could also employ the TSR because this index enables the detection of limiting stoichiometric mismatches and comparisons between various taxa, habitats and foods. Therefore, the TSR index serves as a convenient tool that facilitates the detection of elements that colimit development and comparisons of the severity of the limitations imposed by various foods on different consumers. On that basis, testable hypotheses can be generated to better understand both (1) the biomass and nutrient flow within and between ecosystems and (2) the nutritional ecology of organisms and the relationship between organisms and their various food sources, including plant–insect interactions. For an example of the application of the TSR in conservation biology, see Filipiak (2019).
of xylophages with wood-inhabiting fungi mitigate the mismatch.

The advantage of using chemical element proportions as a basic component of every ecosystem constituent renders it possible to identify large-scale events that may have an effect on individuals at both the local and overall global scales. For instance, a recent meta-analysis revealed a global decline in invertebrate populations in response to nitrogen (N) and phosphorus (P) enrichment (Nessel et al., 2021). A similar analysis focused on aquatic ecosystems concluded that N and P enrichment influences multiple trophic levels, with implications for water nutrient management (Ardon et al., 2021). Both studies, published in 2021, were the first to demonstrate global, mult trophic chemical cycles and linking elemental ratios to observed changes in the environment could be important when conservation efforts in one place can affect other places around the globe (Sodhi et al., 2011), as well as when evidence-based science is used to support agreements between countries and global agreements on specific topics, e.g., related to the use of fertilizers (Brownlie et al., 2021). This knowledge is needed to wisely address ongoing and future global changes.

4. Conservation of insect pollinators

Pollinators support human wellbeing and are involved in ecosystem functioning via their interactions with plants (Matias et al., 2017; Ollerton, 2017, 2021a; Potts et al., 2016). Although the ecological and agricultural importance of insect pollinators is evident, our knowledge regarding pollinator biology and functioning in ecosystems is incomplete (Ollerton, 2021a). Important points are understanding how the nutritional quality and diversity of food resources affect pollinators via nutritional limitations. Furthermore, our knowledge of nutrient cycling via the environment–soil–plant-pollen/nectar–pollinator pathway and related effects on organismal health and fitness on the functioning of ecosystems is extremely limited (Filipiak, 2018b; Filipiak et al., 2021; Ollerton, 2021a, 2021b).

4.1. Different perspectives on nutrition in pollinator conservation studies

The proportion of nutrients in food regulates animal health and fitness (Simpson and Raubenheimer, 2012; Sterner and Elser, 2002). We are familiar with the idea that organisms feed on organic molecules available in the form of compounds such as proteins, lipids, carbohydrates, phospholipids, vitamins, and essential amino acids. This perspective was traditionally incorporated into studies concerning nutritional ecology and the conservation of pollinators, contributing crucial knowledge (e.g., Carnell et al., 2020; Goulson et al., 2015; LeBuhn and Vargas Luna, 2021; Moerman et al., 2017; Roger et al., 2017; Roulston and Cane, 2002; Sedivy et al., 2011; Spitt et al., 2021a, 2021b; Trinkl et al., 2020; van der Stuijs and Vaage, 2016; Vanbergen, 2013; Vanderplanck et al., 2014; Vaudo et al., 2015, 2020, and literature cited therein). Although this idea is factually correct and beneficial as the central point of studies on nutrition within the context of organismal biology, other ideas or perspectives are possible (Krama et al., 2022; Krams et al., 2021; Lau et al., 2022). Organic compounds are crucial when considering the direct interactions between consumers and food (Simpson and Raubenheimer, 2012), but they represent only part of the story in which the entire ecosystem is involved (Kaspari, 2021; Sterner and Elser, 2002). Notably, the ‘all-macromolecule’ approach assumes that all proteins, lipids or carbohydrates are equally important for organisms. In reality, different macromolecules belonging to the same group may have various functions in organismal physiology—e.g., specific proteins may be needed to form structures in the body, while others are needed to produce enzymes, hormones or antibodies. Similarly, when a large proportion of total carbohydrates in food are structural compounds (e.g., lignin, cellulose or chitin), the food quality for consumers is different than when a large proportion of total carbohydrates are sugars (e.g., fructose, sucrose, lactose or glucose).

Additionally, incorporating the many organic components that make food nutritionally balanced into a single study is practically impossible because of their wide diversity (considering all physiologically important proteins, lipid acids, vitamins, and sugars in a single study would require a significant amount of time and work, and these data would also be challenging to analyze statistically). In contrast, when using a biogeochemical approach, it is not assumed that all elements have similar functions in organismal physiology, development and body-building because only specific elements with known functions are considered (Frausto da Silva and Williams, 2001; Kaspari, 2021; Sterner and Elser, 2002). Moreover, since only approximately 25 elements build organismal bodies (Kaspari and Powers, 2016), it is practically possible to consider all of them in a single study as factors making the diet stoichiometrically balanced. Therefore, ionomics and ecological stoichiometry could complement the traditional ‘all-macromolecule’ approach, as a broader perspective is needed to better understand and predict the functioning of pollinators in their changing environments (compare with Lau et al., 2022; Jones and Rader, 2022). However, the main advantage of an ecological stoichiometry and ionomics approach over an ‘all-macromolecule’ approach is that the former can be used to study whole ecosystems (e.g., via the environment–soil–plant–pollinator pathway). This is because immutable atoms of chemical elements cycle in ecosystems, whereas the demand for macromolecules can be studied only at the organismal level since organic compounds are immutable and short-lived and play a role only in direct nutritional interactions between a specific consumer and its host.

Considering the nutritional niches of pollinators, homogenous landscapes decrease the abundance of pollinators, whereas diverse habitats benefit pollinating species (Parreiro et al., 2022). In agricultural landscapes, for instance, diversified farming systems and ecological intensification of agriculture are recommended to protect pollinating insects (Dicks et al., 2016; Goulson et al., 2015; LeBuhn and Vargas Luna, 2021). However, providing a food base for pollinators is mainly understood as planting flower-rich habitats to provide a source of nectar and pollen; therefore, current protection activities apply only the plant–pollinator interaction perspective (Vaudo et al., 2015). Using ionomics and ecological stoichiometry, we can broaden this perspective. Ionomics and ecological stoichiometry allow us to study not only the effects of diverse floral habitats on pollinators, e.g., if certain plants provide stoichiometrically balanced pollen for pollen-eating pollinators but also whether the stoichiometry of pollen changes due to other factors (e.g., soil depletion) and whether this change in plant quality imposes constraints on pollen-eating pollinators (e.g., bees). There have been no detailed investigations of stoichiometric mismatches in the environment–soil–plant–pollen–pollinator pathway, but the scarce literature on pollen stoichiometry and its effects on pollinators suggests that shifts in pollen stoichiometry can have consequences for the well-being and abundance of pollinators (Abbas et al., 2014; Filipiak et al., 2022). Overall, because ecological stoichiometry and ionomics consider the basic building blocks of the animate and inanimate world, i.e., the atoms of chemical elements and their ratios, they allow researchers to take into account many trophic levels (soil, plant tissues and products, and herbivores), as well as various abiotic factors (fertilization and soil depletion) and their direct and indirect interactions, at the same time to provide the bigger picture needed to design efficient conservation practices.

4.2. Juvenile feeding guilds of insect pollinators

Protecting pollinators is often understood simplistically as providing them with large amounts of nectar and pollen. In fact, pollinator dietary needs can be understood as a two-dimensional process characterized by the contradictory, sometimes conflicting, needs of immature stages and adults occupying different feeding guilds. Insect pollinator studies have focused on adults, neglecting the fact that different life stages of
pollinators belong to varied feeding guilds (these may include folivores, pollinivores, sap suckers, saprophages or predators; please refer to Ollerton (2017)) and that they may rely on various nutritionally (im)balanced food sources. Consequently, our knowledge regarding the nutritional constraints imposed on pollinators by ontogenetic shifts in diet use is limited. Importantly, the evolution, ecology and diversity of insect pollinators may be shaped by the nutritional quality of their juvenile food, which is used to develop a fully functional adult body that is then maintained by energy obtained from nectar. This aspect of the ecology and functioning of pollinators remains unclear, hindering the implementation of successful pollinator conservation actions toward all pollinators beyond commonly studied bees. Until recently, no convenient tool has facilitated identifying and comparing the fitness-limiting effects imposed on consumers by the nutritional composition of their juvenile foods. We propose the use of the trophic stoichiometric ratio index (TSR) to understand how various pollinators are limited by proportions of nutrients in their juvenile foods, as presented in the paragraph below.

Because the quantity of food that may be consumed during juvenile development is limited and definitive, food quality, reflected in either stoichiometric matches or mismatches, may impair the growth, development and fitness of organisms (Kay et al., 2005; Kay and Vrede, 2008) (Box 2 and Fig. 3). The nutritional demand of the pollinator can be compared with the supply of nutrients in juvenile food using the trophic stoichiometric ratio index (TSR; Filipiak, 2018a, 2019; Box 3). For example, the TSR can be used to study whether the development, growth, and fitness of a butterfly species feeding on a certain host plant under specific environmental conditions may be limited. For this purpose, one could test for stoichiometric matching between the plant leaves consumed by the butterfly caterpillar and the butterfly adult body, which is built based on nutrients consumed during larval development. Another example is flies (Diptera). Adult dipterans are important pollinators (Ollerton, 2017), whereas their juvenile stages may consume other insect larvae, dead organisms, or grass stems (Hambäck et al., 2009). The performance of Diptera pollinators will therefore strongly depend on the wellbeing of the juveniles feeding on food sources not necessarily related to floral diversity. In the final example, let us consider a more complex and more nature-relevant study in which investigators assess how various insect pollinators (e.g., beetles, butterflies, flies, and bees) depend on field-edge flower plantings. One can imagine that to include every component of the related trophic chain and every interaction between components of this system, a common currency is needed that is easy to determine and that remains unchanged when cascading across levels and ramifying within the system. Such a currency is the concentration of elements, based on which their ratios can be calculated (Kaspari, 2021). Thus, to assess how certain plant communities would affect pollinators, the TSR value for each of the species can be determined, considering for example that (1) Lycaena titrus caterpillars feed on leaves of the host plant Rumex acetosa (Raharivololoinaina et al., 2021), (2) Hoplitis adunca oligoleptic bee larvae prefer pollen from Echium sp. (Sedivy et al., 2011), and (3) Acrodera globulus larvae are actually parasitoids of spiders (Bristowe, 1931). This example highlights that two of the three considered species depend strongly on plants in their juvenile stage, with only one depending on pollen, while the performance of the third species would depend on the presence of host spiders. In conclusion, studies considering the nutritional demands of pollinators should not solely focus on pollen and nectar and on direct interactions between adult pollinators and nectar-providing plants but should also focus on other compartments of the ecosystem, which together shape the nutritional landscape in which pollinators function (Fig. 1). Accordingly, the use of ionomics and ecological stoichiometry can yield new, critical knowledge with which to implement pollinator conservation efforts and to conserve ecosystem services provided by pollinators related to the functioning of food webs.

5. CO2-driven nutrient dilution

The factors shaping organismal biology at the local level may generate stronger or different consequences when combined with global-scale phenomena (Gerard et al., 2020; Jamieson et al., 2017; Ziska et al., 2016). For example, an increase in atmospheric CO2 leads to nutrient dilution in plant tissues, increasing the stoichiometric mismatches experienced by consumers, including humans consuming vegetables, fruits and cereal products (Loeadze, 2014; Welf et al., 2020b). Knowledge of the effect of CO2-driven nutrient dilution on the functioning of organisms, food webs and ecosystems, as well as on human wellbeing, is practically nonexistent. Nutrient dilution has not been considered when examining global changes and outlining measures to be implemented against climate change. For example, much focus has recently been placed on the CO2 fertilization hypothesis—i.e., increased global photosynthesis due to CO2 fertilization and plants absorbing CO2 released by humans into the atmosphere (Ainsworth and Long, 2021; Gonamo et al., 2021; Keenan et al., 2021; Walker et al., 2021). The CO2 fertilization hypothesis is considered a mechanism with only positive effects on ecosystems. This process was identified as a highly valuable ecosystem service providing humanity with more time to take action against climate change (Walker et al., 2021). Importantly, however, the nutrient dilution hypothesis (Welf et al., 2020b) suggests being more critical and careful when assessing the effects of plant CO2 fertilization because this process may impose a negative effect on plant consumers that may further negatively affect the whole food chain. CO2 fertilization results in plants experiencing luxuriant growth. Nevertheless, at the same time, plant tissues are nutritionally diluted—i.e., plant tissues exhibit an increased ratio of carbon to other nutrients (C/X), resulting in an overall decreased nutritional value.

Nutrient dilution was indicated as a global phenomenon, posing a challenge to Earth’s herbivore populations (Welf et al., 2020b). Robinson et al. (2012) noted that under elevated CO2 levels, plants increase their biomass as the total content of plant carbohydrates increases by 23 %, with approximately +50 %, +39 %, and +8 % concurrent increases in starch, total nonstructural carbohydrates, and soluble sugars, respectively. However, simultaneously, plant nitrogen decreases by 16 %, amino acids decrease by 14 %, and soluble proteins decrease by 10 % (Robinson et al., 2012). This process has negative effects on herbivores (Zvereva and Kozlov, 2006)—e.g., decreases in the growth rate, food assimilation, body size, and fecundity and an increase in development time (Hamann et al., 2021; Robinson et al., 2012). Additionally, plant nutrient dilution imposes a direct negative effect on human wellbeing by worsening the nutritional quality of our everyday food (Ebi and Loeadze, 2019; Loeadze, 2014). For example, protein and mineral concentrations in human food could decrease by 5–15 % and B vitamins could decrease by 30 % due to elevated atmospheric CO2 levels (Ebi and Loeadze, 2019). A CO2-related decrease in the quality of human food might have serious negative implications for public health globally, affecting billions of people (even currently, food deficiencies in Zn and Fe cause 63 million deaths annually) (Ebi and Loeadze, 2019; Myers et al., 2014). Consequently, it is critical to gain knowledge on nutrient dilution attributable to CO2 and its effects on food chains, ecosystems, and human wellbeing and to implement actions aimed at mitigating these negative effects.

Elevated atmospheric CO2 directly affects the stoichiometric phenotypes of plant tissues and products via the increased ratio of carbon to other nutrients (C/X). This phenomenon can be easily translated to plant nutritional value. Therefore, ionomics and ecological stoichiometry provide the most straightforward method by which to determine the effects of increased CO2 on plant-based food via the study of elemental concentrations and ratios.

A change in the perception of CO2-driven plant fertilization is needed. To advocate for such a change and provide local stakeholders, national or subnational governmental agencies and policymakers with science-based results, as well as to increase awareness among citizens and consumers, we need to understand the mechanisms and processes
that are responsible for CO\textsubscript{2}-driven nutrient dilution. We emphasize that ecological stoichiometry and ionomics can serve as tools with which to elucidate these mechanisms and support other approaches.

6. Concluding remarks

Focusing only on physiological, behavioral, and life history phenomena is insufficient to better understand the mechanisms and patterns associated with organismal ecology and gain the knowledge required to implement conservation efforts. When studying and discussing these phenomena, organisms must be regarded as entities deeply entrenched in and dependent on biogeochemistry. Ionomics and ecological stoichiometry generate questions regarding the origin and function of physiological phenomena, enabling connections among organisms, their life history strategies, evolution and interactions with biotic (e.g., plants–pollinators) and abiotic (e.g., CO\textsubscript{2}) factors occurring in the environments inhabited by these organisms. Knowledge concerning how biogeochemical phenomena may shape biodiversity is needed to wisely manage ongoing and future global changes. Human-induced changes in the amounts and ratios of essential nutrient elements supplied by ecosystems shape organismal communities locally and globally, altering the functioning of the biosphere and ultimately deteriorating human well-being. Now, the gaps among organismal biology, ecosystem ecology and global environmental factors must be bridged to gain the knowledge needed to better understand how ongoing global changes will impact the biosphere and our lives. Therefore, it is reasonable to consider ionomics and ecological stoichiometry in studies focusing on organismal ecology, behavior, ecophysiology, conservation biology and other areas with an organismal focus to generate questions regarding unsolved biological problems (please refer to the examples in Box 4). This could allow a better understanding and prediction of how global environmental changes affect organisms and how to mitigate the negative consequences of these changes.

Data availability

No data were collected for this study.

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Declaration of competing interest

The authors have no conflict of interest to report.

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