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An Operational Framework for the Advancement of a Molecule-to-Biosphere Stoichiometry Theory

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Biological stoichiometry is an approach that focuses on the balance of elements in biological interactions. It is a theory that has the potential to causally link material processes at all biological levels—from molecules to the biosphere. But the lack of a coherent operational framework has so far restricted progress in this direction. Here, we provide a framework to help infer how a stoichiometric imbalance observed at one level impacts all other biological levels. Our framework enables us to highlight the areas of the theory in need of completion, development and integration at all biological levels. Our hope is that this framework will contribute to the building of a more predictive theory of elemental transfers within the biosphere, and thus, to a better understanding of human-induced perturbations to the global biogeochemical cycles.

Keywords: biological organization, biological stoichiometry, consumer-driven nutrient recycling, ecological theory, theory integration, growth-rate hypothesis, light:nutrient hypothesis

INTRODUCTION

Ecological stoichiometry studies the balance of chemical elements in ecological interactions (Sterner and Elser, 2002). Most hypotheses in ecology are born from the clever integration of previously unrelated assumptions and observations (Pickett et al., 2007d). Ecological stoichiometry is a great illustration of this principle since it came as a eureka combination of two observations: the demonstration that zooplankton can increase the growth rate of phytoplankton through the recycling of limiting nutrients (Sterner, 1986) and the shift in phytoplankton limitation between phosphorus (P) and nitrogen (N) that sometimes results from manipulations of the zooplankton community species composition (Elser et al., 1988). The result was a model of how zooplankton N and P composition could drive phytoplankton limitation through differential recycling of N and P (Sterner, 1990). The hypothesis was then called the Consumer-Driven Nutrient Recycling Hypothesis (Sterner et al., 1992). Hypotheses grow into fully-fledged theories through further integration of new observations, concepts, hypotheses and models, thus increasing their contribution to the understanding of the phenomena they are meant to explain (Pickett et al., 2007c; Marquet et al., 2014). Accordingly, the Consumer-Driven Nutrient Recycling hypothesis grew up into the field of ecological stoichiometry by incorporating more hypotheses, such as the growth rate and light:nutrient hypotheses (Sterner et al., 1997; Elser et al., 2000c). The depth and breadth of ecological stoichiometry then expanded through the integration of empirical observations and experimental results from increasingly diverse habitats, ecosystems and trophic interactions (Sardans et al., 2012). One cannot help but be struck by the vitality of the theory, expressed in a large number of mechanistic hypotheses and testable predictions, as well as in the wide scope of biological phenomena it now encompasses: from freshwater plankton interactions to, for example, the evolution of terrestrial plant genomes (Acquisti et al., 2009), the growth of cancerous tumors (Elser et al., 2003) or the macroevolution of life during the early Cambrian period (Elser et al., 2006). Thus, the theory shows the greatest potential in the midst of many contemporary ecological theories to unify ecology across all biological levels, from molecules to the biosphere (Sterner and Elser, 2002; Elser, 2006; Hessen et al., 2013). Some even argue, with good reason, that the theory should now be called "Biological Stoichiometry," since it no longer restricts itself to the study of ecological patterns (Elser et al., 2000c).

But completeness—breadth of scope and diversity of components—is not the only axis along which a theory can grow (Sterner and Schulz, 1998). Two other axes are the development of each component toward more realism and applicability; and integration, the connection among components toward better articulation (Pickett et al., 2007c). The ultimate objective of a theory being to generate understanding, it must also be judged by the advancement it provides to our comprehension of natural patterns (Pickett et al., 2007a; Marquet et al., 2014). Only when organized into a logical framework that assembles its components into an explicit structure, can a theory correctly predict or explain occurring natural patterns (Pickett et al., 2007b). Natural patterns are generally the result of complex multi-scale hierarchical processes (O'Neill, 1986), and so, most of the fundamental and urgent questions in ecology nowadays are multi-scale and integrative (Irschick et al., 2013; Sutherland et al., 2013). The logical framework of an ecological theory should thus typically be nested and hierarchical as well as integrated, both in terms of its internal components and with other theories.

In the case of biological stoichiometry, foundations for such a logical framework have already been laid, notably in the canon book by Sterner and Elser (2002) and more recently in review articles (Hall, 2009; Sardans et al., 2012; Hessen et al., 2013). Despite offering a panorama of the insights gained from applying the stoichiometric approach to processes spanning from the physiological to the ecosystem level, those reviews do not provide the kind of framework that is needed to help the theory progress along the three axes of completeness, development and integration. Not enough efforts have been made to integrate and organize the various stoichiometric breakthroughs into one coherent framework. Moreover, links between mechanisms at the lower and higher ends of the biological organization levels are often inferred but seldom fully explicated (Schade et al., 2005).

Here, we offer a methodological framework that describes the processes that need to be investigated at each biological level in order to characterize the repercussions of a stoichiometric imbalance at one level over all the other levels. This framework is operational rather than descriptive. It explains "how to" derive consequences of stoichiometric imbalances rather than "what" will be those consequences. As such, it is adaptable to all biological systems and open to further development. Armed with this framework, we surveyed the literature, in order to assess the current understanding of stoichiometric patterns and processes at each biological level (see our framework on **Figure 1**). We focus particularly on the degree of completeness of current understanding (i.e., whether are there any important considerations missing or not), the degree of development (how reliable are the proposed concepts and hypotheses?) and the degree of integration (how are other theories, approaches and knowledge considered and included?). We selected readings from the stoichiometry literature, from seminal publications by Liebig and Playfair (1840) and Redfield (1934) to the most recent literature (>900 articles read). Articles were first selected using generic search engines (Web of Science, Scopus) and generic keywords (biological OR ecological AND stoichiometr*). Articles were then more selectively pursued according to their relevance to the component of the framework evaluated and the elements that we assessed as in need of completion, development or integration. Our evaluation of each framework component is discussed below in separate sections. We have also summarized the elements that we deemed in need of enhancement according to the three axes of completeness, development and integration in **Tables 1, 2**.

FRAMEWORK DEFINITION

Our framework is organized along a rendition of the classical biological levels, defined by their stoichiometry, the distribution of elements within them, and connected by the processes that mediate the repercussions of changes in the stoichiometry of one level upon another (**Figure 1**). We are aware that there is no universally agreed-upon description of hierarchical levels in biology, arguably because such a description depends to a large extent on the specificities of the system studied (Allen and Hoekstra, 1993). So, we open the possibility for adapting the choice and definition of levels to the specificities of the systems to which the framework is applied. Also, we acknowledge that the highest conventional biological levels can be defined at any spatial and temporal scale (Allen and Hoekstra, 1990). Ecosystems for example can be as small as a drop of water or as incommensurable as an ocean (O'Neill, 1986). So the landscape and biosphere levels in our framework should not be understood according to the common-sense definition of the terms. We define a landscape as a set of connected ecosystems, themselves operational units defined according to the aims of the investigators, be it a moss patch, a water pool or a continental forest. The biosphere is the surrounding medium that circulates unbounded between the ecosystem units. Populations are the sum of individuals from the same species (or any other relevant taxonomic unit) contained in one ecosystem unit that can reproduce or exchange genetic information at the timescale considered; community is the ensemble of populations present in a unit ecosystem. Levels from

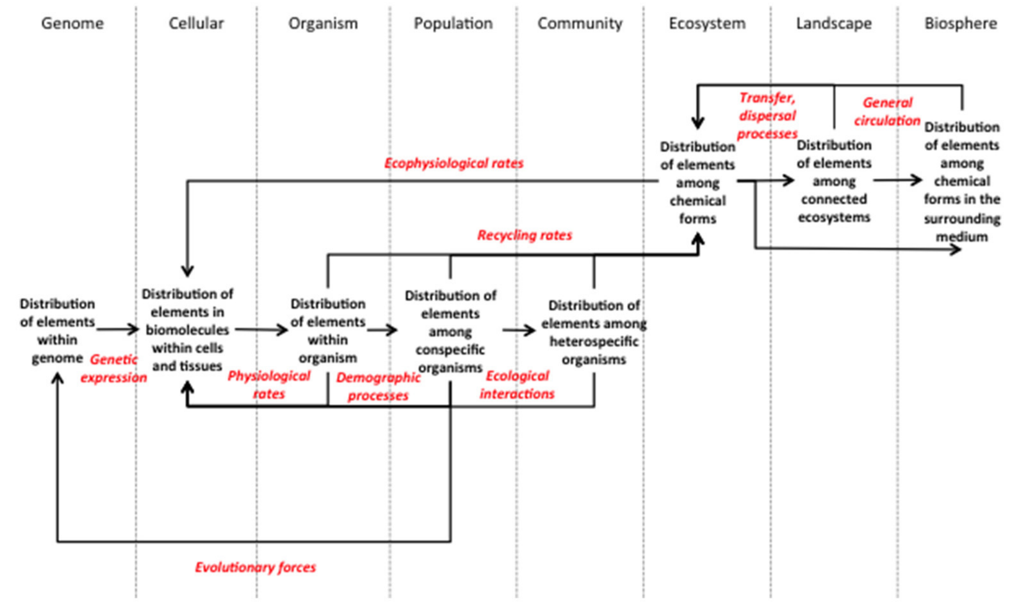

FIGURE 1 | Framework for a molecule-to-biosphere stoichiometry theory. This framework presents explicitly the biological levels and processes that need to be investigated in order to characterize the repercussions of a stoichiometric imbalance at one level over all the other levels. Each biological level should be described by the patterns of elemental distribution within it. As the framework shows, the processes investigated should go beyond the fluxes and rates of elements between components that are classically considered in stoichiometric studies. Any process affecting the structure of a biological level should be considered if the changes provoked relate to changes in the distribution of elements. Numerous examples are discussed within the text.

the organism and below are scale independent. We also include tissues as part of the cellular level to the extent that the cells that compose them answer uniformly to the factors affecting their stoichiometry.

The other elements of the framework are the processes that relate changes in the elemental distribution of a given level to the stoichiometric properties of the other levels (**Figure 1**). They are the medium by which imbalances in the stoichiometry of one level reverberate throughout all biological levels. In practical terms, they are the processes whose rates have to be measured by investigators interested in the multi-scale effects of stoichiometry. The framework reveals that the cellular, organism and ecosystem levels are essential nodes that cannot be bypassed when connecting high and low levels (**Figure 1**). Obviously, regional processes may affect individual organisms only if they influence the local ecosystem that embeds them. Within the local ecosystem, changes in the distribution of elements among chemical forms may impact organisms only if they affect at least one ecophysiological rate, altering the distribution of elements within cells. This highlights the central role of metabolism and ecosystem processes in connecting the biotic and abiotic cycles of elements. Ecophysiological rates and evolutionary forces are the only processes that enable the highest levels to reach the lowest levels (genomic and cellular). They are also the processes that allow organisms to adapt to changes in stoichiometry at larger scales. Biotic adaptation can then lead to further larger-scale changes through recycling processes, thus closing the feedback loop of stoichiometry from molecules to the biosphere.

BIOLOGICAL LEVELS

Stoichiometric studies can be found for all levels, some of them having acquired a foundational character in ecology, often solidifying into paradigms (e.g., Liebig and Playfair, 1840; Redfield, 1958; Tilman, 1982). The emergence of the biological stoichiometry approach made use of these paradigms, sometimes unaltered, sometimes developing them further, and sometimes challenging them (e.g., for the Redfield ratio paradigm, Cleveland and Liptzin, 2007; Sterner et al., 2008; Flynn, 2010; Loladze and Elser, 2011; Sardans et al., 2012). New paradigms have also been developed for various biological levels, and integrations with other ecological theories attempted. In this section, we briefly discuss the contribution of stoichiometric approaches to our understanding of the elemental distribution within each biological level, as well as the areas still in need of improvement, starting from genomes, the lowest level, to the biosphere.

Genome

Nucleic acids are known to be N-rich and, singularly, P-rich molecules (Sterner and Elser, 2002). But only recently has the new field of stoichiogenomics started working on a comparison between the elemental compositions of the genomes of various organisms (Elser et al., 2011). Intriguing differences in N content between wild plants and domesticated crops were revealed (Acquisti et al., 2009). As one Guanine-Cytosine (GC) pair contains 8 N atoms, one more than an Adenine-Thymine (AT) pair, correlations between the GC and N contents of genomes has been postulated (McEwan et al., 1998) but hotly

TABLE 1 | Brief summary of the major advances at each biological level of our framework for a molecule-to biosphere stoichiometry theory and of the elements of understanding identified as in need of improvement.

	Major advances	In need of development	Needed for completeness	Theories for integration
BIOLOGICAL LEVELS				
Genome	Genome elemental content reflects selective pressures	Stoichiometric differences within and between genomes	Elements more loosely associated to genomes such as transition metals	
Cellular	Association between given pools of elements, biomolecules and organelles (e.g., N and chloroplasts)	Contribution of storage organelles and molecules	Cellular components besides chloroplasts and ribosomes (mitochondria, intracellular membranes…)	Ionomics
Organisms	C:N:P composition of major taxa such as unicellular algae, vascular plants and crustacean zooplankton	Neglected taxonomic groups	Other elements besides C, N, and P	
Populations	Intraspecific variability mainly determined by environmental conditions, growth and body size in autotrophs	Mechanistic model for degree of homeostasis in heterotrophs	Major determinants of intraspecific variability in heterotrophs	Physiological homeostasis Developmental biology
Communities	Species in local competitive communities should converge toward similar stoichiometries Functional traits can explain some variations within communities Species diversity and body size are factors affecting community stoichiometries	Scale resolution from biomes to local communities More data on stoichiometric imbalances in realized interactions and across trophic levels	Patterns in stoichiometry-related traits (threshold elemental ratios, growth efficiencies…)	Community ecology theories (coexistence theory, neutral theory, etc.)
Ecosystems	Ecosystems should be close to co-limitation by multiple elements	Extensive monitoring of local elemental limitations for classically studied elements C, N, P and other elements such as K, Mo and Fe	Role of catchment properties and of the regional context	
Landscapes	Increasing role of watershed as water bodies decrease in size Important role for depth along the water column and for the biota along soil profile	Interaction between mixing and stoichiometry along the water column	Stoichiometry patterns along connected terrestrial landscapes	Hydrodynamics
Biosphere	Local heterogeneity in in elemental distribution on emerged lands and to a lesser extent in oceans	Global P distribution in the biosphere	Global distribution of other elements such as K, Fe and Mo	

The elements singled out here have been divided into those in need of development (if they have been already tackled in the literature, but insufficiently) and those needed for completeness (if they have not been tackled in the literature, or only rudimentarily). The integration column lists the relevant theories and fields whose integration would greatly promote understanding of stoichiometry at the corresponding level.

debated (Bragg and Hyder, 2004). Correlation between genome size and P content is also controversial (Hessen et al., 2010b; Vieira-Silva et al., 2010). There is another more subtle way for stoichiometric constraints to imprint on the genome of organisms. The N contents of codons and the amino acids they encode are positively correlated, resulting in a strong relationship between the nitrogen:carbon (N:C) ratio of genomes and proteomes across prokaryotic species (Bragg and Hyder, 2004). Hence, organisms under selection for lower N in their proteins should also see their genome N content decrease, although many other genomic processes may obscure the picture (Gunther et al., 2013). Regarding P, it is the causal association between rDNA structure, rRNA expression, cellular P content and growth rate that is likely to affect the structure of genomes (Weider et al., 2005). Despite these notable breakthroughs, the field of stoichiogenomics is at its early stages. Still lacking is information on potential differences in the stoichiometry of various types of sequences (eu- and heterochomatin, introns and exons, transposons, etc.), of distinct physical structures of genomes (chromosomes, telomeres, centromeres, etc.), as well as differences between the genomes of different organelles (e.g., chloroplasts and mitochondria), cell types (e.g., immune cells, or syncitia) and species (**Table 1**). Other elements beside C, N, and P are worth assessing too. For example, a rather old study by Kearns and Sigee (1979) suggests that some transition metals in cells, like nickel and copper, are mainly associated with chromosomes in dinoflagellates. Thus, differences in genome size among dinoflagellates may result in differences in transition metal contents.

Cellular

Genomes represent only a small fraction of a cell's biomass. Major pools of elements in cells are proteins and nucleotides for N, RNA and phospholipids for P, and carbohydrates and lipids for

TABLE 2 | Brief summary of the major advances at each biological level of our framework for a molecule-to biosphere stoichiometry theory and of the elements of understanding identified as in need of improvement for each process of our framework for a molecule-to biosphere stoichiometry theory.

	Major advances	In need of development	Needed for completeness	Theories for integration
PROCESSES				
Genetic expression	Fundamental links between rRNA production, rDNA gene structure, total P, and growth rate Relation between elemental content and level of expression of genes activated by a given elemental limitation	Organisms beyond classical models such as *E. coli*, *A. thaliana* and *Daphnia*	Interactive effects of multiple elements	Systems biology; Nutrigenomics
Ecophysiological rates	Feedback through increased investment in consumption of scarce resources, leading to co-limitation	Explore alternative resource acquisition strategies	Chemical side effects of elemental resources (e.g., O and anoxia; cations and salinity). Effects of the chemical environment.	Nutritional biology; Environmental chemistry
Physiological rates	Growth penalties for strictly homeostatic organisms under both limitation and excess of given elements The Growth rate Hypothesis and light:nutrient Hypothesis	Molecular and cellular mechanisms at the basis of empirical growth-stoichiometry patterns	A theory of homeostasis. Diseases linked to stoichiometric imbalances	Systems biology; Nutrigenomics
Demographic processes	Somatic growth and reproduction are affected by elemental limitation	Effects of stoichiometry on mortality and dispersal	Density-dependence and demographic stochasticity relationships with stoichiometry. Study of taxa beyond crustaceans	Population biology
Evolutionary forces	N limitation shape N content and gene expression of plant genomes	Measurement of natural selection mechanisms on stoichiometric properties	Other types of evolution (sexual selection, genetic drift, gene flow...)	Evolutionary biology
Ecological interactions	Limitation of herbivores and detritivores by mineral content of their resources Host-pathogen interactions are affected by the stoichiometry of the host	Growth limitation in trophic levels above primary consumers Other dimensions of food quality besides stoichiometry	Inclusion of non-trophic interactions	Multi-level framework
Recycling rates	Consumer-Driven Nutrient Recycling Hypothesis	Chemical and spatio-temporal variability in recycling. Effects of species diversity. Feedback loops between the chemical environment and recycling.	Effects of organisms on the stoichiometry of outputs and inputs in ecosystems	Biodiversity-Ecosystem Functioning theory
Transfer rates	Importance of dispersing organisms and of boundaries between ecosystems	Data reporting transfer rates of multiple elements simultaneously	Conceptual and predictive frameworks for coupled elemental transfer rates	Meta-ecosystems Nutrient spiraling Lagrangian models
General circulation	Dominant effects of plants and humans on global circulation of elements	Study of abiotic and biotic processes together	Study of multiple elements simultaneously	General circulation models

The elements singled out here have been divided into those in need of development (if they have been already tackled in the literature, but insufficiently) and those needed for completeness (if they have not been tackled in the literature, or only rudimentarily). The integration column lists the relevant theories and disciplines whose integration would greatly promote understanding of the stoichiometric role of the corresponding processes.

C (Sterner and Elser, 2002). Hence, the stoichiometry of cells is to all intents and purposes the result of the relative investment of the cell in those few dominant macromolecules (Vrede et al., 2004). This fundamental understanding allows us to predict the stoichiometry of cells in many cases. For example, actively photosynthesizing leaves should show high N:C ratios, because of their heavy investment in RubisCo and other photosynthesis proteins (Field and Mooney, 1986; Evans, 1989). The Growth Rate Hypothesis (Elser et al., 1996) states that fast growing cells should have high contents of ribosomal RNA, and thus also of P, such as in rapidly dividing cancerous cells (Elser et al., 2007b). There can also be a special association between a macromolecule type and a specific cellular structure, e.g., between chlorophyll and chloroplasts, lipids and membranes, or rRNA and ribosomes, resulting in an association between specific metabolic processes and specific elements (Sterner and Elser, 2002; Allen and Gillooly, 2009). Relatively neglected in stoichiometry are storage organelles and associated storage molecules (**Table 1**). In many organisms—like in most autotrophs and prokaryotes (Lee, 1996; Raven, 1997), storage is a major process that may disrupt the functional link described above between cell stoichiometry and other organelles (Lukas et al., 2011), as well as play many other unforeseen roles (e.g., the many roles of polyphosphates, in Bjorkman, 2014). The role of other cellular components, such as mitochondria and intracellular membranes has been given very little consideration too. Elements beside C, N and P have seldom been analyzed at the cellular level in mainstream biological stoichiometry, outside the realm of unicellulars (Ho et al., 2003). They are however the major concern of the whole field of ionomics and both approaches certainly benefit from each other (Salt et al., 2008), revealing intriguing and potentially meaningful correlations among various elements (Loladze, 2014; Jeyasingh et al., 2017).

Organism

Knowledge of the C:N:P composition of species has greatly expanded since the first systematic measurements done on a couple of zooplankton taxa (Andersen and Hessen, 1991). The current datasets allow generalities to be drawn, as well as comparisons among various taxa, life forms, trophic levels and habitats to be performed (Sardans et al., 2012). However, besides the C, N, and P triptych, knowledge of other elements is still limited even though it is potentially of great ecological significance. For example, the oxygen content (O) of organisms may be a signature of their physiological conditions and of the type of molecules they store (Fagerbakke et al., 1996; **Table 1**; see also Han et al., 2011). Biases in the groups of organisms represented in datasets also exist, with unicellular algae, terrestrial vascular plants, crustacean zooplankton—mostly herbivorous—and insects overrepresented (but see Amatangelo and Vitousek, 2008; Martinson et al., 2008; Xia et al., 2014; Danger et al., 2016 for examples of recent attempts at evening the balance).

Population

Intra-specific variability in elemental stoichiometry is less well documented than inter-specific variability. There are different ways to measure variability within a population: according to ontogenetic stages (Main et al., 1997; Meunier et al., 2016), driven by a master trait such as body size or reproductive status (Mendez and Karlsson, 2005), controlled by genotypes, environmentally driven (DeMott et al., 2004), or as stochastic inter-individual variability. Teasing apart all these sources of variation is anything but straightforward and only a few attempts have been made so far, revealing a surprisingly large effect of abiotic conditions on supposedly homeostatic organisms (e.g., El-Sabaawi et al., 2012). Intraspecific variability in autotrophs is notoriously large and determined to a great extent by environmental conditions, with little difference between genotypes (Agren, 2008; Agren and Weih, 2012). Interestingly, ontogenetic stage and body size also strongly affect autotroph stoichiometry, reflecting the fundamental links between growth rate, biomolecules and elements as described in the Growth rate hypothesis (Agren, 2008; Elser et al., 2010). Heterotrophs are classically viewed as maintaining a strict stoichiometric homeostasis, but the paradigm is slowly shifting toward the view that the degree of homeostasis differs from strict to loose in heterotrophic species (Persson et al., 2010; Meunier et al., 2014). It is still unclear what determines the degree of homeostasis (**Table 1**). Potential candidates are ecological factors such as mortality rates (Wang et al., 2012) and the degree of osmotrophy (bacteria, fungi, and flagellates are often highly non-homeostatic, see Godwin and Cotner, 2015; Golz et al., 2015; Danger et al., 2016). Under natural conditions, non-homeostatic species, or conformers—to borrow the concept from physiological studies of homeostasis, are likely to show more intraspecific variability than homeostatic species, or regulators (Meunier et al., 2014). But the latter may still see substantial stoichiometric variability between different life stages or genotypes. It will be important to study the extent of these two sources of intraspecific variability and their effects on populations and nutrient fluxes in ecosystems, likely by integrating elements from the field of developmental biology.

Community

There are numerous studies that examine how elemental composition varies within local communities (Sterner and George, 2000; He et al., 2006; Hattenschwiler et al., 2008). Technical developments in electron microscopy (Gundersen et al., 2002) and microspectroscopy (Hall et al., 2011) allows for such studies in unicellular organisms too. Despite increasing data availability, comparatively few generalities on stoichiometric variability have been drawn (but see Sardans et al., 2012). One reason might be that such studies have not separated scales clearly, mixing data taken from one locality with other data from other localities (**Table 1**). For example, McGroddy et al. (2004) show that variability in N:P ratios is lower within than between biomes. Phylogeny may contribute to this pattern as was found in plants (Broadley et al., 2004) and insects (Woods et al., 2004). The resource-ratio theory may provide some theoretical underpinning as to why local communities feeding on shared resources might converge toward the same stoichiometry, the one ensuring co-limitation by the multiple shared resources (Cherif and Loreau, 2007; Danger et al., 2008). Functional traits may also explain some of the local variation in ratios. For example, N:P ratios are higher in graminoids and stress-tolerant plants than in forbs and ruderals (Gusewell, 2004). Body size is a recurring trait affecting stoichiometry distribution within local communities (Vanni et al., 2002). Other potential factors affecting inter-specific differences in stoichiometry within and between communities are reviewed in Carnicer et al. (2015). Alternatively, neutral processes might control stoichiometric patterns in communities as they may do for abundance distributions (Chave, 2004). Combination of multiple community ecology theories would certainly improve our understanding of community stoichiometry, since competition theory alone does not explain the high biodiversity found in, for example, phytoplankton communities (Passarge et al., 2006).

Species diversity is a factor that has received special interest recently, both as a factor affecting (Striebel et al., 2009; Abbas et al., 2013) and being affected by stoichiometry (Evans-White et al., 2009; Lewandowska et al., 2016). The study by Guiz et al. (2016) is unique in its attempts at causally explaining both the mean and variation in stoichiometry within local communities and suggests an intriguing convergence in the mean and variance of C:N ratios between plant communities established on different soil fertilities.

Vertical diversity, the number of trophic levels, is another dimension of biodiversity that has garnered some attention from stoichiometry. Causal interactions between food chain length and variation in stoichiometry across trophic levels have been touched upon lately, but without any general conclusions drawn yet (Doi, 2012; Peace, 2015). Few generalities have been found regarding systematic stoichiometric differences across trophic levels, beyond the known fact that herbivores are generally poorer in C than their food, but show similar N:P ratios among habitats (Elser et al., 2000a; **Table 1**). For secondary consumers and higher trophic levels, studies have found increases, decreases or no change in N and P when climbing the food chain (Lemoine et al., 2014). Missing are more studies measuring the stoichiometric imbalances between predators and their prey in realized interactions (Malzahn et al., 2010; Lemoine et al., 2014), as well as measuring efficiencies and other important metabolic parameters if one wants to infer consequences on nutrient cycling (Doi et al., 2010).

Ecosystem

Generic knowledge of the balance of N and P in major ecosystems has been available for a long time. In terrestrial systems, chronosequence analyses suggest that terrestrial vegetation shifts from N limitation to P limitation as soils age, N_2 fixation increases N stocks, and erosion depletes soil P (Vitousek and Farrington, 1997). Hence, it is assumed that P is limiting in the tropics and on old bedrocks, while N is limiting in soils recently sedimented or newly exposed by deglaciation. In oceans, the classical work by Redfield has ingrained the view that total C:N:P ratio in pelagic waters is constant around a mean value of 105:15:1 (Redfield, 1958), with competition between N-fixer and non-fixer phytoplankton as the main regulating process (Lenton and Klausmeier, 2007). In freshwater systems, lakes are assumed to be P limited in temperate areas, because C and N can be incorporated into lakes from their vast atmospheric reservoirs (Schindler, 1977), while N limitation was noted for some large lakes in the tropics (Hecky and Kilham, 1988) and some humic lakes in Scandinavia (Jansson et al., 2001). But with biological stoichiometry, there was a renewed interest in measuring the balance of elements in ecosystems, and the classical paradigms depicted above has seen many challenges (Sterner, 2008). The current image emerging is that of ecosystems that are co-limited, or close to co-limitation, unless high imbalances or perturbations in the relative inputs of elements in the ecosystem occur (Elser et al., 2007a). Recent advances even advocate for light limitation in boreal lakes which are rich in colored dissolved organic matter (Karlsson et al., 2009). Anthropogenic alterations of the biogeochemical cycles may also push ecosystems toward limitation by new elements such as K or Mo (van Groenigen et al., 2006). Hence, the general rules about the balance of elements in ecosystems require constant revision as new studies at the local scale emerge (**Table 1**). Important lessons from the analysis of an extensive regional lake database (Hessen et al., 2009) are the significance of catchment properties (type and density of terrestrial vegetation), and of the regional context (N or S deposition intensity) in determining lake stoichiometry. The importance of the landscape context should prompt further distantiation from the "lake as a microcosm" paradigm (Jenkins, 2014).

Landscape

The stoichiometric focus in lake studies greatly highlighted the role of the watershed in determining the nutrient status of freshwater bodies (Frost et al., 2009; Hessen et al., 2009). But it also describes a decreasing influence of landscape as the sizes of water bodies increase, with an increasing convergence toward Redfield ratios from lakes to coastal areas to oceanic water bodies (Sterner et al., 2008). Depth is an equally important spatial dimension in aquatic ecosystems. Vertical profiles of nutrients along the water column, and the role of salinity, temperature and turbulence in their generation are classical material of hydrodynamics and aquatic ecology textbooks (Barnes et al.,, 1991). Additions taken from stoichiometry to these classical approaches look very promising already, indicating important interactions between water mixing and stoichiometric properties of organisms (Diehl et al., 2005; Frassl et al., 2014; **Table 1**).

Terrestrial ecology lags behind in terms of characterizing stoichiometry at the landscape level. Studies searching for differences in elemental availabilities between forests and grasslands for example yielded unresolved contrasting results (Cleveland and Liptzin, 2007; Bond, 2010). There are obvious factors that may affect soil nutrient availabilities between adjacent areas, such as age, vegetation type, or local climate. But there is a lack of knowledge about stoichiometric variation along connected terrestrial ecosystems, for example along a shared hill slope (Porder et al., 2005; **Table 1**). Stoichiometric approaches proved more beneficial when it comes to vertical profiles in soils, demonstrating a great effect of the biota on the relative distribution of elements along soil depth (Jobbagy and Jackson, 2001). Despite recent efforts, understanding landscape variation in ecosystem stoichiometry remains a challenge (Chadwick and Asner, 2016) and considering supplies from the biosphere is often necessary to balance large-scale elemental budgets (Chadwick et al., 1999).

Biosphere

Recent intensive sampling campaigns, global survey tools and data sharing allow for a better mapping of stoichiometry over continents and oceans (Cleveland and Liptzin, 2007; Elser et al., 2010; Weber and Deutsch, 2010), although P may require more data (Wang et al., 2010). Even less information is available on other elements (**Table 1**). The emerging picture so far is that local heterogeneity marks elemental distributions on emerged lands, and to a lesser extent in oceans (Key et al., 2004). Atmospheric circulation mixes gases very efficiently in the atmosphere despite persistent spatial and temporal variations (Wunch et al., 2011). But for other elements, like P and sulfur, homogenization is not fast enough compared to their turnover in the atmosphere, and so, deposition is localized around their sources of supply (Garland, 1978; Mahowald et al., 2008). Their radius of impact can still be surprisingly large as, for example, P from Saharan dust is known to fertilize American ecosystems (Okin et al., 2004).

PROCESSES

Processes are generally harder to measure than standing stocks of elements. They often require specific methods and equipment, as well as manipulative experiments, which may be different among elements that must be measured simultaneously in stoichiometric studies. Despite these complications, there are a large number of studies reporting on the various processes affecting the stoichiometry of all biological levels. The picture emerging from these studies, its beacons and shadows, are briefly discussed in this section.

Genetic Expression

Various genetic, biochemical and physiological methods have already been used in order to characterize genetic responses to stoichiometric imbalances (reviewed in Wagner et al., 2013). Studies of the genetic regulation of nutrient limitation has a strong tradition outside of the biological stoichiometry umbrella, mostly from the study of classical model organisms such as the bacterium *Escherichia coli*, the plant *Arabidopsis thaliana* and the yeast *Saccharomyces cerevisiae* (see, e.g., KEGG PATHWAY Database[1]; Broadley and White, 2009; Broach, 2012). The field seems now ready to move to the next step, from a reductionist to systemic approach, based on approaches such as systems biology and nutrigenomics (Muller and Kersten, 2003; Ruffel et al., 2010; **Table 2**). In parallel, the stoichiometric approach has provided its own novel perspective, by demonstrating, e.g., a fundamental causal link between the number of rDNA copies in a genome, the length and composition of the associated regulatory IGS regions, the cell ribosomal content, its total P content and somatic growth (Elser et al., 2000c; Weider et al., 2005). Stoichiometry sheds a unique light on the link between the economy of elements in organisms and genome structure by showing that the bulk elemental composition of the genetic material itself matters. Genes answering to a given elemental limitation tend to contain less of the limiting element and to code for proteins that do similarly (Gilbert et al., 2013). The two approaches of nutritional genetics and stoichiometry increasingly exchange methodologies (Wagner et al., 2013), but results and conclusions rarely flow in between. For example, a highly cited, comprehensive investigation of the interactive effects of C and N availability on gene expression regulation (Gutierrez et al., 2007) has gone un-cited in the stoichiometry literature so far.

Ecophysiological Rates

Rates of resource acquisition by organisms as modulated by elemental availability in their environment is an old topic in biology at least since the 1940s (Monod, 1947). The general rule is that of a negative feedback resulting from the availability of a given resource: the lower the availability, the higher the investment of the consumer to acquire it. Stoichiometry has made a substantial contribution to the subject by adding concerns about the potential role of other essential elements. On optimisation grounds, it is expected that organisms should use the excess availability of non-limiting elements to increase their acquisition of the limiting elements until co-limitation by all essential elements is reached (Darchambeau et al., 2003; Klausmeier et al., 2004a; Cherif and Loreau, 2007). However, a number of mechanisms may prevent co-limitation establishing in practice, like limits to physiological adaptation (Klausmeier et al., 2004b). Organism needs are complex, and resource acquisition strategies may have ultimate goals beyond just insuring immediate maximum growth for an organism (Flynn, 2009; **Table 2**). Besides, variations in the availabilities of various resources tend to be coupled under natural circumstances (Lemoine et al., 2014), sometimes in conjunction with under-appreciated limiting factors, such as water availability (Sardans et al., 2008). Hence multifactorial analyses beyond the usual N and P (sometimes also C) limitation experiments should be extended to include simultaneous variations in combined resources. Besides, the molecules that contain the essential resources may have peripheral chemical properties that otherwise affect growth, e.g., they may be toxic or change the pH of cells (McGrath and Quinn, 2000). They may also play other roles in the metabolism, for example as ions maintaining constant osmolality (e.g., Na, K, and Ca) or as electron donors/acceptors (e.g., O, N, and S). Such side effects have been considered in classical nutritional biology, but mostly ignored in stoichiometry. It is only recently that consideration of factors such as salinity and anoxia in stoichiometry emerged (Marino et al., 2006; Helton et al., 2015; Tadonleke et al., 2016). Even fewer studies have attempted to integrate the role of elements as biomass components with their other chemical functions (but see Payn et al., 2014). Environmental chemistry should thus be better integrated into the stoichiometric analyses of ecophysiological rates (**Table 2**).

Physiological Rates

Organisms have to match elemental demands set by genetic expression with the ecophysiological rates of resource uptake. They do this through various physiological processes that redistribute elements within the organism or between the organism and its environment, as well as through feedbacks that regulate the genetic expression. Elemental metabolism in primary producers and in some model microorganisms like *E. coli* and *S. cerevisiae* is an established part of research. So-called genome-scale metabolic models now offer the possibility to quantitatively predict the effects of changes in resource availabilities or of mutations in genes (e.g., Liu et al., 2010). On the other hand, stoichiometric studies generally concentrate on designing simple models describing the link between elements and growth in autotrophs and osmotrophs (Cherif, 2016). These models are mostly empirically-based and to a great extent divorced from the potential molecular and cellular underpinning mechanisms, which is both a strength and weakness for such models (Flynn, 2008). When it comes to consumers, classical stoichiometric theories assume strict homeostasis of elemental composition, resulting in strong constraints on the physiological fluxes of elements, particularly excretion (Sterner, 1990). This vision of homeostasis in heterotrophs is increasingly challenged (Persson et al., 2010). The quest is now for a mechanistic understanding

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[1] KEGG PATHWAY Database. Available online at: http://www.genome.jp/kegg/pathway.html (Online).

of the determinants of the degree of homeostasis in organisms (Meunier et al., 2014; **Table 2**). The main physiological consequence of strict homeostasis is a decrease in growth rate because one element becomes limiting (Sterner and Hessen, 1994). Another consequence is an increase in the costs related to the regulation of the elements in excess, which may also lead to a decrease in growth (Boersma and Elser, 2006). Tolerating changes in stoichiometry by lowering the content of the limiting element, or storing the elements in excess, are strategies that dampen the sensitivity of a species to elemental deficiencies (Mulder and Bowden, 2007; Seidendorf et al., 2010) and may even prove competitively advantageous under both constant and variable environments (Grover, 1991; Grover and Chrzanowski, 2006). The stoichiometry theory has specifically emphasized two ecologically relevant stoichiometric rearrangements: the decrease in P content under P limitation, through a decrease in ribosome numbers (the "Growth rate hypothesis," see Elser et al., 1996) and the storage of excess C by plants when light and CO_2 are non-limiting (the "Light:nutrient hypothesis," see Sterner et al., 1997). Maintaining health and immunity in the face of a varying environment is a fundamental homeostatic feature, a fact acknowledged by nutrigenomics (Afman and Muller, 2006) but overlooked by stoichiometry (**Table 2**). If stoichiometric imbalances trigger diseases, then consequences for the organisms may go beyond a decrease in growth rate or reproductive output. More generally, stoichiometric adjustments that affect the life history traits of organisms, should display a variety of demographic and ecological consequences.

Demographic Processes

Classical population biology teaches us that life-history traits determine the demographic processes that set the structure and dynamics of populations (Tuljapurkar and Caswell, 1997). However, classical stoichiometric theories mainly considered the effects of elemental limitation on somatic growth, and more rarely its effects on life history traits (reviewed in Moe et al., 2005). Fecundity was generally found to be affected by poor diet quality (Sterner, 1998; Urabe and Sterner, 2001; Zandona et al., 2011). Few studies focussed on stoichiometry-related mortality (Sterner et al., 1993; Nelson et al., 2001; Declerck et al., 2015; **Table 2**). Only a couple of studies look into links between stoichiometry and dispersal or migration (Sterner and Schwalbach, 2001; Huberty and Denno, 2006). Empirically, much of this work concentrated on *Daphnia* and copepods at the expense of other taxa (Sterner and Schulz, 1998; Urabe and Sterner, 2001; Jeyasingh and Weider, 2005; but see Bertram et al., 2006). Hence, the effects of nutrient limitation, more specifically P limitation, on life-history traits in those organisms are reasonably well understood. But we know only of one study that put this information to use in a P-limited population model by Nakazawa (2011). One intriguing result from this study, but in line with most recent population ecology theory (Roos and Persson, 2013), is that, assuming that P limitation affects mainly somatic growth, more P-limited populations should be dominated by P-rich juveniles, and hence be more P-rich (Nakazawa, 2011). More models releasing simplifying assumptions are needed, as well as experimental data outside of the crustacean realm. Other fundamental concepts in population biology, such as demographic stochasticity and density dependence (feedbacks from the population to the organism and cellular levels), are virtually untouched by the stoichiometry theory so far. In short, a stoichiometric theory of demography is sorely lacking (**Table 2**).

Evolutionary Forces

If sustained over a sufficiently long time, changes in a population structure that are underlain by differences among genomes should result in evolution. Many studies have postulated evolution through adaptation to stoichiometric constraints. Evidence for N limitation shaping the DNA composition of plant genomes, and for P limitation decreasing genome size, P content (Hessen et al., 2010a) and P recycling efficiency (Elser et al., 2000b) has been presented. Evolutionary adaptation requires variability in traits, heritability and correlation to fitness. For a given trait, careful experiments and models examining the mechanisms of natural selection are required. Very few stoichiometric studies committed to examine these mechanisms, either through models (Branco et al., 2010; Yamamichi et al., 2015) or experiments (Declerck et al., 2015; Lind and Jeyasingh, 2015). The absence of mechanistic underpinnings to most evolutionary stoichiometric hypotheses exposes them to criticism (Worman and Kimbrell, 2008; Vieira-Silva et al., 2010; Gunther et al., 2013; **Table 2**). Moreover, other mechanisms for evolution besides natural selection, such as genetic drift and gene flow, are not yet addressed by any stoichiometric hypotheses (but see Morehouse et al., 2010 for sexual selection).

Ecological Interactions

Ecological interactions are the cornerstones of ecological stoichiometry. The theory established the idea that herbivores are most often limited in their growth by the mineral content of their resources, because most autotrophs are richer in C than their consumers (Elser et al., 2001). Later, mineral limitation was also demonstrated in detritivores (Frost et al., 2002). Subsequently, both deficits and excesses of mineral elements were found to adversely affect the growth rate of consumers (Boersma and Elser, 2006). Secondary consumers were first deemed to be limited by energy, since their prey have similar elemental contents, but given that excess elements can impact growth negatively and that consumer stoichiometry is more variable than previously thought, the jury is still out on whether limitation by resources other than energy is possible (Boersma et al., 2008; Lemoine et al., 2014; **Table 2**). Besides, imbalance in the stoichiometry of a prey may be associated with other changes in prey quality that may impact predators, an acknowledged but often neglected complication (Mitra and Flynn, 2005). The stoichiometric approach has extended its predictions beyond the immediate effect of stoichiometric imbalances on the growth of the consumer. For example, consumer-driven nutrient recycling predicts that primary consumers should affect the availability of elements at the ecosystem level (Elser and Urabe, 1999) and therefore influence coexistence criteria of primary producers (Grover, 2002); the light:nutrient hypothesis predicts that increased photosynthetic C fixation with increasing light availability should result in widespread mineral limitation throughout the food web (Sterner et al., 1997); a stoichiometric approach to host-pathogen interactions predict that strength of infections should depend on the stoichiometry of the host resources (Smith et al., 2005; Aalto et al., 2015); and stoichiometrically-explicit food webs models suggest food quality-driven changes in trophic cascade strength (Hall et al., 2007). However, those derived predictions often proved difficult to demonstrate unequivocally in theory or experiments (e.g., Daufresne and Loreau, 2001; Sommer et al., 2004; Faithfull et al., 2011; Pulkkinen et al., 2014) probably because the conjectured mechanisms take place at various biological levels and thus need the type of multi-level framework we endeavor to sketch here. Another explanation is that neglecting non-trophic interactions (Kefi et al., 2012) and feedback loops between ecological interactions and physiological rates may have potent stoichiometric effects on higher-level processes (Leroux and Schmitz, 2015).

Recycling Rates

A clear conceptual advance gained from the stoichiometry theory is the connection between stoichiometric consumer-to-resource imbalances and the ratios of elements recycled by consumers (Sterner, 1990). This approach, however, has abstracted release rates as spatially, temporally and chemically uniform. But recycling by consumers is known to be spatially localized (Augustine, 2003), temporally fluctuating (Blackburn et al., 1998) and chemically variable (Anderson et al., 2005). This variability bears important consequences for the overall effects of recycling (Kato et al., 2007; Ramin et al., 2012; **Table 2**). Recycling rates are predominantly metabolic rates (i.e., excretion and egestion rates). As such, body size and temperature are important rate controllers in concert with stoichiometry (Cross et al., 2015). Recent integration of both stoichiometry and metabolic ecology approaches generally improved rate predictions (Vanni and McIntyre, 2016). The overall chemical conditions, such as anoxia levels, also interact with stoichiometry to determine recycling (Steenbergh et al., 2013). Oxygen minima zones are thus likely to affect and be affected by the recycling rates of essential elements (Stramma et al., 2010; Penn et al., 2016). This example points to the importance of considering the potential feedbacks between the chemical environment and recycling (**Table 2**). Research in biodiversity-ecosystem functioning relationships has otherwise shown that species diversity affects elemental rates within ecosystems (Hooper et al., 2005), as well as biomass production and stoichiometry of primary producers (Striebel et al., 2009). However, interactive effects of stoichiometry and biodiversity on recycling rates are still poorly understood and in need of further development (Hillebrand et al., 2014). In the long term, it has been shown that it is recycling of the forms that are not available to other organisms that determine the impact of a consumer on nutrient availability in its ecosystem (Paterson et al., 2002; Vanni et al., 2013). This impact depends on the quantity and quality of matter that it subtracts from its environment through, e.g., sedimented feces, recalcitrant carcasses or emigration. Potential control of the consumer on the inputs of elements in the ecosystem needs to be considered similarly (e.g., through N fixation, immigration). Hence, the effects of recycling are intimately related to transfer rates among ecosystems, because elements that are removed from an ecosystem are obligatorily added to another ecosystem thus affecting both ecosystems.

Transfer Rates

Translocation of elements among ecosystems has been an early scientific concern, defining the field of biogeochemistry (Gorham, 1991). However, the role of living organisms in the coupling of the fluxes of multiple elements has only been conceptualized and generalized to all ecosystems with the birth of the stoichiometric approach (Sterner and Elser, 2002). On the theoretical level, Schade et al. (2005) attempted to model the interaction of ecosystems through transfers of elements among them with an extension of the classical resource-ratio theory (Tilman, 1982), insisting on the importance of dispersing organisms and of boundaries in altering the stoichiometry of the transferred material and of the recipient ecosystem. Usage of this framework remains limited however, probably because of a relative paucity in data reporting the transfer rates of multiple elements simultaneously (reviewed in Sitters et al., 2015; **Table 2**). Other unifying frameworks, such as meta-ecosystems, are worth exploring as well (Loreau et al., 2003; Manzoni and Porporato, 2011; Marleau et al., 2015).

General Circulation

Shortcuts to localized transfers between adjacent ecosystems take place when elements are redistributed on larger scales by the atmospheric and oceanic circulations. Multiple processes put elements in general circulation: erosion, evapotranspiration, respiration, and most important, human-mediated processes such as fossil fuel burning. Other processes ensure that those elements fall back on local ecosystems. Some are physical (atmospheric deposition, precipitation, upwelling), others are mediated by living organisms (photosynthesis, N-fixation, fertilizer production by humans). Those processes are rarely studied together, or for multiple elements simultaneously (**Table 2**). Because of their sheer biomass and level of activity, plants (Wassen et al., 2013) and humans (Penuelas et al., 2013) are the biotic components that most affect the general circulation of elements. Explicit stoichiometric considerations increased the predictability of general circulation models that include the potential effects of these biotic drivers on the dynamics of the biosphere (Thornton et al., 2009; Penuelas et al., 2013).

CONCLUSION: A ROADMAP FOR A MULTILEVEL, COMPREHENSIVE THEORY OF STOICHIOMETRY

Our framework provides a roadmap of the way a given stoichiometric imbalance at a given biological level, or alteration in a given stoichiometric process can cascade to other biological levels by affecting higher- or lower-level processes. The survey of the literature structured by our framework, although non-exhaustive, shows that the theory has proved astonishingly vigorous despite its relatively young age, as judged by its degree of completeness and development. But we also identified, for each level and each process of the framework, areas in need of completion, development, or articulation with other relevant non-stoichiometric theories (see **Tables 1, 2** for a summary). Stoichiometric theories for population dynamics and community composition appear to us as most urgently needed. Populations and communities obey constraints that are beyond physiology. These two biological levels may thus result in departures from the physiological rules that are used by stoichiometry theories to predict the flows of multiple elements. Various disciplines have already developed reliable theories, concepts and methodologies related to these areas in need of development, which are highly relevant to the stoichiometric approach. But lack of familiarity with other fields from the stoichiometry side, and lack of a comprehensive view on the stoichiometric approach on the other side, is likely to hinder integration, unless the links between fields are explicitly laid out, like in our framework.

By highlighting many areas in need of improvement, our framework indicates that the stoichiometry approach has not yet delivered a predictive theory of elemental transfers within the biosphere. But, we have every hope that our framework will help the theory reach a level of maturity such that it will be able to consistently relate local, microscopic processes to global, macroscopic processes. Current general circulation models often flagrantly ignore lower-scale biological processes for lack of a proper methodology, potentially restraining our capacity to accurately predict future global change. Our framework is one step in this direction.

AUTHOR CONTRIBUTIONS

All authors contributed to the conception and design of the study and to the selection, analysis and interpretation of the relevant literature. MC coordinated the writing of the manuscript. CF, CM, JS, WU, and FR revised the manuscript critically. All authors approve the manuscript in its current form and agree to be accountable for all aspects of the work.

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