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2023

Original citation:

El-Sabaawi, R. W., Lemmen, K. D., Jeyasingh, P. D., & Declerck, S. A. J. (2023). SEED: A framework for integrating ecological stoichiometry and eco-evolutionary dynamics. *Ecology Letters*, *26*(S1). https://doi.org/10.1111/ele.14285

Received: 7 November 2022 | Revised: 1 June 2023 | Accepted: 4 June 2023

DOI: 10.1111/ele.14285

ECOLOGY LETTERS WILEY

PERSPECTIVE

SEED: A framework for integrating ecological stoichiometry and eco-evolutionary dynamics

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Editor: Cyrille Violle

Abstract

Characterising the extent and sources of intraspecific variation and their ecological consequences is a central challenge in the study of eco-evolutionary dynamics. Ecological stoichiometry, which uses elemental variation of organisms and their environment to understand ecosystem patterns and processes, can be a powerful framework for characterising eco-evolutionary dynamics. However, the current emphasis on the relative content of elements in the body (i.e. organismal stoichiometry) has constrained its application. Intraspecific variation in the rates at which elements are acquired, assimilated, allocated or lost is often greater than the variation in organismal stoichiometry. There is much to gain from studying these traits together as components of an 'elemental phenotype'. Furthermore, each of these traits can have distinct ecological effects that are underappreciated in the current literature. We propose a conceptual framework that explores how microevolutionary change in the elemental phenotype occurs, how its components interact with each other and with other traits, and how its changes can affect a wide range of ecological processes. We demonstrate how the framework can be used to generate novel hypotheses and outline pathways for future research that enhance our ability to explain, analyse and predict eco-evolutionary dynamics.

KEYWORDS

carbon, eco-evolutionary feedbacks, ecological stoichiometry, intraspecific variation, microevolution, nitrogen, nutrient, phenotypic plasticity, phosphorus, traits

INTRODUCTION

In recent years there has been increased recognition that **microevolution** can occur rapidly, that is on the same timescales as many ecological processes (see Box 1 for definitions of the terms in bold) (Hendry, 2017; Sanderson et al., 2022; Thompson, 1998). Empirical and theoretical studies show that **intraspecific variation** can have large effects on many ecological processes including population dynamics, species interactions and nutrient cycling (Des Roches et al., 2018; Raffard et al., 2019). The term '**eco-evolutionary dynamics**' refers to the interactions of ecological and evolutionary processes on similar, overlapping timescales (Bassar et al., 2021; Hairston et al., 2005). A better understanding of eco-evolutionary dynamics is critical as humans alter selection regimes at unprecedented rates (Darimont et al., 2009; Sanderson et al., 2022).

Understanding the interactions between ecological processes and microevolution requires knowledge of how selection alters heritable phenotypic variability of traits within populations, how this variation influences ecological processes, and how these processes **feedback** to alter selection through changes in the biotic and abiotic environment. Studies of eco-evolutionary dynamics have typically focused on fitness-related traits like morphology, body size, or life history (Hendry, 2017). These studies have provided exciting insights, but this

BOX 1 Glossary of terms used in the paper in alphabetical order

Classical phenotype: All traits that can be measured at the level of the organism that are not expressed in terms of elements, including, for example, growth rate, life history traits, secondary reproductive traits, morphology, etc. Classical traits that influence fitness are a major focus of evolutionary biology and eco-evolutionary dynamic studies.

Eco-evolutionary dynamics (and feedbacks): Eco-evolutionary dynamics are the interactions between evolutionary and ecological dynamics on overlapping timescales. Feedbacks occur when these dynamics alter selection.

Ecological effects: In the paper this term refers to the effects of microevolutionary changes on an ecological process that can manifest in individuals, populations, communities or the ecosystem.

Ecological stoichiometry: A conceptual framework that expresses all biological entities (e.g. individuals, populations, functional groups or ecosystem components) as ratios of essential elements, and uses mass balance to quantify the fluxes of elements through and between these entities. Ecological stoichiometry is often used to understand how organisms interact with their diets, other organisms or the ecosystem.

Elemental phenotype (and elemental traits): The acquisition, assimilation, allocation and losses (including into reproduction) of the elements by the organism, which ultimately determine the quantities and proportions of elements in its body, and which are measured in element-specific fluxes, pools, efficiencies, concentrations or ratios (Table 1). Traits that make up the elemental phenotype are sometimes also referred to as 'stoichiometric' traits (Leal, Seehausen, & Matthews, 2017).

Intraspecific variation: Variation in traits measured within species, which might be caused by genetic or phenotypic variation.

Mass balance: is the application of the laws of conservation of mass (or elements). Matter cannot be created or destroyed in biologically mediated reactions, and the reactions have to have the same elements in their reactants and products. Therefore, an increase in elements in one entity (e.g. organism) has to be balanced by an increase in the acquisition of that element from the diet or a decrease in its loss rates.

Microevolution: Allele frequency change within a population, which typically occurs on short temporal scales.

Nutrient recycling (also known as consumer-mediated nutrient recycling): The process by which waste products of organisms serve as nutrient sources for others (Atkinson et al., 2017). For example, dissolved inorganic forms of N and P in the excreta of fish and zooplankton are taken up by algae in lakes (Vanni, 2002)

Organismal stoichiometry: The molar ratios of elements in the bodies of the organism (e.g. C:P, C:N, N:P) (Table 1). In ecological stoichiometry, organismal stoichiometry of metazoans is assumed to vary as a result of biochemical variation driven by trait investment. For example, growth rate (a trait) requires increased synthesis of mRNA (a P-rich biochemical), which can therefore increase body P (and decrease N:P and C:P) in the bodies of some taxa (more examples in Box 2).

Resurrection ecology: A method that revives long-dormant organisms via hatching of dormant life stages such as seeds, eggs and spores/cysts, allowing direct quantification of phenotypes over time spans longer than the average human lifespan (Weider et al., 2018) (see example in Box 4).

Space-for-time substitutions: When a contemporary spatial gradient is used to simulate long-term temporal ecological change, such as when temperature or rain-shadow gradients are used to simulate climate change dynamics (Wogan & Wang, 2018).

Stoichiometric mismatch: A difference in the elemental ratios (e.g. C:P) between organisms and their prey or their diets. For example, in herbivores, stoichiometric mismatches occur when an essential element such as P is limiting in the environment. This causes primary producers to have much higher organismal C:P and N:P than the herbivores. When pronounced, stoichiometric mismatch typically causes stress and triggers a range of physiological or behavioural adjustments in the consumer. Long-term stoichiometric mismatch has been shown to act as a selection factor (Declerck et al., 2015).

approach also has limitations. It remains challenging to predict how and why microevolution generates ecological change, or to explain these effects when they arise (Hendry, 2017; Thompson et al., 2021), and it has been difficult to make general inferences beyond specific model systems (Schoener, 2011). Furthermore, most eco-evolutionary dynamics studies have overlooked the impact of microevolution on how organisms acquire, use or dispose of essential elements, which is important for a wide range of ecological processes.

Ecological stoichiometry studies how the relative supply and demand of essential elements (e.g. carbon [C], phosphorus [P], nitrogen [N], etc.) influences biological interactions. It measures the ratios of essential elements in organisms, their food sources or different aspects of their environment, and uses **mass balance** to quantify the fluxes of elements among organisms or between organisms and their environment (Sterner & Elser, 2002). Because it is possible to measure the same elements in all matter, ecological stoichiometry can make mechanistic connections across multiple levels of biological organisation from genes to the ecosystem, facilitating generalisation (Elser et al., 2000). It has been used to explore how organisms influence nutrient cycling (Atkinson et al., 2017), and how elemental availability in resources shapes consumer phenotypes, populations and communities (Declerck et al., 2015; Moe et al., 2005; Roy Chowdhury & Jeyasingh, 2016; Schlüter et al., 2014; Turner et al., 2017).

The early successes of using ecological stoichiometry to explain ecological patterns and processes (e.g. Bridgham et al., 1995; Hassett et al., 1997; Sterner et al., 1992) rapidly led to the suggestion that it could also be useful in understanding evolutionary questions (Elser, 2006; Kay et al., 2005). Early studies posited that the relative abundance of elements in organisms (also known as **organismal stoichiometry**) is driven by their biochemical composition, which is driven by their traits (Reiners, 1986; Sterner & Elser, 2002). In other words, variation in elemental content among and within metazoan taxa reflects their evolutionary history, and could be used to understand past evolutionary trajectories in which the selective environment may have favoured or constrained investment in a given trait (Kay et al., 2005). This ability of elemental ratios to connect phenotypes to the selective environment led Elser (2006) to advocate for using stoichiometry to understand the connections between ecosystem ecology and evolutionary biology, which at the time were viewed as disparate fields. Ecological stoichiometry later played a key role in demonstrating the capacity for evolution and ecology to interact when Matthews et al. (2011) presented a model formalising how heritable phenotypic changes caused by selection within a population (i.e. heritable variation in nutrient uptake rates of a primary producer) could modify ecosystem processes (i.e. **nutrient recycling** and zooplankton grazing rates). Given its ability to link ecology to microevolutionary processes, and microevolution to ecological processes, ecological stoichiometry was quickly identified as uniquely suited to study eco-evolutionary dynamics and feedbacks (Jeyasingh et al., 2014; Leal, Seehausen, & Matthews, 2017). Using ecological stoichiometry to investigate a wide range of evolutionary questions including eco-evolutionary dynamics is a rapidly increasing area of study (e.g. Declerck et al., 2015; Isanta-Navarro et al., 2022; Larsen et al., 2019; Roy Chowdhury et al., 2015; Schlüter et al., 2014; Turner et al., 2017; Yamamichi et al., 2015).

The majority of attempts to integrate ecological stoichiometry with evolutionary biology, and later with eco-evolutionary dynamics have strongly focused on organismal stoichiometry (e.g. Elser, 2006; Kay et al., 2005; Box 2), with mixed success. Although correlations between organismal stoichiometry and trait investment appear to hold across species, resulting in phylogenetic differences in elemental composition (Allgeier et al., 2021; Andrieux et al., 2021; Atkinson et al., 2020; González et al., 2018), they are far more complex and variable within species (Box 2). Furthermore, research shows that how organisms acquire, assimilate, allocate or dispose of elements often display higher levels of phenotypic plasticity and greater amounts of genetic variation than organismal stoichiometry itself (Leal, Seehausen, & Matthews, 2017; Lemmen et al., 2019). Because these **elemental traits** encompass fluxes of elements within organisms, among organisms or between organisms and their environments, they have a more direct mechanistic link to a range of ecological processes than organismal stoichiometry. Compared to organismal stoichiometry, elemental traits may therefore be expected to have both a higher microevolutionary potential and a larger ecological impact. While studies have begun to investigate intraspecific variation in elemental traits beyond organismal stoichiometry, research in this area is still in its infancy (Leal, Seehausen, & Matthews, 2017). Their study, nevertheless, holds great promise for revealing eco-evolutionary dynamics that have been largely ignored until now.

We believe that the application of ecological stoichiometry can vastly improve mechanistic understanding of eco-evolutionary dynamics in many systems. However, to be successful in this pursuit, it is important to consider a wider range of elemental traits than organismal stoichiometry, and to explore their ecological consequences. Here we present a conceptual framework to enhance the integration between traditional approaches to eco-evolutionary dynamics and the elemental perspective of ecological stoichiometry. The framework is based on the **'elemental phenotype'** (Jeyasingh et al., 2014), a concept that is very useful because it takes into account all of the traits of elemental processing, and allows us to articulate how they are linked to each other and to traits that are typically studied in evolutionary biology (e.g. somatic, morphological, behavioural traits, etc.). One of the key advances that the framework makes is the explicit incorporation of causal links among traits of the elemental phenotype and a range of specific ecological processes, which will help guide future research. Although we emphasise metazoan examples in this paper, the general approach and basic principles could undoubtedly be applied to microbes or plants equally well.

BOX 2 On the complex link between organismal stoichiometry and trait investment

The growth rate hypothesis posits that somatic growth is fuelled by protein synthesis which requires Phosphorus (P)-rich mRNA, thus faster growing organisms will have high body P content (Sterner & Elser, 2002). A positive correlation between growth rate and body P (measured as %P of body dry mass) has been observed in a number of organisms, both within and across species (Elser et al., 2003). Furthermore, growth-rate based differences in body P (and body N:P ratios) explain changes observed in zooplankton community composition following alterations in nutrient limitation in lakes (Elser et al., 1988). However, the relationship between intraspecific genetic variation in growth rate and body P appears to be highly variable across taxa and studies (Isanta-Navarro et al., 2022; Lemmen et al., 2023; Liess et al., 2013; Prater et al., 2017; Sherman et al., 2017; Weider et al., 2004). A recent systematic reassessment suggests that the relationship between body P and growth rate is relatively weak (Isanta-Navarro et al., 2022). One hypothesis that has been proposed to explain this uncoupling is that variation in P utilisation efficiency might allow organisms to achieve higher growth rates under P limiting conditions, and without altering body P content (Arnold et al., 2004; Frisch et al., 2014; Isanta-Navarro et al., 2022; Lemmen et al., 2023). In other words, genetic divergence in one or several traits related to elemental processing may allow the organism to achieve higher growth rates without influencing organismal stoichiometry. The observation that the relationship between growth rate and body P varies among genotypes of *Daphnia* suggests that different strategies for dealing with high growth rate are possible within the same species (Prater et al., 2017).

The growth rate hypothesis has been developed and tested primarily in small organisms and zooplankton that do not have a skeleton. In vertebrates, P variation should be driven by bone, which contains high concentrations of P, and which represents the largest pool of P in the body (Gillooly et al., 2005). Body P variation appears to be correlated with the degree of skeletal investment across vertebrate species, where bonier taxa have a higher concentration of body P than less bony taxa (Frost et al., 2006; Hendrixson et al., 2007). The most detailed investigation of how intraspecific bony trait variation affects the elemental phenotype has occurred in the threespine stickleback (*Gasterosteus aculeatus*). This species displays heritable variation in boney defensive traits such armour coverage and pelvic girdle thickness (Bell & Foster, 1994; Colosimo et al., 2005; Peichel et al., 2001). Early studies hypothesised that increased armour investment should increase body P, leading to a reduction of organismal N:P and C:P ratios. However, bony armour coverage has been observed to positively correlate with body P in some but not all stickleback populations (Durston & El Sabaawi, 2017; Leal, Best, et al., 2017; Rudman et al., 2019). Studies have also shown that several elemental traits in sticklebacks co-vary with bony armour phenotypes, including allocation, excretion and assimilation (El-Sabaawi et al., 2016; Leal, Best, et al., 2017; Rudman et al., 2019). Investigations are ongoing, but it appears likely that much like growth rate in *Daphnia*, bony trait investment can occur via multiple strategies, and can be facilitated by multiple traits of the elemental phenotype. The framework proposed in this paper can be used to investigate why different genotypes or populations of the same species utilise different strategies for meeting the elemental demands of trait investment.

A FRAMEWORK FOR INTEGRATING STOICHIOMETRY AND ECO-EVOLUTIONARY DYNAMICS

The proposed framework for integrating ecological Stoichiometry and Eco-Evolutionary Dynamics (SEED) (Figure 1) maps the various pathways through which selection can alter ecological processes through microevolutionary changes in an organism's phenotype. The upper part of Figure 1 shows eco-evolutionary dynamics as they are most commonly depicted in the current literature (Hendry, 2017), where phenotypic trait change in response to selection can lead to **ecological effects** at multiple levels of organisation (populations, communities and the ecosystem), some of which may feedback to alter selection. The SEED framework proposes that any change in a trait must be accommodated by changes in how organisms consume, metabolise, accumulate or eliminate elements, that is, the 'elemental phenotype', which encompasses all elemental traits not just organismal stoichiometry. Selection can also act directly on the elemental phenotype. Furthermore, elemental traits can have wide-ranging ecological effects (lower part of Figure 1). The overall effects of microevolution on ecological processes will therefore reflect the interaction between elemental and non-elemental traits. To utilise this framework we must therefore first explore the elemental phenotype, then clarify how it relates to other phenotypic traits, and then investigate its capacity to generate ecological effects.

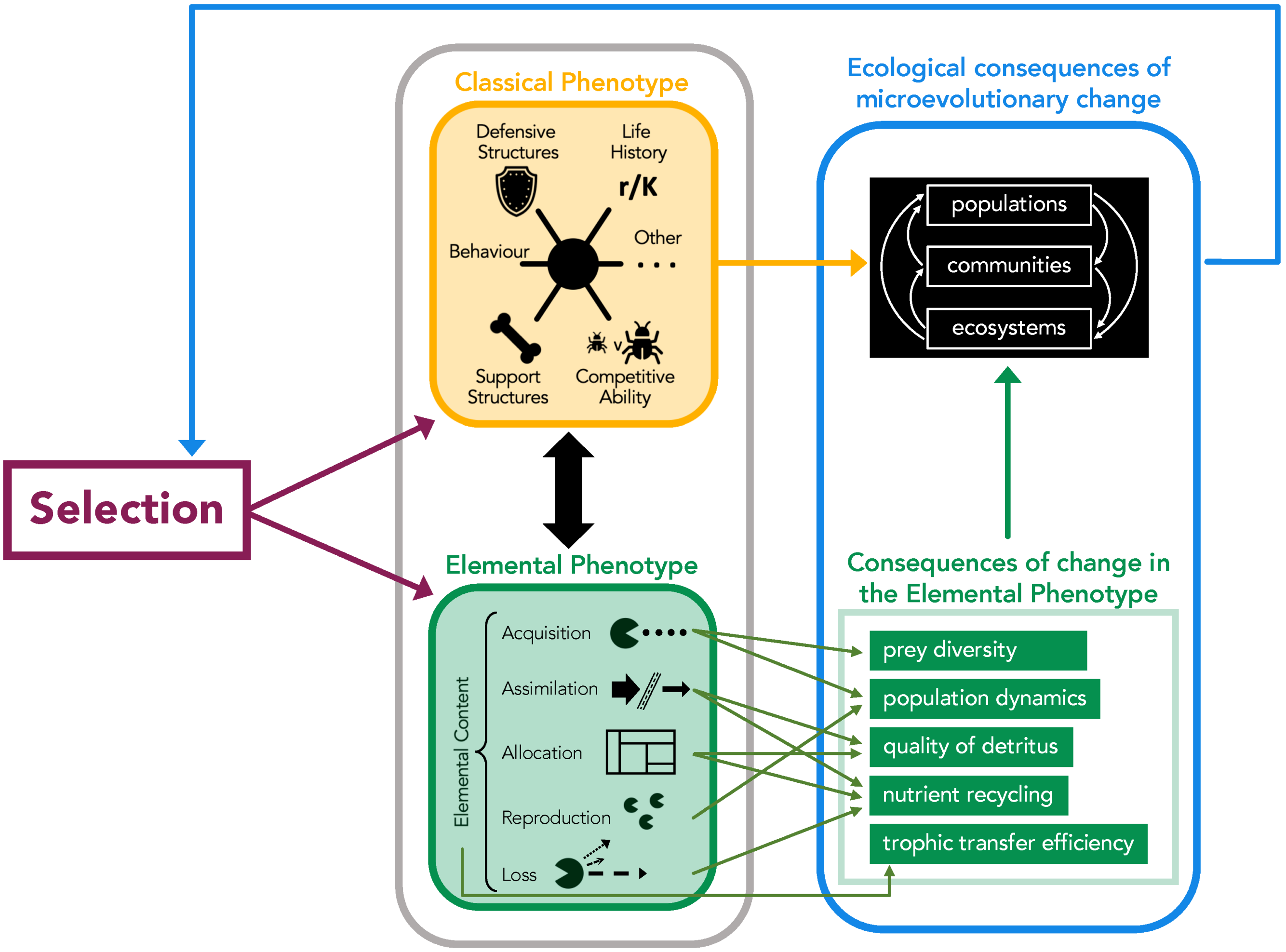

FIGURE 1 A framework for the integration of ecological Stoichiometry with Eco-Evolutionary Dynamics (SEED). The framework highlights the different ways by which selection might result in the evolutionary modification of elemental traits and how such change alters ecological processes. Eco-evolutionary dynamics arise when genetically determined phenotypic change affects ecological dynamics at the level of populations, communities, or ecosystems. Feedbacks arise when these effects alter selection. SEED makes a conceptual distinction between a 'classical' and 'elemental phenotype'. The elemental phenotype refers to body elemental content (or organismal stoichiometry) and their underlying element-specific physiological rates (see Figure 2 and Table 1 for elaboration). The classical phenotype refers to all other non-elemental traits (e.g. growth rate, morphology, defence or life history, etc.). Both phenotypes are interdependent and constrain each other (double arrow). Any change in the classical phenotype must be accommodated by the elemental phenotype, and conversely all physiological rates of the elemental phenotype need to be realised by traits of the classical phenotype. The elemental phenotype can also evolve in response to selection caused by environmental factors (such as those that generate stoichiometric mismatches). Change in the elemental phenotype can generate a wide range of ecological effects through a variety of mechanisms. While much of the studies on eco-evolutionary dynamics focus on classical traits (the upper part of the figure), the SEED framework emphasises that ecological effects of evolutionary change and its potential feedback to selection regimes will often result from modifications in both classical and elemental traits (green arrow).

What is the elemental phenotype?

Any organism is composed of a dynamic pool of different elements, each with continuous influxes and effluxes at different rates (Figure 2a) (Sterner & Elser, 2002). Dictated by biochemical constraints, an organism can only survive, grow and reproduce when the quantities and relative proportions of each of these elements in this pool remain within confined ranges. Given that the relative availability of elements in the environment can differ from organismal requirements, heterotrophic organisms strive towards maintaining their relative elemental composition (i.e. organismal stoichiometry) through the homeostatic regulation of several element-specific physiological rates, involving both gain and loss processes (Figure 2b). In addition, to support specific functions such as growth, reproduction, or defence, elements need to be allocated to specific body compartments.

Because the concentrations of elements in the body and organismal stoichiometry reflect the net result of a number of fundamental element-specific physiological processes, each of which can be considered a quantitative trait, their microevolutionary dynamics cannot be understood without knowledge of changes in these underlying processes. To explain the important but largely

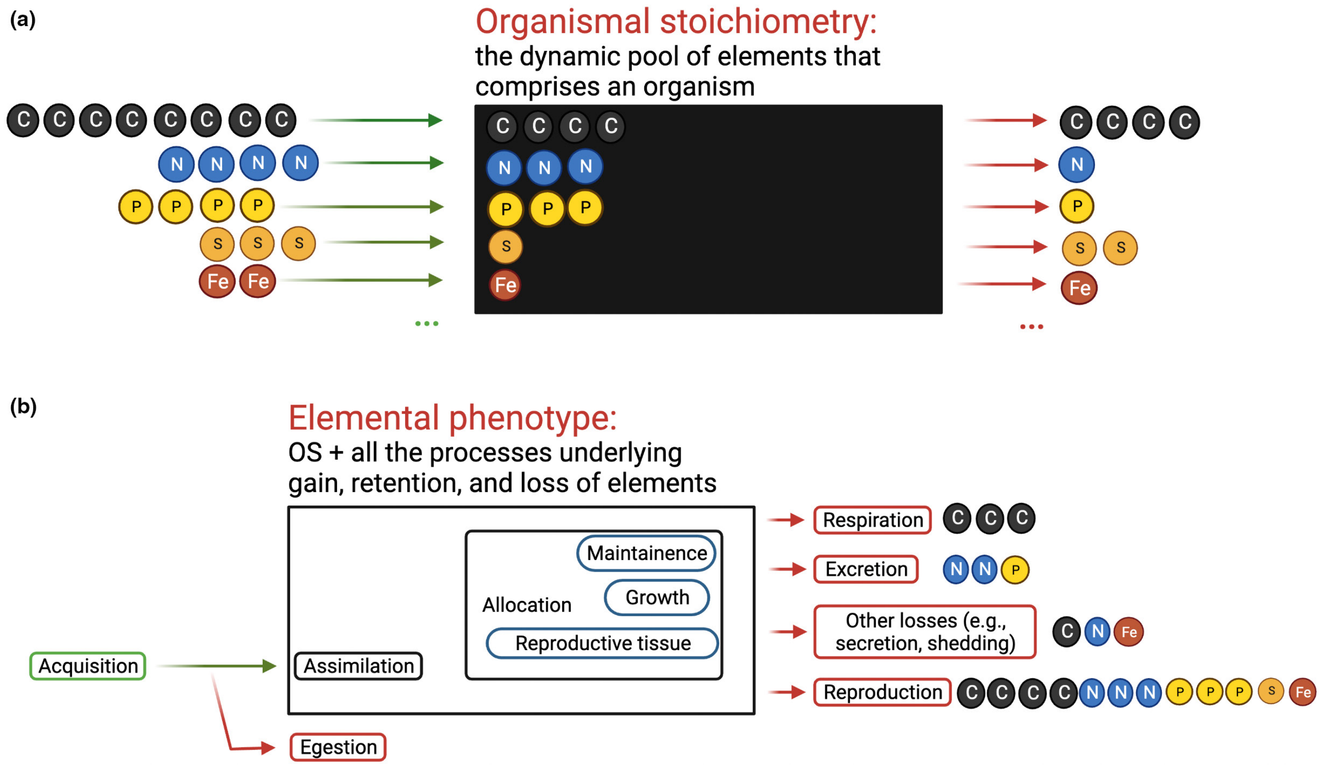

FIGURE 2 In ecological stoichiometry metazoans are viewed as pools of elements that are balanced by gains and losses (a). Five elements are depicted for heuristic purposes (carbon, nitrogen, phosphorus, sulphur and iron), but this perspective can involve any of the 20-odd biologically active elements. The sizes of the elemental symbols denote relative abundance in the three phases: gains, elements retained in the organism (i.e. organismal stoichiometry, OS), and losses, which obey the principle of mass balance. In the elemental phenotype (b), elements are gained from the environment (predominantly ingested as food in metazoans), assimilated in the body of an organism then allocated among different functions, and the used remainder is lost to the environment. Assuming similar gains and organismal stoichiometry as in (a), the elemental phenotype illuminates the stoichiometry of key subprocesses in the gain, assimilation, allocation, and loss terms. Note that the proportions of the elements can be unique to each type of allocation (e.g. allocation to growth vs. reproduction; not depicted) and loss (e.g. respiration, excretion) traits.

neglected intraspecific variation observed in these traits, Jeyasingh et al. (2014) introduced the concept of the ‘elemental phenotype’, defined as a combination of several traits: body elemental Content (and organismal stoichiometry), Acquisition, Assimilation, Allocation and Excretion of elements (abbreviated as CAAA&E). However, this definition limits the utility of using the elemental phenotype to study eco-evolutionary dynamics because it ignores key processes that are required for understanding the ecological effects of microevolutionary change. Furthermore, because the current definition does not include other loss terms beyond excretion, it is not possible to use the principle of mass balance to quantify fluxes of elements between organisms and their environments (Hessen et al., 2013; Sterner & Elser, 2002), which is required for characterising their ecological effects. For this reason, we here redefine the elemental phenotype as the amounts and ratios of all elements that constitute an organism as well as all their underlying gain and loss processes. More specifically, we expand the definition of the elemental phenotype proposed by Jeyasingh et al. (2014) to encompass a wider range of traits (Table 1 and Figure 2b) including: (1) acquisition, defined as the input rates of elements (e.g. element-specific ingestion rates), (2) assimilation, defined as the rate by which elements are assimilated through the gut and are made available for physiological processes, (3) allocation, defined as the rates or proportions by which elements are allocated to different body tissues or structures, (4) reproduction, defined as the investment of elements into reproductive tissues, some of which might be subsequently ‘lost’ from the organism, (5) losses, defined as the rate by which elements leave the body through a variety of processes, including egestion, excretion, respiration, secretion, moulting, shedding, etc. and (6) the overall quantities and ratios of elements that make up the body (i.e. organismal stoichiometry).

The inclusion of reproduction is an important update to the previous definition of the elemental phenotype. Reproductive traits such as fecundity, clutch size, offspring size, etc., are of central interest to evolutionary biologists and ecologists because of their fitness and demographic implications, respectively (Stearns & Hoekstra, 2000). They are often studied from a non-elemental perspective, using units such as mass, offspring number, offspring size, etc. (e.g. Reznick &

TABLE 1 The traits of the elemental phenotype with examples of their units of measurement and ecological responses that their variation might generate. The definitions of these traits are intentionally flexible so that they can be adapted to any study system or question. The traits are measured as rates for single elements, which can be converted to ratios, or efficiencies. For example, assimilation can be expressed either as the rate by which an element is absorbed through the gut wall, the ratio of two elements absorbed through the gut wall, or as the proportion of an ingested element that is assimilated (assimilation efficiency).

Trait	Definition	Example units of measurement	Potential ecological response
Acquisition	Rate at which an element enters an organism from the environment	μmole element; μmole of organism^{-1} time^{-1}; μmole element individual^{-1} time^{-1}	1. Diversity or biomass of prey (resources) 2. Consumer-resource interaction strength
Assimilation	Rate at which an element becomes available for cellular metabolism Or Efficiency at which ingested element is assimilated; mass of assimilated element relative to what is ingested	μmole element available for metabolism time^{-1} Dimensionless ratio or fraction	1. Nutrient recycling 2. Biomass (growth) prodution
Allocation	Rate at which an element is allocated to a specific tissue Or Mass of element allocated in one tissue vs. another	μmole element in target tissue; μmole element in hemoceal^{-1} time^{-1}; μmole element time^{-1} Dimensionless ratio or fraction	1. Nutrient recycling (e.g. allocation of an element to tissues that are frequently shed such as exoskeleton, skin, etc.) 2. Population dynamics 3. Survival (e.g. allocation of Ca from bones to eggs might increase risk of injury to parent)
Reproduction	Rate at which an element is allocated to germ cells (in the case of sexual reproduction), or secondary sexual characteristics or any body part that gives rise to new individuals. OR Ratio of elements in reproductive compartments vs. other tissues	μmole element to target cells or tissue time^{-1} Dimensionless ratio or fraction	1. Nutrient recycling (e.g. allocation of elements to secondary reproductive organs that shed such as antlers) 2. Population dynamics
Elemental losses (e.g. excretion, respiration, egestion, shedding, etc.)	Rate at which element is lost from the body OR Fraction of assimilated or ingested element that is lost	μmole element μmole organism¯1 time^{-1}; μmole element individual^{-1} time^{-1} Dimensionless ratio or fraction	1. Nutrient recycling 2. Nutrient burial (sedimentation) 3. Decomposition rates 4. Decomposer biomass or diversity
Body elemental content Organismal stoichiometry	Total quantities (pools) or concentration of elements in the body of an organism at a given moment in time Ratios of elements in the organism at a given moment in time	μmole element; μmole element μmole of organism; μmole element individual^{-1}; % element concentration in body dry or wet mass molar ratios of different elements in the body of the organism	1. Changes in how elements are stored in the ecosystem 2. Transfer of elements to other trophic levels 3. Generation of stoichiometric mismatches

Bryga, 1996; Swanson et al., 2016). Not surprisingly, reproductive traits have been widely investigated in the context of eco-evolutionary dynamics because demographic characteristics can mediate selective pressures, as well as the ecological impact of a population (e.g. ecological impact of a population is positively related to its size or density) (Farkas & Montejo-Kovacevich, 2014; Turcotte et al., 2013) (Box 3). In contrast, the elemental cost of reproduction is not as well studied, despite evidence indicating distinct elemental content and turnover rates between somatic and reproductive tissue (Cothran & Thiel, 2020). For example, bird eggs require calcium (Ca) for their shells, and the availability of Ca has been hypothesised to limit bird reproduction in Ca-poor areas (Graveland & Drent, 1997). Female birds can potentially meet this increased Ca demand by a variety of mechanisms, including increased ingestion of Ca-rich diets prior to reproduction, or re-allocating Ca from skeletal structures (Reynolds & Perrins, 2010). Male, and some female, cervids require large amounts of Ca and P for their antlers during the mating season, and they can acquire these elements by targeted consumption, or reallocation

BOX 3 The case of the Trinidadian guppy, an example of how elemental and non-elemental (classical) traits, and their ecological effects, interact with each other

The Trinidadian guppy (*Poecilia reticulata*) is a well-studied model system in which the contemporary evolution of life history traits has been hypothesised to generate eco-evolutionary dynamics and potentially, eco-evolutionary feedbacks (Reznick & Travis, 2019). Work on guppies provides an example of two core ideas of the framework presented in this paper: (i) Elemental and non-elemental (classical) traits coevolve and (ii) The ecological effects of microevolution result from the combined actions of elemental and classical traits.

Adaptation to the presence or absence of predators (carnivorous fish) selects for contemporary, heritable changes in guppy life history phenotypes. Guppies adapted to predators (high predation guppies) mature at a smaller size, and have a larger number of smaller offspring per clutch compared to guppies not adapted to predators (low predation guppies) (Reznick et al., 2001; Reznick & Bryga, 1996; Reznick & Endler, 1982). Common gardening experiments have shown that wild-caught low and high predation guppies have large, contrasting effects on a wide range of ecological processes including population dynamics, community composition, and ecosystem processes (Bassar et al., 2015; Bassar, Marshall, et al., 2010; El-Sabaawi et al., 2015; Palkovacs et al., 2009).

Adaptation to predation also results in heritable variation in elemental traits of guppies including organismal stoichiometry and excretion (Dalton et al., 2017), as well as gut characteristics, which influence assimilation efficiency (Sullam et al., 2015). High predation guppies have higher per-capita N and P excretion rates than low predation guppies (Bassar, López-Sepulcre, et al., 2010). However, because of their smaller average body size and smaller population densities, high predation guppy populations overall have a smaller contribution to nutrient recycling than low predation guppies (Bassar, Marshall, et al., 2010; El-Sabaawi et al., 2015). The phenotypic effect of guppy evolution on nutrient recycling therefore results from the interactions of classical traits (body size and life history phenotype) and elemental traits (excretion), and is influenced and mediated by population characteristics (density and size structure). Outstanding questions in this system include characterising the relative importance of genetic and plastic variation in nutrient recycling in natural guppy populations, and characterising genetic and plastic variation in other elemental traits such as egestion, respiration and assimilation.

from the skeleton (Dryden, 2016). Considering reproduction from an elemental perspective therefore allows us to connect variation in reproductive traits to ecological consequences beyond demography. It should be noted that, unlike allocation into somatic tissues, allocation of elemental resources to reproductive tissue are mostly 'lost' from the organism as gametes, eggs, offspring or antlers. Reproduction, therefore, represents a special case among the elemental phenotype components because it involves both allocation and loss processes that vary over the lifespan of the organism.

Another significant update to the elemental phenotype definition is the inclusion of other elemental losses beyond excretion. Excretion is typically defined as the release of dissolved nutrients such as ammonium, phosphate, dissolved organic carbon (Atkinson et al., 2017; Parr et al., 2019), etc., which are used by primary producers and microbes. It contributes to nutrient recycling, which is especially important for maintaining primary production in ecosystems where the environmental supply of nutrients is limiting (Allgeier et al., 2017; Atkinson et al., 2017; Sterner, 1986; Vanni, 2002). It has received much attention both within ecological stoichiometry (Sterner & Elser, 2002) and in studies of eco-evolutionary dynamics (El-Sabaawi, 2017). However, elemental losses can also occur via a variety of other mechanisms, such as egestion, moulting, and secretion, that may affect other organisms or ecosystem processes as we will explore later. The explicit incorporation of all potential elemental loss terms also allows us to use mass balance to quantify elemental fluxes, and greatly enhances our ability to make connections between microevolutionary changes and their ecological effects.

One of the fundamental features of the elemental phenotype is that body elemental content and organismal stoichiometry represent the net outcome of all of the other traits of the elemental phenotype. As a result, any plastic or genetic change in these traits requires a change in one or more of the other traits of the elemental phenotype. However, the absence of variation in body elemental content or organismal stoichiometry does not exclude variation in other traits of the elemental phenotype. For example, organisms can allocate elements from one tissue to the other without changing their overall elemental content (Leal, Best, et al., 2017) (Box 2). Traits of the elemental phenotype can also covary such that the effect of a change in one trait on organismal stoichiometry may be partly, or entirely, compensated by a change in another trait. For example, if organisms over-consume a non-limiting element (e.g. C), in their attempt to meet the demand for a limiting nutrient (e.g. P), they can deploy a range of strategies including increased storage of the non-limiting element (increasing organismal C:P), or its increased release (increasing C respiration rates without changing organismal C:P) (Darchambeau et al., 2003; Hessen & Anderson, 2008). This example is based on studies examining plastic covariation in elemental traits, but genetic correlations among nutritional traits have also been reported (Marchesi et al., 2021). Hence genetic correlations among elemental traits are likely, although we currently lack the data to investigate them in metazoans (but see Leal, Best, et al., 2017; Sherman et al., 2017). Nonetheless, the evolutionary change in the elemental phenotype will likely involve more than one trait, emphasising the need for a multi-trait perspective.

How does the elemental phenotype relate to other (classical) traits?

Demonstrating the utility of the elemental phenotype for the study of eco-evolutionary dynamics requires us to understand how elemental phenotypes relate to the diverse array of traits that have been studied in evolutionary biology. To facilitate this comparison, Jeyasingh et al. (2014) make the conceptual distinction between the elemental phenotype, and the **classical phenotype**, with the latter encompassing any trait that is not measured in terms of elements, including morphology, growth rate, life history, behaviour, etc. Thus far, the majority of studies on eco-evolutionary dynamics focus on these classical traits (as portrayed in the upper portion of Figure 1). The SEED framework assumes that elemental and classical phenotypes are inextricably linked (double arrow in Figure 1). Any change in the classical phenotype has to be accommodated by the elemental phenotype and will potentially be constrained by the availability of elements in the environment and by the limits of the elemental phenotype (i.e. limitations in one or more of the physiological rates in Table 1). On the other hand, all physiological rates that constitute the elemental phenotype are realised by classical traits, and therefore any phenotypic or adaptive changes in these rates will need to be mediated by traits of the classical phenotype.

Experimental and observational studies suggest that genetic variation in classical traits is associated with genetic variation in one or more components of the elemental phenotype. The links between genetic variation in growth rate or bone investment and the elemental phenotype have been well-studied (Box 2). Although less widely studied, existing evidence also suggests that selection on reproductive traits alters a range of elemental traits. Selection on life history phenotypes in the Trinidadian guppy (*Poecilia reticulata*) has been shown to alter several elemental traits including excretion and organismal stoichiometry (Dalton et al., 2017) (Box 3). Investment in sexually selected morphological traits can also affect the elemental phenotype as has been shown in amphipods (*Hyalella azeteca*; Goos et al. (2017)).

An important classical trait whose influence on elemental traits is likely important, but remains to be resolved, is body size. A wide range of classical traits have been shown to scale with body size, although there are more interspecific than intraspecific studies (Sibly et al., 2012). There is also evidence for allometric scaling of N and P excretion across and within species (Allgeier et al., 2015; El-Sabaawi et al., 2015; Guernon et al., 2019; Vanni & McIntyre, 2016). However, intraspecific body size dependence of other elemental traits is in general poorly documented, and is likely to be influenced by or confounded with ontogeny (Maino & Kearney, 2015) or developmental stage (Capps et al., 2015; Knapp et al., 2021). Importantly, existing evidence suggests that elemental traits (e.g. rates of elemental acquisition, assimilation) might not scale with the same allometric exponents (Maino & Kearney, 2015), and, it is not clear how some elemental traits such as egestion correlate with body size within species (May & El-Sabaawi, 2022). Given that body size can evolve in response to a wide range of selective factors, including anthropogenic activity (e.g. Hunt & Roy, 2006; Teplitsky & Millien, 2014), it will be important to further understand its influence on the elemental phenotype.

The above examples illustrate how selection on classical traits can indirectly lead to selection on elemental traits. However, environmental variation can also cause selection on the elemental phenotype in more direct ways. For example, environmental variation in elemental supply can cause **stoichiometric mismatches** between organisms and their diets, selecting for microevolutionary changes in acquisition, organismal stoichiometry, assimilation or excretion (Declerck et al., 2015; Frisch et al., 2014; Lemmen et al., 2023; Tobler et al., 2016). Such evolutionary responses in the elemental phenotype will likely alter the classical phenotype because the fluxes of elements that constitute the elemental phenotype (Table 1) are realised and controlled by combinations of behavioural, morphological, physiological and biochemical ‘classical’ traits. For example, assimilation is controlled by a variety of factors including gut enzyme activity, gut microbes and gut morphological characteristics (Karasov & Douglas, 2013), while the ability to sense and taste nutrients is controlled by a set of anatomical and physiological features (Demi et al., 2021). Furthermore, variation in diet quality can itself select for differential investment in life history traits such as fecundity (Swanson et al., 2016). The mechanisms and pathways by which elemental and classical phenotypes interact are therefore diverse and ubiquitous, and characterising how they influence and constrain each other will be key for elucidating eco-evolutionary dynamics.

What are the ecological effects of intraspecific variation in the elemental phenotype?

The effects of phenotypic variability on ecological processes are increasingly addressed by making the distinction between response and effect traits (Raffard et al., 2017). In this context, the emphasis of the SEED framework on the elemental phenotype is very relevant since each trait of the elemental phenotype can potentially respond to selection, and can also generate an ecological effect (Table 1) (Leal, Seehausen, & Matthews, 2017). The successful integration between ecological stoichiometry and eco-evolutionary dynamics will therefore require knowledge of how traits of the elemental phenotype evolve in response to environmental change, and how such changes will affect ecological processes. Furthermore, variation in the elemental phenotype can have a wide range of ecological effects on population dynamics, species interactions, community composition and ecosystem processes (Table 1). To the best of our knowledge, most of these links have not been previously considered in the eco-evolutionary dynamics literature, despite evidence suggesting that both genetic and plastic variation in these traits has ecological consequences.

Of the traits in Table 1, the ecological effects arising from microevolutionary changes in excretion are the most extensively studied (El-Sabaawi et al., 2015; Guernon et al., 2019; Moody et al., 2018; Tobler et al., 2016). Variation in element-specific excretion and egestion affect the relative rates through which inorganic nutrients and organic substrate are recycled to primary producers and microbes, and can therefore alter their elemental composition, biomass or production rates (Atkinson et al., 2017; Halvorson et al., 2017; Liess et al., 2015; Roy Chowdhury & Jeyasingh, 2016; Vanni, 2002). In response to dietary P limitation, the elemental phenotype of *Daphnia* evolves such that they retain more of the dietary P in their bodies, and reduce the recycling of dissolved P (Frisch et al., 2014; Roy Chowdhury & Jeyasingh, 2016). Algae grown in the same microcosms as these *Daphnia* have higher C:P and N:P ratios, demonstrating how elemental traits operate as both response and effect traits, and suggesting a potential eco-evolutionary feedback on *Daphnia* via the elemental composition of their diet (Box 4).

However, even in studies characterising the effects of the elemental phenotype on nutrient recycling, much remains unknown about broader ecological impacts. For example, evolutionary changes in the organismal stoichiometry of primary consumers such as the ones shown by Roy Chowdhury and Jeyasingh (2016) may also affect energy transfer efficiency to higher trophic levels, as well as the condition of secondary consumers (Boersma et al., 2008; Dickman et al., 2008; Malzahn et al., 2007; Schoo et al., 2012). Furthermore, not much is known about other loss processes beyond excretion such as egestion or moulting. In response to dietary P limitation *Daphnia* has been shown to decrease the allocation of P to the carapace, resulting in low P concentrations in the moults (He & Wang, 2020). *Daphnia* shed their carapace several times over their lifespan, and moults serve as a food source for invertebrate detritivores and microbial decomposers, or can be buried in the sediments (Hessen & Alstad Rukke, 2000; Mira, 2000). Variations in the allocation of elements in a process such as moulting can therefore influence community composition, the productivity of specific groups of decomposers, decomposition rates of the moults and nutrient burial rates, but the capacity of microevolution to influence these processes has not been investigated. He and Wang (2020) also showed that P-limited *Daphnia* decreased the allocation of P to their eggs, suggesting a potential effect on population dynamics and demography.

Intraspecific variation in the elemental phenotype of consumers can potentially affect the biomass and community structure of their prey. For example, large stoichiometric mismatches can cause consumers to increase their overall consumption rates (i.e. compensatory feeding) (Boersma & Plath, 2001; Fink & Von Elert, 2006; Flores et al., 2014), which can increase interaction strength between consumers and their resources (Declerck et al., 2015), potentially destabilising communities (Ratzke et al., 2020). Alternatively, stoichiometric mismatches can also cause organisms to specifically target prey rich in the limiting element (i.e. selective feeding), which can potentially alter the composition and diversity of prey communities (Fuchs & Franks, 2010; Meunier et al., 2016). Modelling studies have demonstrated that microevolution of selective feeding of zooplankton can generate eco-evolutionary dynamics in phytoplankton–zooplankton interactions (Branco et al., 2018).

The examples above demonstrate that the elemental phenotype concept greatly expands our ability to study the effects of microevolution on ecological processes, but clearly much more research is needed in this area. Furthermore, an important consequence of the SEED framework is that the overall effects of microevolution on ecological processes will emerge from the interactions of the ecological impacts of both classical and elemental phenotypes, as illustrated by the Trinidadian guppy example (Box 3). For the sake of conciseness, we have exclusively focused on the direct (i.e. per-capita) effects

BOX 4 Progress and limitations of stoichiometric studies on *Daphnia* in the context of eco-evolutionary dynamics

The water flea *Daphnia* is one of the most frequently used model organisms in both ecological stoichiometry and eco-evolutionary dynamics (Miner et al., 2012). The extensive amount of work done on this model system makes it ideal for illustrating some of the cornerstones and benefits of the SEED framework.

Many of the genetically explicit studies performed on the stoichiometry of *Daphnia* have been motivated by two general types of questions: (i) is there genetic variation in the organismal stoichiometry (e.g. C:P) of a population? If so, what traits underlie such variation? and (ii) Does variation in the elemental ratios of the diet (or stoichiometric mismatches) differentially impact the fitness of genotypes? (e.g. Elser et al., 2000; Jeyasingh & Weider, 2005; Seidendorf et al., 2007).

Frisch et al. (2014) utilised methods in resurrection ecology and palaeogenetics to study a population of *Daphnia pulicaria* inhabiting a Minnesota lake that became eutrophic because of increasing P concentrations in the environment over the last century. While genotypes established by hatching resting eggs from sediments of varying ages (i.e. before, during eutrophication) revealed no differences in organismal stoichiometry (C:P), they differed in P retention, indicating more efficient use of body P by clones dating from before eutrophication, when environmental supply of P was low. Roy Chowdhury and Jeyasingh (2016) found that such differences in P use physiology impacted the growth rate and C:P stoichiometry of cohabiting algae in microcosms, indicating the potential for an eco-evolutionary feedback mediated by diet quality. These studies clearly demonstrate the need to address the elemental phenotype beyond organismal stoichiometry, and show that a singular focus on organismal stoichiometry alone impedes a deeper understanding of how genetic adaptation affects the organism and how it may alter the impact of a population on important ecosystem functions.

However, although more extensive than others, these studies have also ignored other key traits of the elemental phenotype (e.g. ingestion rates, reproductive allocation, moulting losses, egestion, C respiration and dissolved organic carbon secretion). As highlighted by the SEED framework (Figure 1), a more complete assessment of the elemental phenotype and the link between its traits and specific ecosystem functions will allow for a more profound understanding of the causes and consequences of adaptation. For example, variation among genotypes in P losses due to differences in egestion or moulting (He & Wang, 2020), could derive ecological changes in element sedimentation, burial, or remineralisation, and could have a very different ecological effect than differences in P excretion and its associated impacts on algal growth and stoichiometry (Roy Chowdhury & Jeyasingh, 2016). These examples show that even in our most well-studied taxa, more work is needed to refine our understanding of the elemental phenotype.

The SEED framework also proposes that the understanding and prediction of microevolutionary responses requires consideration of the heritability of and genetic covariance among traits. However, as discussed above, existing data are very limited and biased towards one or a few traits of the elemental phenotype (e.g. organismal stoichiometry). In their study of *Daphnia pulicaria* genotypes established from resting eggs, Sherman et al. (2017) reported a significant association between P content and P assimilation, but no significant relationships between P content and the other traits. However, several significant positive associations among the three other traits (than P content) were observed (see Figure S1 in Sherman et al., 2017). Thus, a rapid genetic shift in the value of one of the traits of the elemental phenotype will most likely cause correlated shifts in other traits with potentially unique ecological impacts.

The extent to which genetic variation in the traits of the elemental phenotype is visible to selection can be altered by the environment. For example, Sherman et al. (2017) observed the greatest variance in P acquisition among genotypes in P-limited conditions, while the greatest variation was found in P retention under benign (i.e. non-limiting) conditions. Thus, populations of *Daphnia* inhabiting lakes with contrasting P supply can experience contrasting selection on different elemental traits, leading to distinct ecological effects, with one impacting predation/grazing rates with the other impacting nutrient recycling (Sterner, 1986). These studies suggest that an approach that addresses the genetic variance within and covariances among multiple elemental phenotype traits has much to contribute to understanding the mechanisms that drive eco-evolutionary dynamics.

of elemental phenotype, but this framework can be extended to include indirect effects such as those mediated by population density (Hendry, 2019), especially as more information about the interactions of elemental phenotype and population dynamics becomes available (Box 3).

FUTURE RESEARCH UTILISING AND HONING THE SEED FRAMEWORK

The framework we have proposed is a significant advancement in the application of ecological stoichiometry to the study of eco-evolutionary dynamics. By expanding the definition of the elemental phenotype, we make it more useful for assessing the ecological effects of microevolution. By distinguishing between elemental and classical traits, and demonstrating their mutual interdependence, we have a road map for integrating ecological stoichiometry with a wide range of eco-evolutionary dynamics studies. By demonstrating that variation in the elemental phenotype can generate wide-ranging ecological effects, we significantly expand our understanding of the ecological consequences of microevolutionary change. The first, and probably most immediate, advantage of this framework is that it can guide us in formulating more specific hypotheses about potentially important but hitherto underexplored mechanisms underlying eco-evolutionary dynamics, which can then be studied theoretically and tested empirically. The second is that it highlights the kind of data that are needed to make further progress in this area of research.

Using the SEED framework to generate hypotheses

Based on this framework, we can hypothesise that microevolutionary change in the elemental phenotype in response to increased demands for a specific element will potentially involve four basic responses: increased ingestion, increased assimilation efficiency, reduced loss rates and/or a change in allocation. These responses may be accomplished in different ways, can occur independently or in combination, and each with potentially unique ecological effects. For example, we mentioned previously that an organism can meet the demand for an element by increasing acquisition through compensatory feeding or selective feeding. Each of these responses will be associated with unique changes in the classical phenotype of the organism and will generate different ecological effects. Adaptation through compensatory feeding will involve behavioural and morphological changes that result in increased per-capita acquisition rates of prey, potentially resulting in a stronger top-down control of the lower trophic level. In contrast, adaptation via selective feeding will likely involve different behavioural and morphological traits (e.g. sensory abilities and taste detection) and is expected to have a stronger impact on the composition and diversity, rather than on the overall biomass of prey communities.

Adaptive increases in assimilation efficiency will be facilitated by changes in gut morphology, digestive enzymes or microbiome–host interactions, and will result in a depletion of the focal element in egested material, potentially affecting its nutritional quality for detritivores. Reduced loss rates may involve reduced excretion rates, or a reduction of the concentration of the element in other waste products (e.g. secretion, moults etc.), which will affect relative recycling rates of element, the organismal stoichiometry of organisms that use these recycled elements, trophic transfer efficiency or the condition of consumers. Loss rates may also be reduced by decreasing the allocation of the element to offspring, which might affect population dynamics and demography.

In the SEED framework selection on the elemental phenotype can occur either via environmental variation (for example, stoichiometric mismatches), or indirectly from the elemental demands of classical traits. These selection pathways have been mostly studied independently in the literature (but see Lemmen et al., 2023). Putting them in the same framework allows us to develop hypotheses about how the same elemental trait can respond to different selective factors, and how responses to the same selective factor can vary depending on context in which selection is occurring. In the case where organisms need to invest more of a specific element in a classic trait (e.g. growth rate or defensive morphology, Box 2), we can hypothesise that an increase in the somatic content of that element, and therefore a change in organismal stoichiometry, is expected when the availability of the element is non-limiting. In cases where the availability of the element is limited, organisms might meet these demands by using the element differently, such as through the reallocation from other tissues, or by using the element more efficiently. Such a perspective might reconcile differences observed among studies or across populations. For example, it would be interesting to test whether environmental P availability explains why body P increases with growth rate in some, but not all, populations of *Daphnia*, or why body P increases with armour investment in some, but not all populations in the threespine stickleback (Box 2).

The hypotheses and scenarios in the previous paragraph deal with variation in the elemental phenotype that is caused by demands of classical traits. In contrast, when selection arises from a stoichiometric mismatch, organisms are likely to evolve strategies that allow more efficient use of the limiting element. In the latter case, the concentration of that element in the body will either remain constant (Lemmen et al., 2023), or be reduced through elemental sparing (Merchant & Helmann, 2012; Turner et al., 2017) or elemental substitution (Price & Morel, 1990; Van Mooy et al., 2009). More likely than in the case of classic trait evolution, evolutionary responses to stoichiometric mismatch will involve strategies to dispose of excess elements. For example, if herbivores increase their overall feeding rates in response to dietary P limitation, and as a result over-consume dietary C, then they will require strategies to deal with this excess C such as increasing its loss rates or allocation to lipid storage (Darchambeau et al., 2003; Hessen & Anderson, 2008; Warbrick-Smith et al., 2006).

Using the SEED framework to guide future research

One of the benefits of this framework is that it allows us to identify the kinds of data that we will need to make substantial progress in understanding the evolution of elemental traits, as well as their ecological consequences. Current gaps in our understanding include the characterisation and quantification of: (i) the traits of the elemental phenotype, including sources of genetic and plastic variation, how the traits covary with each other, as well as how they covary with classic traits, and (ii) the potential range of effects of this variation on ecological processes. Below we suggest how we can use a wide range of tools and approaches to achieve these objectives.

Despite some recent progress in characterising the causes of intraspecific variation in elemental traits (Jeyasingh et al., 2014;Leal, Seehausen, & Matthews, 2017; Lemmen et al., 2019), much remains unknown about the genetic variation in the elemental phenotype or how its traits covary (Box 4). Common garden experiments have been used to assess how some elemental traits vary among genotypes, and how genotypes vary in response to the environment (i.e. plastic variation) (Leal, Seehausen, & Matthews, 2017; Lemmen et al., 2019). These experiments are the ideal approach for characterisation and quantification of trait variation. However, in order to move forward in the use of ecological stoichiometry to understand eco-evolutionary dynamics, key parameters (e.g. heritability of traits, genetic covariation among traits, etc.) will need to be estimated from empirical studies that quantify multiple traits of the elemental phenotype across generations with a known pedigree. The resulting genetic variance–covariance matrices (i.e. the G-matrix) will be a powerful tool for not only capturing the genetic linkages and potential trade-offs among traits, but also for predicting microevolutionary responses of populations to specific selection agents, especially at short, ecological timescales (Arnold et al., 2008). Existing inbred populations of metazoans (Ankeny & Leonelli, 2011), created to understand the evolution of various quantitative (classical) traits, are particularly suitable for such experiments. Quantifying elemental phenotype traits in such populations will expand our understanding of the relationship between classical and elemental traits, while also helping to isolate the genetic basis of quantitative elemental traits (Lynch & Walsh, 1998).

Experimental evolution is another powerful and complementary tool to explore how microevolutionary adaptation to novel selection pressures is associated with genetic changes in the elemental phenotype and its interactions with the classical phenotype, while also providing a way to test predictions based on the G-matrix (Arnold et al., 2008). Several model metazoans (e.g. the water flea *Daphnia*, the rotifer *Brachionus*, the fruit fly *Drosophila*, the nematode *Caenorhabditis*, the zebrafish *Danio*) are particularly amenable for such experiments because of their short generation times, small body sizes and ease of culture. Exposing replicate populations to specific selection pressures, followed by common garden experiments, will allow us to study evolutionary modifications in the elemental and classical phenotypes simultaneously. Such experiments will cast light on which traits respond to which type of selection factor and, importantly, how classical traits and elemental traits covary in their responses. These experiments can test how evolutionary responses to selection on classical traits (e.g. body size, growth rate, predator avoidance behaviour, etc.) induce changes in the elemental phenotype and the impact of elemental availability on evolutionary trajectories. Alternatively, they can test how variation in elemental supply and stoichiometric mismatches alter both elemental and classic phenotypes. Although initial attempts with experimental evolution in a stoichiometric context have yielded encouraging results, they have focused on specific hypotheses and have so far involved an incomplete characterisation of the elemental phenotype (Declerck et al., 2015; Lemmen et al., 2023).

While it is clear we need more carefully designed experiments that allow us to evaluate evolutionary responses in the elemental phenotype, an understanding of eco-evolutionary dynamics will not be complete until the ecological effects of microevolution are catalogued and understood (Figure 1). As we have demonstrated in this paper, it is likely that heritable intraspecific variation in the traits of the elemental phenotype will have a wide range of ecological effects, but aside from nutrient recycling, few have been investigated. Common gardening experiments are an experimental approach that is frequently used to characterise the ecosystem consequences of microevolutionary change in a focal species (Matthews et al., 2011). In contrast to common garden experiments where the emphasis is on the organism, common gardening experiments focus on the response of the ecosystem. In these experiments, populations of the focal organism that are composed of genotypes extracted from laboratory, or natural populations that have genetically diverged from a common ancestral population under different selection regimes, are placed in replicated mesocosms that contain a typical food web under natural conditions (e.g. Bassar, Marshall, et al., 2010; Harmon et al., 2009, etc.). The focal populations are allowed to develop and interact with the co-existing communities and mesocosm environments while a range of ecological processes is monitored. Consequently, ecological differences between the treatments can then be unambiguously attributed to differences in the evolutionary history of the focal populations. We believe that common gardening experiments can provide key insights into how heritable intraspecific variation in the elemental phenotype impacts ecosystem processes, especially if they use genotypes from the mapping populations or experimental evolution trials described above.

Although studying model organisms in controlled conditions will be important for generating new insights into the integration of ecological stoichiometry and eco-evolutionary dynamics, inferences arising from a few taxa in abstracted conditions have limitations (Farris, 2020). It is important to characterise how eco-evolutionary dynamics occur in the 'real world' especially if we are to understand the full effect of human activities on natural ecosystems (Hendry, 2019). However, working with natural populations is challenging because of their complexity and the difficulty of teasing apart causal factors. We need innovative approaches that can glean relevant information from natural populations, such as those that use genomics and bioinformatics (Rudman et al., 2018). Another approach is to work with clones or genotypes extracted from natural or anthropogenic gradients. Examples include, but are not limited to, the use of **resurrection ecology experiments** (Frisch et al., 2014; Weider et al., 2018) (Box 4) or **space-for-time substitution** studies (e.g. Wogan & Wang, 2018 but see Damgaard, 2019).

While new studies are emerging with the genotypic replication required to reliably observe selection on traits and trait correlations in natural conditions (e.g. Rudman et al., 2022), the use of common gardening experiments to isolate and quantify the environmental consequences of such selection is challenging. One productive way to explore eco-evolutionary dynamics using the SEED framework will be for ecologists to collaborate with geneticists already studying mapping populations for various reasons such as those interested in morphological classical traits (e.g. colouration; Hubbard et al., 2015), or traits related to nutrition, which is a major focus in agricultural or aquaculture systems (e.g. meat quality; Li et al., 2022). Note that species on which substantial genetic information exists typically lack comparatively substantial ecological information (e.g. *Drosophila*), while species with substantial ecological information lack concomitant genetic understanding (e.g. *Daphnia*). Future studies will need to bridge this gap, with integrative approaches blending population genomic data from wild populations with quantitative genomic data from laboratory populations (e.g. Stinchcombe & Hoekstra, 2008).

CONCLUSIONS

This SEED framework demonstrates that an approach rooted in ecological stoichiometry, and based on the elemental phenotype, has great potential to expand our understanding of eco-evolutionary dynamics. However, it is important to note that in addition to the current interest in characterising eco-evolutionary dynamics, there is a much wider movement in ecology to characterise the ecological effects of any source of intraspecific variation, whether plastic or genetic (Bolnick et al., 2011; Miner et al., 2005; Violle et al., 2012). We envisage that this framework will be useful for understanding the ecological effects of intraspecific trait variation in general, and will apply to a broader range of research questions beyond eco-evolutionary dynamics.

In developing this framework we have advocated for researchers to expand their focus beyond organismal stoichiometry, and to study all components of the elemental phenotype. In order to do so we will need to quantify the genetic variation in, and genetic covariance between, elemental traits at an intraspecific level, and then assess their ecological effects. The spirit of this framework is to foster collaborations among different kinds of biologists (e.g. physiologists, evolutionary biologists, community ecologists), and across disciplinary divides (e.g. evolutionary biology, aquaculture, agriculture and ecosystem science) to rigorously study the elemental phenotype, the way it evolves, how it interacts with other traits, as well as its ecological effects. In addition to such an academic motivation, a focus on elements to capture the interactions between ecology and evolution has another pressing motivation: forecasting the consequences of rapid changes to biogeochemical cycles in the Anthropocene.

AUTHOR CONTRIBUTIONS

Rana W. El-Sabaawi, Kimberley D. Lemmen, Punidan D. Jeyasingh and Steven A. J. Declerck contributed equally to the development of ideas in this manuscript and made substantial contributions to writing. Rana W. El-Sabaawi led and coordinated the effort.

ACKNOWLEDGEMENTS

We thank P Frost and the co-organisers of the 2015 Conference for Biological Stoichiometry who facilitated a workshop that started our collaboration, and ultimately provided the nucleus for this manuscript. D Durston and J Goos contributed to early discussions of the ideas presented in the paper. K Lemmen acknowledges support by grant no. 823.01.011 of the Earth and Life Sciences Division (ALW) of the Netherlands Organization for Scientific Research (NWO). Comments from four anonymous reviewers, E May, R Bassar, J Travis, A Hendry, and members of A Hendry's lab group at McGill University greatly improved this paper.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14285.

DATA AVAILABILITY STATEMENT

There is no data associated with this manuscript.

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How to cite this article: El-Sabaawi, R.W., Lemmen, K.D., Jeyasingh, P.D. & Declerck, S.A.J. (2023) SEED: A framework for integrating ecological stoichiometry and eco-evolutionary dynamics. *Ecology Letters*, 26(Suppl. 1), S109–S126. Available from: https://doi.org/10.1111/ele.14285