Trends in Ecology & Evolution

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Opinion

The Ecology and Evolution of Stoichiometric Phenotypes

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Ecological stoichiometry has generated new insights into how the balance of elements affects ecological interactions and ecosystem processes, but little is known about the ecological and evolutionary dynamics of stoichiometric traits. Understanding the origins and drivers of stoichiometric trait variation between and within species will improve our understanding about the ecological responses of communities to environmental change and the ecosystem effects of organisms. In addition, studying the plasticity, heritability, and genetic basis of stoichiometric traits might improve predictions about how organisms adapt to changing environmental conditions, and help to identify interactions and feedbacks between phenotypic evolution and ecosystem processes.

Trends

There is growing evidence for intraspecific variation in stoichiometric traits of animals, for a genetic basis of this variation, and for rapid evolution of these traits. In light of such observations, ecological stoichiometry has the potential to address evolutionary processes and identify mechanisms by which environmental heterogeneity drives the origins of biological diversity.

We suggest that addressing the evolution of stoichiometric reaction-norms could help in understanding when, and to what extent, variability in elemental phenotype in natural populations is due to plasticity of stoichiometric traits or genetic variation. We also propose strengthening the link between stoichiometric trait variability and fitness by building on nutritional geometry theory and function-valued methods. In addition, and because stoichiometric traits may not only respond to environmental variation but also influence ecosystem dynamics, studying the elemental phenotypes can contribute to our understanding of the nature of eco-evolutionary feedbacks.

Ecological Stoichiometry: A Functional Trait Perspective

There is a growing interest in understanding intraspecific functional trait variability so as to make better predictions about population dynamics, species interactions, and ecosystem functioning [1,2]. Although **stoichiometric traits** (see Glossary) are useful for connecting organisms to ecosystem processes [3–5], little is known about how intraspecific variation in these traits mediates ecological and evolutionary dynamics. Stoichiometric traits are an integral part of ecological stoichiometry (ES) theory, which focuses on the balance of multiple elements in ecological interactions and ecosystem processes [6]. Stoichiometric traits can vary among species [5–7], populations, and individuals of the same species [8–10], can influence how organisms affect energy flow and nutrient cycling in ecosystems (i.e., as functional effect traits) [6,11], and can mediate evolutionary responses to environmental variation and change (i.e., as functional response traits) [4,5]. Recent studies have also begun to document the occurrence [8,12,13] and ecological consequences [3,14] of rapid evolution of stoichiometric traits. Overall, such stoichiometric traits are a useful focal point for studying both interactions and feedbacks between phenotypic evolution and ecosystem processes.

ES theory posits that performance (e.g., growth rate) is partly determined by the match between the stoichiometry of resources and organism elemental phenotype (EP), which comprises multiple stoichiometric traits. However, what is the relationship between stoichiometric traits and fitness variation, and, more generally, how do organisms adapt to elemental imbalances in their diet or their resource uptake? Increasing nutrient supply can impact on the evolution of life-history traits by changing allocation trade-offs, particularly those associated with nutrient imbalances that negatively influence performance [15,16]. For example, we might expect either directional selection on stoichiometric traits to reduce elemental imbalances between a population and its resources [15,17], or fluctuating selection to maintain stoichiometric trait variation within populations when there is variation in resource quality through time. It is also possible that agents of selection on stoichiometric traits vary in their importance over the lifetime of organisms [15]. Juveniles and adults often vary in their **nutritional** needs because the nutritional demands for rapid growth (e.g., high dietary phosphorus, P) early in life might differ from those for

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reproduction later in life (e.g., dietary lipids). Overall, the fitness consequences of maintaining (or not maintaining) stoichiometric **homeostasis** remain poorly understood.

We discuss here how stoichiometric traits can be an important intersection between ecological interactions, evolutionary dynamics, and ecosystem processes. To illustrate this, we review the primary drivers of intraspecific variation in the EP and the evidence that stoichiometric traits can evolve, potentially via multiple agents of natural selection. We advocate a better understanding of how stoichiometric trait variability [e.g., %P, %nitrogen (N), and the N:P ratio] relates to fitness variation, and suggest that studying the evolution of stoichiometric reaction norms might help to disentangle the role of **phenotypic plasticity** and genetic variation in determining the EP. We highlight how approaches from nutritional geometry (e.g., [18,19]) and function-valued methods (e.g., [20,21]) can help strengthening the link between fitness variation and elemental imbalances between consumers and their resources. We end by discussing how stoichiometric traits can improve our understanding of eco-evolutionary dynamics and feedbacks between ecology and evolution.

EP Variability: Causes and Consequences

The EP is made up of multiple stoichiometric traits associated with the composition, acquisition, assimilation, allocation, and excretion of key elements of an individual organism [22] (Box 1). Autotrophs are more stoichiometrically variable than heterotrophs owing to their rapid response to nutrient availability and ability to store nutrients [6]. For heterotrophs, there is growing evidence of variation in homeostasis among species, among individuals within populations [4,9], and within individuals throughout their ontogeny [10,17].

Variation in EP between and within populations is often attributed either to spatial heterogeneity in resource quantity and quality [9,23], or to non-spatial sources of intraspecific variation in EP, including body size, diet, morphology, and sex [7,10,24]. In addition, variation in EP among individuals has been attributed to variation in the cellular concentration (e.g., by weight) of nucleic acids, such as RNA and DNA, particularly when there is variation in ploidy or in elemental allocation associated with growth [12,25–27]. Such genomic variation at the cellular level can affect organismal stoichiometry, and thereby shape the nutritional quality of organisms (either as prey or detritus), and modify energy fluxes through the food web [11].

Glossary

Growth rate hypothesis (GRH): predicts that rapid growth often has comparatively higher P demand to support increased allocation to P-rich ribosomal RNA to meet the demands of protein synthesis.

Heritability: variation of a trait that is explained by genetic differences. It can be calculated as the ratio of genetic to total variance (including environmental).

Homeostasis: physiological mechanisms that maintain the internal environment of an organism in a relatively constant state. In ecological stoichiometry, homeostatic processes reduce variation in the elemental composition of an organism despite changes in resource stoichiometry.

Nutrition: interaction of nutrients available in food with physiological functions of an organism (metabolism, growth, reproduction, health, and disease) that affect resource ingestion, assimilation, and excretion.

Phenotypic plasticity: a single genotype expresses multiple phenotypes in response to environmental cues, with each phenotype matching a different selective optimum. The range of phenotypes produced by a particular genotype exposed to different environmental conditions can be assessed using reaction norms.

Stoichiometric traits: individual measures of elemental composition, assimilation, allocation, or excretion that are usually defined by their elemental content or ratios between elements.

Box 1. Agents and Targets of Selection

Phenotypic traits are defined as quantifiable measurements of an organism and can evolve when there is covariance between phenotype and fitness. The stoichiometric traits that define the elemental phenotype (EP) of an organism can both evolve in response to environmental selection and modify the environmental conditions that might determine selection pressures.

The EP is made up of several traits, such as organismal elemental composition (e.g., % of dry mass or the ratio of elements), which determines how acquired nutrients are used and recycled. These stoichiometric traits might affect the survival, growth, and reproduction of individuals, and consequently be targets of selection. Potential selection agents such as nutrient availability (i.e., food quantity and/or quality) and predation pressure are likely to affect fitness through changes in element allocation from routine metabolic processes to demanding physiological traits occurring during growth and reproduction, which can also reroute energy allocation away from homeostatic processes. Food quality affects the growth rate of consumers and therefore can be considered a selection agent. The selection targets would be the physiological mechanisms driving nutritional demand that are affected by food quality. Another target of selection might be genome size because it is composed of nucleotides and amino acids that require key elements, such as N and P, which are reallocated from DNA to RNA to sustain rapid growth [26,58]. Consequently, the N and P content of food have been suggested to act as selection agents in nutrient-limited environments because they can mediate the relative success of individuals differing in genome size, particularly between diploid and polyploid organisms [11,25]. Parasitism might also be a selection agent driving the evolution of EPs through nutrient-driven within-host infection dynamics [59].