

# A three-way perspective of stoichiometric changes on host–parasite interactions

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**Changes in environmental nutrients play a crucial role in driving disease dynamics, but global patterns in nutrient-driven changes in disease are difficult to predict. In this paper we use ecological stoichiometry as a framework to review host–parasite interactions under changing nutrient ratios, focusing on three pathways: (i) altered host resistance and parasite virulence through host stoichiometry (ii) changed encounter or contact rates at population level, and (iii) changed host community structure. We predict that the outcome of nutrient changes on host–parasite interactions depends on which pathways are modified, and suggest that the outcome of infection could depend on the overlap in stoichiometric requirements of the host and the parasite. We hypothesize that environmental nutrient enrichment alters infectivity dynamics leading to fluctuating selection dynamics in host–parasite coevolution.**

## Anthropogenic nutrient enrichment alters disease dynamics: how and why?

Anthropogenic disturbances in global biogeochemical cycles of nitrogen (N) and phosphorus (P) have not only led to increased nutrient loading in the environment but also to changed carbon (C) to nutrient ratios (C:N:P) available to organisms. Based on the assumptions of ecological stoichiometry, C:N:P of resources are reflected in the stoichiometric content of the organisms consuming those resources (Box 1). For example, spatial imbalances in atmospheric loading of N cause spatial variation in N:P ratios in organisms, with a shift towards higher N:P in organisms in areas with high loading of N [1,2]. Owing to fundamental differences in allocation of these three key elements (C, N, P) to major biomolecules (e.g., nucleic acids, amino acids), or to chemical structures between organisms [3] and in their life-history strategies, changes in C:N:P ratios will either favor or impinge upon the function and fitness of organisms. The elemental ratio (C:N:P) in a resource thus defines resource quality for a

consumer. For example, decreases in environmental C:P ratios (i.e., increase in P) are likely to favor fast growing organisms that allocate P strongly to P-rich ribosomal RNA (rRNA), which is needed for protein synthesis and growth [4,5]. By changing population dynamics, increased nutrient loading has the potential to modify species interactions at different trophic levels and in different ecosystem functions [2,6,7].

In recent years, increases in parasitic and infectious diseases have been connected to increased nutrient loading in the environment [8–10]. These studies have mainly focused on resource quantity-driven changes in disease dynamics, examining increased host production under conditions of nutrient enrichment. However, parasites can also be considered as consumers, and thus changes in their resource quality – in other words, in the stoichiometric content of hosts – could alter their fitness and function in similar ways as resource quality-driven changes in producer stoichiometric content affect herbivores (Box 1). Indeed, to predict how and why hosts and parasites respond at the individual, population, and ecosystem levels to changed ratios of elemental nutrients, the framework provided by ecological stoichiometry can be utilized (Box 1). Based on the assumptions of ecological stoichiometry, anthropogenic increases in N and P concentrations in the environment would not only support the growth of individual hosts and host populations but would also increase the nutrient content of hosts, thus increasing resource quality and availability to parasites. By contrast, increased nutrient levels could also facilitate host resistance and hence suppress parasite growth and transmission.

We review here what is known about the effects of environmental nutrient changes on host–parasite interactions in a stoichiometric framework. We focus on endoparasites, which exploit host tissues or storage biomolecules metabolized from the food (described e.g., in [11]). We propose a three-pathway perspective (Figure 1). Pathway 1 focuses on the interactions between individual hosts and parasites modified by nutrient levels. Pathway 2 describes how environmental nutrient levels change parasite transmission efficiency via altering host population density. With respect to pathways 1 and 2, we review the effects that changes in environmental nutrient ratios are likely to

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Keywords: ecological stoichiometry; host–parasite coevolution; infection dynamics; nutrient ratios; resource quality.

1471-4922/

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### Box 1. Ecological stoichiometry

Sterner and Elser [100] define ecological stoichiometry as: 'the balance of multiple chemical substances in ecological interactions and processes, or the study of this balance. Also sometimes refers to the balance of energy and matter'.

The assumptions that ecological stoichiometry makes are based on the law of conservation of matter, which states that the 'amount of matter in a closed system is conserved' and that 'in an ordinary chemical reaction, the total mass of the products must equal the total mass of the reactants'. From the perspective of ecological stoichiometry, this means that all elements in the resources that an organism consumes must be converted either into biomass of that organism or into waste (Figure 1) [100].

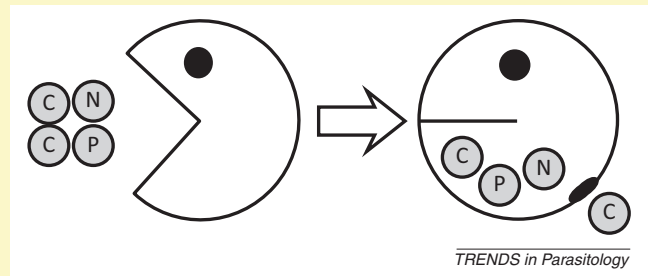
All organisms are built from three key elements: carbon (C), nitrogen (N), and phosphorus (P). C is the main component of biomolecules involved in energy metabolism (e.g., lipids and carbohydrates), while N and P are constituents of biomolecules (e.g., nucleic acids, amino acids) and of functional and structural compounds [100]. In ecosystems, N and P are the usually the two elements that limit biomass production – in other words, are 'nutrients' – whereas C is generally found in excess, meaning that the environmental C:N and C:P ratios are high [101]. Most studies on ecological stoichiometry have focused on P because it is necessary for building essential compounds for life (DNA, RNA, and ATP) and is more commonly found to limit growth of organisms than N (as reviewed in [102]).

Each organism has a unique elemental content, in other words the ratio between carbon and nutrients (C:N:P), reflecting the extent to which it allocates elements to major biomolecules and to chemical structures [3]. This again is related to the life-history strategy of the organism. Indeed, one of the central concepts in ecological stoichiometry, the growth rate hypothesis (GRH), suggests that fast-growing organisms have low C:P and N:P ratios (high P content) because they allocate P strongly to P-rich ribosomal RNA (rRNA) which is needed for protein synthesis and growth [4,5]. GRH is most applicable to small heterotrophic P-limited organisms [102], and does not apply under special conditions: for example, under co-limitation of essential nutrients [103].

The connection between life-history traits and stoichiometric composition of an organism means that acquisition of C and elemental nutrients in imbalanced ratios impinges on the function

and fitness of the organism. Each organism has a defined threshold elemental ratio (TER) after which it transitions from energy limitation to elemental limitation [102]. Some organisms need to maintain constant chemical compositions under varying resource quality (resource C:N:P) – in other words, they are more stoichiometrically homeostatic than others. Autotrophs are generally considered to be less homeostatic than consumers and suffer less from imbalanced resource quality because they can incorporate excess C into structures and storage matter. Consumers are considered to be more stoichiometrically homeostatic. They allocate resources strongly towards nucleic acids and to other N- and P-rich compounds needed for growth and reproduction, and consequently need to maintain high nutrient content and require high quantities of nutrients (low C:N:P) [100]. When consuming resources with imbalanced C:N:P, they suffer from reduced function and fitness and need to actively remove excess C [102]. Previous studies in ecological stoichiometry have focused on producer–herbivore interactions because there is significant stoichiometric mismatch between plant and animal tissue. However, poor resource quality (high C:N:P) may cascade up to the food chain to constrain secondary and tertiary consumers [104], and possibly parasites [28].

Water fleas from the genus *Daphnia* have been the main study organisms in ecological stoichiometry because they are common herbivores in aquatic ecosystems and have high P requirements, meaning that they commonly suffer from P-limitation [101].



**Figure 1.** Law of conservation of matter in consumer–resource interactions. All the elements gained are either incorporated into new biomass of the consumer or are secreted as waste.

have on host–parasite coevolution. Pathway 3 then describes how nutrient-driven changes in the host community can modify host–parasite interactions.

#### Pathway 1. Nutrient-driven within-host infection dynamics

In pathway 1 we focus on the interactions at the level of a host individual (Figure 1). At the onset of the infection process, parasite infectivity will largely depend on factors other than host nutrients, such as genetic compatibility between the parasite and the host [12]. However, after successful onset and establishment of infection, the parasite is able to retrieve host resources and even to manipulate host resource allocation to acquire energy and nutrients. For example, host 'castrating' parasites make the host divert resources from reproduction to growth, which the parasites in turn exploit for their propagule production [13,14]. Some microbes have been found to trigger biosynthesis and degradation pathways of the hosts to acquire essential biochemical compounds [15,16].

Following the assumptions of ecological stoichiometry, higher environmental nutrient levels can be expected to cascade via the food web from primary producers into increased resource quality for consumer-hosts. However, whether these higher-quality hosts (higher resource

quality for parasites) will result in increased parasite fitness is determined by resource allocation between host resistance and parasite growth. If the host is able to invest elemental resources into resistance before parasite exploitation, higher resource quality (low C:N or C:P) could lead to decreased parasite load, even though such resistance mechanisms may be costly to the host [17]. In accordance, a nutrient-supplemented high-quality diet has been documented to lead to increased immune activity and/or reduced parasite multiplication rate (e.g., [18–23]). However, if the parasite is able to steal the nutritional elements before the host can allocate them to immune defense, higher host quality (high amount of P and/or N) can lead to increased parasite growth rate and production of infective propagules within individual hosts (Figure 2). Higher nutrient (N and/or P) availability has been found to promote the replication of various parasites, including fungal foliar pathogens in plants [24], bacteria and fungi in corals [25,26], trematodes in snails [27], and bacteria and fungi in water fleas [28,29]. In addition, host resource-driven increases in parasite replication rate have been found to enhance the negative effect of parasites on host fitness (i.e., parasite virulence) [20,30]. Parasite fitness may also depend on host tolerance, in other words the ability of the host to maintain normal physiological functions when

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