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Think ratio! A stoichiometric view on biodiversity–ecosystem functioning research

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Abstract

Ecological stoichiometry (ES) has become one of the most pervasive theoretical frameworks in environmental sciences and biology in the last two decades. ES allows predicting processes on all organizational levels from subcellular structures to ecosystems by relating the elemental composition and demand of organisms to the relative availability of resources. However, ES has been rarely used to understand and predict the relationship between biodiversity and ecosystem functioning (BEF), although ES would be ideally suited as it makes predictions on both population processes underlying biodiversity as well as on matter transformations underlying ecosystem processes. Here, we propose to link the two fields of research on ES and BEF relationships and highlight a number of potential avenues for further research. First, we cast a stoichiometric view on drivers of biodiversity change. Second, we address the stoichiometric underpinning of biodiversity–productivity relationships. Third, we discuss potential interactions between stoichiometry and diversity in a food web context.

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Zusammenfassung

Ökologische Stöchiometrie (ecological stoichiometry, ES) hat sich in den letzten beiden Jahrzehnten zu einer der grundlegenden Theorien der Umweltwissenschaften und der Biologie entwickelt. Durch den Vergleich von elementarer Zusammensetzung von Organismen und ihren Ressourcenansprüchen mit der relativen Verfügbarkeit der Ressourcen sagt ES Prozesse auf allen Organisationsebenen von subzellulären Strukturen bis hin zu Ökosystemen voraus. Allerdings wurde ES bisher selten angewandt um den Zusammenhang zwischen Biodiversität und Ökosystemfunktion zu verstehen, obwohl ES ideal dazu geeignet wäre, da es sowohl Vorhersagen zu Prozessen macht, die Biodiversität beeinflussen, als auch zu Materieflüssen und –transformationen, auf denen wichtige Ökosystemfunktionen basieren. In diesem Artikel untersuchen wir den Zusammenhang dieser beiden Forschungsfelder und zeigen zukünftige Forschungsfelder anhand von drei Themen auf: i) stöchiometrische Aspekte der Treiber des Biodiversitätswandels, ii) stöchiometrische Grundlagen des Zusammenhangs zwischen Biodiversität und Produktivität, iii) potentielle Interaktionen zwischen Biodiversität und Stöchiometrie im Nahrungsnetzkontext.

Keywords: Ecological stoichiometry; Biodiversity; Ecosystem functioning; Coexistence; Biodiversity; Productivity; Eutrophication

Introduction

The concept of ecological stoichiometry (ES) describes the balance of elements in ecological processes, the term deriving originally from the mass balance in chemical reactions. ES has a long history in ecology with early investigations on the constraints of mass balance reaching back to the 19th century (Liebig 1840; Lotka 1925; Redfield 1934; Redfield, 1958). More recently, ES has developed towards a general ecological framework linking cellular processes, organism physiology, and trophic interactions to processes within and across ecosystems (Sterner & Elser 2002). It has gained increasing attention in community ecology in order to explain the consumer responses to prey food quality (Hillebrand, Borer, et al. 2009), resource competition between consumer species (Hall 2004), and consumer effects on prey nutrient composition via nutrient recycling (Hillebrand, Frost, & Liess 2008).

Most work in the field of ecological stoichiometry has focused on the importance of material imbalances at the interface between consumers and their prey. Cellular elemental composition can differ greatly especially between herbivorous primary consumers and their autotroph prey due to their different physiology. Nutrient uptake and carbon fixation in photoautotrophs, like phytoplankton or vascular plants, mainly depend on the availability of mineral resources and light. Nutrient assimilation and CO_2 fixation are physiologically separated, such that fluctuations in resource availability and ratios are partly reflected in autotrophs′ elemental composition (Ågren 2004; Hillebrand et al. 2013). Consequently, autotrophs can exhibit a broad plasticity in elemental composition.

In contrast, consumer species show a more confined stoichiometry and relatively high nutrient contents compared to autotrophs (Elser et al. 2000; Persson et al. 2010). As a result, the flexibility in autotrophic cellular elemental ratios can have major consequences for heterotrophs because maximal growth and reproduction of consumers depend on optimal elemental concentrations in their food. Therefore, consumers' demand for essential nutrients and the relatively plastic balance of these nutrients in their prey can create elemental mismatches. In consequence of the simultaneous carbon and nutrient assimilation, consumers have to cope with excess carbon or nutrient concentrations in their food by regulating their cellular nutrient content via excretion or respiration, which is commonly known as homeostasis (Frost, Evans-White, Finkel, Jensen, & Matzek 2005; Persson et al. 2010). Moreover, elemental mismatches alter ingestion rates of consumers, with different consequences at the individual level (compensatory feeding, avoidance) and the population level (reduced abundance and consumption through reduced growth efficiency) (Hillebrand, Borer, et al. 2009).

Thus, consumer species with high nutrient demands can become nutrient limited rather than carbon limited. As enhanced light availability increases autotroph biomass, grazers are assumed to benefit from the surplus of the food concentration. However, enhanced light intensities also increase the carbon:nutrient ratios in autotrophs and thereby alter food quality for heterotrophic grazers, either reducing quality if the consumers are rather nutrient-limited (Urabe & Sterner 1996; Urabe et al. 2002) or increasing it if nutrients are in excess (Boersma & Elser 2006). Consequently, elemental imbalance in plant-animal interactions can affect herbivore performance and elemental recycling efficiency (Sterner & Elser 2002; Urabe et al. 2002). Yet, since the nutritional requirements vary between different taxonomical groups, changes in community composition and species richness may alter the stoichiometric interactions in food webs.

The potential consequences of elemental imbalances for trophic interactions are crucial in the face of expanding human alteration of the global biogeochemical cycles. During the past decades, anthropogenic nutrient input into the biosphere has almost doubled due to P-mining and the industrial manufacture of ammonium (Haber-Bosch-method) for