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Towards a mechanistic understanding of the impacts of nitrogen deposition on producer–consumer interactions

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ABSTRACT

Nitrogen (N) deposition has increased substantially since the second half of the 20th century due to human activities. This increase of reactive N into the biosphere has major implications for ecosystem functioning, including primary production, soil and water chemistry and producer community structure and diversity. Increased N deposition is also linked to the decline of insects observed over recent decades. However, we currently lack a mechanistic understanding of the effects of high N deposition on individual fitness, species richness and community structure of both invertebrate and vertebrate consumers. Here, we review the effects of N deposition on producer–consumer interactions, focusing on five existing ecological frameworks: C:N:P ecological stoichiometry, trace element ecological stoichiometry, nutritional geometry, essential micronutrients and allelochemicals. We link reported N deposition-mediated changes in producer quality to life-history strategies and traits of consumers, to gain a mechanistic understanding of the direction of response in consumers. We conclude that high N deposition influences producer quality *via* eutrophication and acidification pathways. This makes oligotrophic poorly buffered ecosystems most vulnerable to significant changes in producer quality. Changes in producer quality between the reviewed frameworks are often interlinked, complicating predictions of the effects of high N deposition on producer quality. The degree and direction of fitness responses of consumers to changes in producer quality varies among species but can be explained by differences in life-history traits and strategies, particularly those affecting species nutrient intake regulation, mobility, relative growth rate, host-plant specialisation, ontogeny and physiology. To increase our understanding of the effects of N deposition on these complex mechanisms, the inclusion of life-history traits of consumer species in future study designs is pivotal. Based on the reviewed literature, we formulate five hypotheses on the mechanisms underlying the effects of high N deposition on consumers, by linking effects of nutritional ecological frameworks to life-history strategies. Importantly, we expect that N-deposition-mediated changes in producer quality will result in a net decrease in consumer community as well as functional diversity. Moreover, we anticipate an increased risk of outbreak events of a small subset of generalist species, with concomitant

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declines in a multitude of specialist species. Overall, linking ecological frameworks with consumer life-history strategies provides a mechanistic understanding of the impacts of high N deposition on producer–consumer interactions, which can inform management towards more effective mitigation strategies.

Key words: life-history strategy, insect decline, nutritional ecology, global change, stoichiometry, ecological ionomics, food quality, eutrophication, trophic mismatch.

CONTENTS

I. INTRODUCTION

The global nitrogen cycle has been altered greatly by human activities in the Anthropocene (Crutzen, 2002), with anthropogenic nitrogen (N) fixation currently exceeding natural fixation rates (Vitousek *et al.*, 1997; Galloway & Cowling, 2002; Elser, 2011; Fowler *et al.*, 2013). As a result, deposition of reactive N from the atmosphere has increased substantially since the second half of the 20th century (Holtgrieve *et al.*, 2011; Smith, Tilman & Nekola, 1999; Galloway & Cowling, 2002), with present deposition hotspots in northwest Europe, eastern USA, India and eastern China (Jia *et al.*, 2016). The increase of available N into the biosphere is a global problem; it includes all major biomes and has major implications for ecosystem functioning (Smith *et al.*, 1999; Bobbink *et al.*, 2010; Elser *et al.*, 2009*b*; Ryther & Dunstan, 1971; Sala *et al.*, 2000). Well-documented impacts include effects on primary production (e.g. Stevens *et al.*, 2015), soil and water chemistry (e.g. van Breemen, Driscoll & Mulder, 1984; Hogg, Squires & Fitter, 1995; Houdijk, 1993; De Graaf *et al.*, 1998) and plant community structure and diversity (e.g. Bobbink, Hornung & Roelofs, 1998; Stevens *et al.*, 2010, 2011; Field *et al.*, 2014; Bobbink *et al.*, 2010). Anthropogenic N deposition is hypothesised to have contributed to the insect decline observed over recent decades (Hallmann *et al.*, 2017, 2021; Wagner *et al.*, 2021; Cardoso *et al.*, 2020). However, we currently lack a mechanistic understanding of how increased N deposition impacts both invertebrate (Stevens, David & Storkey, 2018; Throop & Lerdau, 2004; Meunier *et al.*, 2016) and vertebrate consumers.

Recent studies have shown that increased N deposition affects consumers through a number of pathways that directly or indirectly affect their habitat quality (Nessel *et al.*, 2021; Nijssen, WallisDeVries & Siepel, 2017). These include changes in the habitat of a species that are quantitative (food abundance, visibility or accessibility), physical (changes in microclimatic conditions, reduced reproductive habitat resulting from increased biomass production) and chemical (altered food quality or changes in chemical stressors). For the chemical pathways in particular, major knowledge gaps exist about the mechanisms through which increased N deposition affects producer quality and how this ultimately affects consumer fitness, species richness and community structure (Stevens *et al.*, 2018).

A mechanistic understanding of how N deposition impacts the fitness of consumers has proved elusive. There are different ecological frameworks, each offering a different perspective on how N deposition changes producer nutritional quality and making general predictions on how this in turn affects consumer fitness. However, in many cases, responses of specific consumer species to increased N availability are fundamentally different among species (Zhu *et al.*, 2023), indicating that a one-size-fits all explanation does not exist. Indeed, impacts of nutritional changes in producers on consumers not only depend on changes in producer chemistry, but also on the 'nutritional niche' a given organism occupies. This 'nutritional niche' is itself an aspect of a species' life-history strategy, which is a set of co-evolved traits that enable a species to cope with the opportunities and constraints it experiences in the natural environment (Verberk, Noordwijk & Hildrew, 2013).

Here we suggest a way forward by reviewing the effects of N deposition on producer quality and consumer fitness. We do so by first synthesising the different nutritional frameworks in ecology, separating between effects of N deposition on consumer fitness (Fig. 1, panel 1) and how these can be explained from effects on producer nutritional quality (Fig. 1, panel 2). With these frameworks, we scale from elements (ecological stoichiometry) to a range of biochemicals,

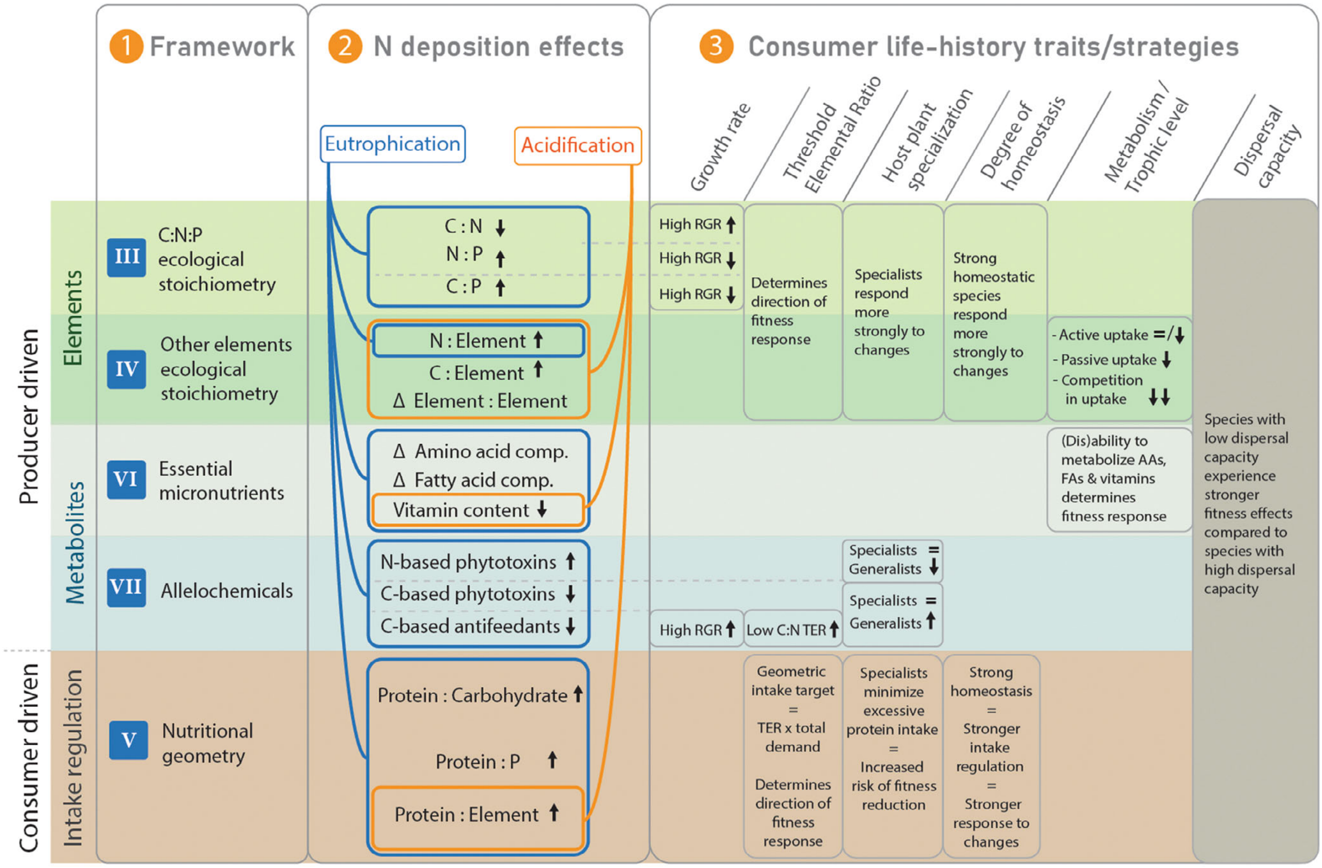

Fig. 1. Schematic overview of N deposition impacts on producer nutritional quality per ecological framework and the hypothesised interactions with consumer life-history traits and strategies reviewed herein, predicting consumer responses to N-deposition-mediated change. Panel 1 organises each framework based on the type of nutrients and subject focus (producer-chemistry driven *versus* consumer-behaviour driven). Panel 2 summarises the effects of N deposition on corresponding producer nutritional quality. A distinction is made between eutrophication (blue boxes) and acidification (orange) effects. Panel 3 summarises the degree and/or direction of effects of such changes on consumer fitness, through interactions with life-history traits and/or strategies. Numbers III to VII indicate the corresponding sections of this article in which these mechanisms are described. AAs, amino acids; FAs, fatty acids; RGR, relative growth rate; TER, threshold elemental ratio.

including macronutrients (nutritional geometry), essential micronutrients, and allelochemicals, for each framework. Responses of consumers are then contextualised by integrating them with their life-history traits and strategies for each framework (Fig. 1, panel 3), which we expect to prove valuable for explaining species-specific responses to N deposition and enrichment (Nessel *et al.*, 2021). Throughout the review we highlight fruitful directions and testable hypothesis for future research. A mechanistic understanding rooted in life-history strategy of consumer species will aid in predicting species responses, and help in designing the best mitigating measures and management practices.

II. PRODUCER–CONSUMER INTERACTION FRAMEWORKS

For reference, we first provide a brief summary description of the frameworks covered in this review, particularly on the specific scopes and subjects covered by each framework.

(1) C:N:P ecological stoichiometry

Carbon (C), nitrogen (N) and phosphorus (P) are the main building blocks of species biomass. C:N:P ecological stoichiometry focuses on the balance between energy (as carbon) and macronutrients (such as N and P) to describe ecological interactions, including those between producers and consumers (Sterner & Elser, 2002; Reiners, 1986; Hessen *et al.*, 2013). Producer quality thereby is defined as the degree of similarly between the C:N:P stoichiometry of producers and consumers.

(2) Other elements ecological stoichiometry

A total of 21 elements are considered essential for organismal functioning, and the relative availability of a much wider range of elements besides the macronutrients C, N and P may influence organismal functioning (Huang & Salt, 2016; Salt, Baxter & Lahner, 2008; Jeyasingh *et al.*, 2017). The majority of these elements are tightly coupled to distinct organismal functions, for example through their incorporation in specific enzymes. For many of these elements, the relative content and needs differ markedly between producers and consumers (Jeyasingh *et al.*, 2017; Kaspari, 2021).

(3) Nutritional geometry

Consumers are known to be able to regulate the intake of carbohydrates and protein, by measuring the content of these biochemicals in food items *via* taste receptors and by coupling this to internal demand (Abisgold & Simpson, 1988; Simpson *et al.*, 1991). The degree to which a consumer regulates protein and carbohydrate intake differs among species and can be measured 'geometrically' in specifically designed feeding experiments (Raubenheimer & Simpson, 1993).

(4) Essential micronutrients

Many biochemical compounds are essential for organismal functioning. The ability to synthesise these is not universal among organisms. First-order consumers often rely on the production of complex biomolecules by primary producers, and higher order consumers typically lose the ability to synthesise complex molecules that are produced by their prey or host species. Essential micronutrients are thus defined as those that are vital for organismal functioning, including compounds such as amino acids, fatty acids and vitamins that consumers cannot synthesise themselves.

(5) Allelochemicals: antifeedants and phytotoxins

Many producers are able to synthesise compounds (allelochemicals) that are involved in grazing resistance. Such allelochemicals can be fully C based, or can also contain N. Allelochemicals are subdivided into two groups (van Genderen, Schoonhoven & Fuchs, 1996), where one functions *via* impairment of nutrient uptake efficiency (antifeedants), and another operates through inhibition of vital organismal functioning of consumers (phytotoxins).

III. C:N:P ECOLOGICAL STOICHIOMETRY RESPONSES TO INCREASED N DEPOSITION

(1) Effect of N deposition on producer C:N:P ratios

Nitrogen is among the major limiting nutrients for plant growth in many natural and semi-natural ecosystems (Cech *et al.*, 2008; Fay *et al.*, 2015; Elser *et al.*, 2007; Olde Venterink *et al.*, 2003; Meunier *et al.*, 2016). When N is no longer limiting, producer growth becomes (co)-limited by other resources such as P, K, Fe, light, CO_2 (in aquatic ecosystems), or water (in terrestrial ecosystems) (Aerts & Bobbink, 1999; Harpole *et al.*, 2011). A further increase in available N results in higher cellular or tissue content of N-based compounds such as proteins (Sardans, Rivas-Ubach & Penuelas, 2012*a*). Primary producers exhibit a higher stoichiometric plasticity than consumers since nutrients are acquired *via* separate pathways and cellular requirements can be regulated by reducing or increasing tissue protein content (Geider & La Roche, 2002; Liefer *et al.*, 2019), or through nutrient reallocation (Güsewell, 2004). Non-limiting elements can accumulate in storage molecules, such as phospholipids and certain amino acid-based storage polymers (Elser *et al.*, 2010; Geider & La Roche, 2002; Sterner & Elser, 2002). Reduced availability of a limiting nutrient and/or increased availability of a non-limiting nutrient can thus cause significant changes in primary producers C:N:P stoichiometry (Gonzalez *et al.*, 2017; Garcia *et al.*, 2018). Under high N availability, elemental ratios of primary producers generally shift towards lower C:N and higher N:P ratios (Sardans *et al.*, 2012*a*; Geider & La Roche, 2002; Hillebrand *et al.*, 2013; Elser *et al.*, 2009*b*). On a community level, producer C:N:P stoichiometry could also alter through N-deposition-mediated shifts in species composition, as different phytoplankton and vascular plant species have been shown to differ in their C:N:P stoichiometry (Garcia *et al.*, 2018; Hillebrand *et al.*, 2013; Güsewell, 2004; Vogels *et al.*, 2020; Wassen *et al.*, 2021).

(2) Stoichiometric effects of N deposition on consumers

Impacts of high N deposition on producers may also cascade to higher trophic levels and follow stoichiometrically predictable patterns. For example, consumer fitness may increase due to lowered C:N ratios and thereby reduced mismatches between consumers and their food (Kurze, Heinken & Fartmann, 2017; White, 1993; Brunsting & Heil, 1985; Taboada, Marcos & Calvo, 2016; Kerslake, Woodin & Hartley, 1998). However, increased N deposition was also shown to reduce consumer fitness (Kurze, Heinken & Fartmann, 2018; Fischer & Fiedler, 2000) or diversity (Lee, Nakamura & Hiura, 2017). In aquatic ecosystems, P limitation in consumers occurs frequently (for a review see Hessen *et al.*, 2013), but (co-)limitation by N is common (Elser *et al.*, 2007), resulting in reduced performance under low N supply for tadpoles (Stephens *et al.*, 2017), rotifers (Golz, Burian & Winder, 2015) and copepods (Van Nieuwerburgh, Wänstrand & Snoeijs, 2004). Thus, increased N deposition can either enhance or reduce consumer performance in terrestrial as well as aquatic ecosystems, depending on the experienced nutrient limitation under prevailing conditions. Increased N deposition may also increase consumer fitness initially, but then as N deposition remains high, the system may shift from N to P limitation, which in turn will limit consumer growth and development (Elser *et al.*, 2009*a*; Bergström *et al.*, 2018).

In contrast to primary producers, consumers tend to be more stoichiometrically homeostatic (Persson *et al.*, 2010; Kagata & Ohgushi, 2006), and consumer tissue C:N, C:P, as well as N:P ratios are generally lower than those of producers (Sardans, Rivas-Ubach & Peñuelas, 2012*b*; Fagan *et al.*, 2002; Hessen *et al.*, 2013; Sterner & Elser, 2002; Hessen, 2008; Elser *et al.*, 2000*a*). High tissue C:N content often negatively influences herbivore performance, reproduction or density in terrestrial (Throop, 2005; Throop & Lerdau, 2004; Couture, Servi & Lindroth, 2010; Loaiza, Jonas & Joern, 2008, 2011; Kagata & Ohgushi, 2006, 2007; Lebigre *et al.*, 2018; Hessen, 1992; White, 1993) and aquatic (Kiørboe, 1989; Burian *et al.*, 2018; Thomas *et al.*, 2022) ecosystems. Producers have also been shown to have a higher mean N:P ratio compared to consumers (Elser *et al.*, 2000*a*), which may indicate that herbivores are often (co-)limited by P. Indeed, various studies have reported negative (Zhu *et al.*, 2019; Zehnder & Hunter, 2009; Cease *et al.*, 2012; Kay *et al.*, 2007; Nijssen & Siepel, 2010; Pöyry *et al.*, 2017; Fischer & Fiedler, 2000; Vogels *et al.*, 2017, 2021; Kurze *et al.*, 2018) or optimum (Joern & Behmer, 1997, 1998) herbivore responses to increased producer N content and/or N:P ratio. In other words, more N led to enhanced P shortage in producers, thereby reducing the performance of consumers. When examining the outcome of studies focusing on the effect of (experimentally) increasing P availability relative to N over a range of producer N:P ratios, clear fitness gains can be observed from alleviating P shortage and these seem to occur at molar N:P ratios of 38 or higher (Fig. 2; see online Supporting Information, Table S1). At the same time, P can also be in excess relative to N, and fitness reduction effects of increasing P availability seems to occur at molar N:P ratios of 22 or lower in terrestrial consumers (Fig. 2).

(3) Degree and direction of consumer response to changed C:N:P ratios

The degree of nutrient limitation is not only determined by producer stoichiometry, but also by the specific needs of the consumers, as determined by the organisms' tissue and metabolic stoichiometry. This is partially determined by phylogenetic drivers (Gonzalez *et al.*, 2011; Hendrixson, Sterner & Kay, 2007; González *et al.*, 2018; Woods *et al.*, 2004; Fagan *et al.*, 2002), as well as by species traits that influence consumers' C:N:P stoichiometry, such as growth rate, skeleton investment, ontogeny, size and trophic position (see Table 1 for an overview).

The degree of C:N:P homeostasis in consumers determines the degree of fitness costs a consumer encounters under conditions of suboptimal food stoichiometry. The degree of stoichiometric homeostasis has been found to differ among consumers (Golz *et al.*, 2015; Meunier, Malzahn & Boersma, 2014). Strict stoichiometric homeostasis optimises growth, as optimal conditions for cellular processes are maintained. A more flexible stoichiometry allows for storage of elements (Meunier *et al.*, 2014), which can be beneficial for species feeding on a diverse diet with food items differing in C:N:P stoichiometry. The species-specific C:N:P stoichiometry thus determines the optimal food C:N:P ratio at which maximum growth is achieved, while the degree of homeostasis determines the severity of fitness costs associated with changes in food C:N:P stoichiometry. Both factors are important determinants of the response of consumers to N-deposition-driven changes in food C:N:P stoichiometry. The threshold elemental ratio (TER; Urabe & Watanabe, 1992) incorporates a species' specific C:N:P stoichiometry and its ability to regulate homeostasis, by assuming quadratic relationships between producer elemental ratios and consumer performance (Sterner & Elser, 2002). The TER thus equates to the optimum C:N; C:P and/or N:P ratio for growth, and the associated fitness curve shows the degree of fitness costs encountered at suboptimal food C:N:P (Fig. 3). Specialist consumers are hypothesised to have narrower TER performance curves than generalists, since strong homeostatic regulation is preferred over a low degree of homeostasis within this strategy. Consumers specialised on food with a high C:N or C:P ratio have been proposed to be more susceptible to reduced C:N or C:P ratios in

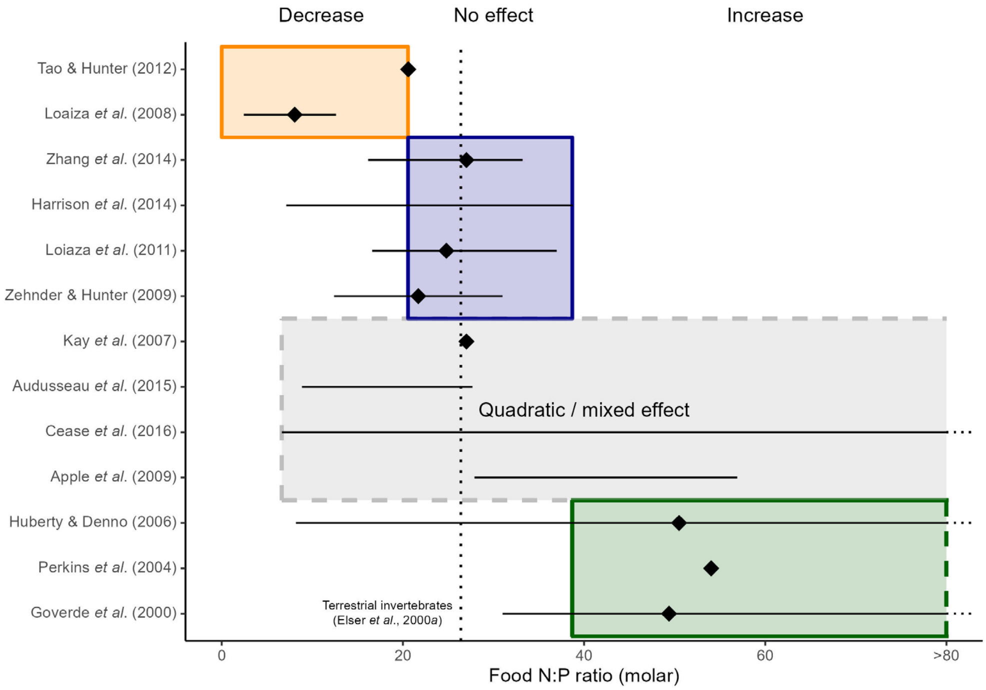

Fig. 2. Relationship between consumer fitness response to dietary P supplements in relation to food N:P ratios in experimental herbivore fitness effect studies. For each study, mean (diamonds, when retrievable) and/or minimum and maximum (horizontal lines, when retrievable) food N:P ratios used in the study are plotted. Studies are sorted by experimental outcome, as indicated. Coloured rectangles indicate suggested boundaries of dietary limitation (orange: N; green: P, blue: other element or co-limitation). Studies that reported a quadratic or mixed response to increasing dietary P either reported a broad N:P ratio range or a range at the boundary of decrease – no effect and no effect – increase (grey rectangle). Vertical dotted line: mean N:P ratio of terrestrial invertebrates reported by Elser *et al.* (2000*a*). For a detailed description of experimental setup and outcome of each study, see Table S1.

producers (Boersma & Elser, 2006), because species adapted to these food types have a relatively high TER, as was shown for C:N. Specialist consumers of N-poor food are therefore hypothesised to be more prone to experience fitness losses due to high N-deposition-mediated changes in producer C:N and N:P ratios than generalist consumers. Experimental support for this hypothesis is reported by several authors (Behmer, 2009; Simpson *et al.*, 2004; Warbrick-Smith *et al.*, 2009) who found that host plant specialists regulate excess N intake more strongly than C compared to generalists. By contrast, high-N specialists will be N limited under natural conditions more frequently, resulting in fitness increases rather than fitness losses under increased N deposition. In short, consumers that express traits leading to high body tissue C:N and/or low N:P ratio (Table 1) may also exhibit a high TER for C:N and a low TER for N:P, and will thereby be more likely to experience negative consequences from N deposition as this will shift the food stoichiometry toward lower C:N and higher N:P ratios (Fig. 2). By contrast, this may also reveal potential winners under high N-deposition conditions, which are expected to exhibit N-dependent traits, with lower TERs for C:N and higher TERs for N:P. The degree of specialisation of the consumer ultimately determines the response rate to N-deposition-driven changed producer stoichiometry.

The number of studies linking TERs to various consumer traits and life-history strategies is still limited. Yet, partial support for trait-related changes in TERs was found by whole-community studies of European butterflies. Univoltine, low-dispersive monophagous species were found to feed on host plants relatively rich in P, while highly dispersive polyphagous species were found to feed on plants with lower P content. For trait combinations between these two extremes, there was a quadratic trend for plant tissue N concentration (Carnicer *et al.*, 2012, 2013, 2015). Thus, host-plant specialists tend to feed on low N:P plants, while polyphagous species tend to feed on higher N:P plants. Moreover, multivoltine, large polyphagous (i.e. generalist) butterflies and Diptera consuming host plants with high N generally have shown positive population trends during recent decades, in contrast to (smaller) specialist species. This suggests that large generalist butterfly and Diptera species occupy a comparatively low C:N and high N:P niche, whereas small specialists are found in a niche with low C:P and N:P ratios (Hambäck *et al.*, 2009; Pöyry *et al.*, 2017). These findings suggest that high N deposition may benefit generalists at the cost of specialists, and that these impacts are stoichiometrically predictable.

To understand the stoichiometric consequences of N deposition on consumers, the trait-based TER approach

Table 1. Reported relationships between species traits and consumer C, N and P content and C:N, C:P and N:P ratio. Arrows indicate direction of change in elemental content or ratios as a result of a given trait; = indicates no or minor change in elemental content or ratio. For each trait, the proposed underlying mechanism and supporting references are also provided.

Trait	C	N	P	C:N	C:P	N:P	Mechanism
High relative growth rate (RGR)	=	=	↑	=	↓	↓	High ribosomal RNA (rRNA) content is positively correlated with growth rate (Elser *et al.*, 1996, 2000*b*; Watts *et al.*, 2006; Van Geest *et al.*, 2010; Sardans *et al.*, 2012*b*), increasing P requirements over N.
Increasing size	↑	↑	↓	↑	↓	↑	RGR decreases allometrically with size, resulting in lower tissue P content with size (Woods *et al.*, 2004; Sterner & Elser, 2002; Gonzalez *et al.*, 2011; Elser *et al.*, 1996). C, N and C:N ratio increases with size (González *et al.*, 2018), due to increased allocation of N to muscle tissue and C to fat reserves.
Increasing vertebrate skeleton investment	=	=	↑	=	↓	↓	Bone tissue apatite is rich in P and bone tissue investment increases allometrically with size (Elser *et al.*, 1996; Sterner & Elser, 2002; Hendrixson *et al.*, 2007; Knapp *et al.*, 2021; Pilati & Vanni, 2007; Sterrett *et al.*, 2015; Gonzalez *et al.*, 2011).
Increasing insect exoskeleton investment	↑	↑	=	=	↓	↓	Chitin contains C and N but no P (Andrieux *et al.*, 2021), thus tissue relative C and N content increases with increased investments in exoskeleton tissue.
Endothermy	↑	=	=	↑	↑	=	More C allocated to fat reserves (Klaassen & Nolet, 2008) to sustain thermoregulation.
Ontogeny: immature invertebrates relative to adults	=	↑	↑↑	↓	↓	↓	Immature stages exhibit increased N, but relatively stronger increased P content, resulting in lower C:N, C:P and N:P tissue ratio (Main *et al.*, 1997; Mathews *et al.*, 2018)
Ontogeny: holometabolism relative to hemimetabolism	=	↓	↑	=	=	↓	Holometabolous insects contain more P and less N than hemimetabolous insects (Fagan *et al.*, 2002; Woods *et al.*, 2004; Villar-Argaiz *et al.*, 2021)
Predators relative to herbivores	=	↑	↑↑	↓	↓	↓	Predators contain more N and P than herbivores. (Fagan *et al.*, 2002; González *et al.*, 2018). Tissue P increases more than tissue N (Gonzalez *et al.*, 2011), thus N:P is lower in relation to herbivores.

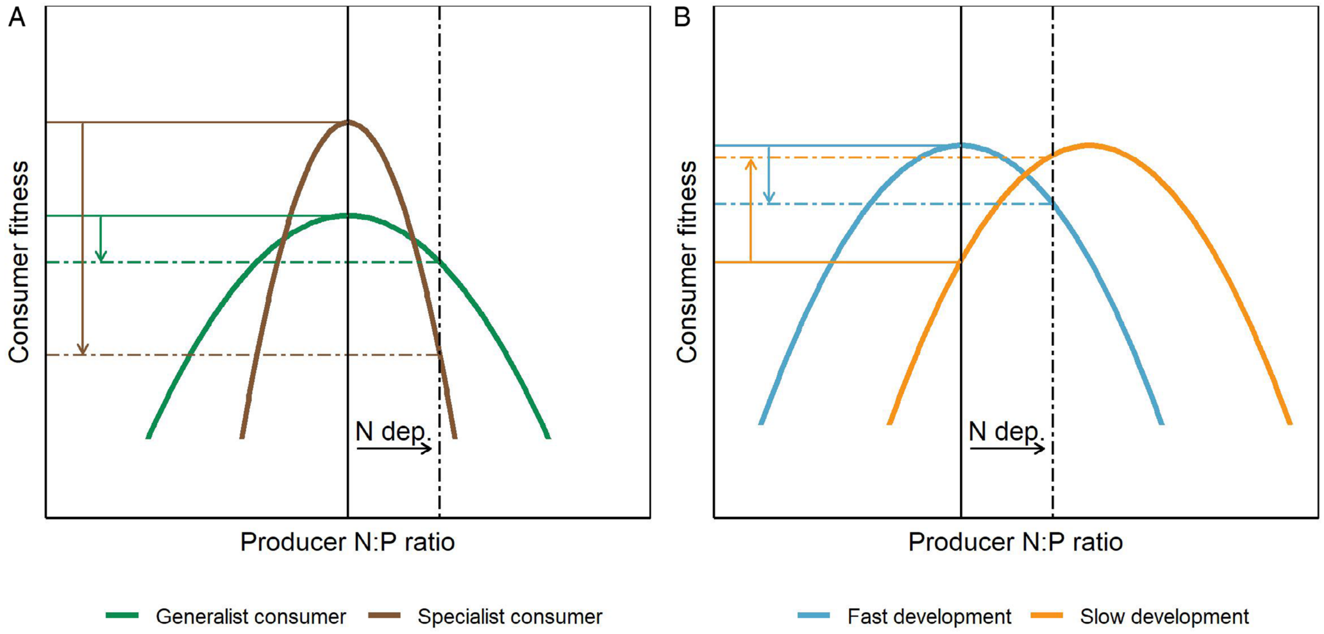

Fig. 3. Conceptual representation of the fitness responses to changed producer tissue N:P ratio of a generalist *versus* specialist consumer (A), and species that differ in the location of the threshold elemental ratio (TER) due to different life-history strategies, here a fast-growing *versus* slow-growing consumer (B). Peaks of the quadratic curves represent the TER; fitness loss occurs when deviating from this TER. The solid vertical line denotes producer N:P ratio under ambient conditions, and the dashed vertical line shows increased producer N:P ratios as result of N deposition (N dep.), indicated by the horizontal arrow. Solid horizontal lines indicate fitness of the corresponding consumer under ambient conditions, and dashed horizontal lines show the resulting fitness under N-deposition-mediated increases in N:P ratio. Vertical arrows indicate the degree and direction of fitness shifts resulting from a changed plant tissue N:P ratio.

might provide a valuable framework in future high N-deposition effect studies. We note, however, that not all consumers are equally likely to encounter negative consequences of N-deposition-mediated shifts from N limitation to limitation by P. For example, phloem feeders circumvent whole plant tissue feeding by only ingesting dissolved nutrients. As the N:P ratio of phloem sap is often much lower than that of leaf tissue (Tao & Hunter, 2012), phloem feeders are typically highly N limited, and a shift to P limitation under increased N deposition is therefore highly unlikely to occur.

IV. OTHER ELEMENTS ECOLOGICAL STOICHIOMETRY RESPONSES TO INCREASED N DEPOSITION

(1) Elemental mismatch between producers and consumers

Other elements than C, N, and P are also essential for the functioning of organisms. In producers and consumers, elements such as potassium (K), calcium (Ca) and magnesium (Mg) are required for cellular functioning and homeostatic regulation. Moreover, trace metals such as iron (Fe), zinc (Zn), manganese (Mn), nickel (Ni), copper (Cu) and cobalt (Co) play key roles in various enzymatic processes, all potentially influencing growth of primary producers as well as consumers (Twining & Baines, 2013). In consumers, metal ions furthermore play a role in enforcing physical structures such as mandibles and ovipositors (Mattson & Scriber, 1987; Quicke *et al.*, 2008; Polidori, García & Nieves-Aldrey, 2013). Of the 21 elements identified as essential for organismal functioning, six elements [sodium (Na), chromium (Cr), lithium (Li), arsenic (As), Ni and Co] are essential for consumers but not for producers, and six other essential elements (Ca, Fe, Mn, Zn and Cu) are found in substantially higher concentrations in herbivore consumers compared to producers (Kaspari, 2021). This means that the identities of macro- and micronutrients are not necessarily the same for consumers and producers. To avoid confusion, we here explicitly use the terms trace elements, micronutrients and macronutrients in reference to their increasing requirements (in abundance) for consumers.

In animal tissue, Na reaches concentrations several orders of magnitude higher compared to primary producers, and recent studies proved that plant tissue Na content often limits herbivore population density (Borer *et al.*, 2019; Prather *et al.*, 2018; Welti *et al.*, 2019, 2020). Grasshopper densities are also positively associated with plant tissue Mg, K and Cu content, indicating a role of trace elements in addition to Na (Joern, Provin & Behmer, 2011). The elemental composition of pollen varies considerably among species (Filipiak *et al.*, 2017), and for several trace elements the stoichiometric ratio between pollen and consumers is large enough to infer limitation for wild bee and honey bee populations (Filipiak, 2018; Filipiak *et al.*, 2017). Consumer tissue elemental content also influences the relative needs of consumers. In contrast to vertebrates, which have much higher body Ca content than most invertebrates as Ca is allocated in large quantities to bone formation, herbivorous invertebrates have much lower Ca demands. However, some groups such as isopods, millipedes and snails use Ca as a structural element in exoskeleton formation, and therefore do require higher quantities of Ca from their food (Graveland, 1995). In ungulate herbivores, deficiencies in Ca appear far less common than for other elements, including Na, Cu Zn, Mn, and Se (Ohlson & Staaland, 2001; Pareja-Carrera *et al.*, 2018; Huo, He & Shen, 2020; Estevez *et al.*, 2009; Becker, Kauffman & Anderson, 2010).

(2) N-deposition effects on producer elemental stoichiometry

Increases in N deposition may affect the relative content of micro- and macronutrients in producers. For example, the N:element ratios in terrestrial plant foliage has been found to increase through increased N uptake (Tian *et al.*, 2019), and trace element content of plant tissue has been found to decrease *via* dilution effects due to increased net primary production under increased N availability (Jonard *et al.*, 2015). In aquatic producers, trace element contents may similarly decrease due to growth dilution processes (Gormley-Gallagher, Douglas & Rippey, 2016), which may be induced by N deposition. N deposition may furthermore have indirect effects on trace elements. For example, increased soil acidification (partially attributable to N deposition; van Breemen *et al.*, 1984; Horswill *et al.*, 2008; Dorland *et al.*, 2013) may enhance trace element imbalance as the availability of base cations (Ca, Mg, K, Na) decreases and that of acid cations (Al, Fe, Mn) increases under increased soil acidification (Gilliam, Adams & Peterjohn, 2020). Furthermore, root uptake of trace elements can be disrupted as result of a N-deposition-driven increase in Al toxicity (Rout, Samantaray & Das, 2001; De Graaf *et al.*, 1997) and NH_4^+ toxicity (De Graaf *et al.*, 1998; Lucassen *et al.*, 2003; van den Berg *et al.*, 2005; Paulissen *et al.*, 2016; Gerendas *et al.*, 1997; Britto & Kronzucker, 2002), or through decreased root colonization and/or activity of mycorrhizal fungi under increased N deposition (de Witte *et al.*, 2017; Yesmin, Gammack & Cresser, 1996). Overall, N deposition is expected to reduce both the relative and absolute quantities of trace elements and macronutrients in producers.

(3) N-deposition-driven elemental stoichiometry effects on consumers

Currently, only weak evidence exists that enhanced N deposition induces a shortage, excess, or imbalance of (trace) metals for consumers (Nijssen *et al.*, 2017; Baines *et al.*, 2016), revealing a major knowledge gap in our understanding of the impacts of producer nutrition on consumer performance. The impact of N deposition on elemental mismatch may, however, be as large as those reported for mismatches in C:N:P stoichiometry. For instance, shifts in the elemental composition of both producer and consumer was shown to explain the variation in response of an aquatic consumer toward P limitation (Jeyasingh *et al*., 2020). Such responses may become more common when high N deposition leads to a shift from N to P limitation, although such responses in both producers and consumers remain to be tested. Moreover, N-deposition-driven acidification of soils may affect consumers with Ca-bearing exoskeletons, such as isopods, millipedes and snails, as this exoskeleton will dissolve at low pH. This in turn has been linked to Ca deficiency in vertebrates, like insectivorous birds that supplement their diet with Ca-rich food (Graveland & Van Gijzen, 1994; Bures & Weidinger, 2003; Dawson & Bidwell, 2005; Gosler & Wilkin, 2017; Graveland *et al*., 1994; Ormerod *et al*., 1991; Tyler & Ormerod, 1992; Mahony, Nol & Hutchinson, 1997). Such Ca deficiencies affect reproductive success (Graveland & vanderWal, 1996; Graveland & Drent, 1997) and community structure (Schlender *et al*., 2007) of birds. Ramsay & Houston (1999), however, found no evidence for Ca deficiency, even under highly acidified site conditions. Different Ca-uptake strategies among bird species (Schlender *et al*., 2007) have been proposed to determine species sensitivity to reduced Ca availability. However, even at sites without apparent Ca deficiencies, application of Ca increased snail abundance and population density of various bird species (Pabian *et al*., 2012; Pabian & Brittingham, 2007, 2011).

V. NUTRITIONAL GEOMETRY RESPONSES TO INCREASED N DEPOSITION

(1) Protein and carbohydrate intake regulation

The production of proteins and other biochemicals rich in N is strongly regulated by the availability of N, and generally increases with N deposition when limitation is alleviated. By contrast, production of C-rich carbohydrates and fatty acids was shown generally to increase when C is in relative excess (Sterner & Elser, 2002; Geider & La Roche, 2002; Gao *et al*., 2018). In consumers, mechanisms have evolved that enable regulated intake of these nutrients (Fig. 4A, B; Behmer, 2009), by steering feeding volume (compensatory feeding) and feeding selection (complementary feeding) in response to the relative availability of these nutrients in their food (Bernays & Bright, 1991; Berner, Blanckenhorn & Korner, 2005; Fig. 4A). The degree to which consumers regulate protein intake differs among species, life stages and life-history strategies (Raubenheimer & Simpson, 1993, 2004; Simpson *et al*., 2002), and the species-specific optimum protein: carbohydrate intake ratio can also differ markedly among consumers, often even among co-occurring closely related species (Behmer & Joern, 2008).

The degree to which animals regulate their protein and carbohydrate intake can be visualised using intake arrays (Fig. 4; Behmer, 2009; Simpson & Raubenheimer, 1993). By plotting the cumulative amount of protein and carbohydrate consumed by a consumer forced to feed on a specific biochemical ratio (Fig. 4B) for several of these ratios (Fig. 4C, D), the resulting intake pattern can be assessed visually and compared to the ideal ratio, defined as the intake target. Using these arrays, two often-encountered intake optimization rules can be identified. Consumers utilising the closest distance rule (Fig. 4C) regulate intake and excess intake to closely optimise the resulting total intake towards the target, resulting in an arch-shaped pattern around the intake target (Raubenheimer & Simpson, 1993). Consumers utilising the fixed proportion rule (Fig. 4D) follow a life-history strategy in which consuming an excess of nutrient X is helpful in achieving maximum assimilation efficiency of nutrient Y and *vice versa*, resulting in an inclined line through the intake target (Raubenheimer & Simpson, 2003). Early-instar nymphal *Locusta migratoria* and *Schistocerca gregaria* follow the closest distance rule, while in adults an intake array indicating fixed proportion rule emerges (Raubenheimer & Simpson, 1993, 2003, 2004). In *S. gregaria*, solitary phases follow the closest distance rule, while gregarious individuals ingested more of an excess nutrient, resulting in a fixed proportion intake array (Simpson *et al*., 2002). This shift has been attributed to differences in the chance of encountering complementary food items in the environment. Solitary individuals have a lower probability of encountering complementary food items than do gregarious individuals, resulting in an evolutionary pressure stimulating the gregarious phase to ingest more excess nutrients. Generalist herbivores often show a fixed proportion intake strategy, while specialists often strictly regulate intake in order to minimise associated fitness costs and, hence, should follow the closest distance strategy (Behmer, 2009). Another important finding is that excretion of excess protein comes with relatively high costs compared to carbohydrates, resulting in a generally more strict intake regulation for protein than that for carbohydrates (Behmer, 2009).

While intake regulation for protein and carbohydrates is well documented, evidence for compensatory or complementary feeding behaviour for P-containing compounds is less unequivocal. For terrestrial invertebrates, compensatory feeding for P is rarely found, even when fitness was significantly influenced by P intake relative to N intake (Perkins *et al*., 2004; Visanuvimol & Bertram, 2010; but see Cease *et al*., 2016; Harrison *et al*., 2014). For vertebrate ungulates however, compensatory feeding for P through geophagia and/or osteophagia has been well documented (Blair-West *et al*., 1989; Dixon *et al*., 2019; Wallisdevries, 1996), which may have evolved as a result of relative high P requirements for bone formation in this group (Sterner & Elser, 2002). Various studies on aquatic herbivores also provide evidence of compensatory feeding through higher feeding rates under P-limited conditions (Fink & Von Elert, 2006; Suzuki-Ohno, Kawata & Urabe, 2012; Zhou & Declerck, 2019). Whether compensatory feeding for P is indeed more common in aquatic invertebrates and terrestrial vertebrates as compared to terrestrial invertebrates, remains to be elucidated. Either way, the degree to which a species exhibits

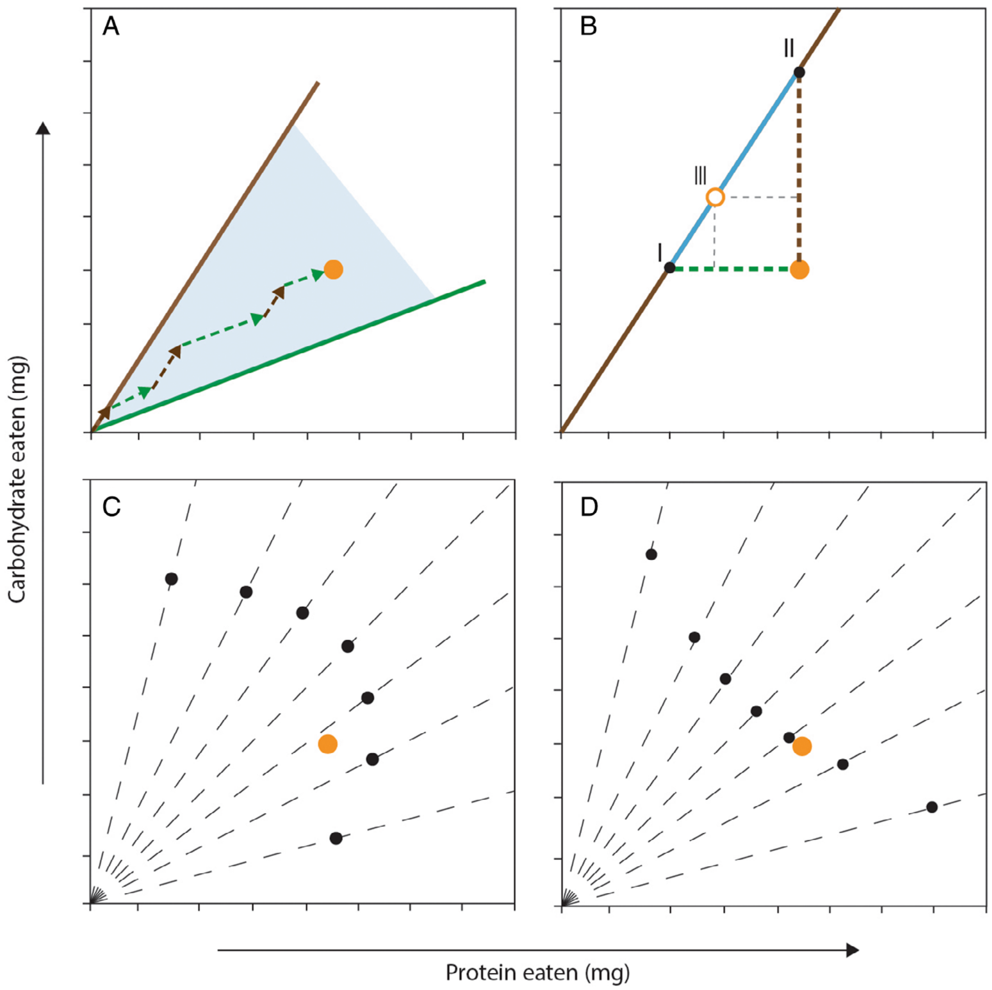

Fig. 4. Summary of the geometric framework [A and B derived from Behmer (2009); C and D derived from Raubenheimer & Simpson (2004)]. The intake target for protein and carbohydrate (yellow dot) is the amount and ratio of protein and carbohydrate where maximum fitness is realised. (A) Consumers that are allowed to feed on two complementary nutritionally imbalanced food items are able to reach the intake target by switching meals (arrows) depicted by brown and green lines. (B) If a consumer is confronted with food of suboptimal quality without the ability to mix diets, it can choose to eat until it reaches the intake target for carbohydrate (position I), resulting in protein-intake deficit; to eat until it reaches the intake target for protein (position II), resulting in excess carbohydrate intake; or to reach a point of compromise, relatively close to the intake target (position III). (C) Species that exhibit the closest distance approximation employ a feeding strategy that results in a 'best approach' to the specific intake target when fed with food types differing in protein:carbohydrate ratios (depicted as dotted lines), resulting in an intake array of realised intake levels (black dots) resembling a concave curve surrounding the intake target. (D) Species that employ a fixed proportion feeding strategy (Raubenheimer & Simpson, 2003) allow for overeating the excess nutrient relative to the limiting nutrient, resulting in a straight line or slightly convex curve surrounding the intake target. The extent to which a consumer employs either of these strategies is correlated with diet breadth and life-history strategy (Raubenheimer & Simpson, 2003).

compensatory feeding for P will ultimately affect its sensitivity to P limitation.

(2) Differential effects of N deposition on feeding strategies

The effects of N deposition on consumer performance have not been studied within the nutritional geometric framework, but the general rules identified from this field of study allow us to make several predictions. First, nutritional geometry studies make clear that different species have distinctly different intake targets, both in absolute amounts of required nutrient intake and in protein: carbohydrate ratios, analogous to the TER concept in ecological stoichiometry. N-deposition-driven changes in producer protein:carbohydrate ratios will benefit those species with intake targets that match the resulting producer ratio more closely, while species that experience a distancing from their optimal intake target will experience fitness declines. Second, species that perform a strict intake-regulation strategy (i.e. closest distance optimizers) will experience greater fitness costs when N deposition shifts the protein: carbohydrate ratio away from the intake target. Third, consumers that mainly regulate for protein intake (i.e. avoid overconsumption of N) will most likely experience reduced fitness due to N-deposition-driven increased protein content, since this regulation strategy reduces their ability to account for accompanying dilution effects of other elements, including P (for terrestrial consumers) and all other macro- and micronutrients. Fourth, analogous to predictions from a stoichiometric perspective, N-deposition-mediated changes in protein: carbohydrate ratios will affect low-dispersing host-plant specialists (closest distance optimizers) to a much greater degree than high-dispersing host-plant generalists (fixed proportion optimizers).

VI. ESSENTIAL MICRONUTRIENTS RESPONSES TO INCREASED N DEPOSITION

(1) Amino acids

As shortage of a single amino acid (AA) can limit the production of particular proteins and thereby disrupt the cellular processes that these proteins govern (e.g. enzymes), essential AAs can be seen as micronutrients. Many studies link high N deposition to changes in AA physiology in plants. The composition of free AAs changes markedly as a result of high N availability (Perez-Soba, Stulen & Vandereerden, 1994; Huhn & Schulz, 1996), and the accumulation of free AAs, especially the relatively N-rich arginine, is even used as a biomarker for N deposition (e.g. Pitcairn *et al.*, 2003). However, total AA composition did not differ between plants under high or low N deposition (van den Burg *et al.*, 2014; Nijssen & Siepel, 2010). Most AAs are incorporated into protein, and RuBisCO, the most common protein in plants as it is responsible for CO_2 fixation, is also used as AA storage protein. The AA composition of this protein will thus largely reflect whole plant tissue AA composition, even under increased N availability. However, minor reductions of less-dominant AAs, which do not stand out in the entire plant AA profile may still be critically important for herbivores that rely on the availability of such AAs. The composition and levels of AAs in *Daphnia magna* remained largely unaltered across a range of food quality treatments (Taipale *et al.*, 2018). However, when *Daphnia magna* was stripped of its microbiome, its population development and fecundity showed a strong decrease that may have resulted from limitation of essential AAs otherwise provided by bacteria (Peerakietkhajorn *et al.*, 2015). In terrestrial invertebrates, aphids are known to rely on AA-synthesising *Buchnera* symbionts that allow the host to feed on phloem sap, which has a highly imbalanced AA composition (Douglas, 2003). Such provisioning of biochemicals by the microbiome may provide invertebrate hosts with higher resilience to N-deposition-driven AA deficiency. However, the existence and strength of such symbiotic relationships likely differs across invertebrate consumer species. In bird studies, symptoms of AA deficiencies in eggs are observed frequently, but these cannot be readily attributed to N deposition as this requires a more thorough understanding of the reproduction strategy, dietary and other sources of AAs, and how these are affected by N deposition (Van den Burg, 2021). Because such data are largely unavailable, we cannot assess whether AA deficiencies in wild birds occur due to N deposition. However, signs of AA limitation were found in producers, insectivores and predators in forests experiencing high N deposition (van den Burg *et al.*, 2014).

(2) Fatty acids

Eutrophication and N-deposition-driven shifts in the primary producer community composition can alter fatty acid (FA) availability in aquatic ecosystems. FA deficiencies are mostly reported for consumers in aquatic ecosystems and often involve linoleic acid, linolenic acid, or long-chained poly unsaturated FAs (PUFAs) with two unsaturated carbon bonds, and highly unsaturated FAs (HUFAs) with 3–6 unsaturated carbon bonds (Gomes *et al.*, 2016; Twining *et al.*, 2016; Thomas *et al.*, 2022). Docosahexaenoic acid (DHA) is among the most dominant HUFAs present in aquatic consumers, and changes in DHA concentrations in the food may alter their performance (Twining *et al.*, 2016; Thomas *et al.*, 2022). Variations in DHA content in producers may derive from shifts in the abundance of single producer species, as well as shifts in producer community composition because phylogenetic groups vary in their DHA content. For example, diatoms and dinoflagellates contain low levels of DHA, while levels in chlorophytes and cyanobacteria are higher (Gomes *et al.*, 2016). Terrestrial plants contain PUFAs but few HUFAs, presumably because the double bonds in these compounds are easily broken by oxygen or reactive oxygen species in the atmosphere (Twining *et al.*, 2016).

HUFAs are necessary to maintain membrane fluidity and are precursors to vital signalling molecules such as the eicosanoids, which have key functions in the regulation of inflammatory diseases (Gomes *et al.*, 2016). In zooplankton, shortages of HUFAs result in reduced growth rates and fecundity, and similarly in fish larvae HUFA limitation led to reduced growth and survival (Taipale *et al.*, 2018). As HUFAs are vital for organismal functioning, they are bioaccumulated, preferentially stored, and spared in fat burning as compared to other FAs (Twining *et al.*, 2016). As a result, carnivores are expected to be less prone to HUFA deficiencies compared to first-order consumers (Larson *et al.*, 2017). Animals that have diets typically rich in HUFAs and/or DHA have poor to no capacity to make these compounds from PUFA precursors (Twining *et al.*, 2016), including aquatic first-order consumers like *Daphnia* (Larson *et al.*, 2017). If N deposition promotes protein synthesis and cellular growth, thereby increasing HUFA demand, this may lead to HUFA deficiencies, particularly in aquatic consumers, which will be aggravated when N deposition favours low-HUFA-containing species like diatoms (Gomes *et al.*, 2016).

(3) Vitamins

Vitamins play an essential role in a range of cellular functions including growth, reproduction, C assimilation, and DNA synthesis. There is a lack of direct reports on the relationships between N deposition and vitamin contents, although for vitamins A, B1, B2, and B12 reduced trace element availability resulting from soil acidification or changes in AA composition might ultimately result in shortages of these vitamins.

Vitamin A has an important function in visual perception as well as in growth and reproduction, maintenance of mucous membranes, and in controlling cerebrospinal fluid pressure (Leeson & Summers, 2001). Vitamin A deficiencies are not likely to arise from a lack of dietary intake but could be a result of Zn deficiency, which is essential for enzymatic synthesis of vitamin A (Smith *et al.*, 1973; Smith, 1980; Dijkhuizen & Wieringa, 2001). Deficiency in Zn resulting from soil acidification can ultimately lead to Vitamin A deficiency symptoms in consumers.

Riboflavin (vitamin B2) is a precursor molecule of two redox coenzymes, both essential in the Krebs cycle and also in the beta-oxidation of fatty acids (McDonald *et al.*, 1995). Production of riboflavin in producers is probably not affected by N deposition, but riboflavin binding proteins in consumers may be reduced due to deficiencies in essential AAs (van den Burg *et al.*, 2014), and these deficiencies may then cascade higher up the food chain. Riboflavin concentrations in eggs of great tits (*Parus major*) are lower in forests affected by N deposition and soil acidification, and embryos in failed eggs of sparrowhawks (*Accipiter nisus*) often show signs of vitamin B2 deficiency (van den Burg, 2009). Riboflavin deficiency symptoms in consumers may be best understood as a side effect of AA deficiencies (van den Burg *et al.*, 2014), but this hypothesis remains to be tested.

Cobalamin (vitamin B12) is an animal vitamin containing the element Co, and sources of cobalamin in primary producers are scarce (Milewski & Diamond, 2000; Leeson & Summers, 2001). Cobalamin is involved in DNA and AA synthesis, FA and carbohydrate metabolism, red blood cell synthesis and myelin production in the nervous system (Leeson & Summers, 2001). Soil acidification can cause leaching of Co and thereby lead to reduced Co availability (Daroub & Snyder, 2007). Large herbivores have been proposed to be particularly susceptible to Co limitation and resulting cobalamin deficiency (Milewski & Diamond, 2000). However, cobalamin is actively stored in liver tissue (McDonald *et al.*, 1995), and shortage will only occur under chronic Co limitation. Cobalamin deficiency can thus be regarded as a possible secondary effect of N deposition, promoted by increased soil acidification.

Thiamine (Vitamin B1) is a co-factor in many physiological pathways, such as carbohydrate and AA metabolism (Ejsmond *et al.*, 2019). Its key functions make thiamine a vital compound for plants, many microbes, and animals. Thiamine synthesis is limited to plants, fungi and microbes, and among these taxa some can completely synthesise thiamine while others need precursor molecules (Kraft & Angert, 2017; Ejsmond *et al.*, 2019). Thiamine deficiency in consumers can lead to impaired functioning of mitochondria, nervous system and the immune system (Kraft & Angert, 2017), ultimately resulting in reproductive failure, increased mortality and possibly also population decline in the case of systemic thiamine deficiency (Ejsmond *et al.*, 2019). Thiamine deficiency can occur in aquatic ecosystems, caused by the production of thiaminases as antifeedants in planktonic algae (Kraft & Angert, 2017; Harder *et al.*, 2018). However, some fish species appear to accumulate thiaminases from their food without any detrimental fitness effects (Kraft & Angert, 2017) and use these accumulated enzymes as antifeedants against higher order carnivores themselves. As such, thiaminase-induced thiamine deficiencies can alter population dynamics throughout the entire food chain. Eutrophication can cause shifts in the algal community resulting in higher thiaminase production, especially by cyanobacteria (Sylvander, Häubner & Snoeijs, 2013). As such, thiaminase-induced thiamine deficiencies can alter population dynamics throughout the entire food chain and will occur more frequently under increased nutrient inputs.

To summarise, there is some evidence that N deposition may lead to changes in AA, FA and vitamin availability in producers, which may have negative consequences for first and higher order consumers. However, detailed knowledge is still largely lacking.

VII. ALLELOCHEMICALS RESPONSES TO INCREASED N DEPOSITION

(1) Antifeedants *versus* toxins

Secondary compounds may protect producers against consumers, and can generally be subdivided into two groups, antifeedants and toxins (van Genderen *et al.*, 1996). Compounds that (mainly) function *via* impairment of nutrient uptake efficiency are here referred to as antifeedants, while those that function *via* impairment of vital organismal functioning of consumers (e.g. blocking or disruption of signal transduction in synaptic transfer) are referred to as toxins. In general, N-containing secondary compounds act more often as toxins, leading to impaired functioning of consumers through direct toxic effects on organismal functioning. Such compounds include non-proteinogenic AAs, cyanogenic glycosides, alkaloids and glucosinolates (Palo & Robbins, 1991; van Genderen *et al.*, 1996). Strictly C-based compounds can function either as antifeedants, including (condensed) tannins, latex-forming polyisoprenes, and lignin, or as toxins, including flavonoids, terpenes, and steroids. In aquatic ecosystems, phytoplankton can also produce a range of toxic compounds that may, in some cases, negatively affect consumers, although the ecological roles of these compounds as grazing deterrents is still under debate (Cusick & Sayler, 2013; Ger, Hansson & Lurling, 2014). Common toxins include N-rich alkaloids, such as saxitoxin, produced by cyanobacteria and dinoflagellates, as well as peptide-based microcystins and nodularins, produced by cyanobacteria

(Gobler *et al.*, 2016). During the course of evolution, many consumers co-evolved with host primary producer species and often have co-evolved physiological mechanisms that significantly reduce or nullify the phytotoxic effects of the allelochemicals produced by the host plant (Agrawal *et al.*, 2012). For specialist consumers, it is thus less likely that increased concentrations of phytotoxins in their food will lead to highly impaired functioning. For generalist consumers however, increased phytotoxin concentrations will often result in strong negative responses as these organisms usually show poor growth and survival on these plants (Agrawal *et al.*, 2012). For consumers feeding on plants utilising an antifeedant strategy, both specialist and generalist consumers will show comparable growth impairment under increased antifeedant concentrations in the food plant, as these compounds act more generally on the efficacy of nutrient acquisition, affecting specialists and generalist consumers equally.

(2) Impact of N deposition on producers

N deposition exerts effects on the producer organisms' defence system and thus affects producer quality for consumers. In aquatic systems, phytoplankton cellular levels of N-containing compounds such as saxitonin and microcystins were shown to depend strongly on N availability and decrease when N was limited (Gobler *et al.*, 2016; Van de Waal *et al.*, 2009, 2013). With excess N under P limitation, cellular levels of these compounds were also shown to increase (Van de Waal *et al.*, 2013; Brandenburg *et al.*, 2020). Thus, N-containing toxins depend directly on N availability, and generally increase when phytoplankton cells contain a relative excess of N over C and/or P. Moreover, several toxic and/or allelopathic compounds in harmful algal bloom species were shown to be inversely related to nutrient availabilities. This may be due to an increase in C-based allelochemicals, which were shown to increase under N- and P-limited conditions (Van de Waal *et al.*, 2014). Enhanced N deposition may thus stimulate synthesis of some secondary compounds, while limiting the synthesis of others (Granéli, Weberg & Salomon, 2008). In aquatic as well as terrestrial systems, a general rule is that with increasing N input, levels of N-containing allelochemicals are elevated, but those of C-based antifeedants are reduced (Hofland-Zijlstra & Berendse, 2009; Bandau *et al.*, 2015; Campbell & Vallano, 2018; Nybakken *et al.*, 2018). In a recent meta-analysis of N-deposition experiments in terrestrial ecosystems, concentrations of C-based secondary compounds (polyphenolics and phenolics) were found to significantly decrease with increased N supply (Sun *et al.*, 2020). The proposed mechanism responsible for this effect is prioritising the use of C for growth instead of defence when C becomes more limiting (Nybakken *et al.*, 2018). However, under conditions of chronic increased N input, soil acidification often results in severe growth impairment (Emmett *et al.*, 1998). Thus, under chronic or high N-deposition levels, growth dilution effects on C-based secondary compounds may be reduced or nullified.

(3) Consequences of N deposition for consumers

Only a few studies directly assessed the impacts of N deposition on the synthesis of antifeedants and toxins, and their consequences for higher trophic levels. Yet, various studies assessed responses towards N availability. For example, in terrestrial systems, high foliar NO_x exposure was shown to increase plant tissue alkaloid concentrations, resulting in reduced caterpillar performance (Campbell & Vallano, 2018). In a N-fertilisation experiment with Douglas fir (*Pseudotsuga menziesii*), increasing N supply resulted in reduced concentration of phenolics (Joseph *et al.*, 1993). Consequently, growth of gypsy moth (*Lymantria dispar*) caterpillars feeding on high-N- (and hence low-phenolic-)containing needles was significantly higher. However, to what degree lower phenolics contribute to an increase in growth remains unclear, since it coincided with higher N content of the needles, which also proved beneficial for caterpillar growth. For instance, an increase in larval developmental rate of winter moth (*Operophtera brumata*) caterpillars, a generalist species feeding on woody plant leaves, was shown to result solely from an increase in food quality (here lower C:N ratio of *Calluna vulgaris*; Kerslake *et al.*, 1998), because phenolic content did not change significantly in N-treated plants in this study. In aquatic systems, toxic secondary compounds produced by phytoplankton may have negative effects on grazers, including immobilisation, reduced growth, and mortality (e.g. see Turner, 2006; Ger *et al.*, 2016). Although toxins in phytoplankton generally follow clear nutrient-dependent shifts, and may thereby alter consumer performance, this has not explicitly been assessed. Moreover, the relationship between toxin content and grazer performance is complicated by a number of factors, including evolutionary adaptation of grazers in their detoxification, and/or the ability of some zooplankton species to feed selectively on more edible, less toxic phytoplankton (Turner & Tester, 1997; Ger *et al.*, 2016; Turner, 2006).

In summary, impacts of increased N deposition on allelochemicals are non-linear and depend on the nature of nutrient limitation of the producer, the allelochemical involved and the elements they contain (C-based *versus* N-containing), their mode of toxicity and the strategy of the consumer to cope with allelochemicals. Other modulating factors include the effects of soil acidification on allelochemical production and growth dilution, and the effect of N-deposition-driven changes in producer community structure and subsequent changes in allelochemical composition of the producer community. Future studies integrating these aspects are required to understand better the potential consequences of N deposition on producer–consumer interactions in aquatic and terrestrial systems.

VIII. DISCUSSION AND FUTURE PERSPECTIVES

Highly increased deposition of N can impact the nutritional quality of producers through several pathways, ranging from relatively straightforward changes (C:N:P stoichiometric shifts), through secondary changes (nutrient dilution and/or acidification impacts), to complex interactions involving biochemical synthesis processes. The latter may, for example, involve secondary changes in the synthesis and availability of AAs, FAs, vitamins and allelochemicals. Currently, the majority of published work focuses on the least complex ecological stoichiometry framework, and only a small number of papers exist on how N deposition modulates biochemical synthesis pathways. This means that for a mechanistic understanding of the impacts of N deposition on food quality for consumers and its consequences in the food web, much progress still has to be made, especially in the emerging fields of ionomics (i.e. elemental stoichiometry beyond C:N:P) and metabolomics (i.e. vitamins, AAs, FAs). The role of trace elements and micronutrients as (co-)limiting nutrients, influencing species performance and community composition is, however, becoming increasingly apparent (Kaspari & Powers, 2016). Aside from Ca limitation in vertebrate insectivores driven by soil acidification, studies on the effects of highly increased N deposition on producer–consumer elemental stoichiometric interactions are largely lacking. Even fewer studies are available on the effects of N deposition on the metabolome of producers and the resulting impacts on consumer populations. These limitations aside, the current available literature reviewed here leads us to several conclusions, predictions and hypotheses that may aid in focusing future research efforts and directions.

First, based on our findings and perhaps the most obvious, we conclude that a change in producer quality induced by N deposition is most pronounced in naturally oligotrophic ecosystems. Such environments are often naturally co-limited by N and P and increasing N availability therefore often results in increasing P limitation in both producers and consumers. Often, these same environments are also vulnerable to acidification, resulting in decreased trace-element availability or changed elemental ratios in producers, potentially affecting consumer fitness.

Second, we show that N deposition-driven changes in C:N:P and elemental ratios in producers can lead to changes in biosynthesis pathways, ultimately affecting micronutrient availability and antifeedant or toxin concentrations in producers. Studies are needed to unravel both direct impacts of N deposition on complex nutritional pathways, such as essential AAs, allelochemicals, FAs and vitamin synthesis, as well as indirect impacts through community shifts in producers, soil acidification and trace element limitation.

Third, the degree and direction of a consumer's fitness response to changed producer quality are not equal but depend on the life-history strategy of the consumer. Specifically, the direction of a consumer's response to changes in producer C:N:P stoichiometry will depend on the relative mismatch with the consumer-specific TER, while the magnitude of such a change will depend on the degree of C:N:P homeostasis. This homeostasis, in turn, is shaped by the consumers phylogeny, ontogeny and physiology.

Fourth, the nutrient intake strategy of a consumer further determines its sensitivity to N-deposition-mediated changes in producer quality. A thorough understanding of nutritional intake regulation mechanisms, which are often linked to specific life-history strategies and/or life stages of the consumer, is therefore pivotal in order to predict consumer responses to changed food quality.

The effect of N deposition through essential metabolites and allelochemicals is also partially determined by species traits and life-history strategies, including feeding guilds, trophic level and the presence or absence of endosymbionts. Future studies aiming to understand the impact of N deposition on either individual consumer species or community responses should link soil, water and producer chemical and physiological mechanisms to species traits, trait combinations and life-history strategies of consumers (Fig. 1; see Table 1 for additional trait interactions with altered C:N:P stoichiometry).

Building on trait-based approaches to consumer nutrition under increased N deposition, we hypothesise the following:

(1) Specialist consumers of naturally nutrient-poor producers are more likely to experience fitness loss resulting from high N deposition. (*i*) Species with high relative growth rates (RGRs), with corresponding high P demands, or species specialised on low N:P producers are more likely to experience fitness loss, while slow-growing generalist species are less likely to experience severe fitness costs. (*ii*) Generalist species adapted to high-N producers or species feeding on extremely low-N:P food (e.g. phloem feeders) are likely to experience fitness benefits.
(2) Invertebrates with holometabolous development are more vulnerable to changes in food quality than hemimetabolous species, due to generally lower body N:P ratios and their inability to compensate for nutrient shortages during pupal development.
(3) Differences in life-history strategies result in different elemental composition of consumers, and these are often shaped by physiological and physical properties (e.g. bone formation, cuticular hardening) of the consumer. N-deposition-induced changes in producer elemental stoichiometry will differentially affect consumer fitness through these differences in consumer elemental composition.
(4) The fitness response to deficiencies in complex metabolites is likely to differ greatly across species, with species relying on these metabolites from food sources experiencing major fitness costs compared to species that can synthesise these metabolites themselves. This should result in a higher incidence of fitness losses in species higher up in the food chain, as the ability to synthesise complex biochemicals has often been lost in predators and parasites during evolutionary history.
(5) Consumer species specialised on producers that synthesise N-containing allelochemicals will only show a moderate fitness decline under increased N deposition, while generalist consumer species feeding on such producers will suffer stronger fitness loss under high N deposition. By contrast, generalist consumer species will increase in fitness when feeding on plants utilising a C-based phytotoxic and/or antifeedant strategy, resulting in more frequent pest outbreaks.

Overall, we hypothesise that N-deposition-induced changes in producer quality generally result in a net decrease in absolute and functional diversity of the consumer community (Haddad, Haarstad & Tilman, 2000; Nessel *et al.*, 2021), as the above-mentioned hypothesised mechanisms will promote outbreak events of a small subset of (often generalist) species, and concomitant declines in a multitude of other (often specialist) species. The proposed hypotheses should be tested using field and laboratory experiments in order to increase our mechanistic understanding of the effects of increased N deposition on consumers. The emerging insights will provide a scientific basis for predicting the outcomes of emission-reduction measures and should help to improve restoration measures to mitigate the environmental impacts of increased atmospheric deposition of reactive N compounds.

IX. CONCLUSIONS

(1) N-deposition-driven producer quality change is most pronounced in naturally oligotrophic, poorly buffered ecosystems.
(2) Changes in C:N:P and other elemental ratios in producers can underlie changes in biosynthesis pathways, affecting essential metabolite availability and antifeedant or toxin concentration in producers.
(3) The degree and direction of a consumer's fitness response to a change in producer quality can be predicted by the life-history strategy and the nutrient intake strategy of the consumer.
(4) Linking soil, water and producer chemical and physiological mechanisms to consumer species traits, trait combinations or life-history strategies has proved invaluable in predicting species responses in nutritional ecology. We propose five hypotheses that incorporate trait-based approaches to N-deposition-driven changes in consumer nutrition.
(5) Overall, we hypothesise that N-deposition-induced changes in producer quality result in a net decrease in absolute and functional diversity of the consumer community, with increased pest outbreaks of a small number of mostly generalist species and decreased performance in a multitude of mostly specialist species.

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XI. REFERENCES

Abisgold, J. D. & Simpson, S. J. (1988). The effect of dietary protein levels and haemolymph composition on the sensitivity of the maxillary palp chemoreceptors of locusts. *Journal of Experimental Biology* **135**(1), 215–229.

Aerts, R. & Bobbink, R. (1999). The impact of atmospheric nitrogen deposition on vegetation processes in terrestrial, non-Forest ecosystems. In *The Impact of Nitrogen Deposition on Natural and Semi-Natural Ecosystems* (ed. S. J. Langan), pp. 85–122. Springer, Dordrecht.

Agrawal, A. A., Petschenka, G., Bingham, R. A., Weber, M. G. & Rasmann, S. (2012). Toxic cardenolides: chemical ecology and coevolution of specialized plant–herbivore interactions. *New Phytologist* **194**(1), 28–45.

Andrieux, B., Signor, J., Guillou, V., Danger, M. & Jabot, F. (2021). Body stoichiometry of heterotrophs: assessing drivers of interspecific variations in elemental composition. *Global Ecology and Biogeography* **30**(4), 883–895.

Apple, J. L., Wink, M., Wills, S. E. & Bishop, J. G. (2009). Successional change in phosphorus stoichiometry explains the inverse relationship between herbivory and lupin density on Mount St. Helens. *PLoS One* **4**(11), e7807.

Audusseau, H., Kolb, G. & Janz, N. (2015). Plant fertilization interacts with life history: variation in stoichiometry and performance in nettle-feeding butterflies. *PLoS One* **10**(5), e0124616. https://doi.org/10.1371/journal.pone.0124616.

Baines, S. B., Chen, X., Vogt, S., Fisher, N. S., Twining, B. S. & Landry, M. R. (2016). Microplankton trace element contents: implications for mineral limitation of mesozooplankton in an HNLC area. *Journal of Plankton Research* **38**(2), 256–270.

Bandau, F., Decker, V. H. G., Gundale, M. J. & Albrectsen, B. R. (2015). Genotypic tannin levels in *Populus tremula* impact the way nitrogen enrichment affects growth and allocation responses for some traits and not for others. *PLoS One* **10**(10), e0140971.

Becker, S., Kauffman, M. J. & Anderson, S. H. (2010). Nutritonal condition of adult female Shiras moose in Northwest Wyoming. *Alces* **46**, 151–166.

Behmer, S. T. (2009). Insect herbivore nutrient regulation. *Annual Review of Entomology* **54**, 165–187.

Behmer, S. T. & Joern, A. (2008). Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences* **105**(6), 1977–1982.

Bergström, A.-K., Karlsson, J., Karlsson, D. & Vrede, T. (2018). Contrasting plankton stoichiometry and nutrient regeneration in northern arctic and boreal lakes. *Aquatic Sciences* **80**(2), 24.

Bernays, E. A. & Bright, K. L. (1991). Dietary mixing in grasshoppers – switching induced by nutritional imbalances in foods. *Entomologia Experimentalis et Applicata* **61**(3), 247–253.

Berner, D., Blanckenhorn, W. U. & Korner, C. (2005). Grasshoppers cope with low host plant quality by compensatory feeding and food selection: N limitation challenged. *Oikos* **111**(3), 525–533.

Blair-West, J. R., Denton, D. A., Nelson, J. F., McKinley, M. J., Radden, B. G. & Ramshaw, E. H. (1989). Recent studies of bone appetite in cattle. *Acta Physiologica Scandinavica. Supplementum* **583**, 53–58.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., et al. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* **20**(1), 30–59.

Bobbink, R., Hornung, M. & Roelofs, J. G. M. (1998). The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* **86**, 717–738.

Boersma, M. & Elser, J. J. (2006). Too much of a good thing: on stoichiometrically balanced diets and maximal growth. *Ecology* **87**(5), 1325–1330.

Borer, E. T., Lind, E. M., Firn, J., Seabloom, E. W., Anderson, T. M., Bakker, E. S., Biederman, L., La Pierre, K. J., MacDougall, A. S., Moore, J. L., Risch, A. C., Schutz, M. & Stevens, C. J. (2019). More salt, please: global patterns, responses and impacts of foliar sodium in grasslands. *Ecololy Letters* **22**(7), 1136–1144.

Brandenburg, K., Siebers, L., Keuskamp, J., Jephcott, T. G. & Van de Waal, D. B. (2020). Effects of nutrient limitation on the synthesis of N-rich phytoplankton toxins: a meta-analysis. *Toxins* **12**(4), 221.

Britto, D. T. & Kronzucker, H. J. (2002). NH_4^+ toxicity in higher plants: a critical review. *Journal of Plant Physiology* **159**(6), 567–584.

Brunsting, A. M. H. & Heil, G. W. (1985). The role of nutrients in the interactions between a herbivorous beetle and some competing plant species in heathlands. *Oikos* **44**(1), 23–26.

Bures, S. & Weidinger, K. (2003). Sources and timing of calcium intake during reproduction in flycatchers. *Oecologia* **137**(4), 634–641.

Burian, A., Grosse, J., Winder, M. & Boschker, H. T. S. (2018). Nutrient deficiencies and the restriction of compensatory mechanisms in copepods. *Functional Ecology* **32**(3), 636–647.

Campbell, S. A. & Vallano, D. M. (2018). Plant defences mediate interactions between herbivory and the direct foliar uptake of atmospheric reactive nitrogen. *Nature Communications* **9**(1), 4743.

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kwak, M. L., Mammola, S., Ari Noriega, J., *et al.* (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation* **242**, 108426.

Carnicer, J., Brotons, L., Stefanescu, C. & Peñuelas, J. (2012). Biogeography of species richness gradients: linking adaptive traits, demography and diversification. *Biological Reviews* **87**(2), 457–479.

Carnicer, J., Sardans, J., Stefanescu, C., Ubach, A., Bartrons, M., Asensio, D. & Penuelas, J. (2015). Global biodiversity, stoichiometry and ecosystem function responses to human-induced C-N-P imbalances. *Journal of Plant Physiology* **172**, 82–91.

Carnicer, J., Stefanescu, C., Vila, R., Dincă, V., Font, X. & Peñuelas, J. (2013). A unified framework for diversity gradients: the adaptive trait continuum. *Global Ecology and Biogeography* **22**(1), 6–18.

Cease, A. J., Elser, J. J., Ford, C. F., Hao, S. G., Kang, L. & Harrison, J. F. (2012). Heavy livestock grazing promotes locust outbreaks by lowering plant nitrogen content. *Science* **335**(6067), 467–469.

Cease, A. J., Fay, M., Elser, J. J. & Harrison, J. F. (2016). Dietary phosphate affects food selection, post-ingestive phosphorus fate, and performance of a polyphagous herbivore. *Journal of Experimental Biology* **219**(1), 64–72.

Cech, P. G., Kuster, T., Edwards, P. J. & Olde Venterink, H. (2008). Effects of herbivory, fire and N_2-fixation on nutrient limitation in a humid African savanna. *Ecosystems* **11**(6), 991.

Couture, J. J., Servi, J. S. & Lindroth, R. L. (2010). Increased nitrogen availability influences predator-prey interactions by altering host-plant quality. *Chemoecology* **20**(4), 277–284.

Crutzen, P. J. (2002). Geology of mankind. *Nature* **415**(6867), 23.

Cusick, K. D. & Sayler, G. S. (2013). An overview on the marine neurotoxin, saxitoxin: genetics, molecular targets, methods of detection and ecological functions. *Marine Drugs* **11**(4), 991–1018.

Daroub, S. H. & Snyder, G. H. (2007). The chemistry of plant nutrients in soil. In *Mineral Nutrition and Plant Disease* (eds L. E. Datnoff, W. H. Elmer and D. M. Huber), pp. 1–7. The American Phytopathological Society, St. Paul.

Dawson, R. D. & Bidwell, M. T. (2005). Dietary calcium limits size and growth of nestling tree swallows *Tachycineta bicolor* in a non-acidified landscape. *Journal of Avian Biology* **36**(2), 127–134.

De Graaf, M. C. C., Bobbink, R., Roelofs, J. G. M. & Verbeek, P. J. M. (1998). Differential effects of ammonium and nitrate on three heathland species. *Plant Ecology* **135**(2), 185–196.

De Graaf, M. C. C., Bobbink, R., Verbeek, P. J. M. & Roelofs, J. G. M. (1997). Aluminium toxicity and tolerance in three heathland species. *Water Air and Soil Pollution* **98**(3–4), 229–239.

de Witte, L. C., Rosenstock, N. P., van der Linde, S. & Braun, S. (2017). Nitrogen deposition changes ectomycorrhizal communities in Swiss beech forests. *Science of the Total Environment* **605**, 1083–1096.

Dijkhuizen, M. A. & Wieringa, F. T. (2001). *Vitamin A, iron and zinc deficiency in Indonesia: micronutrient interactions and effects of supplementation*. PhD Thesis: Wageningen University.

Dixon, R. M., Fletcher, M. T., Goodwin, K. L., Reid, D. J., McNeill, D. M., Yong, K. W. L. & Petherick, J. C. (2019). Learned behaviours lead to bone ingestion by phosphorus-deficient cattle. *Animal Production Science* **59**(5), 921–932.

Dorland, E., Stevens, C. J., Gaudnik, C., Corcket, E., Rotthier, S., Wotherspoon, K., Jokerud, M., Vandvik, V., Soons, M. B., Hefting, M. M., Aarrestad, P. A., Alard, D., Diekmann, M., Dupre, C., Dise, N. B., *et al.* (2013). Differential effects of oxidised and reduced nitrogen on vegetation and soil chemistry of species-rich acidic grasslands. *Water Air and Soil Pollution* **224**(9), 13.

Douglas, A. E. (2003). The nutritional physiology of aphids. In *Advances in Insect Physiology* (Volume **31**), pp. 73–140. Academic Press, London.

Ejsmond, M. J., Blackburn, N., Fridolfsson, E., Haecky, P., Andersson, A., Casini, M., Belgrano, A. & Hylander, S. (2019). Modeling vitamin B1 transfer to consumers in the aquatic food web. *Scientific Reports* **9**(1), 10045.

Elser, J. J. (2011). A world awash with nitrogen. *Science* **334**(6062), 1504–1505.

Elser, J. J., Andersen, T., Baron, J. S., Bergstroem, A.-K., Jansson, M., Kyle, M., Nydick, K. R., Steger, L. & Hessen, D. O. (2009*a*). Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science* **326**(5954), 835–837.

Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B. & Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* **10**(12), 1135–1142.

Elser, J. J., Dobberfuhl, D. R., MacKay, N. A. & Schampel, J. H. (1996). Organism size, life history, and N:P stoichiometry: toward a unified view of cellular and ecosystem processes. *BioScience* **46**(9), 674–684.

Elser, J. J., Fagan, W. F., Denno, R. F., Dobberfuhl, D. R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S. S., McCauley, E., Schulz, K. L., Siemann, E. H. & Sterner, R. W. (2000*a*). Nutritional constraints in terrestrial and freshwater food webs. *Nature* **408**(6812), 578–580.

Elser, J. J., Fagan, W. F., Kerkhoff, A. J., Swenson, N. G. & Enquist, B. J. (2010). Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. *New Phytologist* **186**(3), 593–608.

Elser, J. J., Kyle, M., Steger, L., Nydick, K. R. & Baron, J. S. (2009*b*). Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition. *Ecology* **90**(11), 3062–3073.

Elser, J. J., Sterner, R. W., Gorokhova, E., Fagan, W. F., Markow, T. A., Cotner, J. B., Harrison, J. F., Hobbie, S. E., Odell, G. M. & Weider, L. J. (2000b). Biological stoichiometry from genes to ecosystems. *Ecology Letters* **3**(6), 540–550.

Emmett, B. A., Boxman, D., Bredemeier, M., Gundersen, P., Kjønaas, O. J., Moldan, F., Schleppi, P., Tietema, A. & Wright, R. F. (1998). Predicting the effects of atmospheric nitrogen deposition in conifer stands: evidence from the NITREX ecosystem-scale experiments. *Ecosystems* **1**(4), 352–360.

Estevez, J. A., Landete-Castillejos, T., Martínez, A., García, A. J., Ceacero, F., Gaspar-López, E., Calatayud, A. & Gallego, L. (2009). Antler mineral composition of Iberian red deer *Cervus elaphus hispanicus* is related to mineral profile of diet. *Acta Theriologica* **54**(3), 235–242.

Fagan, W. F., Siemann, E., Mitter, C., Denno, R. F., Huberty, A. F., Woods, H. A. & Elser, J. J. (2002). Nitrogen in insects: implications for trophic complexity and species diversification. *The American Naturalist* **160**(6), 784–802.

Fay, P. A., Prober, S. M., Harpole, W. S., Knops, J. M. H., Bakker, J. D., Borer, E. T., Lind, E. M., MacDougall, A. S., Seabloom, E. W., Wragg, P. D., Adler, P. B., Blumenthal, D. M., Buckley, Y. M., Chu, C., Cleland, E. E., *et al.* (2015). Grassland productivity limited by multiple nutrients. *Nature Plants* **1**(7), 15080.

Field, C. D., Dise, N. B., Payne, R. J., Britton, A. J., Emmett, B. A., Helliwell, R. C., Hughes, S., Jones, L., Lees, S., Leake, J. R., Leith, I. D., Phoenix, G. K., Power, S. A., Sheppard, L. J., Southon, G. E., *et al.* (2014). The role of nitrogen deposition in widespread plant community change across semi-natural habitats. *Ecosystems* **17**(5), 864–877.

Filipiak, M. (2018). A better understanding of bee nutritional ecology is needed to optimize conservation strategies for wild beesthe application of ecological stoichiometry. *Insects* **9**(3), 9030085.

Filipiak, M., Kuszewska, K., Asselman, M., Denisow, B., Stawiarz, E., Woyciechowski, M. & Weiner, J. (2017). Ecological stoichiometry of the honeybee: pollen diversity and adequate species composition are needed to mitigate limitations imposed on the growth and development of bees by pollen quality. *PLoS One* **12**(8), 0183236.

Fink, P. & Von Elert, E. (2006). Physiological responses to stoichiometric constraints: nutrient limitation and compensatory feeding in a freshwater snail. *Oikos* **115**(3), 484–494.

Fischer, K. & Fiedler, K. (2000). Response of the copper butterfly *Lycaena tityrus* to increased leaf nitrogen in natural food plants: evidence against the nitrogen limitation hypothesis. *Oecologia* **124**(2), 235–241.

Fowler, D., Coyle, M., Skiba, U., Sutton, M. A., Cape, J. N., Reis, S., Sheppard, L. J., Jenkins, A., Grizzetti, B., Galloway, J. N., Vitousek, P., Leach, A., Bouwman, A. F., Butterbach-Bahl, K., Dentener, F., *et al.* (2013). The global nitrogen cycle in the Twentyfirst century. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**(1621), 164.

Galloway, J. N. & Cowling, E. B. (2002). Reactive nitrogen and the World: 200 years of change. *Ambio: A Journal of the Human Environment* **31**(2), 64–71.

Gao, B., Liu, J., Zhang, C. & Van de Waal, D. B. (2018). Biological stoichiometry of oleaginous microalgal lipid synthesis: the role of N:P supply ratios and growth rate on microalgal elemental and biochemical composition. *Algal Research* **32**, 353–361.

Garcia, N. S., Sexton, J., Riggins, T., Brown, J., Lomas, M. W. & Martiny, A. C. (2018). High variability in cellular stoichiometry of carbon, nitrogen, and phosphorus within classes of marine eukaryotic phytoplankton under sufficient nutrient conditions. *Frontiers in Microbiology* **9**, 543.

Geider, R. & La Roche, J. (2002). Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis. *European Journal of Phycology* **37**(1), 1–17.

Ger, K. A., Hansson, L. A. & Lurling, M. (2014). Understanding cyanobacteria-zooplankton interactions in a more eutrophic world. *Freshwater Biology* **59**(9), 1783–1798.

Ger, K. A., Urrutia-Cordero, P., Frost, P. C., Hansson, L.-A., Sarnelle, O., Wilson, A. E. & Lürling, M. (2016). The interaction between cyanobacteria and zooplankton in a more eutrophic world. *Harmful Algae* **54**, 128–144.

Gerendas, J., Zhu, Z. J., Bendixen, R., Ratcliffe, R. G. & Sattelmacher, B. (1997). Physiological and biochemical processes related to ammonium toxicity in higher plants. *Zeitschrift Fur Pflanzenernahrung Und Bodenkunde* **160**(3), 239–251.

Gilliam, F. S., Adams, M. B. & Peterjohn, W. T. (2020). Response of soil fertility to 25 years of experimental acidification in a temperate hardwood forest. *Journal of Environmental Quality* **49**(4), 961–972.

Gobler, C. J., Burkholder, J. M., Davis, T. W., Harke, M. J., Johengen, T., Stow, C. A. & Van de Waal, D. B. (2016). The dual role of nitrogen supply in controlling the growth and toxicity of cyanobacterial blooms. *Harmful Algae* **54**, 87–97.

Golz, A.-L., Burian, A. & Winder, M. (2015). Stoichiometric regulation in micro- and mesozooplankton. *Journal of Plankton Research* **37**(2), 293–305.

Gomes, A. D., Tolussi, C. E., Boëchat, I. G., Pompêo, M. L. M., Cortez, M. P. T., Honji, R. M. & Moreira, R. G. (2016). Fatty acid composition of tropical fish depends on reservoir trophic status and fish feeding habit. *Lipids* **51**(10), 1193–1206.

González, A. L., Céréghino, R., Dézerald, O., Farjalla, V. F., Leroy, C., Richardson, B. A., Richardson, M. J., Romero, G. Q. & Srivastava, D. S. (2018). Ecological mechanisms and phylogeny shape invertebrate stoichiometry: a test using detritus-based communities across Central and South America. *Functional Ecology* **32**(10), 2448–2463.

Gonzalez, A. L., Dezerald, O., Marquet, P. A., Romero, G. Q. & Srivastava, D. S. (2017). The multidimensional stoichiometric niche. *Frontiers in Ecology and Evolution* **5**, 110. https://doi.org/10.3389/fevo.2017.00110.

Gonzalez, A. L., Farina, J. M., Kay, A. D., Pinto, R. & Marquet, P. A. (2011). Exploring patterns and mechanisms of interspecific and intraspecific variation in body elemental composition of desert consumers. *Oikos* **120**(8), 1247–1255.

Gormley-Gallagher, A. M., Douglas, R. W. & Rippey, B. (2016). Metal to phosphorus stoichiometries for freshwater phytoplankton in three remote lakes. *PeerJ* **4**, e2749.

Gosler, A. G. & Wilkin, T. A. (2017). Eggshell speckling in a passerine bird reveals chronic long-term decline in soil calcium. *Bird Study* **64**(2), 195–204.

Goverde, M., van der Heijden, M. G. A., Wiemken, A., Sanders, I. R. & Erhardt, A. (2000). Arbuscular mycorrhizal fungi influence life history traits of a lepidopteran herbivore. *Oecologia* **125**(3), 362–369.

Granéli, E., Weberg, M. & Salomon, P. S. (2008). Harmful algal blooms of allelopathic microalgal species: the role of eutrophication. *Harmful Algae* **8**(1), 94–102.

Graveland, J. (1995). *The quest for calcium: calcium limitation in the reproduction of forest passerines in relation to snail abundance and soil acidification*. PhD Thesis: University of Groningen.

Graveland, J. & Drent, R. H. (1997). Calcium availability limits breeding success of passerines on poor soils. *Journal of Animal Ecology* **66**(2), 279–288.

Graveland, J. & van der Wal, R. (1996). Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines. *Oecologia* **105**(3), 351–360.

Graveland, J. & Van Gijzen, T. (1994). Arthropods and seeds are not sufficient as calcium sources for shell formation and skeletal growth in passerines. *Ardea* **82**(2), 299–314.

Graveland, J., Vanderwal, R., Vanbalen, J. H. & Vannoordwijk, A. J. (1994). Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature* **368**(6470), 446–448.

Güsewell, S. (2004). N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist* **164**(2), 243–266.

Haddad, N. M., Haarstad, J. & Tilman, D. (2000). The effects of long-term nitrogen loading on grassland insect communities. *Oecologia* **124**(1), 73–84.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* **12**(10), e0185809.

Hallmann, C. A., Ssymank, A., Sorg, M., de Kroon, H. & Jongejans, E. (2021). Insect biomass decline scaled to species diversity: general patterns derived from a hoverfly community. *Proceedings of the National Academy of Sciences* **118**(2), e2002554117.

Hambäck, P. A., Gilbert, J., Schneider, K., Martinson, H. M., Kolb, G. & Fagan, W. F. (2009). Effects of body size, trophic mode and larval habitat on Diptera stoichiometry: a regional comparison. *Oikos* **118**(4), 615–623.

Harder, A. M., Ardren, W. R., Evans, A. N., Futia, M. H., Kraft, C. E., Marsden, J. E., Richter, C. A., Rinchard, J., Tillitt, D. E. & Christie, M. R. (2018). Thiamine deficiency in fishes: causes, consequences, and potential solutions. *Reviews in Fish Biology and Fisheries* **28**(4), 865–886.

Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E. S., Elser, J. J., Gruner, D. S., Hillebrand, H., Shurin, J. B. & Smith, J. E. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters* **14**(9), 852–862.

Harrison, S. J., Raubenheimer, D., Simpson, S. J., Godin, J. G. J. & Bertram, S. M. (2014). Towards a synthesis of frameworks in nutritional ecology: interacting effects of protein, carbohydrate and phosphorus on field cricket fitness. *Proceedings of the Royal Society B-Biological Sciences* **281**(1792), 20140539. https://doi.org/10.1098/rspb.2014.0539.

Hendrixson, H. A., Sterner, R. W. & Kay, A. D. (2007). Elemental stoichiometry of freshwater fishes in relation to phylogeny, allometry and ecology. *Journal of Fish Biology* **70**(1), 121–140.

Hessen, D. O. (1992). Nutrient element limitation of zooplankton production. *The American Naturalist* **140**(5), 799–814.

Hessen, D. O. (2008). Efficiency, energy and stoichiometry in pelagic food webs; reciprocal roles of food quality and food quantity. *Freshwater Reviews* **1**(1), 43–58.

Hessen, D. O., Elser, J. J., Sterner, R. W. & Urabe, J. (2013). Ecological stoichiometry: an elementary approach using basic principles. *Limnology and Oceanography* **58**(6), 2219–2236.

Hillebrand, H., Steinert, G., Boersma, M., Malzahn, A., Meunier, C. L., Plum, C. & Ptacnik, R. (2013). Goldman revisited: faster-growing phytoplankton has lower N:P and lower stoichiometric flexibility. *Limnology and Oceanography* **58**(6), 2076–2088.

Hofland-Zijlstra, J. D. & Berendse, F. (2009). The effect of nutrient supply and light intensity on tannins and mycorrhizal colonisation in Dutch heathland ecosystems. *Plant Ecology* **201**(2), 661–675.

Hogg, P., Squires, P. & Fitter, A. H. (1995). Acidification, nitrogen deposition and rapid vegetational change in a small valley mire in Yorkshire. *Biological Conservation* **71**(2), 143–153.

Holtgrieve, G. W., Schindler, D. E., Hobbs, W. O., Leavitt, P. R., Ward, E. J., Bunting, L., Chen, G., Finney, B. P., Gregory-Eaves, I., Holmgren, S., Lisac, M. J., Lisi, P. J., Nydick, K., Rogers, L. A., Saros, J. E., *et al.* (2011). A coherent signature of anthropogenic nitrogen deposition to remote watersheds of the Northern Hemisphere. *Science* **334**(6062), 1545–1548.

Horswill, P., O'Sullivan, O., Phoenix, G. K., Lee, J. A. & Leake, J. R. (2008). Base cation depletion, eutrophication and acidification of species-rich grasslands in response to long-term simulated nitrogen deposition. *Environmental Pollution* **155**(2), 336–349.

Houdijk, A. L. F. M. (1993). *Atmospheric Ammonium Deposition and the Nutritional Balance of Terrestrial Ecosystems*. PhD Thesis. Katholieke Universiteit Nijmegen.

Huang, X.-Y. & Salt, D. E. (2016). Plant ionomics: from elemental profiling to environmental adaptation. *Molecular Plant* **9**(6), 787–797.

Huberty, A. F. & Denno, R. F. (2006). Consequences of nitrogen and phosphorus limitation for the performance of two planthoppers with divergent life-history strategies. *Oecologia* **149**(3), 444–455.

Huhn, G. & Schulz, H. (1996). Contents of free amino acids in Scots pine needles from field sites with different levels of nitrogen deposition. *New Phytologist* **134**(1), 95–101.

Huo, B., He, J. & Shen, X. (2020). Effects of selenium-deprived habitat on the immune index and antioxidant capacity of Przewalski's gazelle. *Biological Trace Element Research* **198**(1), 149–156.

Jeyasingh, P. D., Goos, J. M., Lind, P. R., Roy Chowdhury, P. & Sherman, R. E. (2020). Phosphorus supply shifts the quotas of multiple elements in algae and *Daphnia*: ionomic basis of stoichiometric constraints. *Ecology Letters* **23**(7), 1064–1072.

Jeyasingh, P. D., Goos, J. M., Thompson, S. K., Godwin, C. M. & Cotner, J. B. (2017). Ecological stoichiometry beyond Redfield: an ionomic perspective on elemental homeostasis. *Frontiers in Microbiology* **8**, 722. https://doi.org/10.3389/fmicb.2017.00722.

Jia, Y., Yu, G., Gao, Y., He, N., Wang, Q., Jiao, C. & Zuo, Y. (2016). Global inorganic nitrogen dry deposition inferred from ground- and space-based measurements. *Scientific Reports* **6**(1), 19810.

Joern, A. & Behmer, S. T. (1997). Importance of dietary nitrogen and carbohydrates to survival, growth, and reproduction in adults of the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia* **112**(2), 201–208.

Joern, A. & Behmer, S. T. (1998). Impact of diet quality on demographic attributes in adult grasshoppers and the nitrogen limitation hypothesis. *Ecological Entomology* **23**(2), 174–184.

Joern, A., Provin, T. & Behmer, S. T. (2011). Not just the usual suspects: insect herbivore populations and communities are associated with multiple plant nutrients. *Ecology* **93**(5), 1002–1015.

Jonard, M., Fürst, A., Verstraeten, A., Thimonier, A., Timmermann, V., Potočić, N., Waldner, P., Benham, S., Hansen, K., Merilä, P., Ponette, Q., de la Cruz, A. C., Roskams, P., Nicolas, M., Croisé, L., *et al.* (2015). Tree mineral nutrition is deteriorating in Europe. *Global Change Biology* **21**(1), 418–430.

Joseph, G., Kelsey, R. G., Moldenke, A. F., Miller, J. C., Berry, R. E. & Wernz, J. G. (1993). Effects of nitrogen and Douglas-fir allelochemicals on development of the gypsy moth, *Lymantria dispar*. *Journal of Chemical Ecology* **19**(6), 1245–1263.

Kagata, H. & Ohgushi, T. (2006). Nitrogen homeostasis in a willow leaf beetle, *Plagiodera versicolora*, is independent of host plant quality. *Entomologia Experimentalis et Applicata* **118**(2), 105–110.

Kagata, H. & Ohgushi, T. (2007). Carbon-nitrogen stoichiometry in the tritrophic food chain willow, leaf beetle, and predatory ladybird beetle. *Ecological Research* **22**(4), 671–677.

Kaspari, M. (2021). The invisible hand of the Periodic Table: how micronutrients shape ecology. *Annual Review of Ecology, Evolution, and Systematics* **52**(1), 199–219.

Kaspari, M. & Powers, J. S. (2016). Biogeochemistry and geographical ecology: embracing all twenty-five elements required to build organisms. *The American Naturalist* **188**(S1), S62–S73.

Kay, A. D., Schade, J. D., Ogdahl, M., Wesserle, E. O. & Hobbie, S. E. (2007). Fire effects on insect herbivores in an oak savanna: the role of light and nutrients. *Ecological Entomology* **32**(6), 754–761.

Kerslake, J. E., Woodin, S. J. & Hartley, S. E. (1998). Effects of carbon dioxide and nitrogen enrichment on a plant-insect interaction: the quality of *Calluna vulgaris* as a host for *Operophtera brumata*. *New Phytologist* **140**(1), 43–53.

Kiørboe, T. (1989). Phytoplankton growth rate and nitrogen content: implications for feeding and fecundity in a herbivorous copepod. *Marine Ecology Progress Series. Oldendorf* **55**(2), 229–234.

Klaassen, M. & Nolet, B. A. (2008). Stoichiometry of endothermy: shifting the quest from nitrogen to carbon. *Ecology Letters* **11**(8), 785–792.

Knapp, D. D., Smith, L. L. & Atkinson, C. L. (2021). Larval anurans follow predictions of stoichiometric theory: implications for nutrient storage in wetlands. *Ecosphere* **12**(4), e03466.

Kraft, C. E. & Angert, E. R. (2017). Competition for vitamin B1 (thiamin) structures numerous ecological interactions. *The Quarterly Review of Biology* **92**(2), 151–168.

Kurze, S., Heinken, T. & Fartmann, T. (2017). Nitrogen enrichment of host plants has mostly beneficial effects on the life-history traits of nettle-feeding butterflies. *Acta Oecologica* **85**, 157–164.

Kurze, S., Heinken, T. & Fartmann, T. (2018). Nitrogen enrichment in host plants increases the mortality of common Lepidoptera species. *Oecologia* **188**(4), 1227–1237.

Larson, J. H., Richardson, W. B., Vallazza, J. M., Bartsch, L. A. & Bartsch, M. R. (2017). Using a gradient in food quality to infer drivers of fatty acid content in two filter-feeding aquatic consumers. *Aquatic Sciences* **79**(4), 855–865.

Lebigre, C., Vanderbeken, C., Turlure, C. & Schtickzelle, N. (2018). Host plant nitrogen enrichment has both positive and negative effects on the larval growth of a specialist butterfly. *Ecological Entomology* **43**(4), 494–505.

Lee, J., Nakamura, M. & Hiura, T. (2017). Does large-scale N fertilization have time-delayed effects on insects community structure by changing oak quantity and quality? *Arthropod-Plant Interactions* **11**(4), 515–523.

Leeson, S. & Summers, J. (2001). *Scott's Nutrition of the Chicken*, Fourth Edition. University Books, Canada.

Liefer, J. D., Garg, A., Fyfe, M. H., Irwin, A. J., Benner, I., Brown, C. M., Follows, M. J., Omta, A. W. & Finkel, Z. V. (2019). The macromolecular basis of phytoplankton C:N:P under nitrogen starvation. *Frontiers in Microbiology* **10**, 763.

Loaiza, V., Jonas, J. L. & Joern, A. (2008). Does dietary P affect feeding and performance in the mixed-feeding grasshopper, (Acrididae) *Melanoplus bivitattus*? *Environmental Entomology* **37**(2), 333–339.

Loaiza, V., Jonas, J. L. & Joern, A. (2011). Grasshoppers (Orthoptera: Acrididae) select vegetation patches in local-scale responses to foliar nitrogen but not phosphorus in native grassland. *Insect Science* **18**(5), 533–540.

Lucassen, E., Bobbink, R., Smolders, A. J. P., van der Ven, P. J. M., Lamers, L. P. M. & Roelofs, J. G. M. (2003). Interactive effects of low pH and high ammonium levels responsible for the decline of *Cirsium dissectum* (L.) Hill. *Plant Ecology* **165**(1), 45–52.

Mahony, N., Nol, E. & Hutchinson, T. (1997). Food-chain chemistry, reproductive success, and foraging behaviour of songbirds in acidified maple forests of Central Ontario. *Canadian Journal of Zoology* **75**(4), 509–517.

Main, T. M., Dobberfuhl, D. R. & Elser, J. J. (1997). N:P stoichiometry and ontogeny of crustacean zooplankton: a test of the growth rate hypothesis. *Limnology and Oceanography* **42**(6), 1474–1478.

Mathews, L., Faithfull, C. L., Lenz, P. H. & Nelson, C. E. (2018). The effects of food stoichiometry and temperature on copepods are mediated by ontogeny. *Oecologia* **188**(1), 75–84.

Mattson, W. J. & Scriber, J. M. (1987). Nutritional ecology of Woody plants: nitrogen, water, Fiber, and mineral considerations. In *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates* (eds F. Slansky and J. G. Rodriguez), pp. 105–146. Wiley & Sons, Inc., New York.

McDonald, P., Edwards, R. A., Greenhalg, J. F. D. & Morgan, C. A. (1995). *Animal Nutrition*, Fifth Edition. Pearson Education Limited, Harlow.

Meunier, C. L., Gundale, M. J., Sánchez, I. S. & Liess, A. (2016). Impact of nitrogen deposition on forest and lake food webs in nitrogen-limited environments. *Global Change Biology* **22**(1), 164–179.

Meunier, C. L., Malzahn, A. M. & Boersma, M. (2014). A new approach to homeostatic regulation: towards a unified view of physiological and ecological concepts. *PLoS One* **9**(9), e107737.

Milewski, A. V. & Diamond, R. E. (2000). Why are very large herbivores absent from Australia? A new theory of micronutrients. *Journal of Biogeography* **27**(4), 957–978.

Nessel, M. P., Konnovitch, T., Romero, G. Q. & González, A. L. (2021). Nitrogen and phosphorus enrichment cause declines in invertebrate populations: a global meta-analysis. *Biological Reviews* **96**(6), 2617–2637.

Nijssen, M. & Siepel, H. (2010). The characteristic fauna of inland drift sands. In *Inland Drift Sand Landscapes* (eds J. Fanta and H. Siepel), pp. 255–278. KNNV Uitgeverij, Zeist.

Nijssen, M. E., WallisDeVries, M. F. & Siepel, H. (2017). Pathways for the effects of increased nitrogen deposition on fauna. *Biological Conservation* **212**, 423–431.

Nybakken, L., Lie, M. H., Julkunen-Tiitto, R., Asplund, J. & Ohlson, M. (2018). Fertilization changes chemical defense in needles of mature Norway spruce (*Picea abies*). *Frontiers in Plant Science* **9**, 770.

Ohlson, M. & Staaland, H. (2001). Mineral diversity in wild plants: benefits and bane for moose. *Oikos* **94**(3), 442–454.

Olde Venterink, H., Wassen, M. J., Verkroost, A. W. M. & De Ruiter, P. C. (2003). Species richness–productivity patterns differ between N-, P-, and K-limited wetlands. *Ecology* **84**(8), 2191–2199.

Ormerod, S. J., Ohalloran, J., Gribbin, S. D. & Tyler, S. J. (1991). The ecology of dippers *Cinclus-cinclus* in relation to stream acidity in upland Wales – breeding performance, calcium physiology and nestling growth. *Journal of Applied Ecology* **28**(2), 419–433.

Pabian, S. E. & Brittingham, M. C. (2011). Soil calcium availability limits forest songbird productivity and density. *Auk* **128**(3), 441–447.

Pabian, S., Rummel, S., Sharpe, W. & Brittingham, M. (2012). Terrestrial liming as a restoration technique for acidified forest ecosystems. *International Journal of Forestry Research* **2012**. https://doi.org/10.1155/2012/976809.

Pabian, S. E. & Brittingham, M. C. (2007). Terrestrial liming benefits birds in an acidified forest in the northeast. *Ecological Applications* **17**(8), 2184–2194.

Palo, R. T. & Robbins, C. T. (1991). *Plant Defenses against Mammalian Herbivory*. CRC Press, London.

Pareja-Carrera, J., Rodríguez-Estival, J., Martinez-Haro, M., Ortiz, J. A. & Mateo, R. (2018). Age-dependent changes in essential elements and oxidative stress biomarkers in blood of red deer and vulnerability to nutritional deficiencies. *Science of the Total Environment* **626**, 340–348.

Paulissen, M. P. C. P., Bobbink, R., Robat, S. A. & Verhoeven, J. T. A. (2016). Effects of reduced and oxidised nitrogen on rich-fen mosses: a 4-year field experiment. *Water, Air, & Soil Pollution* **227**(1), 18.

Peerakietkhajorn, S., Tsukada, K., Kato, Y., Matsuura, T. & Watanabe, H. (2015). Symbiotic bacteria contribute to increasing the population size of a freshwater crustacean, *Daphnia magna*. *Environmental Microbiology Reports* **7**(2), 364–372.

Perez-Soba, M., Stulen, I. & Vandereerden, L. J. M. (1994). Effect of atmospheric ammonia on the nitrogen-metabolism of scots pine (*Pinus sylvestris*) needles. *Physiologia Plantarum* **90**(4), 629–636.

Perkins, M. C., Woods, H. A., Harrison, J. F. & Elser, J. J. (2004). Dietary phosphorus affects the growth of larval *Manduca sexta*. *Archives of Insect Biochemistry and Physiology* **55**(3), 153–168.

Persson, J., Fink, P., Goto, A., Hood, J. M., Jonas, J. & Kato, S. (2010). To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. *Oikos* **119**(5), 741–751.

Pilati, A. & Vanni, M. J. (2007). Ontogeny, diet shifts, and nutrient stoichiometry in fish. *Oikos* **116**(10), 1663–1674.

Pitcairn, C. E. R., Fowler, D., Leith, I. D., Sheppard, L. J., Sutton, M. A., Kennedy, V. & Okello, E. (2003). Bioindicators of enhanced nitrogen deposition. *Environmental Pollution* **126**(3), 353–361.

Polidori, C., García, A. J. & Nieves-Aldrey, J. L. (2013). Breaking up the wall: metal-enrichment in ovipositors, but not in mandibles, co-varies with substrate hardness in gall-wasps and their associates. *PLoS One* **8**(7), e70529.

Pöyry, J., Carvalheiro, L. G., Heikkinen, R. K., Kühn, I., Kuussaari, M., Schweiger, O., Valtonen, A., van Bodegom, P. M. & Franzén, M. (2017). The effects of soil eutrophication propagate to higher trophic levels. *Global Ecology and Biogeography* **26**(1), 18–30.

Prather, C. M., Laws, A. N., Cuellar, J. F., Reihart, R. W., Gawkins, K. M. & Pennings, S. C. (2018). Seeking salt: herbivorous prairie insects can be co-limited by macronutrients and sodium. *Ecology Letters* **21**(10), 1467–1476.

Quicke, D. L. J., Wyeth, P., Fawke, J. D., Basibuyuk, H. H. & Vincent, J. F. V. (2008). Manganese and zinc in the ovipositors and mandibles of hymenopterous insects. *Zoological Journal of the Linnean Society* **124**(4), 387–396.

Ramsay, S. L. & Houston, D. C. (1999). Do acid rain and calcium supply limit eggshell formation for blue tits (*Parus caeruleus*) in the UK? *Journal of Zoology* **247**, 121–125.

Raubenheimer, D. & Simpson, S. J. (1993). The geometry of compensatory feeding in the locust. *Animal Behaviour* **45**(5), 953–964.

Raubenheimer, D. & Simpson, S. J. (2003). Nutrient balancing in grasshoppers: behavioural and physiological correlates of dietary breadth. *Journal of Experimental Biology* **206**(Pt. 10), 1669–1681.

Raubenheimer, D. & Simpson, S. J. (2004). Organismal stoichiometry: quantifying non-independence among food components. *Ecology* **85**(5), 1203–1216.

Reiners, W. A. (1986). Complementary models for ecosystems. *American Naturalist* **127**(1), 59–73.

Rout, G., Samantaray, S. & Das, P. (2001). Aluminium toxicity in plants: a review. *Agronomie* **21**(1), 3–21.

Ryther, J. H. & Dunstan, W. M. (1971). Nitrogen, phosphorus, and eutrophication in the coastal marine environment. *Science* **171**(3975), 1008–1013.

Sala, O. E., Chapin, F. S. III, Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M. n., Poff, N. L., *et al.* (2000). Global biodiversity scenarios for the year 2100. *Science* **287**(5459), 1770–1774.

Salt, D. E., Baxter, I. & Lahner, B. (2008). Ionomics and the study of the plant ionome. *Annual Reviews of Plant Biology* **59**, 709–733.

Sardans, J., Rivas-Ubach, A. & Penuelas, J. (2012*a*). The C:N:P stoichiometry of organisms and ecosystems in a changing world: a review and perspectives. *Perspectives in Plant Ecology Evolution and Systematics* **14**(1), 33–47.

Sardans, J., Rivas-Ubach, A. & Peñuelas, J. (2012*b*). The elemental stoichiometry of aquatic and terrestrial ecosystems and its relationships with organismic lifestyle and ecosystem structure and function: a review and perspectives. *Biogeochemistry* **111**(1), 1–39.

Schlender, M., Skibbe, A., Kappes, H. & Topp, W. (2007). Complex responses of songbirds to soil acidification of managed beech forests in Central Europe. *Ecosystems* **10**(4), 579–587.

Simpson, S. J., James, S., Simmonds, M. S. J. & Blaney, W. M. (1991). Variation in chemosensitivity and the control of dietary selection behaviour in the locust. *Appetite* **17**(2), 141–154.

Simpson, S. J. & Raubenheimer, D. (1993). A multilevel analysis of feeding-behavior – the geometry of nutritional decisions. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **342**(1302), 381–402.

Simpson, S. J., Raubenheimer, D., Behmer, S. T., Whitworth, A. & Wright, G. A. (2002). A comparison of nutritional regulation in solitarious- and gregarious-phase nymphs of the desert locust *Schistocerca gregaria*. *Journal of Experimental Biology* **205**, 121–129.

Simpson, S. J., Sibly, R. M., Lee, K. P., Behmer, S. T. & Raubenheimer, D. (2004). Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour* **68**, 1299–1311.

Smith, J. C. (1980). The vitamin A-zinc connection: a review. *Annals of the New York Academy of Sciences* **355**(1), 62–75.

Smith, J. C., McDaniel, E. G., Fan, F. F. & Halsted, J. A. (1973). Zinc: a trace element essential in vitamin A metabolism. *Science* **181**(4103), 954–955.

Smith, V. H., Tilman, G. D. & Nekola, J. C. (1999). Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution* **100**(1), 179–196.

Stephens, J. P., Stoler, A. B., Sckrabulis, J. P., Fetzer, A. J., Berven, K. A., Tiegs, S. D. & Raffel, T. R. (2017). Ontogenetic changes in sensitivity to nutrient limitation of tadpole growth. *Oecologia* **183**(1), 263–273.

Sterner, R. W. & Elser, J. J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, New Jersey.

Sterrett, S. C., Maerz, J. C. & Katz, R. A. (2015). What can turtles teach us about the theory of ecological stoichiometry? *Freshwater Biology* **60**(3), 443–455.

Stevens, C. J., David, T. I. & Storkey, J. (2018). Atmospheric nitrogen deposition in terrestrial ecosystems: its impact on plant communities and consequences across trophic levels. *Functional Ecology* **32**(7), 1757–1769.

Stevens, C. J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D. J. G., Bleeker, A., Diekmann, M., Alard, D., Bobbink, R., Fowler, D., Corcket, E., Mountford, J. O., Vandvik, V., Aarrestad, P. A., Muller, S. & Dise, N. B. (2010). Nitrogen deposition threatens species richness of grasslands across Europe. *Environmental Pollution* **158**(9), 2940–2945.

Stevens, C. J., Lind, E. M., Hautier, Y., Harpole, W. S., Borer, E. T., Hobbie, S., Seabloom, E. W., Ladwig, L., Bakker, J. D., Chu, C., Collins, S., Davies, K. F., Firn, J., Hillebrand, H., Pierre, K. J. L., *et al.* (2015). Anthropogenic nitrogen deposition predicts local grassland primary production worldwide. *Ecology* **96**(6), 1459–1465.

Stevens, C. J., Manning, P., van den Berg, L. J. L., de Graaf, M. C. C., Wamelink, G. W. W., Boxman, A. W., Bleeker, A., Vergeer, P., Arroniz-Crespo, M., Limpens, J., Lamers, L. P. M., Bobbink, R. & Dorland, E. (2011). Ecosystem responses to reduced and oxidised nitrogen inputs in European terrestrial habitats. *Environmental Pollution* **159**(3), 665–676.

Sun, Y., Guo, J., Li, Y., Luo, G., Li, L., Yuan, H., Mur, L. A. J. & Guo, S. (2020). Negative effects of the simulated nitrogen deposition on plant phenolic metabolism: a meta-analysis. *Science of the Total Environment* **719**, 137442.

Suzuki-Ohno, Y., Kawata, M. & Urabe, J. (2012). Optimal feeding under stoichiometric constraints: a model of compensatory feeding with functional response. *Oikos* **121**(4), 569–578.

Sylvander, P., Häubner, N. & Snoeijs, P. (2013). The thiamine content of phytoplankton cells is affected by abiotic stress and growth rate. *Microbial Ecology* **65**(3), 566–577.

Taboada, A., Marcos, E. & Calvo, L. (2016). Disruption of trophic interactions involving the heather beetle by atmospheric nitrogen deposition. *Environmental Pollution* **218**, 436–445.

Taipale, S. J., Kahilainen, K. K., Holtgrieve, G. W. & Peltomaa, E. T. (2018). Simulated eutrophication and browning alters zooplankton nutritional quality and determines juvenile fish growth and survival. *Ecology and Evolution* **8**(5), 2671–2687.

Tao, L. L. & Hunter, M. D. (2012). Does anthropogenic nitrogen deposition induce phosphorus limitation in herbivorous insects? *Global Change Biology* **18**(6), 1843–1853.

Thomas, P. K., Kunze, C., Van de Waal, D. B., Hillebrand, H. & Striebel, M. (2022). Elemental and biochemical nutrient limitation of zooplankton: a meta-analysis. *Ecology Letters* **25**(12), 2776–2792.

Throop, H. L. (2005). Nitrogen deposition and herbivory affect biomass production and allocation in an annual plant. *Oikos* **111**(1), 91–100.

Throop, H. L. & Lerdau, M. T. (2004). Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. *Ecosystems* **7**(2), 109–133.

Tian, D. S., Reich, P. B., Chen, H. Y. H., Xiang, Y. Z., Luo, Y. Q., Shen, Y., Meng, C., Han, W. X. & Niu, S. L. (2019). Global changes alter plant multi-element stoichiometric coupling. *New Phytologist* **221**(2), 807–817.

Turner, J. T. (2006). Harmful algae interactions with marine planktonic grazers. In *Ecology of Harmful Algae* (eds E. Granéli and J. T. Turner), pp. 259–270. Springer Berlin Heidelberg, Berlin.

Turner, J. T. & Tester, P. A. (1997). Toxic marine phytoplankton, zooplankton grazers, and pelagic food webs. *Limnology and Oceanography* **42**(5part2), 1203–1213.

Twining, B. S. & Baines, S. B. (2013). The trace metal composition of marine phytoplankton. *Annual Review of Marine Science* **5**(1), 191–215.

Twining, C. W., Brenna, J. T., Hairston, N. G. Jr. & Flecker, A. S. (2016). Highly unsaturated fatty acids in nature: what we know and what we need to learn. *Oikos* **125**(6), 749–760.

Tyler, S. J. & Ormerod, S. J. (1992). A review of the likely causal pathways relating the reduced density of breeding dippers *Cinclus cinclus* to the acidification of upland streams. *Environmental Pollution* **78**(1–3), 49–55.

Urabe, J. & Watanabe, Y. (1992). Possibility of N or P limitation for planktonic cladocerans: an experimental test. *Limnology and Oceanography* **37**(2), 244–251.

van Breemen, N., Driscoll, C. T. & Mulder, J. (1984). Acidic deposition and internal proton sources in acidification of soils and waters. *Nature* **307**(5952), 599–604.

Van de Waal, D. B., Tillmann, U., Zhu, M. M., Koch, B. P., Rost, B. & John, U. (2013). Nutrient pulse induces dynamic changes in cellular C:N:P, amino acids, and paralytic shellfish poisoning toxins in *Alexandrium tamarense*. *Marine Ecology Progress Series* **493**, 57–69.

Van de Waal, D. B., Smith, V. H., Declerck, S. A. J., Stam, E. C. M. & Elser, J. J. (2014). Stoichiometric regulation of phytoplankton toxins. *Ecology Letters* **17**(6), 736–742.

Van de Waal, D. B., Verspagen, J. M. H., Lürling, M., Van Donk, E., Visser, P. M. & Huisman, J. (2009). The ecological stoichiometry of toxins produced by harmful cyanobacteria: an experimental test of the carbon-nutrient balance hypothesis. *Ecology Letters* **12**(12), 1326–1335.

van den Berg, L. J. L., Dorland, E., Vergeer, P., Hart, M. A. C., Bobbink, R. & Roelofs, J. G. M. (2005). Decline of acid-sensitive plant species in heathland can be attributed to ammonium toxicity in combination with low pH. *New Phytologist* **166**(2), 551–564.

van den Burg, A. B. (2009). Limitations of owl reproduction in the wild: is there a role for food quality besides quantity? *Ardea* **97**(4), 609–614.

van den Burg, A. B. (2021). The quality of protein sources for egg production in tawny owls and Sparrowhawks. *Airo* **29**, 467–476.

van den Burg, A. B., Dees, A., Huigens, T., Bijlsma, R. J. & de Waal, R. W. (2014). *Voedselkwaliteit en biodiversiteit in bossen van de hoge zandgronden*. Directie Agrokennis, Ministerie van Economische Zaken, Den Haag.

Van Geest, G. J., Sachse, R., Brehm, M., Van Donk, E. & Hessen, D. O. (2010). Maximizing growth rate at low temperatures: RNA:DNA allocation strategies and life history traits of Arctic and temperate *Daphnia*. *Polar Biology* **33**(9), 1255–1262.

van Genderen, H., Schoonhoven, L. M. & Fuchs, A. (1996). *Chemisch-ecologische flora van Nederland en Belgie. Een inleiding over aard en ecologische betekenis van secundaire plantestoffen*. KNNV, Utrecht.

Van Nieuwerburgh, L., Wänstrand, I. & Snoeijs, P. (2004). Growth and C:N:P ratios in copepods grazing on N- or Si-limited phytoplankton blooms. *Hydrobiologia* **514**(1), 57–72.

Verberk, W. C. E. P., Noordwijk, C. G. E. v. & Hildrew, A. G. (2013). Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science* **32**(2), 531–547.

Villar-Argaiz, M., López-Rodríguez, M. J. & Tierno de Figueroa, J. M. (2021). Divergent nucleic acid allocation in juvenile insects of different metamorphosis modes. *Scientific Reports* **11**(1), 10313.

Visanuvimol, L. & Bertram, S. M. (2010). Dietary phosphorus availability influences female cricket lifetime reproductive effort. *Ecological Entomology* **35**(3), 386–395.

Vitousek, P. M., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H. & Tilman, D. (1997). Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* **7**(3), 737–750.

Vogels, J. J., Verberk, W. C. E. P., Kuper, J. T., Weijters, M. J., Bobbink, R. & Siepel, H. (2021). How to restore invertebrate diversity of degraded heathlands? A case study on the reproductive performance of the field cricket *Gryllus campestris* (L.). *Frontiers in Ecology and Evolution* **9**(300), 659363. https://doi.org/10.3389/fevo.2021.659363.

Vogels, J. J., Verberk, W. C. E. P., Lamers, L. P. M. & Siepel, H. (2017). Can changes in soil biochemistry and plant stoichiometry explain loss of animal diversity of heathlands? *Biological Conservation* **212**(Part B), 432–447.

Vogels, J. J., Weijters, M. J., Bobbink, R., Bijlsma, R.-J., Lamers, L. P. M., Verberk, W. C. E. P. & Siepel, H. (2020). Barriers to restoration: soil acidity and phosphorus limitation constrain recovery of heathland plant communities after sod cutting. *Applied Vegetation Science* **23**(1), 94–106.

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R. & Stopak, D. (2021). Insect decline in the Anthropocene: death by a thousand cuts. *Proceedings of the National Academy of Sciences* **118**(2), e2023989118.

WallisDeVries, M. F. (1996). Nutritional limitations of free-ranging cattle: the importance of habitat quality. *Journal of Applied Ecology* **33**(4), 688–702.

Warbrick-Smith, J., Raubenheimer, D., Simpson, S. J. & Behmer, S. T. (2009). Three hundred and fifty generations of extreme food specialisation: testing predictions of nutritional ecology. *Entomologia Experimentalis et Applicata* **132**(1), 65–75.

Wassen, M. J., Schrader, J., van Dijk, J. & Eppinga, M. B. (2021). Phosphorus fertilization is eradicating the niche of northern Eurasia's threatened plant species. *Nature Ecology & Evolution* **5**(1), 67–73.

Watts, T., Woods, H. A., Hargand, S., Elser, J. J. & Markow, T. A. (2006). Biological stoichiometry of growth in *Drosophila melanogaster*. *Journal of Insect Physiology* **52**(2), 187–193.

Welti, E. A. R., Roeder, K. A., de Beurs, K. M., Joern, A. & Kaspari, M. (2020). Nutrient dilution and climate cycles underlie declines in a dominant insect herbivore. *Proceedings of the National Academy of Sciences* **117**(13), 7271–7275.

Welti, E. A. R., Sanders, N. J., de Beurs, K. M. & Kaspari, M. (2019). A distributed experiment demonstrates widespread sodium limitation in grassland food webs. *Ecology* **100**(3), e02600.

White, T. C. R. (1993). *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Springer-Verlag, Berlin-Heidelberg.

Woods, H. A., Fagan, W. F., Elser, J. J. & Harrison, J. F. (2004). Allometric and phylogenetic variation in insect phosphorus content. *Functional Ecology* **18**(1), 103–109.

Yesmin, L., Gammack, S. M. & Cresser, M. S. (1996). Effects of atmospheric nitrogen deposition on ericoid mycorrhizal infection of *Calluna vulgaris* growing in peat soils. *Applied Soil Ecology* **4**(1), 49–60.

Zehnder, C. B. & Hunter, M. D. (2009). More is not necessarily better: the impact of limiting and excessive nutrients on herbivore population growth rates. *Ecological Entomology* **34**(4), 535–543.

Zhang, Z. J., Elser, J. J., Cease, A. J., Zhang, X. M., Yu, Q., Han, X. G. & Zhang, G. M. (2014). Grasshoppers regulate N:P stoichiometric homeostasis by changing phosphorus contents in their frass. *PLoS One* **9**(8), e103697. https://doi.org/10.1371/journal.pone.0103697.

Zhou, L. & Declerck, S. A. J. (2019). Herbivore consumers face different challenges along opposite sides of the stoichiometric knife-edge. *Ecology Letters* **22**, 2018–2027.

Zhu, Y., Ma, Q., Zhong, Z., Jiang, M., Bakker, E. S., Harvey, J. A., Veen, G. F., Vhen, C. & Wang, D. (2023). Contrasting effects of nitrogen fertiliser application on the performance of closely related grasshoppers through changes in plant nutrient concentrations. *Ecological Entomology* 1–11. https://doi.org/10.1111/een.13228.

Zhu, Y., Zhong, Z., Pagès, J. F., Finke, D., Wang, D., Ma, Q., Hassan, N., Zhu, H. & Wang, L. (2019). Negative effects of vertebrate on invertebrate herbivores mediated by enhanced plant nitrogen content. *Journal of Ecology* **107**(2), 901–912.

XII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Summary table of methods, reported range and/or mean C:N:P content and corresponding calculated molar ratios of producers and consumers and results of studies used in Fig. 1 on effects of differing dietary C:N:P ratios on insect fitness and growth.

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