Impacts of Nitrogen and Phosphorus: From Genomes to Natural Ecosystems and Agriculture

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Nitrogen (N) and/or phosphorus (P) availability can limit growth of primary producers across most of the world's aquatic and terrestrial ecosystems. These constraints are commonly overcome in agriculture by applying fertilizers to improve yields. However, excessive anthropogenic N and P inputs impact natural environments and have far-reaching ecological and evolutionary consequences, from individual species up to entire ecosystems. The extent to which global N and P cycles have been perturbed over the past century can be seen as a global fertilization experiment with significant redistribution of nutrients across different ecosystems. Here we explore the effects of N and P availability on stoichiometry and genomic traits of organisms, which, in turn, can influence: (i) plant and animal abundances; (ii) trophic interactions and population dynamics; and (iii) ecosystem dynamics and productivity of agricultural crops. We articulate research priorities for a deeper understanding of how bioavailable N and P move through the environment and exert their ultimate impacts on biodiversity and ecosystem services.

Keywords: crops, genome size, nitrogen, nutrients, phosphorus, polyploidy, stoichiometry

INTRODUCTION

Fertilizers are central to the "green revolution," which has seen about half of the world's land converted to agriculture (Kareiva et al., 2007). Nitrogen (N) and phosphorus (P) are the dominant rate-limiting nutrients in most natural systems and the major constituents of agrochemical fertilizers. The consequences of N and P losses from agricultural land, e.g., through runoff and leaching, can span multiple organizational levels and scales in time and space, threatening essential ecosystem services (Smith et al., 1999; Elser, 2012; Fowler et al., 2013). In nature excessive loadings

of N and P are extrinsic drivers that (i) often reduce biodiversity directly (Chapin et al., 2000; Erisman et al., 2008; Lambers et al., 2010), and have indirect effects through (ii) increased local extinction via dominance of a few competitive species, leading to (iii) altered plant community structure (Rohr et al., 2016), (iv) reduced functional trait diversity of communities and ecosystems (Tilman and Lehman, 2001; Díaz et al., 2006), and (v) ultimately reshaping ecosystem services (Millennium Ecosystem Assessment., 2005; **Figure 1**). Examples of such services include the provision of clean water for human needs and leisure, maintaining and regulating soil fertility, and supporting services such as nutrient cycling and the transfer of nutrients through trophic levels (Millennium Ecosystem Assessment., 2005; Bommarco et al., 2013; Harrison et al., 2014).

At the organism level, N and P availability is known to have powerful influences on functional traits and growth rates, but we are only just beginning to understand that genome structure (e.g., genome size, ploidal level) can also play an important role (e.g., Neiman et al., 2009, 2013b; Šmarda et al., 2013; Guignard et al., 2016). At the genomic level, environmental nutrient limitation may constrain cellular processes (e.g., photosynthesis, transcriptomes) and over time may result in divergence of genes and the proteins they encode (Acquisti et al., 2009a,b; Elser et al., 2011; Seward and Kelly, 2016; **Figure 1**).

Thus, the fluxes, feedbacks, and availability of N and P fundamentally impact biota at all levels from genes and genomes to ecosystems, reshaping ecological and ultimately ecosystem processes. It is therefore crucial to understand *how* environmental N and P impact all levels of biological organization, from genome dynamics and cell metabolism, to the structure and functioning of multispecies systems (**Figure 1**). Such research could dramatically improve both the efficacy of biodiversity conservation and the development of more sustainable farming systems with lower N and P demands.

This paper evaluates the roles of N and P (1) in the environment, (2) within organisms, (3) in multispecies systems, and (4) in meeting human needs in the context of rising to the dual challenges of increasing food production and maintaining functional biodiversity to underpin the delivery of essential ecosystem services. It also proposes research priorities in these areas.

(1) N and P in the Environment

Nitrogen and P both underpin photosynthetic processes, cell growth, metabolism, and protein synthesis (Chapin et al., 2011), but their natural sources and rates of supply are very different: in principle, N availability is unlimited as an atmospheric gas, whereas P comes from rock phosphate, renewed with the uplift of continental rock. N and P co-limitation is common across the Earth's ecosystems in all the major biomes (Elser et al., 2007a). Today the primary sources of N and P originate from the massive anthropogenic inputs of fertilizers onto agricultural land (Fowler et al., 2013; **Figure 2**). For instance, industrial N production via the Haber–Bosch process surpassed natural
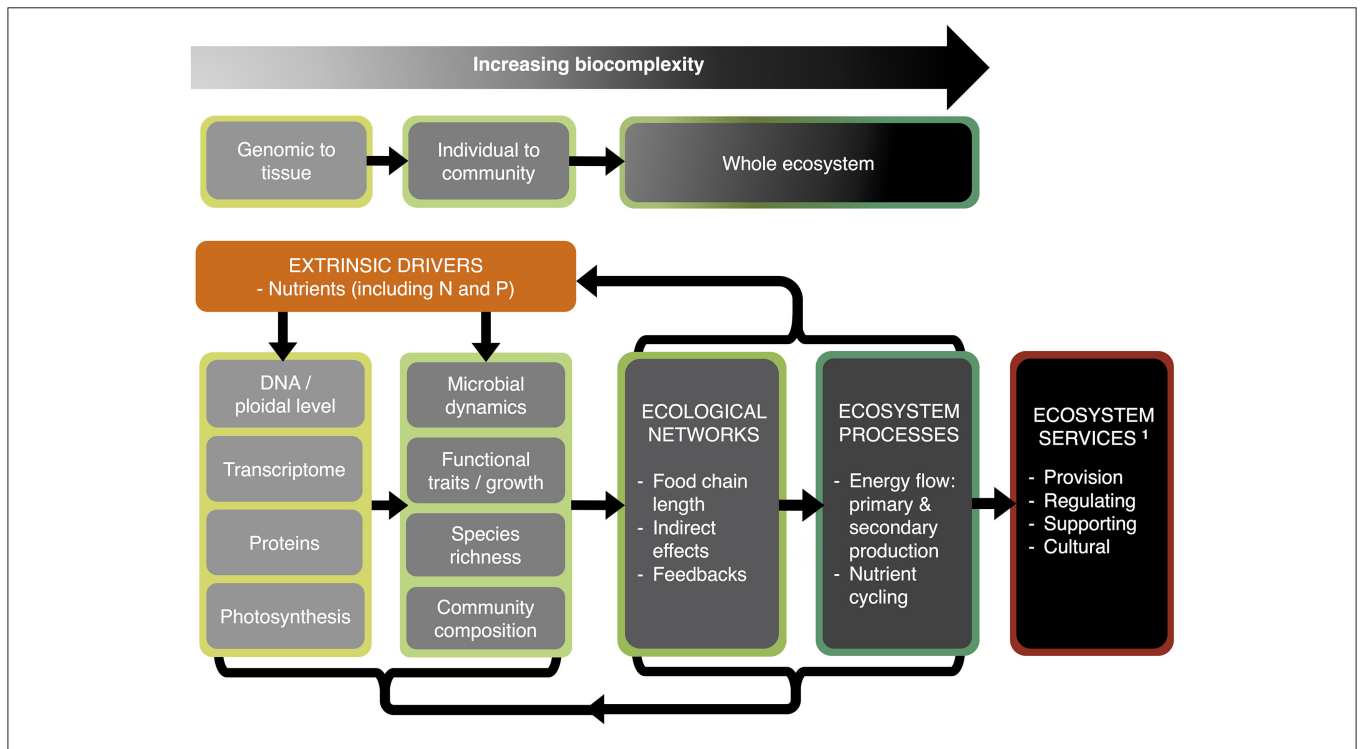

FIGURE 1 | Effects of N and P availability—from genomes to ecosystems. Inputs of nutrients, in particular nitrogen (N) and phosphorus (P), act as extrinsic drivers affecting biological dynamics at the genomic to the ecosystem level, and which in turn feed-back on these drivers. An essential component of the ecosystem is the cycling of nutrients through the food web and back to the atmosphere and soil in inorganic forms. Such ecosystems provide services of benefit to humans. [1]Services as defined by the Millennium Ecosystem Assessment. (2005).

FIGURE 2 | Consumption of N and P fertilizer by year **(A)** globally, and **(B,C)** by world regions, from 1961 to 2014. Data are available from the Food and Agriculture Organization of the United Nations (FAO, 2016).
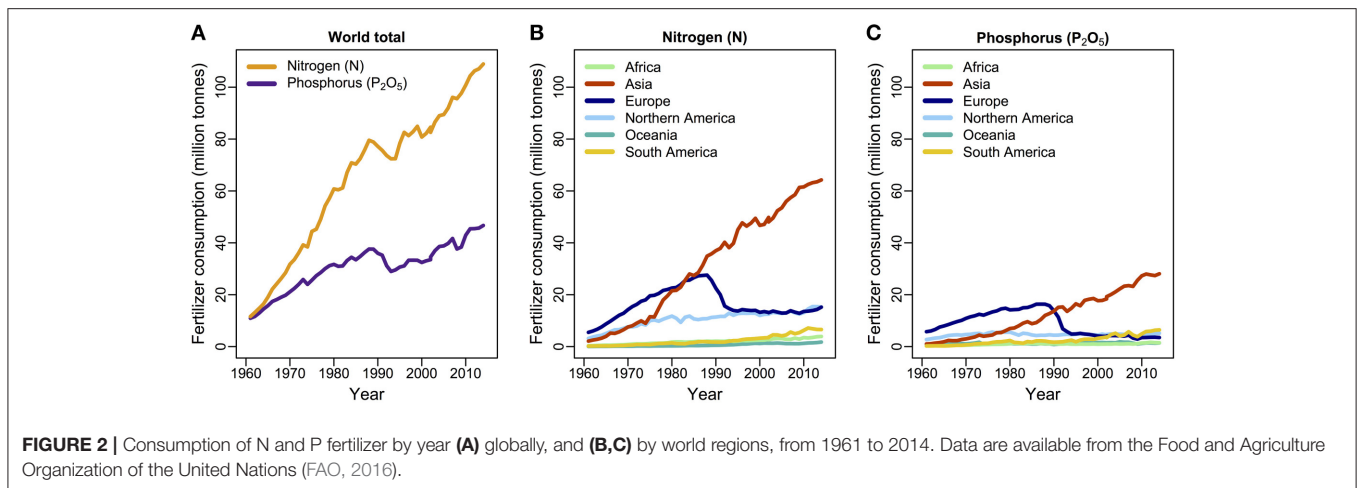
fixation of dinitrogen gas more than 50 years ago. It affects vast areas by increased deposition of oxidized and reduced N with increased runoff of N to freshwater and coastal areas (Galloway et al., 2013).

Anthropogenic N-deposition also originates from nitrogen oxides created during fossil fuel combustion, from nitrogen fixation of cultivated legumes (Ciais et al., 2014), and ammonia produced from animal wastes (Sutton et al., 2013). This elevated N-deposition may shift ecosystems from N to P limitation, with subsequent detrimental ecosystem impacts (Elser et al., 2009, 2010). Conversely, the deposition of P from P-rich dust from sand and agricultural soils may shift some ecosystems from P to N limitation (e.g., mountain lakes: Camarero and Catalan, 2012; Brahney et al., 2015).

In ecosystems, N and P are bound within waste organic products and dead organic matter (e.g., in nucleic acids). They must first be remineralized to release inorganic orthophosphates or dissolved and reduced to inorganic nitrate and ammonia before either element can be absorbed by primary producers (i.e., autotrophic bacteria, algae, plants). The mineralization of organic to inorganic forms of N and P is completed primarily by microorganisms as they metabolize carbon (Spohn and Kuzyakov, 2013). These microorganisms also require N investment to synthesize the alkaline phosphatase enzymes that release P. Because organic N concentrations are higher than those of P, this investment is balanced by N availability and the corresponding gain in P. In terrestrial systems, P cycling is closely linked to mycorrhizal fungi in plant roots that release extracellular phosphatases. If N is applied above a certain threshold, P cycles faster in response to greater N availability for producing phosphatase enzymes. This in turn results in faster rates of P removal and increased P limitation (Vitousek et al., 2010). This implies that elemental imbalances generated at the molecular level can influence elemental stoichiometry in the ecosystem.

In agriculture, nutrients are also lost from ecosystems when crop products are harvested, leaving less plant litter to decompose and fewer nutrients to be returned to the soil. Consequently, fertilizers are added to build and maintain soil fertility. When applied at excessive levels, however, N and P may be lost via leaching, runoff, and erosion (e.g., globally, an estimated 15 million tons of P are lost annually from crop fields due to erosion; Smil, 2000), and an estimated 8 million tons of P are lost in runoff from arable land annually (Cordell et al., 2009). Nitrogen is additionally removed from an ecosystem as N_2 and N_2O gases derived from microbial denitrification (when bacteria use nitrate as a source of oxygen) and anaerobic ammonium oxidation (or anammox, when the oxidation of ammonium is coupled with the reduction of nitrite). With entry into aquatic systems, N and P will trigger eutrophication before being cycled or buried as sediments.

Future Research Priorities

Frequently, the stores, fluxes, and cycling of N and P have been considered separately, partly because of the relative ease of tracing N cycles compared with P. A unified interdisciplinary approach is needed to fully understand macronutrient fate and transport through the ecosystem. It needs to incorporate both terrestrial and aquatic components of the landscape as well as how different macronutrient cycles interact (Grimm et al., 2003; Guenet et al., 2010; Soininen et al., 2015). A better understanding of how N:P supply ratios affect microbial activity (e.g., nitrogen-fixing bacteria and mycorrhizal fungi), and subsequently the flow of these nutrients to and between organisms (e.g., Cherif and Loreau, 2009), may be obtained via controlled experiments. This may help to develop a clearer understanding of the impact of fertilizers on soil and water health and a more informed and environmentally sensitive approach to how we use fertilizers. The urgent need for a more comprehensive understanding is highlighted by the rising concern of a potential global scarcity of P (Cordell et al., 2009).

(2) N and P Usage within Organisms and Genome Structure

Nucleic acids are approximately 39% N and nearly 9% P by mass (Sterner and Elser, 2002), making them among the most N- and P-demanding biomolecules of the cell. Accordingly, the nucleus of eukaryotes represents a substantial sink for N and P.

How this nucleic acid "sink" influences N and P stoichiometry remains unclear, yet these connections are potentially profound: genome size is one of the most variable of all organismal traits, varying 4-fold in mammals, 187-fold in insects, 378-fold in bony fishes, 460-fold in crustaceans (Gregory, 2016), and 2,400-fold in angiosperms (Pellicer et al., 2010). These differences in genome size reflect underlying genomic processes such as (retro)transposon amplification and deletion and whole-genome duplication (polyploidy). All of these processes can influence molecular evolution, gene expression, and organismal phenotype (Neiman et al., 2009, 2013a; Gerstein, 2013; Mayfield-Jones et al., 2013; Ramsey and Ramsey, 2014; Dodsworth et al., 2015; Selmecki et al., 2015; Soltis and Soltis, 2016). Polyploidy in particular has been implicated in the remarkably successful radiations of angiosperms (Soltis et al., 2009; Jiao et al., 2011; Albert et al., 2013; Tank et al., 2015; Van de Peer et al., 2017) and teleost fish (Van de Peer et al., 2009; Braasch and Postlethwait, 2012). Even so, many groups of eukaryotes are characterized by relatively small genomes, arising from genome-streamlining processes such as unequal and illegitimate recombination and chromosomal rearrangements triggered following polyploidy (Leitch and Bennett, 2004; Hessen et al., 2010; Dodsworth et al., 2016). Furthermore, the limited availability of environmental N and P and the expense of building and maintaining nucleic acids and associated proteins necessary to maintain a larger genome and hence cell may, under certain circumstances, act as a selection pressure driving the evolution of smaller genomes.

Selection on N and P use may also have an impact on genome composition. A comparative genomics approach on a set of animal and plant model organisms has shown N-conservation in the transcriptomes of wild plant taxa relative to both crop plants, which have a history of fertilizer application, and animals, which harvest N in organic form from other organisms (Acquisti et al., 2009a,b). Similarly, bias toward lower numbers of N atoms is reported in the highly expressed proteins of bacteria and yeast (Li et al., 2009), and in bacterial and eukaryotic parasites with low-N diets (Seward and Kelly, 2016).

The biochemical link between N and P in growth processes might underpin the broadly convergent ratios reported in many eukaryotic groups, such as the classic Redfield ratio, which states that marine plankton exhibit a mean C:N:P of 106:16:1 (Redfield, 1934; Klausmeier et al., 2004). Most eukaryotes, including microbes (Cleveland and Liptzin, 2007), maintain a certain degree of C, N, and P homeostasis. However, ratios vary with species growth rate (Hillebrand et al., 2013), trophic level, and environmental parameters. For example, N:P ratios range from 21:1 in broadleaved forests to 43:1 in tropical forests (McGroddy et al., 2004), while a more general ratio of 28:1 has been attributed to vascular plants (Chapin et al., 2011). Thus, while *general* ratios have been described, there is considerable variation due to fluctuations in environmental nutrient availability (Güsewell, 2004), phylogeny, and geography.

Biotic stoichiometric ratios are especially good reflections of nutrient availability at the base of the food web, where the scope for plasticity is greatest: proxy measures associated with latitudinal gradients have been described for both terrestrial plants (Reich and Oleksyn, 2004; Kerkhoff et al., 2006) and

marine phytoplankton (Martiny et al., 2013). For example, older tropical soils are richer in N than P, whereas soils of recently glaciated regions at higher latitudes show the opposite pattern, implying reduced N:P ratios in colder areas (Reich and Oleksyn, 2004). Latitudinal and temperature-related changes in N:P likely reflect a higher demand for ribosomes (and thus P) to maintain sufficient protein synthesis at lower temperatures (Toseland et al., 2013; Thrane et al., 2017). This apparent link between temperature and stoichiometry in primary producers is perhaps unsurprising given that temperature drives the rates of many biological processes, including photosynthesis (C gain) and N and P uptake from the environment. At the genomic level, transcription rates in plants also increase with temperature (Sidaway-Lee et al., 2014). The higher demands for ribosomes at lower temperatures may occur to maintain protein synthesis or arise from the increased number of stored immature ribosomes in the nucleolus (Leitch et al., 1995), which can also translate into higher P-demands (and lower N:P) (Woods et al., 2003; Toseland et al., 2013; Thrane et al., 2017).

Future Research Priorities

At an organismal level, functional traits influence fitness via their effects on growth rate, reproduction, and survival (Violle et al., 2007). A stoichiometric perspective leads us to speculate that genome size and ploidal level are important but often ignored functional traits. For example, very large genomes in plants could be selected against in many ecosystems due to their higher demands for N and P. In animals, there may also be selection against larger genomes due to the reduced fitness associated with relatively low developmental rates and the relatively high demand for P invested in RNA (as much as 50–80% of cellular P) for protein synthesis (Hessen and Persson, 2009; Neiman et al., 2013a, but see Larkin et al., 2016). A definitive answer to the question of the extent to which larger genome sizes and higher ploidal levels translate into N and P costs will require characterization of organism-level consequences. For example, the increased N and P demands could be offset by the lower number of cells that are sometimes, but not always, associated with larger genomes (Neiman et al., 2017). Demands may also be offset by more efficient allocation of cellular P to RNA. Indeed polyploidy can rapidly induce a diversity of genetic and epigenetic responses, which can lead to highly variable total transcriptome volumes (Grover et al., 2012), a trait upon which selection can act.

Another key unanswered question is the nature of trade-offs between the genome, transcriptome, proteome, and metabolites for N and P usage, under differing N and P stress, at the cellular, tissue, and organismal levels and in organisms with different genome sizes. Controlled growth experiments under differing nutrient regimes, combined with biochemical, DNA/RNA, and genome analyses, are needed. Understanding the associations between C:N:P ratios and how these elements are partitioned for ribosomal synthesis vs., for example, histone synthesis may not only lead to important insights for organisms within ecosystems, but also provide novel medical insights into cancer dynamics (Elser et al., 2003, 2007b).

(3) The Roles of N and P and Genome Sizes in Species Assemblies

As we move beyond the organism and population levels, we can begin to elucidate some of the roles and consequences of these phenomena on multispecies systems such as communities, food webs, and entire ecosystems. Polyploidy is a genomic trait that may have cascading effects on food webs. For instance, in marine ecosystems, polyploidy may influence the composition of zooplankton communities. Polyploid zooplankton are more common in the Arctic, where a time constraint is imposed by the short growing season (Van Geest et al., 2010). The differential responses between taxa of different ploidal levels could shift the balance of power in both horizontal (competitive) and vertical (consumer-resource) interactions within ecological networks of interacting taxa.

The functional traits of species can influence energy and nutrient fluxes and the resilience of ecosystems to environmental disturbances. Recent evidence suggests that genome structure (i.e., genome size, ploidal level) and nutrient availability can influence plant distributions, community composition, and biomass production in grasslands (Šmarda et al., 2013; Guignard et al., 2016; Segraves, 2017). This possibility is bolstered by large-scale comparative analyses using the Plant DNA C-values database (Bennett and Leitch, 2012) which suggest that plants with large genomes are at greater risk of extinction and are less tolerant of polluted soils and extreme environmental conditions (Vinogradov, 2003; Knight et al., 2005; Greilhuber and Leitch, 2013). Although genome size effects can depend on ploidal level, these data clearly demonstrate that genome structure has ecological consequences that can shape the distribution and persistence of biodiversity.

Variation in DNA and RNA usage in primary producers may also cascade upwards to higher trophic levels. For example, higher ploidal-level representatives of aquatic animals fare better (biomass as well as amount of N and P in their tissues) than their lower ploidal-level congeners, when their diets (composed of primary producers) have relatively high nutrient content. The reverse holds true in low-nutrient conditions (Neiman et al., 2013b; Jeyasingh et al., 2015). Radiotracer assays have also revealed that polyploid *Daphnia* incorporated significantly more ^{33}P and excreted significantly less ^{33}P compared with diploids (Jeyasingh et al., 2015), indicating potentially strong effects of ploidal level on key population and, by extension, community parameters related to consumer-resource interactions. In addition to these "green pathways" that link autochthonous producers to herbivorous consumers, there is clearly the potential for the "brown pathways" that transfer energy and nutrients via detrital feeding links to also be affected by N and P and genome structure. For instance, terrestrial leaf litter fuels the base of many freshwater food webs and the main determinants of its consumption are its C:N:P stoichiometry, which is shaped by the taxonomic and functional attributes of the plants as well as environmental nutrient conditions (e.g., Hladyz et al., 2009; Woodward et al., 2012). Consequently, if the C:N:P stoichiometry of terrestrial plants is itself linked to genome size, genome attributes of these plants have clear potential to shape

ecosystem-level processes and the trophic basis of production of the higher trophic levels in the food web. How, and to what extent, these influences are manifested in natural ecosystems also could depend on the extent of nutrient enrichment from agriculture within the surrounding landscape.

Future Research Priorities

Polyploids and taxa with larger genome sizes should be more common where nutrients are more abundant (Lewis, 1985; Leitch and Bennett, 2004; Leitch and Leitch, 2008; Hessen et al., 2010; Neiman et al., 2013a; Leitch et al., 2014). Support for these predictions has come from recent studies of freshwater snails (Neiman et al., 2013b) and angiosperms (Šmarda et al., 2013; Guignard et al., 2016). Further data collection on, and empirical tests of, the associations between N and P limitation, genome size, and ploidal-level variation in diverse habitat types and biomes are clearly needed to determine how far such predictions hold across different ecosystems and larger, continental scales. Such investigations may take advantage of geographical information systems and niche modeling approaches.

Organisms are frequently linked in stoichiometric feedback loops (Sterner, 1990; Gruner et al., 2008) within wider elemental cycles. Even so, and perhaps due to the sheer complexity of ecological systems, research is most often focused on top-down (consumer-directed) vs. bottom-up (resource-based) effects within only a small part of the food web. A broader system-level approach that can also include indirect effects or reciprocity is needed. Elemental availability can also play a large role in predator-prey interactions, including nutrient cycling by predators, which, in turn, influences what elements are available to prey (Grover, 2003; Andersen et al., 2004; Sardans et al., 2012). With respect to macro-organisms, plants form the base of the food web; the diversity of plant structures is hypothesized to influence multiple trophic levels via effects on differential nutrient requirements, intake, growth rates, and, thus, food quality for higher trophic levels, either as an autochthonous resource that is processed via the food web's green pathways or as detritus within the brown pathways.

Plants are affected by their environment but they can also modify this environment via shifts in microbial communities that have short- and long-term effects (Putten et al., 2013; Van Nuland et al., 2016). Such ecological feedbacks occur when interactions at one time determine the performance or interactions of organisms at another (Hendry, 2016). The impact of nutrient availability has already been demonstrated to alter eco-evolutionary dynamics in plants (Wooliver et al., 2016) and in fish due to increased eutrophication, resulting in changes to parasite load and individual feeding ecology (Anaya-Rojas et al., 2016; Brunner et al., 2017). Future research will thus not only have to focus on direct effects of N and P on species but also on how they impact the interactions between species at the ecosystem level.

(4) N and P and Genomes—toward Sustainable Agriculture

The world's consumption of N- and P-based fertilizers has increased substantially since the 1960's although that rise is now

largely driven by agriculture across Asia (FAO, 2016; **Figure 2**). As discussed above, N and P availability may influence the productivity of plant taxa differentially, depending on genome structure: when nutrients are in excess, polyploid plants tend to increase more in biomass production and competitiveness than diploids. This increased yield may be one reason why most crops are polyploids (Leitch and Leitch, 2008). The rapid rate of biomass production for which crops are typically selected is associated with high soil nutrient demands. Indeed this high demand for nutrients has essentially been "designed" into our current agricultural systems. That in turn has led to a high dependence for fertilizer inputs, whereby agricultural crops generally display high critical nutrient requirements (N and P) for optimal growth with high product removal. This is not only economically expensive but also biologically inefficient and environmentally destabilizing, with increased potential for collateral damage to aquatic ecosystems via eutrophication. For example, P inputs are two to five times greater than the amount exported in the final product (Simpson et al., 2011), and crops take up only 30–40% of applied N (Kant et al., 2011). Nutrient-use efficiency in crops can be improved by, for example, selection of morphological and physiological traits that maximize nutrient uptake (Richardson et al., 2011), optimizing traits that increase the efficiency of ribosomes (Kreps et al., 2002; Kant et al., 2011; Veneklaas et al., 2012), and reducing the carbon costs of nutrient uptake (Lynch and Ho, 2005). Crops are high in P content with a 15:1 N:P ratio (Veneklaas et al., 2012), in contrast to the 28:1 ratio across vascular plants as a whole. Moreover, high concentrations of P in grain crops are undesirable because P is predominantly stored as phytate, which is indigestible, and which reduces absorption of other nutrients in non-ruminant animals, including humans (Veneklaas et al., 2012). The indigestibility of this form of P means it ends up in our sewage and waterways, and one solution may be to reduce P uptake and/or P concentrations in seeds and grains using genomic approaches (Raboy, 2001; Yamaji et al., 2017).

Future Research Priorities

Many engineering approaches are being considered to help improve the management of N and P in the environment. One key goal is to apply less fertilizer while maintaining or even enhancing agricultural yields. A key part of this process will be to revisit our polyploid crops. To date, much plant breeding has exploited polyploids, where genic diversity is fixed and favorable characters can be selected (e.g., allopolyploids: wheat, cotton, tobacco, sugarcane; autopolyploids: strawberry, alfalfa, banana) (Udall and Wendel, 2006; Renny-Byfield and Wendel, 2014). Yet these crops have been developed in a context of high inputs of N, P, and other nutrients. By contrast, the wild relatives of these crop species typically grow in relatively infertile habitats. By targeting inbred introgressed lines and applying high-throughput sequencing in combination with marker-assisted or genomic selection approaches (Heffner et al., 2009; Xu et al., 2014; Jan et al., 2016; Lv et al., 2016), it may be possible to reduce nutrient requirements and/or improve nutrient-use efficiency (higher yield per unit used of fertilizer) of crop plants. There are significant commercial gains to be made from reducing our

dependency on N- and P-containing fertilizers. For example, increasing N use efficiency by 1% alone could lead to estimated annual savings of $1.1 billion (Kant et al., 2011). Additional reductions in fertilizer use could also come from harnessing the microbiome in plant selection, especially under limiting N and P. Future avenues include the use of bacteria and fungi to increase a plant's uptake of nutrients, in particular P (reviewed in Owen et al., 2015), and to exploit new technologies aiming to inhibit P loss and increase fertilizer recovery (Withers et al., 2015).

CONCLUSION

In defining a "safe-operating space" for humanity in the Anthropocene, Rockström et al. (2009a,b) identified nine planetary boundaries and thresholds for anthropogenic activities to remain globally sustainable. They argued that some of these have already been surpassed, including a proposed boundary of 35 million tonnes (Tg) per year of N_2 removed from the atmosphere, far below the actual annual rate of 121 Tg (Rockström et al., 2009b). We are very close to the proposed boundary of 11 Tg per year of P flowing into oceans, currently at c. 9 Tg per year (Rockström et al., 2009b). However, if freshwater systems are also taken into account, we have also surpassed that P boundary (Carpenter and Bennett, 2011). Because N and P are linked to life systems ranging from global ecosystems (e.g., oceans) to genomes, a more complete understanding and an incorporation of stoichiometric analysis at all levels of biological organization are needed. This is indeed an urgent goal, as it will enable us to maintain or enhance agricultural productivity whilst simultaneously conserving and enriching the biodiversity that is essential for the continued provision of ecosystem services across the globe.

AUTHOR CONTRIBUTIONS

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