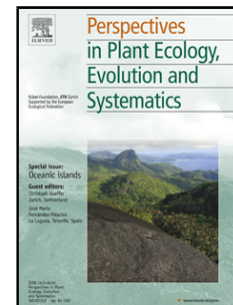


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Recent advances and future research in ecological stoichiometry

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Highlights

- Ecological stoichiometry (ES) studies have growth exponentially in the last years
- ES studies have advanced relating elemental composition with several ecosystem traits
- Biogeochemical niche hypothesis is linking elemental composition with species niche
- The drivers of global change are beyond a general imbalance of ecosystems N:P ratio
- We identify future ES research in the frame of ecosystem function and global change

ABSTRACT

Studies on ecological stoichiometry (ES) have increased rapidly in number in recent years. Continuous exploration of classical concepts such as the growth-rate hypothesis (GRH), which is based on the relationship between the nitrogen:phosphorus (N:P) ratio of organisms and their growth-rate capacity, has identified new patterns and uncertainties, particularly with regard to terrestrial plants and microbial systems. Another concept that has proven to be helpful is the Redfield ratio, which postulates a consistent carbon:nitrogen:phosphorus (C:N:P) molar ratio of 100:16:1 in marine phytoplankton and open oceanic waters, and this ratio is related to the protein:rRNA ratio associated with protein synthesis. ES studies in all types of

ecosystems have demonstrated that shifts in the elemental composition of water, soil, organisms, and communities are linked to the spatiotemporal structure and function of the ecosystem communities. The recent trend of also considering additional bio-elements such as potassium (K), magnesium (Mg) and calcium (Ca), has improved our understanding of how resource availability in complex ecosystems affects basic organism functions such as growth, stress responses, and defensive mechanisms. The biogeochemical or bio-elemental niche hypothesis is a novel tool that uses the concentrations and ratios of several bio-elements to define species niches and to scale up processes at the community and ecosystem levels. Global environmental changes, such as an increase in atmospheric CO₂, drought, N deposition, and species invasion, change the elemental composition of the growth media (soil and water), organisms, and ecosystems. For example, the growing imbalance between N and P that results from very large anthropogenic inputs of reactive N and smaller inputs of P into the biosphere is increasingly affecting the health of both ecosystems and humans. In this review, we summarise recent advances in ecological stoichiometry and identify key questions for future research on the impacts of ES on ecosystem function and structure due to global environmental change.

Keywords: C:N; C:P; N:P; biogeochemical niche; structure of food webs; diversity; phosphorus; nitrogen; carbon cycling

1.Introduction

Studies on ecological stoichiometry (ES) have increased exponentially in number in the last decade. Relationships between the elemental composition of water, soil, and organisms and basic ecological traits such as nutrient cycling, composition and diversity of species communities, spatial distribution of species, trade-offs and synergies with drivers of global change, nitrogen (N₂) fixation and capacity of ecosystem production, have been widely

investigated (Jirousek et al., 2011; Qui et al., 2013; Borer et al., 2015; Deng et al., 2015; Guenther et al., 2015; Tao et al., 2016; Vanni and McIntyre, 2016; Chodkowski and Bernot, 2017; Lee et al., 2017; They et al., 2017; Zhang and Elser, 2017; Delgado-Baquerizo et al., 2018; Zheng et al., 2018; Kranabetter et al., 2019; Moody and Wilkinson, 2019), and novel approaches and hypotheses have been tested and incorporated into theoretical ES models (Loladze and Elser, 2011; Rivas-Ubach et al., 2012; Sardans and Peñuelas, 2015; Gonzalez et al., 2017; Guignard et al., 2017; Peñuelas et al., 2019a).

Classic ES paradigms and lines of research, such as the study of general optimum carbon:nitrogen:phosphorus (C:N:P) ratios across taxa and ecosystems or the growth-rate hypothesis (GRH) have been the objects of several studies in the last decade. As claimed by Redfield et al. (1963), for marine phytoplankton and soils (Cleveland and Liptzin, 2007) and terrestrial plants (MacGroddy et al., 2004), several recent studies have reported optimal C:N:P ratios of particular taxa or ecosystem compartments with great variability around the means. The other classical paradigm, the GRH, based on the relationships between the N:P ratios in organisms and their growth rate capacity and scaling ecological consequences (Elser et al., 2000a, b; Sterner and Elser, 2002), has yielded consistent results in the last decade in many (Loladze and Elser, 2011; Hillebrand et al., 2013; Xing et al., 2016; Zederer et al., 2017; Branco et al., 2018) but not all systems (Yu et al. 2012; Peng et al., 2011a; Martiny et al., 2013; Yan et al., 2015a; Moreno and Martiny, 2018). Despite some exceptions (see below), the GRH, based on the need for high P-rich RNA to support high growth rates, is becoming clearer. These two classical paradigms have frequently been the basis for new solid and expanding lines of study, hypotheses, and approaches in Ecological Stoichiometry ES in the last few years (Box 1).

These new ES approaches have identified more global and consistent couplings of ES with ecosystem and organismic function and structure by including a wider range of elements beyond the concentrations of C, N and P that are typically used (Box 1). For example, new studies have included potassium (K) and/or magnesium (Mg), which are involved in various plant functions, such as water-use efficiency and light capture (Khan et al., 2015; Sardans and Peñuelas, 2015; Xing et al., 2015; Yan et al., 2015b; Pierce et al., 2016; Jochum et al., 2017; Urbina et al., 2017; Wang et al., 2018a) (Box 1).

Novel ES approaches have recently aimed to complement and provide specific and measurable tools applicable to the framework of the classical niche theory, one of the main topics of ecology, which is based on the idea that each genotype/species occupies a specific physical space and has a specific function in its ecosystem (Schoener, 1986). The

biogeochemical niche (BN) hypothesis was proposed by Peñuelas et al. (2008, 2010, 2019) and proposed that each species/genotype should have a singular elemental composition. This hypothesis has been given different names, such as the stoichiometric niche hypothesis (Chimphango et al., 2015; Sardans et al., 2015; Gonzalez et al., 2017; Zamora et al., 2017; Zhao et al., 2018a; Peñuelas et al., 2019a), and has been demonstrated in subsequent studies, as well as in taxa other than plants (Gonzalez et al., 2017; Bartrons et al., 2018; Sanders and Taylor, 2018) (Box 1).

Establishing links between ecosystem function and structure and the C:N:P ratios of communities and media (soil or water) has been the main objective of ES since its origins. . Several recent studies have provided information on how media (water or soil) or food C:N:P ratios affect the structure of food webs in freshwater (Hillebrand and Lehmpfuhl, 2011; Hessen et al., 2013; Elser et al., 2015; Filipiak, 2016; Moorthi et al., 2017; Prater et al., 2017; Vanderploeg et al., 2017; Wagner et al., 2017; Branco et al., 2018; Iannino et al., 2018; Moody et al., 2018; Prater et al., 2018; Zhang et al., 2018b; Bell et al., 2019) and marine ecosystems (Glibert et al., 2011; Galbraith et al., 2015; Bi et al., 2017; Branco et al., 2018; Mousing et al., 2018; Spilling et al., 2019; Tanioka and Matsumoto, 2019). The most intelligible advances, however, have been in terrestrial ecosystems, where conclusions were not possible earlier because of insufficient studies. Studies on terrestrial ecosystems have increased exponentially in the last decade, and sufficient databases are now available to discuss and conclude the link between the characteristics, values, and shifts in media (water or soil) or food C:N:P ratios and their effects on the structure of food webs in terrestrial ecosystems (Fanin et al., 2013; Abbas et al., 2014; Zechmeister-Bolstenstren et al., 2015; Paseka and Grunberg, 2019) Box 1).

There is mounting evidence that link the drivers of global change and shifts in the elemental compositions of water, soil, and organisms and therefore, shifts in ecosystem structure and functioning (Jirousek et al., 2011; Sardans et al., 2012 and 2017a,b; Li et al., 2013; Peñuelas et al., 2013a; Deng et al., 2015; Yuan and Chen, 2015; Carrillo et al., 2016; Yan et al., 2016; Thrane et al., 2017; Velthius et al., 2017; Wang et al., 2017; Yuan et al., 2017; Delgado-Baquerizo et al., 2018; Schmitz et al., 2019). Indeed, ES analysis may be necessary for elucidating and predicting the effects of global environmental change on climate, food security, biodiversity conservation, and the provision of ecosystem services (Van der Velde et al., 2014; Guinard et al., 2017; Leal et al., 2017; Lu and Tian, 2017; Lun et al., 2018; Wang et al., 2018b; Peñuelas et al., 2019b) (Box 1).

Novel complementary techniques to study the elemental composition of water, soil, ecosystem pools, and organisms, as well as of ecosystem structure and function have been proposed (Rivas-Ubach et al., 2012, 2018; Gargallo-Garriga et al., 2015). Metabolomics, for example, has found that the growth of terrestrial plants coincides with the timing of the highest foliar concentrations of N and P and the lowest foliar N:P ratios (Rivas-Ubach et al., 2012), and metatranscriptomics has advanced our understanding of the mechanisms underlying the links between shifts in N:P ratios and species diversity (Alexander et al., 2015).

We review recent advances in ES studies in all types of ecosystems with the following aims: (i) to summarise the current status and understanding of ES paradigms (ii) to identify new emerging hypotheses and generalities, (iii) to understand the impact of global change drivers on ecosystem stoichiometry, and (iv) to reveal key knowledge gaps and targets for future research. We searched the ISI Web of Science using combinations of the following keywords: alien, animal, arid, aridity, availability, available, biogeochemical, biodiversity, carbon, composition, community, concentration, content, consumer, C:K, C:N, CO₂, C:P, deposition, diversity, drought, ecological, ecology, ecosystem, enzyme, fish, foliar, forb, function, functionality, grass, grassland, growth, growth rate, heath, insect, invasion, invasive, invertebrate, lake, leaf, mammal, marine, needle, niche, nitrogen, nitrogen deposition, N fixing, N:K, N:P, ocean, phosphatase, phosphorus, photosynthesis, photosynthetic, phylogenetic signal, phylogeny, plankton, phytoplankton, plant, potassium, P:K, ratio, Redfield, respiration, river, sea, soil, solution, stoichiometric, stoichiometrical, stoichiometry, stream, structure, success, temperature, tree, vertebrates, warming, water and zooplankton.

2. Review of recent research on classical topics

Growth Rate Hypothesis

ES studies of planktonic communities tend to yield results consistent with the GRH (Tables 1 and S1). Only a minority (18%) of the 33 studies published between 2011 and 2019 failed to observe a consistent relationship between the N:P ratio of planktonic organisms and their growth rate (Godwin et al., 2017; Godwin and Cotner, 2018; Table 1). Galbraith and Martiny (2015) developed a mechanistic model based on the variation of the P:C ratio as a linear function of ambient phosphate concentrations and the variation of the N:C ratio as a function of ambient nitrate concentrations, and the model outputs and observational validation data provided evidence that the N:P ratio drove the growth rate when N and P concentrations were high. One of the most convincing studies compiled the results from 55 datasets for phytoplankton around the world; it revealed that phytoplanktonic N:P ratios decreased as

growth rate increased and variance decreased, that is, fast-growing phytoplankton contained more P and had simpler elemental composition (Hillebrand et al., 2013). Some observational and experimental analyses have found negative correlations between water and/or phytoplanktonic N:P ratios and phytoplankton growth rates and a higher growth rate of plankton in diets rich in P (Guenther et al., 2015; Garcia et al., 2016; Fu and Gong, 2017; Krist et al., 2017; Hessen et al., 2017; Rivas-Ubach et al., 2018; among others; Tables 1 and S1). However, a recent study reported that growth rate could be weakly correlated with the rate of intake of dietary P but strongly correlated with the rate of assimilation of ingested P, suggesting that studies should consider shifts in the N:P ratio of the assimilated organic matter rather than shifts in the N:P ratio of the food (Urabe et al., 2018).

Recent studies have provided sufficient data supporting the utility of the GRH and reasons for different growth rates in terrestrial ecosystems (Yu et al., 2012; Zhang et al., 2020). Recent studies indicate that N:P ratios are negatively correlated with the growth of terrestrial plants when the majority of biomass comprises photosynthetic tissue and N and P are mainly allocated to the capture of light and CO₂ and thus to the production of new biomass and growth (Figure 1) (Zhang et al., 2020). The GRH thus applies to N and P concentrations and N:P ratios in photosynthetic tissues during the initial stages of growth or in growing seasons when the majority of metabolic products are invested in growth, and not during periods with water limitation (Wanek and Zotz, 2011; Rivas-Ubach et al., 2012; Liang et al., 2018; Qiao et al., 2018; Sun et al., 2019). Experiments in terrestrial systems under these conditions support the seminal work in communities of freshwater plankton and across a range of biological scales (Andersen and Hessen, 1991; Sterner et al., 1992, 1998; Elser et al., 1996; Sterner and Elser, 2002). Nonetheless, many ES studies have supported the GRH (Peng et al., 2011a; Rivas-Ubach et al., 2012; Yu et al., 2012; Yan et al., 2015a; Huang et al., 2016; He et al., 2017; Jing et al., 2017; Zhang et al., 2019a) (Table 1). Plant N:P ratios and growth rates have been correlated during the initial stages of life, when most N and P are allocated to growth, but not in grasses during advanced stages of growth when the allocation of N and P to organs and functions that are not directly involved in growth increases exponentially (Zhang et al., 2019a) (Figure 1). In contrast to phytoplankton that allocate N and P mostly to growth/reproduction during all vital cycles, higher terrestrial plants large proportions of N and P to functions other than growth as they mature (Kerkhoff and Enquist, 2006; Peñuelas and Sardans, 2009; Rivas-Ubach et al., 2012). A widely accepted hypothesis for mature terrestrial plants states that foliar N:P ratios increase at low growth rates, reaching a maximum, and then N:P ratios become negatively correlated with growth rate (Yu et al., 2012; Niu et al., 2019).

The GRH often does not apply under conditions of low growth rates where aboveground growth is positively correlated with N:P ratios, coinciding frequently with very low concentrations of N and P. This hypothesis is consistent with predictions of a mathematical model that assumes that N allocation to amino acids/proteins (including rubisco) and P allocation to P-rich RNA, projects a linear increase in the N:C ratio with growth rate, and a quadratic positive link between P:C ratio and growth rate wherein N:P ratio increases at low growth rates, reaches a maximum, and then decreases at high growth rates (Agren, 2004). As predicted by the GRH, increase in foliar N and P concentrations are associated with lower N:P ratios because N concentrations increase more slowly than P concentrations (Agren, 2004, 2008; Reich and Oleksyn, 2004; Kerkhoff et al., 2005; Niklas et al., 2005; Niklas and Cobb, 2005; Reich et al., 2010; Sardans et al., 2012b; Sardans et al., 2016a, b; Tian et al., 2018; Wang et al., 2020), and foliar N:P ratios are lower in rapidly growing pioneer plant species than in late-successional slowly growing species in the same biome (Peñuelas et al., 2013b,c; Sardans and Peñuelas, 2013a; Busch et al., 2018). Similarly, differences in foliar N and P concentrations have been reported in domesticated species of wild herbaceous plants used for food, where N and P concentrations increased and N:P ratios decreased as the growth rates of the plants increased (Delgado-Baquerizo et al., 2016).

Limited evidence (a lack of studies) suggests that the GRH also applies in other taxa than plants and green algae. Recently, Six and Elser (2020) observed that in bark beetles, the decrease in C:P and N:P ratios are due to higher allocation of P to P-rich RNA to support growth. Some studies have observed a negative correlation between organismic N:P ratios and growth rates in various taxa, such as Echinoidea (Prado et al., 2014), aquatic macrophytes (Xing et al., 2016), terrestrial invertebrates (Paseka and Grunberg, 2019), and vertebrates (Milanovich et al., 2015). Testing the GRH in more complex and evolutionarily advanced animals, however, is difficult because of the allocation of N and P to functions other than growth, such as in fish where large amounts of P are allocated to bone (Guo et al., 2018). Some studies, for example, suggest that some species can accumulate more P under P limiting conditions; thus, P concentration and growth rate may also be negatively correlated in organisms such as some marine macroalgae (Reff et al., 2012). The GRH may thus apply for correlation between N and P concentrations and N:P ratios in growing cells and tissues. When their growth rate is high, N:P ratios decrease because of the importance of P-rich RNA in accelerating protein synthesis (Sterner and Elser, 2002). As an analogy, both bricks (amino acids and proteins) and bricklayers (P-rich RNA) are needed to build the walls of a house. Even if many bricks are available, the walls cannot be built without bricklayers. This idea underlies

the metabolic basis of the GRH, but we must highlight the few studies that have investigated the relationship between the N:P ratios and growth rates of animals, especially in the initial stages of growth, to conclude whether or not the GRH applies throughout the animal kingdom.

Redfield ratio

Although studies in the last decade have provided some theoretical (molecular and mathematical) support, they do not show full agreement with the Redfield ratio. Redfield et al. (1963) proposed a uniform molar C:N:P ratio of 100:16:1 in marine phytoplankton. Many studies in the last decade with experimental and observational approaches have supported the applicability of the Redfield ratio and its underlying mechanism. One study used published and unpublished N:P ratios of phytoplankton and particulate matter to assess the global patterns of N:P ratios in oceans (Martiny et al., 2013). Overall, the data are not consistent. There has been some evidence on the application of the Redfield ratio in marine and non-marine ecosystems, where optimum N:P ratios may be the consequence of equilibria among several biotic and abiotic factors. For example, many models indicate that marine phytoplankton deviate only slightly from the Redfield ratio (Frigstad et al., 2011; Zhang and Elser, 2017) and that they maintain nearly constant N:P ratios because of compensatory dynamics between active and inactive N fixers that drive the chemistry of open ocean water during nutrient recycling (Augueres and Loreau, 2014), as claimed by Klausmeier et al. (2004). Optimum protein:rRNA ratios in protein synthesis under non-limiting N and P conditions, however, represent an N:P ratio of 16 (molar basis) (Goldman et al., 1979; Loladze and Elser, 2011), which is similar to and supports the Redfield ratio and has also been reported in a meta-analysis of fungi (Zhang and Elser, 2017).

Meta-analyses of published and unpublished data for marine phytoplankton have reported global and regional average ratios that are inconsistent with the Redfield ratio. Data sets of 5631, 5318 and 4965 phytoplanktonic C, N and P concentrations indicated average N:P ratios of 18-28 in warm oceans and 13 in oceans at high latitudes (Martiny et al., 2013). These results are consistent with other compilations and analyses indicating, indicating that the critical N:P ratio in phytoplankton for transitioning from N- to P-limitation may be higher than the Redfield ratio and are consistent with experiments on specific taxa of plankton (Greider and La Roche, 2002; Trautwein et al., 2017). Extensive data analysis in a recent review by Moreno and Martiny (2018) suggested that the physiological mechanisms in organisms play an important role in regulating plankton and community C:N:P stoichiometry in nutrient-rich sites in oceans, whereas in nutrient-poor sites, biogeochemical interactions may regulate the

organisms' C:N:P stoichiometry. Thus, the Redfield ratio remains unconfirmed with two almost clear messages. One message is that biochemical evidence supports optimum conditions for growth, consistent with some studies reporting metadata averages similar to the Redfield ratio, suggesting a natural trend for plankton in open oceans to have C:N:P ratios similar to the Redfield ratio. The other message is that biogeochemical constraints (those linked to the circulation of ocean water) drive the maintenance of planktonic C:N:P stoichiometry in several areas that are significantly different from the Redfield ratio.

Current reports suggest that the Redfield C:N:P ratio is not achieved in freshwater ecosystems, mainly lakes, indicating that inland water bodies have shorter residence times than deep ocean waters, hindering the establishment of biological control (They et al., 2017). This account is consistent with the observations by Elser and Hassett (1994) that the N:P ratio of phytoplankton was higher in lakes than in oceans, whereas the N:P ratio of zooplankton was higher in oceans than in freshwater. After stoichiometric analysis, these authors deduced that the consumer-driven nutrient-recycling ratios might be 4-5-fold higher in lakes than in marine systems. These higher nutrient ratios in freshwater ecosystems could be a general adaptation to the shorter residence time of water in freshwater systems than in marine systems. The influence of external inputs of organic matter and water, and the climatic conditions (volume of water inputs, evapotranspiration) of surrounding environments and the nearest terrestrial ecosystems can also vary greatly among and within sites over time, promoting high variability in C, N, and P concentrations and C:N:P ratios in inland water bodies (Zadereev et al., 2014; Collins et al., 2017; Huang et al., 2018; Ngochera and Bootsma, 2018; Smith and Jarvie, 2018). Nonetheless, the biological control of chemical environments increases as the mean residence time of the water increases, which is consistent with the mechanisms underlying the Redfield ratio (They et al., 2017). Studies investigating the optimum C:N:P ratios in species of freshwater phytoplankton have reported ratios that are very different from the conventional Redfield ratio (Townsend et al., 2008; Middleton and Frost, 2014).

It is noticeable that in a review analysis, soils had a mean atomic C:N:P ratio of 186:13:1 and soil microbial biomass, of 60:7:1, showing that there is a higher accumulation of P than of N and C in microbes and a higher accumulation of N than of C with in soil medium (Cleveland and Liptzin, 2007). This shows the key role of soil microbial community in retaining P in the soil. However, there is a lack of recent studies on soil and soil compartments C:N:P ratio.

N:P across gradients and taxa

Recent analyses of global databases of terrestrial plant species have found that foliar N and P concentrations decrease and N:P ratios increase from polar to tropical latitudes (Li et al., 2018; Zhang et al. 2018a, 2019b), which is consistent with previous seminal studies (McGroddy et al., 2004; Reich and Oleksyn, 2004; Kerkhoff et al., 2005; Yuan and Chen, 2009). This global pattern is consistent with the soil-age hypothesis (Walker and Syers, 1976) and a more recent study (Vitousek et al., 2010), that states that regions at higher latitudes with young soils have a greater capacity to release P from parental minerals than do older soils with long-term weathering of surface parental materials. Ecosystems with old soils can consequently become depleted in P, which may be exacerbated at a global scale because old soils coincide with higher mean annual precipitation and temperature toward tropical regions and thus, have climatic conditions more vulnerable to the leaching and depletion of P (Davidson et al., 2007; Richardson et al., 2008; Hedin et al., 2009; Hou et al., 2018). However, some exceptions have been reported at the regional scale. For example, the N:P ratio increased with latitude in a multispecies study in eastern China (Zhang et al., 2019) and a study on the Loess Plateau (Fang et al., 2019). This pattern was also observed when intraspecific populations along latitudinal gradients were compared across Europe and North America (De Frenne et al., 2013; Sardans et al., 2016a,b). However, most recent reports are generally consistent with a general P limitation for forest growth at low latitudes and with N and P colimitation in cold temperate forests, as in one review (Li et al. 2018); some less recent studies have observed that P limitation is widespread in plants and affects equally distinct terrestrial plant biomes (Elser et al., 2007). Some studies have observed a greater proportional increase in foliar P than in N concentrations across (Tian et al., 2018) and within (Sardans et al., 2016b) species along natural gradients. The effects of human activities on foliar elemental composition along latitudinal gradients have also been detected, wherein anthropogenic N deposition drives foliar N concentrations and N:P ratios in the key forest species of *Pinus sylvestris* (Sardans et al., 2016b) and *Picea abies* (Kang et al., 2011) across Europe.

Similar latitudinal patterns of N:P ratios have been also observed in forest soil microbes and tree roots (Yuan et al., 2011; Li et al., 2014). In contrast to these consistent and similar patterns of changes in N:P ratios in tree foliar and root tissues along latitudinal gradients, no data are available for latitudinal N:P stoichiometry in other types of plants, such as legumes (Liu et al., 2017). Yu et al. (2017), however, found no consistent relationship between N:P ratio of plant belowground biomass and latitude, indicating that nutrient use in aboveground and belowground plant organs was at least partially decoupled..

Foliar N:P ratios at regional scales also vary with temperature and water availability along environmental gradients. For example, foliar N and P concentrations in Tibetan grass

species increased and N:P ratios decreased with decreasing temperature (Fan et al., 2016), and foliar N and P concentrations in Mediterranean climates increased and N:P ratios decreased with increasing water availability, owing to more favorable growth conditions (Sardans et al., 2011; Sun et al., 2017a).

3. Effects of stoichiometry on ecosystem structure and function

We highlighted the lack of ES studies in terrestrial ecosystems in a previous review to evaluate topics such as the GRH, relationships of elemental stoichiometry with trophic web function and species composition in ecosystems and communities (Sardans et al., 2012). Several recent studies have provided further evidence that changes in the N:P ratios of media (water or soil) or food affect the structure of food webs in terrestrial ecosystems (Fanin et al., 2013; et al., 2014; Zechmeister-Bolstenstren et al., 2015; Paseka and Grunberg, 2019) and other studies have observed this link in aquatic ecosystems (Plum et al., 2015; Sitters et al., 2015; Lee et al., 2017; Elser et al., 2018; Zhao et al., 2018b; Nhu et al., 2019). Shifts in organismic stoichiometry throughout trophic webs due to changes in excreted stoichiometry and/or resource use (nutrients, light, water) have provided new insights into the changes in community composition, dynamics, and functionality in freshwater and marine ecosystems (Glibert et al., 2011; Hillebrand and Lehmpfuhl, 2011; Hessen et al., 2013; Plum et al., 2015; Elser et al., 2015; Galbraith and Martiny, 2015; Vanni and McIntyre, 2016; Filipiak, 2016; Moorthi et al., 2017; Vanderploeg et al., 2107; Branco et al. 2018; Moody et al., 2018; Mousing et al., 2018; Prater et al., 2018; Spilling et al., 2019; Tanioka and Matsumoto, 2019). For example, the phenotypic selection of *Synechococcus* cyanobacteria living with a pathogenic phage was affected by the N:P stoichiometry of the medium, and thus, the associated co-evolutionary trophic pathways in the host-microbe community were affected because prey selection depends on the N:P ratios of the medium (Larsen, 2019). Several recent studies of planktonic communities have also observed strong links between the species composition of communities and the water and/or organismic N:P ratios and N and P concentrations through changes in growth rate and/or species dominance as a function of their optimum N and P requirements (Elser et al., 2009a, b; Hessen et al., 2013; Grosse et al., 2017; Branco et al., 2018; Bergstrom et al., 2018), which is consistent with several studies from the 1990s and 2000s.

Changes in bottom-up and top-down fluxes of N and P throughout trophic chains are linked to shifts in diet and N:P ratios of excretion, which are associated with shifts in the overall functioning of aquatic food webs. The selective pressure exerted by zooplankton strongly affects the composition of phytoplanktonic species (Vanderploeg et al., 2017; Branco

et al., 2018). Similar shifts in N:P ratios in fishes have been observed depending on the pressure of predation by other fishes (Moody et al., 2018). These findings support the compensatory feeding hypothesis that states that at high trophic levels, when limited by a specific nutrient, organisms vary their diet by increasing the consumption of food, mainly of those organisms rich in the limiting (Iannino et al., 2018). N-demanding zooplankton promote the abundance of phytoplankton with low N:P ratios, whereas P-demanding zooplankton favor the dominance of phytoplankton with high N:P ratios (Branco et al., 2018). Zebra mussels exert strong feedback on communities of algae and plankton by varying the N:P ratio of their excretions; when seston have low P concentrations and high N:P ratios, zebra mussels eating seston excrete low P, that is, have a high N:P ratio, slowing the growth of most producers but potentially promoting the growth and bloom of N-limited *Microcystis* due to increasing water nitrate concentration (Vanderploeg et al., 2017). The growth, survival, stoichiometry and nutritional quality of a trophic level is thus determined by both food quality (low trophic level) and predatory pressure (high trophic level), correlating all with shifts in elemental composition at the various levels of trophic webs (Bergström et al., 2018; Bell et al., 2019). Predator cues can influence the behavior of *Daphia* sp (zooplankton), increasing its metabolic rate and reducing growth, but the extent of growth reduction depends on the P concentration of the food source (phytoplankton) under a low-P diet (Bell et al., 2019). The molecular mechanisms underlying the impact of low-P diets of zooplankton on growth have been associated with the low expression of several genes involved in growth (Jeyasingh et al., 2011). Aquatic omnivores can increase their consumption of plants when plant stoichiometry is similar to their own, altering the overall web structure and thus, increasing their top-down control of the community composition of aquatic plants (Zhang et al., 2018b). Fishes can affect the stoichiometry of aquatic systems for other mechanisms; for instance, in shallow lakes, the feeding and removal of sediments by fishes affect the C:N:P stoichiometry of suspended particulate matter (He et al., 2019a).

Several recent studies have also reported significant correlations between changes in species growth and the success and shifts in the species composition of trophic webs with changes in N:P ratios and N and P concentrations in the soils and/or organisms in terrestrial ecosystems. Changes in the elemental composition of food affect the species composition of consumer communities not only directly through a bottom-up effect but also indirectly through a top-down effect in response to the feedback to change in the composition and pressure of the predator communities (Chen et al., 2014a). In some relationships such as that between spiders and their prey, the selection of an array of prey species by each spider species is due to stoichiometric imbalances in the predator-prey interactions (Ludwig et al., 2017).

These relationships between shifts in the N:P ratios of the food sources and changes in community composition of the consumer species have been widely observed in pollinators (Abbas et al. 2014), hosts and their parasites (Aalto et al., 2015), invertebrate-microbe trophic webs (Fanin et al., 2013; Sitters et al., 2014; Scharler et al., 2015; Jochum et al. 2017; Shao et al. 2017; Larsen, 2019), plant-animal herbivory (Zhang et al., 2011; Filipiak and Weiner, 2017a, b; Vogels et al. 2017) and predators and their prey (Trubl and Johnson, 2019). A large body of evidence has accumulated on the relationships between community composition and important ecosystem processes, such as the transfer of energy and elements through trophic levels and nutrient cycling associated with changes in organismic N:P ratios in terrestrial ecosystems (Peñuelas et al., 2013a,c and 2019b; and references therein, Zechmeister-Bolstenstren et al., 2015). The magnitude of the role of the dung excreted by large vertebrate herbivores in the control of the distribution and stoichiometry of nutrients within ecosystems can be similar to the role of biological fixation or fires (Cech et al., 2008,2010; Sitters et al., 2014;2015; Veldhuis et al., 2018; Valdes-Correcher et al., 2019). The return of N by excretion of large vertebrate herbivores in savanna ecosystems is much higher than the return of P because the N:P ratio is lower in herbivores than in plants; hence, they need to retain more P, which has a strong top-down effect on ecosystem stoichiometry (Veldhuis et al., 2018). This trend is even higher in large animals because the need for P for bone formation scales exponentially with body size (le Roux et al., 2020) and because metabolic P demand by biomass correlates negatively with body size (Sitters and Olde Venterink 2021a). However, at the same time, a large part of the N in dung and urine is in the form of ammonium, which can be lost easily by volatilisation and leaching, and areas receiving high amounts of macroherbivore excreta can become N limited for plants (Augustine, 2003; Cech et al., 2008). Recently, Sitters and Olde Venterink (2021b) have observed how the differences in dung N:P ratios between two dominant macro-vertebrates in the African savanna drive the competitive relationship between N₂-fixing trees and grasses. For instance, in soils receiving zebra (*Equus quagga burchellii*) dung with a low N:P ratio (3.5) tree seedlings have a competitive advantage by favouring nodulation; in contrast in soils receiving giraffe (*Giraffa camelopardalis*) dung with a low N:P ratio (6.4) grasses have an advantage by suppressing nodulation and tree establishment. Di Palo and Fornara (2017) compared the N:P ratios of soils and plant communities along successional gradients in several grasslands around the world and found that the soil N:P ratios increased, whereas the plant-community N:P ratios remained constant as succession progressed. Similar trends were observed in the Swiss Alps, where N:P in the vegetation did not significantly change with soil successional time (Göransson et al 2016). Even though the N:P ratios of plant communities remained constant, the proportion of distinct

functional groups, i.e. legumes, grasses, and forbs, in the community varied along successional gradients, thus affecting the contribution of species with different N:P ratios and N and P concentrations along the temporal successional gradient without significantly affecting the overall N:P ratio of the plant community (Di Palo and Fornarà, 2017). However, despite this observation of almost constant N:P ratios of plant communities along successional gradients in a determined site, the variation among sites can be large (Olde Venterink et al., 2003; Göransson et al 2016). This result suggests that plant communities rely on internal nutrient mechanisms that regulate the N:P ratio, for the community to depend strongly on plants under particular bedrock and climatic conditions. These interesting findings warrant further research in other communities and successional processes.

Relationships of the species composition and functioning of soil microbes, and decomposers communities and N:P ratios of soil and litter have recently been widely reported. Some examples include the links between the organic composition of soil, C:N:P stoichiometry and the functionality of decomposition (Mooshammer et al., 2014; Heuck and Spohn, 2016; Spohn, 2016) and the structure of decomposer communities (Mooshammer et al., 2014; Lee et al., 2015, 2017; Su et al., 2015; Eo and Park 2016; Spohn, 2016; Delgado-Baquerizo et al., 2017). Soil microbes can adapt to different levels of nutrients, C supply, and litter stoichiometry mainly by affecting community composition and the synthesis of soil enzymes and the proportional synthesis of specific enzymes involved in the mineralization of these different bio-elements (Mooshammer et al., 2014; Achat et al., 2016 and references therein). Changes in soil C:N:P by fertilization also affect the composition and function of microbial communities and thus, litter decomposition by affecting litter stoichiometry (Barantal et al., 2014). Soil microbes partially counteract stoichiometric imbalances in soil organic matter because they retain and slow the cycling of limiting bio-elements and recycle and accelerate the cycling of the most abundant bio-elements (Chen et al., 2019). Similar observations have been reported for the decomposition of the dung of herbivore macro-vertebrates under soil macrofauna control in African savanna (Sitters et al., 2014).

Some studies have reported that biotic relationships between plants and fungi are strongly determined by the level of limitation of litter/soil C, N, and P and their stoichiometric relationships. Fungi and generally all soil microbial decomposers exert feedback on litter/soil stoichiometric variables (Johnson, 2010; Roy et al., 2017; Mei et al., 2019a,b), helping to maintain more balanced C:N:P ratios in plants (Johnson, 2010; Gray et al., 2010). The mycorrhization of terrestrial higher plants is mainly associated with high N availability and low N:P ratios, favouring high mobilisation of soil P and thus, plant P uptake and a more balanced plant N:P ratio (Gray et al., 2010; Wang et al., 2014; Mei et al., 2019a,b; Riley et al., 2019),

which in turn favours high N and P foliar concentrations associated with a low N:P ratio and high growth rate (Chen et al., 2010; Mei et al., 2019a,b; Riley et al., 2019) and a high N-use efficiency (Gray et al., 2010). In support of this, Chagnon and Bradley (2013) observed that a decrease in the soil N:P ratio was associated with a decrease in arbuscular mycorrhizae and corresponding increases in non-mycorrhizal fungi. Severe N limitation, however, can limit plant control of arbuscular mycorrhizal symbiosis, irrespective of the status of P in soil (Friede et al., 2018).

Strong evidence suggests a consistent transition from fast-growing species to more conservative/competitive species in all types of media, coinciding with the transition from non-limiting N and P and low N:P ratios toward N and P limitation and high N:P ratios. Stress-tolerant plants have been associated with high N:P ratios and a more homeostatic stoichiometry, fast-growing ruderal species, with low N:P ratios, and competitor species, with a low homeostatic stoichiometry (Busch et al., 2018; Peñuelas et al., 2019a) (Figure 2). In this context of the relationships between the N:P ratio and plant style of life, Fujita et al. (2014) observed that European endangered plant species frequently live in phosphorus-limited soils and invest very low in reproduction, presenting conservative traits linked to stress-tolerant species which is consistent with previous reports and provides further evidence of plant adaptations to soil N and P conditions driving the distribution of plant species, plant ecological strategies, and style of life. In support of these findings, anthropogenic increases in environmental and organismic N:P ratios due to increasing N emissions (fertilization, fuel combustion, spread of N₂-fixing crop species) have generally been associated with cascading effects in aquatic and terrestrial ecosystems that can favour organisms with lower or fast growth rates, depending on current environmental circumstances, such as the availability of other resources needed for growth, and have finally been associated with changes in the species composition and function of communities (Peñuelas et al., 2013a and 2020 and references therein). For instance, the increase of N availability under human N-eutrophication has been frequently associated with the expansion of fast-growing 'nitrophilous' species (Bobbink et al 2010; Bowman et al 2018). The changes in soil N:P:K ratios strongly affect the competitive relationships among plant species, favouring one over the others due to their different growth capacities, rates of root growth, stem/root flexibility, soil enzyme production, and foliar traits (Sardans et al. 2004;2005;2006; Minden and Olde Venterink, 2019).

The relationships between N:P ratios with community species diversity in terrestrial ecosystems are neither clear nor consistent, particularly in terrestrial ecosystems. For example, studies that have correlated increases in the N:P ratios of media and/or food sources

with reduced diversities of plant (DeMalach, 2018) and animal communities (Wei et al., 2012; Vogels et al., 2017) contradict those that found an increase in the diversity of microbes (Ren et al., 2016 2017; Aanderud et al., 2018) and plants (Pekin et al., 2012; Yang et al., 2018). A higher diversity of plant communities with higher N:P ratios and less variable N:P ratios may be due to a convergence in the optimisation of nutrient uptake among key species (Abbas et al., 2013). However, other studies have reported different N:P ratios in sympatric species to avoid direct competition (Alexander et al., 2015; Urbina et al., 2015, 2017). In a study of 599 grassland communities across Europe, higher species diversity has been observed at intermediate values of community N:P ratios in aboveground biomass under co-limitation of N and P conditions and lower species diversity in grassland communities under N or P limiting conditions (Fujita et al., 2014). This study also observed that higher evolutionary pressure towards a specialisation under a determined environmental stress makes species with higher stress-tolerant traits dominant in the community, which can limit species diversity (Fujita et al., 2014). The highest species diversity was observed at intermediate values of community N:P ratios of aboveground biomass under co-limitation of N and P conditions with a lower number of species in grassland communities under N-or P-limiting conditions (Fujita et al., 2014). Thus, it is difficult to establish a general relationship between the N:P ratio and diversity in terrestrial plant communities.

The link between N:P ratios and diversity in freshwater ecosystems, particularly in lakes, has been well studied, providing clear pathways to account for this link. For example, diversity and N:P ratios tend to be negatively correlated in marine plankton (He et al., 2013) and coastal lagoon phytoplankton (Nhu et al., 2019), which has been attributed to lower rates of transfer of matter and energy along short trophic webs under P limitation (Elser et al., 2010). However, resource stoichiometry is not a unique factor of community diversity. The trophic relationships between phytoplankton and zooplankton are indeed associated with N and P concentrations and N:P ratios through both bottom-up and top-down processes; the N:P ratios of phytoplankton induce selective grazing by zooplankton and thereby, strongly determine phytoplankton community composition (Branco et al., 2018). In conclusion, the multivariate productivity/diversity (MPD) hypothesis sustains a multifactorial equilibrium that relates the diversity of phytoplankton communities with the amount of resources, mainly of P. Thus, the diversity of the producer community would be in equilibrium with the potential number of species that can coexist in accordance with stoichiometric relationships, mainly among the most limiting resources, consumer pressure, and resource use efficiency (Cardinal et al., 2009a,b). The MPD hypothesis also claims that consumer pressure reduces the biomass and richness of producers and that stoichiometry drives the relationship between community

diversity and resource-use efficiency (Hillebrand and Lehmpfuhl, 2011). Thus, it claims that, in general, higher biodiversity is associated with a better partitioning and distribution of multiple resources in communities with a higher number of competing species, showing that under richer N and P (and other resources) availability, biological communities tend to be more diverse to reach the maximum resource-use efficiency and thus, increase overall community productivity (Lewandowska et al. 2016; Nhu et al., 2018). A meta-analysis showed that increased resource supply increases productivity and richness in some (forest and freshwater) but not all (marine, grasslands) ecosystems (Lewandowska et al., 2016), and a phytoplankton study also observed that general community richness is driven by N and P availability but this link also fails when applied to functional groups (Nhu et al., 2018). These studies warrant future research to clarify whether there is a direct and positive link between resource availability and resource-use efficiency and whether higher production and resource availability and use-efficiency are related to higher species diversity.

4. Ecological stoichiometry and global environmental change

Global environmental problems, including increasing anthropogenically mediated imbalances in the N:P ratio and the interactions, feedback, and trade-offs between drivers of global environmental change and soil, water, and organismic N:P ratios have recently been linked to ES (Sturner, 2015; Yuan and Chen, 2015; Sardans et al., 2017a, b; Peñuelas et al., 2013c and 2019a,b; Yue et al., 2017; Wang et al., 2018c,d; Peng et al., 2019). In this section, we summarize the key issues associated with these two aspects of ES.

Anthropogenically mediated imbalances in N:P ratios and P scarcity

Global-scale data indicate an exponential increase in anthropogenic N emission but a much smaller increase in global anthropogenic P addition to ecosystems, leading to an exponential increase in the ratio of anthropogenically mediated N:P emissions that have been reported in natural and managed ecosystems and are expected to continue (Sardans and Peñuelas, 2012; Peñuelas et al., 2012; 2013c, 2019a,b). These imbalances in the N:P ratios have implications on human society due to the challenges they pose to food security, which may be further aggravated by limited reserves of mineable P and the unequal distribution of P fertilizers (Obersteiner et al., 2013; Li et al., 2016; Mew, 2016; Weikard, 2016; Lun et al., 2018). The total global emission of anthropogenic reactive N is similar to the level of natural N₂ fixation, that is, approximately 250 Tg N y⁻¹, whereas reactive P inputs from mineral P fertilisers into the global P cycle is approximately 20 Tg P y⁻¹ (Peñuelas et al., 2019b). The N:P ratio for anthropogenic

emissions is approximately 29 (molar basis), that is, almost twice the Redfield ratio (16, Redfield 1963) and higher than the optimum soil N:P ratio (16-22) for terrestrial plant growth (Peñuelas et al., 2013c, 2019b). The fact that these emissions are geographically asymmetrical and change over time makes the possible impacts stronger in some regions (Houlton et al., 2019). The N:P ratios also continue to increase in the biosphere owing to the continuous increase in N emission. These conditions are unprecedented in the recent history of Earth, particularly the intensity and rate of change, and research is required to predict unknown consequences.

Metropolitan areas, particularly those surrounded by intensely managed cropland, emit high levels of N to the atmosphere and to wastewater with high N and P concentrations and N:P ratios (Zhang et al., 2019d; Peñuelas et al., 2020). The emissions with very much higher N than P concentrations lead to higher levels of N deposition, with slower decay toward the interface between metropolitan and agricultural/remote areas, whereas the N:P ratio is very low and even decreases with distance from metropolitan areas (Sardans et al., 2011; Kim and Kim, 2013; Peñuelas et al., 2020). Conversely, P enrichment and low N:P ratios in aquatic systems, mainly in less renewable water bodies such as lakes and ponds, are due to leaching from cropland and the release of untreated urban/industrial wastewater, mainly in regions without wastewater treatment (Yan et al., 2016; Zhang et al., 2018c). These decreases in water N:P ratios have been linked to the lower mobility of P than N, allowing the accumulation of more P than N in fertilized soil, water and vegetation, decreasing their N:P ratios (Yan et al., 2016; Romero et al., 2020). More mobile N leaches from soil and water; hence, the N:P ratios tend to be high in rivers, especially in estuaries with catchments (Sardans et al., 2012a).

Croplands are frequently sufficiently fertilized with N but not adequately fertilized with P; thus, P tends to accumulate in soils, whereas N is lost by volatilisation and leaching (Peñuelas et al., 2013). This trend of P accumulation in soils is even stronger in cropland areas fertilised with manure or untreated urban/industrial waste, which are richer in P than in N (Dupas et al., 2015; Szögi et al., 2015; Sun et al., 2017; Romero et al., 2020). Following the application of P fertiliser to cropland, P is more prone to absorption into soil components than N and precipitates to form diverse salt species, depending on the pH and mineral composition of the soil (Srinivasarao et al., 2007; Dumas et al., 2011; Arai and Livi, 2013). An estimated 50% of the P fertiliser applied during 2002-2009 has accumulated in cropland soils worldwide (Lun et al., 2018). This increasingly large store of P in soil, which tends to be unavailable for direct plant uptake, constitutes a key global challenge, and efforts are required to improve the P-use efficiency of crops (Li et al., 2015, 2016; Bai et al., 2016; Xi et al., 2016; Liu et al., 2016; Withers

et al., 2018a,b). Thus, cropland soils have low N:P ratios, while the non-cropland ecosystems tend to have higher N:P ratios (Peñuelas et al., 2013c, 2019b). Much of the soil P in croplands, however, is sorbed and not available to plants; thus, crops may still have (effective) N:P ratios that are too high (Sattari et al., 2012).

Thus, asymmetrical shifts in N:P ratios prevail across managed and natural ecosystems. Increase in P content and reductions in N:P ratios in fertilised cropland soils (Dupas et al., 2015; Liu et al., 2016; Sun et al., 2017b; Zhang et al., 2019d; Romero et al., 2020) are particularly intense in areas with high livestock densities and monogastric animal farming, such as poultry and pigs (Szögi et al., 2015). Increasing P concentrations and lower N:P ratios have also been reported in some freshwater ecosystems with low nutrient cycling (mostly lakes and ponds) near areas with high human populations, industrial activities, and/or intensely managed cropland without waste treatment plants (Peñuelas et al., 2013c; Guenther et al., 2015; Yang et al., 2015; Choquette et al., 2019). In contrast, the N:P ratios tend to increase in terrestrial non-cropland ecosystems, such as forests and unmanaged grasslands (Veresoglou et al., 2014; Du et al., 2016; Wang et al., 2017c; Schmitz et al., 2019), large rivers and lakes (Li and Bush, 2015; Pandey and Pandey, 2015; Burson et al., 2016; Tong et al., 2019) and coastal areas (Chen et al., 2014b; Leong et al., 2014; Zirino et al., 2016; Maranger et al., 2018).

The consequences of anthropogenic imbalances in N:P ratios have already been widely observed. N:P increases in media (soil or water) due to high N deposition or loading directly affects organismic N:P ratios and growth, which subsequently drive shifts in the community diversity and trophic web structure and function of ecosystems (Marlotte et al., 2017; Shao et al., 2017; Peñuelas et al., 2019b). N deposition, urban waste and leachates from fertilized agricultural fields have increased water and planktonic N:P ratios in freshwater and coastal ecosystems, reducing the complexity of trophic webs and/or shifting community composition and function (Silkin et al., 2014; Guenther et al., 2015; Burson et al., 2016; Yu et al., 2018a; Moody and Wilkinson, 2019), albeit with some exceptions. For example, decreases in N:P ratios have been recorded in some lakes and water bodies in Japan because of the increased deposition of P derived from atmospheric dust pollution from other countries in south-eastern Asia (Miyazako et al., 2015) and in some European and North American lakes in areas where N deposition has decreased in recent decades (Gerson et al., 2016; Isles et al., 2018). Increasing soil N:P ratios have also been observed in unfertilised terrestrial ecosystems, most often attributed to increasing N deposition (Piklington et al., 2005; Hardtle et al., 2006). Increased N:P ratios in soils (Huang and Yu, 2016; Lu et al., 2017; Yue et al., 2017; Yu et al., 2018b; Xu et al., 2019) tend to lead to increases in organismic N:P ratios (Zötz and Asshoff, 2010; Wanek

and Zötz, 2011; Huang and Yu, 2016; Lu et al., 2017; Cao and Chen, 2018; Yu et al., 2018b; Kranabetter et al., 2019), decreases in organismic growth rates, and associated changes in community structure (Wanek and Zötz, 2011; He et al., 2017; Tischer et al., 2015; Kranabetter et al., 2019; Nair et al., 2019; Sun et al., 2019) and function such as plant/soil nutrient cycling (Schneider et al., 2012; Carrillo et al., 2017; Ulm et al., 2017; Guo et al., 2019). Finally, these N:P imbalances increase the risk of nutrient limitation in the acquisition of C (Peñuelas et al., 2017a; Wang et al., 2020). Nevertheless, when N deposition increases in N-limited sites, it generates a more balanced N:P ratio that can stimulate growth and thus C capture and storage (van Groenigen et al., 2006).

Oligotrophication of lakes and large rivers has also been recently reported in some developed and industrialised countries. China presents an example of the rapid emergence of this phenomenon due to the rapid implementation of wastewater treatment facilities (Tong et al., 2019) that remove approximately 60% of the N and 80% of the P, resulting in water with low N and P concentrations and high N:P ratios (Ibañez and Peñuelas, 2019). This oligotrophication is likely to become more widespread with the introduction and implementation of environmental control measures, wherein changes from anoxic to oxic conditions due to low N and P water concentrations and very high N:P ratios will elicit cascading effects on the community structure in aquatic ecosystems. For example, aerobic species with low growth rates (Sterner and Elser, 2002; Sardans et al., 2012b) such as macrophytes, may become more abundant than species with high growth rates, such as phytoplankton, which are favoured under lower N:P ratios, as observed in several European rivers such as the Ebro since—the past 20–30 years, due to the implementation of wastewater treatment facilities (Ibañez and Peñuelas, 2019) (see section 2.1 and 2.2).

Key trade-offs and feedbacks between drivers of global environmental change and ecosystem N:P ratios

Recent studies have presented clear evidence that, in addition to responding to global-scale anthropogenic emissions and N and P deposition/fertilisation, the stoichiometries of media (soil, water) and organisms can also be altered by the drivers of global environmental change, such as warming, drought or species invasion (Sardans and Peñuelas, 2012; Sardans et al., 2012b; 2017a,b; Peñuelas et al., 2013c, 2019b; Yuan and Chen, 2015; Yue et al., 2017; Kou et al., 2018; Wang et al., 2018c; Yuan et al., 2018; Peng et al., 2019). For example, long-term increases in N:P ratios in water, soil, and organisms have been reported in some areas despite decreases in N deposition (Hessen, 2013; Ferretti et al., 2014; Chen et al., 2016; Goyette et al.,

2016; Sardans et al., 2016a,b; Wang et al., 2017a; Calvo-Fernandez et al., 2018; Schmitz et al., 2019), even though N deposition triggers a greater uptake of P by producers (Long et al., 2016; Deng et al., 2016) that causes lower N:P ratios. We provide examples of the effects of various drivers of global change on ES in later sections.

A more global and consistent association of ES with ecosystemic and organismic function and structure has been achieved with new ES approaches by the inclusion of a wider range of elements than only the concentrations of C, N, and P in models. For example, new studies have included K and/or Mg, which are involved in various plant functions, such as water-use efficiency and light capture (Khan et al., 2015; Sardans and Peñuelas, 2015; Xing et al., 2015; Yan et al., 2015b; Pierce et al., 2016; Jochum et al., 2017; Urbina et al., 2017; Wang et al., 2018a).

Two recent meta-analyses comprising 315 and 386 studies that did not differentiate among plant organs, found an overall decrease in N:P ratios along natural gradients and under controlled field conditions at elevated levels of CO₂ (Yuan and Chen, 2015; Du et al., 2019), and another review of 215 studies (Sardans et al., 2017a), mostly under controlled field conditions, found that increased atmospheric concentrations of CO₂ led to decreased N:P ratios in roots but not in leaves. The ongoing increase in atmospheric CO₂ concentration is thus likely to decrease N:P ratios in plants, consistent with the GRH for plants under favourable growth conditions. However, this relationship with the GRH requires testing, including the dependence of these results on coincident changes in atmospheric N deposition. A study by King et al. (2015) reported an increased in the N:P ratio in one species, a decrease in N:P ratios in three other species, and no change in N:P ratios in the three other species of phytoplankton. Thus, the effects of higher CO₂ levels on stoichiometry may be species-dependent.

Recent experimental studies and meta-analyses have demonstrated that the increases in C:N and C:P ratios in foliar tissues under higher atmospheric CO₂ concentrations are more due to decreases in N and P concentrations than to increases in C concentration (Sardans et al. 2012a). For example, an extensive meta-analysis involving 386 published reports of several types of plants and plant organs found that increasing levels of CO₂ have significantly altered the concentrations of C (+2.19%), N (−9.73%) and P (−3.23%) and the C:N (+13.3%) and N:P (−7.32%) ratios (Du et al., 2019). A more recent meta-analysis (Xu et al., 2019b) and an experimental field study (Wang et al., 2019a) obtained similar results.

The effects of climatic warming on plant N and P concentrations and N:P ratios were much less consistent, in contrast to the effects of atmospheric CO₂ concentrations. The effects

vary among plant organs and studies report differently (Peñuelas et al., 2013c; Yuan and Chen, 2015; Gargallo-Garriga et al., 2015; Zhang et al., 2016a; Sardans et al., 2017a; Yue et al., 2017; Wu et al., 2019; Vicedo et al., 2019). A meta-analysis of 86 studies that did not differentiate among plant organs found an overall increase in N:P ratios along natural temperature gradients, but not in field experiments with controlled warming conditions (Yuan and Chen, 2015). Several studies have reported a decrease in aboveground plant N:P ratios under warming, which were attributed to a greater allocation of P to stems and/or to a greater capacity for plant growth (Dudareva et al., 2018; Wang et al. 2018e, 2019b). A meta-analysis of data from 76 warming manipulation field studies reported an overall increase in plant N:P ratios under warming (Yue et al., 2017). Field experimental warming, however, can also decrease foliar N:P ratios, such as in tropical forests (Wu et al., 2019) or the shoots and roots of the grasses, *Holcus lanatus* and *Alopecurus pratensis* (Gargallo-Garriga et al., 2015). Warming in boreal areas can increase microbial N limitation because the young soils of these regions are frequently N-limited (Vitousek et al., 2010). Stark et al. (2018) observed higher activities of soil enzymes involved in N but not P mineralisation under warming.

Warming affects growth rates and trophic activity in aquatic ecosystems by increasing biological activity (from metabolism to organisms) and can thus affect the uptake, flux and use of N and P, ultimately shifting N:P ratios. However, a lack of studies prevents conclusion. Warming causes phenological advances in zooplankton and triggers top-down grazing pressure, leading to low phytoplanktonic biomass but a higher capacity to produce new biomass due to a lower N:P ratio associated with a higher growth rate, maintaining the increased energy demands of zooplankton (Velthuis et al., 2017). In contrast, some studies observed no significant changes in N:P ratios under elevated temperatures; N:P ratios at higher planktonic trophic levels, such as in *Daphnia*, increased under warming conditions due to larger reductions in P than in N concentrations, particularly under predator pressure (Zhang et al., 2016b). Higher temperatures did not affect the N:P ratios of species of different trophic levels or seston and sediments in a mesocosm study mimicking shallow ponds (Ventura et al., 2008). Janssens et al. (2015) observed increased N and P concentrations under warming conditions with no change in N:P ratios in larvae of the damselfly, *Enallagma cyathigerum*. Higher temperatures did not affect P concentrations in *Daphnia* but decreased the C:P ratio by decreasing total lipid concentrations (Prater et al., 2018). However, several studies have identified higher P demands in planktonic organisms in response to higher temperatures, frequently linked to higher N and overall P uptake and thus, a lower N:P ratio linked to a higher growth rate (Phillips et al., 2017; Lin et al., 2018; Mathews et al., 2018). Thomas et al. (2017)

also observed that the diatom *Thalassiosira pseudomonas* had a higher optimum temperature for growth as higher availability of N and P were, implying that planktonic species would be more vulnerable to warming under low-nutrient conditions than previous models have projected. A turnover of phytoplankton linked to higher C:P and N:P ratios were observed in a long-term warming experiment in freshwater ponds (Yvon-Duricher et al., 2017). A clear understanding of the relationship of aquatic trophic web structure with C:N:P ratio and temperature in aquatic ecosystems is currently not possible.

Long-term relationships between temperature and organismic N and P concentrations and N:P ratios have also been associated with genotypic changes. Cotner et al. (2006) reported that the heterotrophic bacterium *Escherichia coli* had higher C and N but lower P concentrations associated with a shift of P allocation from RNA and protein synthesis to resource acquisition in cell membranes when incubated for several generations at higher temperatures in a mesocosm experiment. Poikilotherms adapted to colder sites had higher N and P concentrations than those adapted to warmer environments, suggesting that the lack of positive catalytic effects of higher temperatures on metabolic reactions of growth have been counterbalanced through evolution, favouring higher N and P concentrations that are associated with the allocation of more N and P to proteins and RNA (Woods et al., 2003).

Changes in soil N and P concentrations and N:P ratios have been widely observed in experimental-warming studies but not along natural altitudinal or latitudinal temperature gradients. For example, increasing temperatures along natural gradients are generally associated with decreasing soil N and P concentrations, whereas the opposite pattern is mostly observed in field experiments with short-term warming, especially for N (Yuan et al., 2017). However, the effects of warmer background temperatures on plant and soil C:N:P ratios along natural gradients are more difficult to distinguish from the effects of precipitation, radiation, or atmospheric N deposition, which are frequently correlated with the geographical temperature gradient (Jiao et al., 2016).

The impact of drought on ES differs in magnitude and direction more in drought manipulation studies than along environmental gradients, linked to increased concentrations of P and mainly N in long-term evolutionary responses (due to species turnover) to aridity in contrast to short-term phenotypic responses (due to intraspecific responses), frequently associated with decreases in N and P concentrations (He and Dijkstra, 2014; Yuan and Chen, 2015; Yuan et al., 2017; Luo et al., 2018a,b). Extensive meta-analyses of ecosystem changes along aridity gradients have revealed increasing plant N:P ratios with intensifying drought

(Yuan and Chen, 2015) and N concentrations increasing more than P concentrations (Sardans et al., 2017a) (Figure 3). However, some studies have observed decreasing plant N:P ratios with increasing drought (Luo et al., 2018b) or no significant effect of drought (Wang et al., 2014; Delgado-Baquerizo et al., 2018). Mechanisms underlying these responses to increasing aridity along natural gradients may be partly due to changes in mycorrhizal symbioses (Johnson et al., 2010; Zhao et al., 2015; Mariotte et al., 2017), turnover of plant species where the relative biomasses of N- and P-rich species increase with aridity (Liu et al., 2019), and nutrient leaching (Sardans and Peñuelas, 2013b, 2014a).

A meta-analysis of field drought-manipulation experiments suggested a general decrease in plant N concentration and a larger decrease in plant P concentration, and thus an increase in N:P ratios, with increasing drought intensity (He and Dijkstra, 2014); however, foliar N and P concentrations under experimental drought conditions varied among studies (Sardans et al., 2013; Sardans et al., 2017b; Luo et al., 2018b). A meta-analysis of manipulative experiments by Yuan and Chen (2015) also observed higher N:P ratios, albeit not significantly, in plants subjected to drier conditions (Figure 3). Foliar N:P ratios tend to increase in response to field-imposed drought, probably because of the greater sensitivity of the mobilisation and subsequent plant uptake of soil P relative to N in systems that are not pre-adapted to dry conditions (Sardans and Peñuelas, 2013b, 2014a; Urbina et al., 2015; Luo et al., 2018a,b; Sardans et al., 2017b).

Decrease in root N:P ratios in response to drought conditions, in contrast to aboveground tissues, have also been reported (Xiao et al., 2016), suggesting a greater allocation of P and N to roots than stems under dry conditions (Figure 3). The allocation of resources (N, P, and K) to roots increases with aridity, albeit in varying proportions, causing lower N:P ratios and higher N and P concentrations in roots than in stems (Gargallo-Garriga et al., 2014, 2015). This allocation has been associated with a higher expression of genes involved in primary metabolism linked to growth, protein synthesis, and pathways of energy transfer in roots whereas the expression of genes involved in anti-stress metabolic pathways were higher in leaves (Gargallo-Garriga et al., 2014, 2015). Short- to intermediate-term shifts in N and P concentrations under experimentally manipulated drought conditions are driven by intraspecific variation and to a lesser extent, by species turnover (Luo et al., 2018b). However, over longer periods, species turnover is the strongest cause of changes in vegetation N:P:K ratios (Olde Venterink et al., 2009). These results strongly suggest that droughts affect trophic webs by altering the nutritional value of plant organs and have asymmetrical effects on above- and belowground trophic webs.

Contrasting stoichiometric responses and shifts have also been observed in soil between natural gradients of aridity and experimental drought manipulation. Soil N and P concentrations tend to decrease with aridity along natural gradients, but N concentrations increased and P concentrations decreased in some manipulation experiments (Yuan et al., 2017). In contrast to responses in plants, soil N and P concentrations tend to decrease in most soil types and biomes with increasing aridity, indicating a proportional shift in N and P concentrations from soil to plants as soil-water content decreases (Yuan et al., 2017). These findings are consistent with the lower N:P ratios in the runoff of leached water in arid soils derived mostly from deeper soil layers because of the lower water table; this process poses a greater threat to soil P than N availability with increasingly arid climate (Sardans and Peñuelas, 2014a). Studies have indicated that the use of N and P by plants becomes increasingly conservative as the environment becomes drier. The increase in plant P concentrations in plants in P depleted drier soils is especially important, suggesting that plants take up and store more P along aridity gradients. Total soil N concentrations, however, can increase in field drought experiments, especially in arid areas (Yuan et al., 2017) (Figure 3).

Plant invasion is a globally emerging driver of environmental change (Seabloom et al. 2015), and the success of invasive plants depends on differences between the elemental compositions of the native and invasive species and soil nutrient availability and stoichiometry (Lannes et al., 2012;2016; Aragon et al., 2014; Wang et al., 2015a,b and 2019b; Sardans et al., 2017b). Plant invasions alter plant/soil N and P cycles (Matzek, 2011; Sardans et al., 2017b) and increase the uptake capacity and use efficiency of limiting nutrients (Leffler et al., 2011; Peng et al., 2011b; Aragon et al., 2014; Wang et al., 2015a,b; 2019c; Ulm et al., 2016; Sardans et al., 2017b; Lannes et al., 2020a). A meta-analysis of 1233 studies found higher N and P concentrations in photosynthetic tissues in invasive than in native species (Sardans et al., 2017b), supporting previous meta-analyses (Pysek et al., 2012; Sardans and Peñuelas, 2012) (Figure 4). Total soil N and available N and P concentrations are higher in invasive species (Vilà et al., 2011; Sardans et al., 2017b), possibly because of a greater capacity to mineralise the plant litter produced (Aragon et al., 2014; Kuebbing et al., 2014). These differences are more pronounced in nutrient-poor than nutrient-rich environments, suggesting different N and P resorption capacities as drivers of differences between invasive and native species and the importance of conservation strategies of nutrient use for the success of alien plants invading nutrient-poor environments (Ens et al., 2015; Sardans et al., 2017b).

Foliar N concentrations are higher and C:N ratios are lower in invasive than native species but the patterns of shifts in N:P ratios and other elemental stoichiometric relationships

(excluding C) are unclear (Sardans et al., 2017b and references therein). The effects of species invasion on N and P cycles may depend on the intensity of other concurrent drivers of environmental change. For example, the impacts of plant invasion on N and P cycles in coastal wetland plant/soil systems in China depends on the increase in flooding intensity mediated by climate change (Wang et al., 2015a,b, 2016b, 2018d). Wang et al. (2016a) reported that high levels of litter production in coastal wetlands during typhoons produced larger and sudden releases of N and P, with low N:P ratios, which potentially can affect soil microbial communities and trophic chains. Such impacts of the projected increase in extreme weather on N and P cycles and their ratios warrant further investigation.

5. Biogeochemical stoichiometry

Several ES studies in recent decades have included elements other than C, N, and P as other elements are also involved in key functions in organisms (Slade 2006; Peñuelas et al. 2019a). For example, elements in plants such as K, Mg, sulfur (S), iron (Fe), calcium (Ca) and zinc (Zn) are involved in photosynthesis, transport of metabolites, enzyme control (co-enzymes), respiration, water flow, internal cell homeostasis and reproduction (Tripler et al., 2006; Naples and Fisk, 2010; Baribault et al., 2012; Rivas-Ubach et al., 2012; Peñuelas et al., 2013c, 2019a,b; Sardans et al., 2015; Kaspari and Powers, 2016; Jeyasingh et al., 2014, 2017; Minden et al., 2020). Similarly, elements other than N, P and K may be limiting in some terrestrial ecosystems and may elicit community-level effects (Naples and Fisk, 2010; Baribault et al., 2012; Lapenis et al., 2013; Lannes et al., 2020b). For example, herbivore fitness may be compromised by the limitation of elements other than N, P and K in food (Filipiak, 2016; Filipiak and Weiner, 2017a,b). N, P, K, Ca, Mg, S, Fe, and silicon (Si) concentrations, along with those of other microelements, affected macrophytic community structure in several lakes on the Yunnan Plateau in China (Xing et al., 2015). Phylogenetic fingerprinting has characterized plants, animals and microbes based on their multi-elemental compositions (Quigg et al., 2011; Leal et al., 2017; Gonzalez et al., 2018).

Ionomic approaches that correlate ecosystem functionality with bio-elements (mainly of mineral origin) have emerged in recent years. Plant ionomics is the study of the relationships between the profiles of mineral elements in plants relative to the concentrations of nutrients and trace elements in the soil and with plant functional traits and gene expression (Salt et al., 2008; Buescher et al., 2010; Baxter et al., 2008, 2012; Huang and Salt, 2016). Some studies have reported that the disruption of a single gene can substantially affect the

concentration of one or more bio-elements (Baxter et al., 2012; Lowry et al., 2012; Jenasingh et al., 2017), thus allowing to identify the genes that control the uptake, storage and use of soil nutrients and trace elements in plants (Baxter et al., 2012; Lowry et al., 2012). Transcriptomic studies have shown that organisms can differentially express different genes and have different levels of expression in response to changing stoichiometric supplies to maintain a specific level of organismic homeostasis (Jeyasingh et al., 2017). These results further allow to identify the effects of the environment and genetics on plant nutrition (Buescher et al., 2010; Lowry et al., 2012; Neugebauer et al., 2018) and physiological status (Baxter et al., 2008), identifying ionomic alleles involved in mineral nutrition and the accumulation and function of trace elements in response to environmental shifts (Baxter et al., 2008). Ionomics has thus allowed several advances in the study of the interaction between bio-elemental content and electrical charge, mostly absorbed from soils, and their impact on plant health, food quality, and/or the identification of hyperaccumulating species (Baxter et al., 2012; Subramanian et al., 2017; Gregory et al., 2017; Alcock et al., 2017). The integration of this information with bioinformatic and genetic tools, such as genomic sequencing, has allowed us to identify the genes that control the uptake, storage, and use of soil nutrients and trace elements in plants (Baxter et al., 2012; Lowry et al., 2012).

Another recent approach, the BN hypothesis, postulates a relationship between the anatomical and functional traits of organisms and communities and their elemental compositions, where species occupy a particular region in the multidimensional space generated by the concentrations and ratios of bio-elements required by individuals of a species. Thus, this approach differs notably from ionomics, despite some overlap. Ionomics aims to account for shifts in ionic composition by identifying specific genes and their role in changing environmental conditions, thus providing information for improving crop nutrition. The BN hypothesis is based on four simple ideas: i) the overall bio-elemental composition (elementome) of a taxonomic group or genotype is based on the differential use and allocation of elements to specific structures and functions, ii) trade-offs between adaptation to competitiveness in a stable environment vs success in a fluctuating environment cause differences in homeostasis and plasticity between species in a strategy continuum, iii) sympatric and co-existing species in equilibrium tend to have distinct elementomes to minimise competitive pressure and iv) recent evolutionary processes in distant clades under similar environmental conditions may converge in functionality and therefore elementomes and BNs of genotypes (Peñuelas et al., 2019a). In contrast, ionomics has aimed to account for shifts in elemental composition (mainly based on metals from the soil) by identifying genes

and their control in changing environmental conditions, providing information for improving crop nutrition, while the BN hypothesis is based on a more general idea linked to the overall direct and indirect “genetic control” (including phenotypic expression) of bio-elements (including C if data are available). This approach is based on the idea that the entire genome of each species determines species-specific functionality and morphology traits (the thus as more distinct these traits are, the more the genomes differ) and thus, determines the distinct uses of different bio-elements, because they, in turn, contribute asymmetrically to different functions and morphologies. Thus, the BN hypothesis can be used without the need to know the control of the expression of specific genes or gene functions.

Recent evidence supports the BN hypothesis (Peñuelas et al., 2011, 2019a) across organisms and ecosystems in plant (Sardans and Peñuelas, 2014b; Sardans et al., 2015, 2016a, 2020; Urbina et al., 2015, 2017; de la Riva et al., 2017; Castellanos et al., 2018; Hu et al., 2018; Reimann et al., 2018; Zhao et al., 2018a), animal (Bartrons et al., 2018; Gonzalez et al., 2018) and microbial communities (Pereira and Berry, 2017) (Figure 4). Foliar elemental composition and stoichiometry are more similar in phylogenetically close species than in distantly related species (Sardans and Peñuelas, 2014b; Sardans et al., 2015, 2016b, 2019), as indicated by studies that have reported the dependence of plant and animal taxonomy and/or phylogeny on organ or body stoichiometry (Zhang et al., 2012; Lovelock et al., 2014; Yang et al., 2015; de la Riva et al., 2017; Wu et al., 2017; Castellanos et al., 2018; Hu et al., 2018; Reimann et al., 2018; Zhao et al., 2018a; Zhang et al., 2019c). Some studies have reported no links between phylogeny and N:P ratios (Sun et al., 2017a), whereas > 90% of recent studies have reported a significant correlation between species elemental composition and taxonomic/phylogenetic distance (Table 2). The trend of different BNs in sympatric species has been demonstrated in plants (Peñuelas et al., 2008; Sardans and Peñuelas, 2014b; Dai et al., 2018; Guiz et al., 2018; Sardans et al., 2021), where changes in the elemental composition of a species depend on biotic factors, such as the degree of interspecific competition (in the presence of competing species or parasites) and ecological interactions (type of relationship, such as mutualism) (Urbina et al., 2015, 2017; Borer et al., 2015). Thus, plants may alter their elemental composition with shifts in their functionality within the range of species-specific phenotypic plasticity for optimising the avoidance of competition and the benefits of biotic relationships (Peñuelas et al., 2019a).

6. Ecological enzyme stoichiometry

The ratios of various soil enzymes involved in the mineralisation of C, N, and P as measures of ecological enzyme stoichiometry (EES) have recently been used in studying ecosystem nutrient limitation (mainly microbe/plant systems), temporal community evolution, changes in nutrient status, nutrient use along natural gradients, and the responses of ecosystems to global environmental change. Integrating elemental stoichiometry with EES allows the assessment of the stoichiometric status and investment in an ecosystem, particularly by soil microorganisms and roots, in the mineralisation and uptake of bio-elements (Tapia-Torres et al., 2015; Yuan et al., 2019). Thus, it enables us to understand the current state of stoichiometry and requirements for maintenance or change. The global mean EES C:N:P ratio of 1:1:1 indicates an equilibrium between microbial elemental composition and detrital organic matter that sustains soil trophic webs; therefore, EES shifts the stoichiometric function of soil organic matter, wherein the stoichiometry of nutrient release is controlled to optimise the stoichiometry of the microbial community (Sinsabaugh et al., 2008, 2009). This EES C:N:P ratio of 1:1:1 is frequently considered the average in local studies, and when a bio-element is scarce at one site, microbes allocate more resources to acquire the scarcely available bio-element (Tapia-Torres et al., 2015). The ratio is an effective tool for monitoring the responses of ecosystems to shifts in resource availability, including those due to global change (Hill et al., 2018).

Shifts in EES may buffer environmental changes that affect soil C:N:P ratios and thus, allow the acquisition of bio-elements that limit growth. For example, decreases in EES N:P and C:P ratios and/or increase in EES C:N ratios have been observed in response to N deposition (Chen et al., 2018; Shen et al., 2019; Dong et al., 2019), increases in atmospheric CO₂ have been correlated with decreases in EES C:N and C:P ratios (Kelley et al., 2011) and higher EES N:P ratios have been recorded with decreasing soil N:P ratio along environmental gradients (Peng and Wang, 2016; Wu et al., 2018; Feng et al., 2019). Other studies comparing soils have yielded results (Wang et al., 2017b; Xu et al., 2017; Zhao et al., 2018c; Fujita et al., 2019) similar to a meta-analysis by Jian et al. (2016), indicating that soil microorganisms invest in enzymes that mineralise and improve the availability of the most limiting bio-elements (Figure 4). In addition, C fertilisation in tundra soils increases C:N and C:P ratios and decreases EES C:N and C:P ratios (Koyama et al., 2013).

A few studies have reported that EES does not effectively lead to the acquisition of growth-limiting bio-elements involved in bacterial growth (Rosinger et al., 2019) and have reported higher activities of soil enzymes involved in soil C and N mineralisation coinciding with higher C and N concentrations in bacteria (Cenini et al., 2016). Tian and Shi (2014) found

no clear relationship between soil C:N and EES C:N ratios, possibly due to the availability of other nutrient sources, despite investment by microorganisms in producing enzymes that mineralise growth-limiting bio-elements. This phenomenon has been reported by Tischer et al. (2014), who observed a trend toward an inverse relationship between the activity of soil phosphatase and soil P availability across rainforest soils, where C and N availability represented soil P availability and affected phosphatase activity. A meta-analysis by Waring et al. (2014) similarly reported that EES N:P ratios were lower in tropical forests than in temperate forests because of the high levels of P limitation that is typical of tropical forests and that phosphatase activity was limited by higher mean annual precipitation and temperature, supporting a study that positively correlated the activities of soil enzymes with soil water content in wet tropical soils (Weintraub et al., 2013). Similarly, the availability of soil water has been positively correlated with the activities of soil enzymes in dry Mediterranean forests and shrublands (Sardans and Peñuelas, 2005,2010; Sardans et al., 2006 and 2008a). Thus, changes to EES C:N:P ratios can be a tool to decrease the variability between soil and microbial (and perhaps plant) C:N:P ratios but the capacity to change EES C:N:P ratios is frequently limited by the availability of bio-elements or by climatic factors.

Thus, some are yet to be answered in this framework to understand the integration of soil, mycorrhiza, and plant stoichiometries using EES as a tool to clarify the mechanisms that drive the competition for soil bio-elemental resources between soil microorganisms and plants. The extent of differences between water, soil, and organismic elemental stoichiometries and that of mineralising enzymes are the key issues that need to be addressed. We suggest a possible hypothesis: equilibria and ecosystem functions are optimised when stoichiometric levels are low. The role of enzymatic stoichiometry in competitive relationships between soil microorganisms and plants is uncertain because plants may shift and influence microbial investment in EES via exudates that increase C availability (Bell et al., 2014; Stock et al., 2019), even though the stoichiometry of soil enzymatic activity is strongly determined by soil and/or microbial stoichiometry and limitation (Wang et al., 2017b; Xu et al., 2017; Zhao et al., 2018c; Fujita et al., 2019; Zhang et al., 2019e).

7. Preliminary evidences of potential risk for humans from increasing stoichiometric imbalances

The increase in C:nutrient ratios in foods due to increasing levels of atmospheric CO₂ has recently been linked to the possibility of affecting human health through nutritional

deficits (Paseka et al., 2019 and references within). The increase in C:N ratio in poor countries, dependent on specific monocrops for food, can be critical in reducing the ratio of proteins versus vitamins/calories in a diet already poor in proteins and vitamins (Zhu et al., 2018). The dilution of other important minerals in human foods account for another potential health risk for humans (Loladze, 2014). The intensification of human mood disorders has been associated with a diet low in Mg (Black et al., 2015). Moreover, the composition of the gut microbial community has been linked to several human disorders and important illnesses (Paseka et al., 2019 and references within). The C:nutrient ratios in foods has clear effects on the composition of microbial communities (Hibbing et al., 2010; Larsen et al., 2019), and dietary N has large effects on the composition of the microbial community of the human gut (Holmes et al., 2017), but the relationships between the shifts in dietary P content and the N:P ratios of the microbial community of the human gut have not been specifically studied.

The stoichiometries of environments and foods have been associated with parasite-host relationships, but not in humans (Aalto et al., 2015; Sanders and Taylor, 2018). The rapid rate of growth of the host that frequently accompanies parasitism is consistent with reports that state that hosts with a low C:P diet had higher rates of viral (Clasen and Elser, 2007) and bacterial infections (Frost et al., 2008). This finding is especially relevant as it reveals a potential threat to human health in countries with diets high in P (Razzaque, 2011; Peñuelas et al., 2017b). Several parasitic diseases in humans that depend on vectors and/or intermediate hosts can alter environmental stoichiometry by affecting these vectors and/or intermediate hosts, thereby affecting the possibility of human infestation (Sanders and Taylor, 2018). For example, the larvae of mosquitoes that transmit the Zika virus to humans grow faster and reach adulthood earlier when they have a N-rich diet, thus decreasing the time period of viral infection for humans (Paige et al., 2019).

There is emerging evidence that shifts in N:P ratios have global and direct consequences for humans (Elser et al., 2006, 2007b; Peñuelas et al., 2017b, 2020a). For example, rapid and widespread shifts in diets and imbalances in N:P ratios due to fertilization may affect the N:P ratios and molecular compositions of staple foods, such as gliadin proteins in gluten that trigger gluten intolerance (Peñuelas et al., 2019d), and shifts in elemental intake (including N:P ratios) may be linked to mortality, the prevalence of illnesses such as cancer and traits such as body size (Peñuelas et al., 2017b, 2020b). Cancerous tissues in humans have 100% higher P concentrations and lower N:P ratios than corresponding noncancerous tissues (Elser et al., 2006 2007b). Cancerous tissues can thus be subjected to P limitation. Thus, ES

studies have immense potential encompassing aspects of human safety and socioeconomics (Figure 4).

8. ES as a tool for understanding the structure and function of global ecosystems

N:P ratios can indicate a range of ecosystem functions; but recent studies have found that the ratios of other bio-elements, such as P, K, and Mg, can also indicate a range of functions (He et al., 2019b).). For example, the P:Ca ratio may indicate the balance between investment in plant biochemical energy and the regulation of cellular physiological processes, and the K:Mg ratio may indicate water regulation and C-cycling mechanisms in plants as physiological processes associated with drought resistance (da Silva et al., 2011; Sardans et al., 2012b; He et al., 2019b). The concept that an ecosystem's elemental composition is associated with the ecosystem's structural and functional traits enables the analysis of concentrations and ratios of bio-elements to indicate the health of the entire ecosystem as well as of compartments, such as soil, water, organisms, and communities. This approach allows us to compare ecosystems along spatial and temporal gradients and to understand the mechanisms and patterns of ecosystem changes and responses, such as shifts in species niches (Gonzalez et al., 2017; Peñuelas et al., 2019a) and complex ecological paradigms, such as successional processes or diversity.

The GRH is conceptually straightforward and elegantly describes mechanisms that link water N:P ratios and N and P concentrations in aquatic systems, but ES uses data from a wider range of bio-elements across ecosystems to test and confirm new generalities within the BN hypothesis, constituting a novel tool that may be used to confirm emerging ecological theories. For example, analyses of a wider range of bio-elements should improve our understanding of the mechanisms and consequences of shifts in elemental composition in ecosystem function and structure (Figure 4).

Imbalances in N:P ratios are emerging as a driver of global environmental change (Peñuelas et al., 2013, 2019b) (Figure 4), but imbalances in the ratios of other bio-elements, such as K:P and Ca:P may also contribute to global change due to differences in bio-elemental mobility and use that are yet to be investigated. For example, interactions among the stoichiometries of bio-elements linked to the drivers of global environmental change, such as C cycling, storage, and fixing in competitive relationships between native and invasive species and the buffering of the effects of N deposition on shifts in ecosystem function and structure, are unknown. Analysis of stoichiometrical relationships at different levels, such as at the level

of bio-elements and of the activity of mineralising enzymes, allow us to confirm the use and uptake of different bio-elements by ecosystem communities and to understand the spatiotemporal distribution of basic ecological traits.

9. Summary of support for ES studies

- The GRH applies when the availability of N and P is high when P limits the capacity for rapid organismic growth by limiting the role of P-rich RNA in protein synthesis, and when lower N:P ratios combined with high concentrations of N and P are associated with increased growth rates in plankton, which lead to increases in the flux of matter and energy throughout trophic webs and in the diversity of trophic levels. The GRH applies to higher plants during the initial phases of seedling growth, when the majority of N and P is allocated to photosynthetic tissue but not during later growth stages when larger amounts of N and P are allocated to non-growth functions and other organs.
- Analysis of the content and ratios of a range of bio-elements other than C, N and P, such as K and Mg, improves our understanding of the implications of shifts in water, soil and organismic elemental compositions and stoichiometries for ecosystem function and structure. The BN hypothesis is emerging as a useful tool in this field (Figure 4).
- ES studies have found that life forms and taxonomic groups with high growth rates, such as fast-growing gymnosperms, contain lower N:P ratios than slow-growing angiosperms (Figure 2, 4).
- The homeostatic stoichiometry of elemental composition is generally more common in organisms than in growth media because organisms have diverse mechanisms for modulating and controlling bio-elemental uptake and internal homeostasis, for example, foliar resorption and root exudation in plants, the synthesis of enzymes in microbes and plants, and the stoichiometric control of animal excretion (Figure 4).
- Fast-growing ruderal species tend to have the lowest levels of stoichiometric homeostasis, whereas slow-growing stress-tolerant species typically have the highest levels, and competitor species have intermediate levels.
- Integration of the elemental stoichiometry of soil, mycorrhiza, and plant systems with EES improves the analysis of global shifts in nutrient cycling and limitation and thus, advances ES studies.
- ES approaches have been used in studies of global environmental change and have found that drivers of global change, such as increasing levels of atmospheric CO₂, drought, warming, and species invasion, directly and indirectly affect water, soil, organismic and community stoichiometries through mechanisms including feedback and interactions. Large global

imbalances in biospheric N:P ratios are driven by the exponential increase in anthropogenic emissions into the atmosphere and terrestrial and aquatic systems (Figure 4). The imbalances are due to the increasing N:P ratios of anthropogenic emissions, the greater mobility of N than P, and the accumulation of P in the vicinity of industrial areas, in cropland soils, and freshwater ecosystems from the application and leaching of untreated waste products under intense livestock production. In contrast, trends toward higher N:P ratios are emerging in unmanaged and rural noncrop ecosystems, particularly forests, grasslands, large rivers, lakes and coastal areas.

10. Key future challenges

- Many key ecological questions remain unanswered, including the links between ecosystem stoichiometry and species diversity, the cycling of and the capacity to store C, emissions of CO₂ and biogenic volatile organic compounds, ecological niches, and species evolution, despite evidence of relationships between water, soil, organismic and community stoichiometries, and associated shifts in the structure and function of ecosystem communities.
- Some interactions at the interface of ecosystem stoichiometry and drivers of global environmental change remain unclear. For example, do increases in atmospheric CO₂ concentrations stimulate the higher uptake of P than N by plants? will the capacity of a species to adapt to increasing drought conditions, as predicted in scenarios of future global environmental change, is linked to N and P use and N:P ratios, and the likely consequent shifts in ecosystem composition and effects on species invasions on N:P ratios, is not known.
- Emerging evidence on the effects of changes in N:P ratios on human health and socioeconomics indicate that further research is needed in this regard.
- Ecosystem-level imbalances in N:P ratios occur globally, with likely impacts on human health and well-being mediated by the effects on socioeconomics and food security. The implications and potential mitigation of these unprecedented changes require urgent attention.

Conflicts of Interest

The authors declare no conflicts of interest.

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Table 1. Relationships of organismic growth rate (GR) with the increase in the N:P ratio.

| Ecosystem | Study type | Main results | Reference |
|-------------------------|-------------------------|--|-----------------------------------|
| | Microcosm | ↓ GR (when nutrients are not limiting) | Bi <i>et al.</i> , 2012 |
| | Metadata review | ↓ GR | Loladze and Elser, 2011 |
| Lakes | Field | ↓ GR | Naddafi <i>et al.</i> 2012 |
| | Mesocosm | ↓ GR | Stahl-Delbanco <i>et al.</i> 2003 |
| Lake | Field | ↓ GR (when nutrients are not limiting) | Tanner <i>et al.</i> 2011 |
| | Microcosm | No conclusive relationships | Guo <i>et al.</i> , 2018 |
| Freshwater ecosystems | Field | ↓ GR | Arbaciauskas <i>et al.</i> , 2013 |
| Coastal waters | Mesocosm | ↓ GR | Prado <i>et al.</i> , 2014 |
| | Review | ↓ GR in phytoplankton | Hillebrand <i>et al.</i> , 2013 |
| | Microcosm | No conclusive relationships | Trommer <i>et al.</i> , 2012 |
| Coastal waters | Field | Unimodal GR response to P | Reef <i>et al.</i> , 2012 |
| | Microcosm | ↓ GR | Rivas-Ubach <i>et al.</i> , 2018 |
| Stream | Field | ↓ GR | Bumpers <i>et al.</i> , 2015 |
| | Mesocosm | ↓ GR | Prado <i>et al.</i> , 2014 |
| Southeastern Pacific | Field | ↓ GR | Franz <i>et al.</i> , 2012 |
| Freshwater | Mesocosm | ↓ GR | Molazadeh <i>et al.</i> , 2019 |
| | Common garden | ↓ GR | Wanek and Zotz, 2011 |
| | Common garden | ↓ GR | Peng <i>et al.</i> , 2011 |
| Panama | Field and common garden | ↓ GR | Wanek and Zotz, 2011 |
| | Common garden | ↓ GR (when nutrients are not limiting) | Yu <i>et al.</i> , 2012 |
| Mediterranean grassland | Field | ↓ GR | Rivas-Ubach <i>et al.</i> , 2012 |
| | Pot experiment | ↓ GR | Liang <i>et al.</i> , 2018 |
| Scrubland | Field | ↓ GR | He <i>et al.</i> , 2017 |
| Temperate forest | Field | ↓ GR | Wang <i>et al.</i> , 2013 |

| | | | |
|---|-----------------------|---|--|
| Crops (<i>Triticum aestivum</i> , <i>Hordeum vulgare</i> and <i>Zea mays</i>) | | ↓ GR in initial growth stages ↑ GR in advanced growth stages | Zhang <i>et al.</i> , 2019 (submitted) |
| <i>Juniperus przewalskii</i> , China | Field | GR ↓ | Wang et al. 2019c |
| Shrubland | Field | Unimodal relationships with GR | Yu <i>et al.</i> , 2012 |
| | Pot experiment | ↓ GR | Yan <i>et al.</i> , 2013 |
| | Greenhouse experiment | ↑ GR | Niu <i>et al.</i> , 2019 |
| Freshwater ecosystems (parasitic species) | Field | GR ↓ | Paseka and Grunberg 2018 |
| Macroinvertebrates of streams | Field | GR ↓ | Demi et al. 2018 |
| Zooplankton of western Pacific | Field | GR ↓ | Chen et al. 2018b |

Table 2. Results of studies testing the relationships between differences in species elemental composition and taxonomy/phylogeny distance.

| Species and/or ecosystem | Study type | Main results (+, significant phylogenetic signal or taxonomic determinism; -, no significant phylogenetic signal or taxonomic determinism) | Reference |
|--|------------|--|---------------------------|
| Main forest tree species of Catalonia | Field | + | Sardans and Peñuelas 2014 |
| Main forest tree species of Europe | Field | + | Sardans et al. 2015 |
| Main forest tree species of Spain | Field | + | Sardans et al. 2016 |
| 98 Mediterranean woody species | Field | + | De la Riva et al. 2017 |
| Dominant plant species in Sonoran Desert | Field | + | Castellanos et al. 2018 |
| Natural gradients in coastal herbaceous wetlands | Field | + | Hu et al 2018 |
| Plants along natural gradient (Norway) | Field | + | Reimann et al. 2018 |
| Root elemental composition of 281 species in Chinese forests | Field | + | Zhao et al. 2018 |
| 702 plant species | Review | + | Zhang et al. 2012 |
| Benthic organisms | Field | + | Lovelock et al. 2014 |
| 48 species of <i>Artemisia</i> from 65 sites across northern China | Field | + | Yang et al. 2015 |
| 348 plant species in Chinese forests | Review | + | Wu et al. 2017 |
| 32 Ericaceae species (China) | Field | + | Zhang et al. 2019 |
| 30 sites containing four <i>Tamarix</i> species | Field | - | Sun et al. 2017 |
| Marine phytoplankton | Mesocosm | - | Garcia et al. 2018 |
| Aquatic heterotrophic bacteria | Mesocosm | + | Godwin and Cotner 2018 |
| Fynbos vegetation | Field | + | Verboom et al. 2017 |
| Microalgae | Review | + | Finkel et al. 2016 |
| Fungi and bacteria in leaf litter | Field | + | Mouginot et al. 2014 |

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|--|------------------------|---|------------------------|
| Marine proteobacteria | Mesocosm | - | Zimmerman et al. 2014 |
| China grassland plant communities | Field | + | Song et al. 2014 |
| 564 Mediterranean plant species | Review | + | Stock and Verboom 2012 |
| Animals of Atacama Desert (Chile) | Field | + | Gonzalez et al. 2011 |
| Rainforest tree species | Field | - | Bai et al. 2019 |
| 203 plant species of a Tibetan meadow | Field | + | Bu et al. 2018 |
| Woody plants, altitudinal gradient (China) | Field | + | Yang et al. 2017a |
| Different trophic groups | Review | + | Gonzalez et al. 2017 |
| Plants along large-scale gradient | Field | + | Yang et al. 2017b |
| 163 shrubland species (China) | Field | + | Yang et al. 2016 |
| 177 plant species in a Karst area (China) | Field | + | Hao et al. 2014 |
| Inner Mongolian plants | Field | + | Liu et al. 2013 |
| 108 plant species from saline environments in Iran | Field | + | Matinzadeh et al. 2019 |
| Chihuahuan Desert gypsophilic plants | Field | + | Muller et al. 2017 |
| Peat mosses | Field | - | Limpens et al 2017 |
| 670 plant species | Review | + | Watanable et al. 2007 |
| 167 plant species (China) | Field | + | Zhang et al. 2018 |
| 564 plant species from five Mediterranean climatic regions | Review | + | Kerkhoff et al. 2006 |
| 87 species from a tropical dry forest in Costa Rica | Field | + | Powers and Tiffin 2010 |
| 71 macroinvertebrate species | Field | + | Gonzalez et al. 2018 |
| Lake communities of different trophic levels | Field | + | Bartrons et al. 2018 |
| Phytoplankton | Review | + | Quigg et al. 2011 |
| 213 species at 199 research sites in the grassland biomes of China | Field | + | He et al. 2008 |
| 48324 vascular plant species (review) | Field | + | Cornwell et al. 2014 |
| 508 Amazonian trees | Field | + | Fyllas et al. (2009) |
| 334 angiosperm species | Greenhouse experiments | + | Neugebauer et al. 2018 |
| 27 desert herbs | Field | + | He et al. (2016) |

| | | | |
|------------------------------|-------|---|---------------------|
| 25 plant species from Brazil | Field | + | Viani et al. (2014) |
|------------------------------|-------|---|---------------------|

Box 1. Classical paradigms of ecological stoichiometry and the main new challenges.

Classical Paradigms and new challenges

| Classical paradigms | Some new challenges |
|---|---|
| <p>GRH Growth rate capacity at cell level depends of the N:P ratio as proxy of protein:RNA ratio. Increased growth rate is favoured by an increase in P-rich RNA (low N:P ratio) under non-limiting N and P conditions</p> <p>Plankton community structure in freshwater ecosystems is related to water N and P concentrations and N:P ratio</p> <p>Redfield ratio Ocean phytoplankton C:N:P (100:16:1 on average)</p> | <p>Are environmental N:P ratios also related to the structure and functions of other ecosystems (terrestrial and marine)?</p> <p>Can we gain more sensitivity and success by relating the elemental composition of medium (soil and water) and community to ecosystem structure, functions, and diversity using elements other than C, N, and P (for example, K, Mg, S, Ca, etc.)?</p> <p>How do the main drivers of global change affect the relation between ecosystem stoichiometry and ecosystem functionality, composition, and diversity?</p> <p>Do components of homeostasis <u>and flexibility</u>/plasticity of stoichiometry exist among the main bio-elements across different taxa and environmental gradients</p> <p>How do shifts in ecosystem stoichiometry (for instance, in response to global change) impact human health and wellness?</p> |

Figure captions

Figure 1. Terrestrial plant N:P ratios and growth rates have been correlated during the initial stages of life when most N and P are allocated to growth but not during advanced stages of growth when the allocation of N and P to organs and functions not directly involved in growth increases exponentially.

Figure 2. Stress-tolerant plants have been associated with high N:P ratios and a more homeostatic stoichiometry, fast-growing ruderal species have been associated with low N:P ratios, and competitor species, with N:P ratios between that of stress-tolerant and ruderal species.

Figure 3. General results of shifts in N:P ratios in plant/soil systems in field drought manipulation experiments and along aridity gradients.

Figure 4. New achievements and open scenarios of ecological stoichiometric studies in the last years.

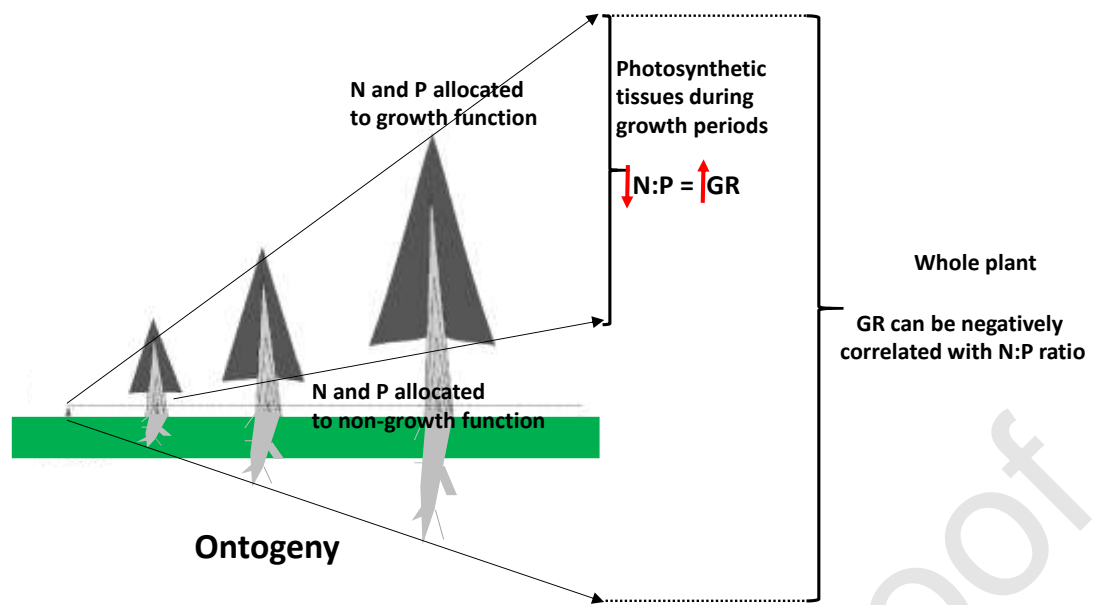


Figure 1

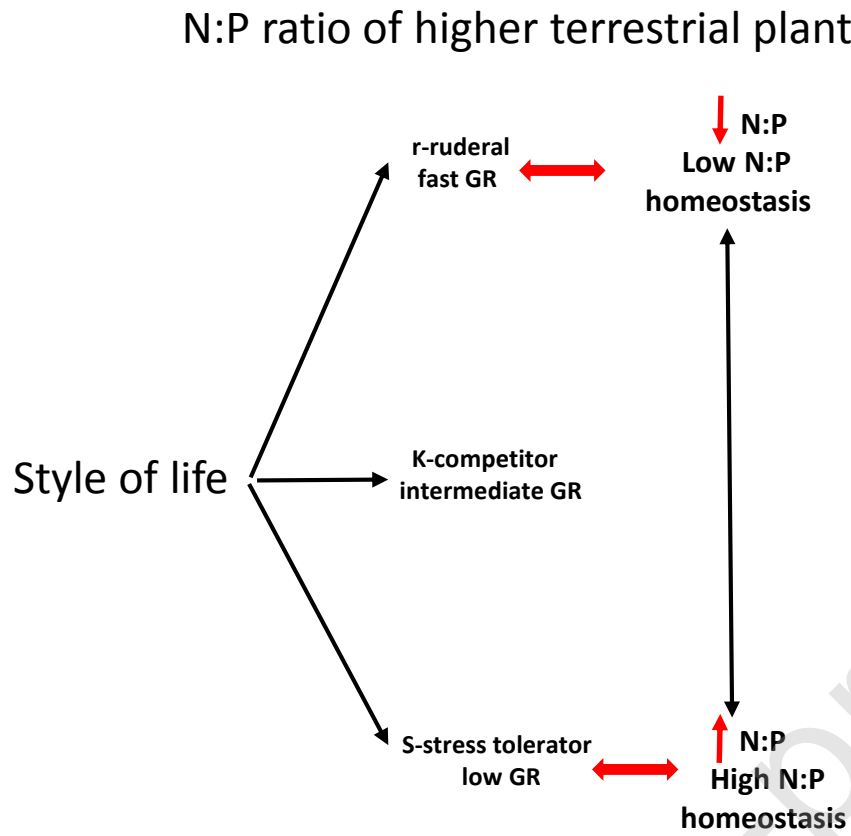


Figure 2

Relationships of N:P ratios with drought or aridity in plant/soil systems

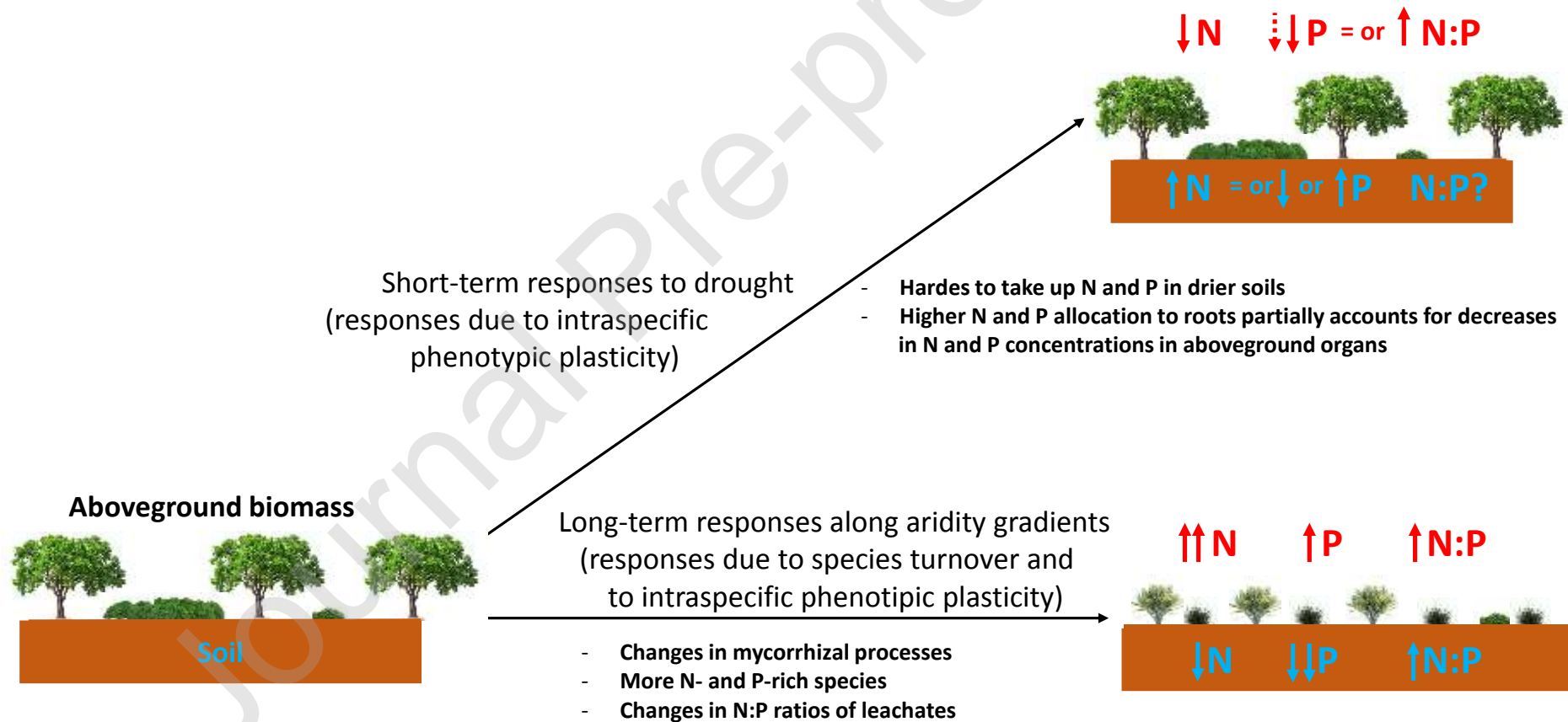


Figure 3

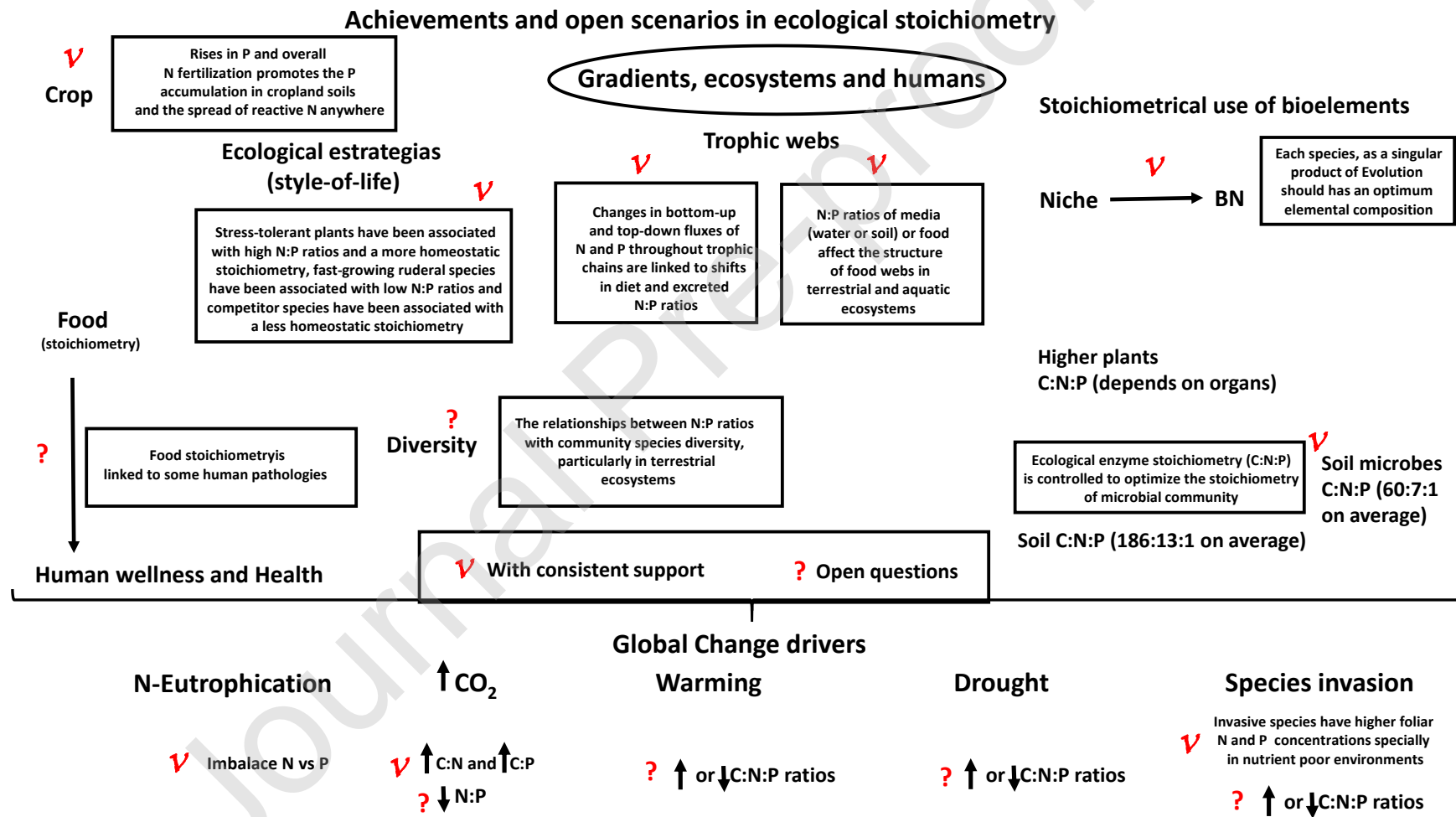


Figure 4