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Global biodiversity, stoichiometry and ecosystem function responses to human-induced C-N-P imbalances

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Abstract

Global change analyses usually consider biodiversity as a global asset that needs to be preserved. Biodiversity is frequently analysed mainly as a response variable affected by diverse environmental drivers. However, recent studies highlight that gradients of biodiversity are associated with gradual changes in the distribution of key dominant functional groups characterized by distinctive traits and stoichiometry, which in turn often define the rates of ecosystem processes and nutrient cycling. Moreover, pervasive links have been reported between biodiversity, food web structure, ecosystem function and species stoichiometry. Here we review current global stoichiometric gradients and how future distributional shifts in key functional groups may in turn influence basic ecosystem functions (production, nutrient cycling, decomposition) and therefore could exert a feed-back effect on stoichiometric gradients. The C-N-P stoichiometry of most primary producers (phytoplankton, algae, plants) has been linked to functional trait continua (i.e. to major axes of phenotypic variation observed in inter-specific analyses of multiple traits). In contrast, the C-N-P stoichiometry of higher-level consumers remains less precisely quantified in many taxonomic groups. We show that significant links are observed between trait continua across trophic levels. In spite of recent advances, the future reciprocal feedbacks between key functional groups, biodiversity and ecosystem functions remain largely uncertain. The reported evidence, however, highlights the key role of stoichiometric traits and suggests the need of a progressive shift towards an ecosystemic and stoichiometric perspective in global biodiversity analyses.

Keywords

stoichiometry; biodiversity; species richness; ecosystem function

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Introduction: Global changes in biodiversity and Earth system stoichiometry

During the last centuries human activities have significantly altered both global biodiversity patterns and nutrient cycling, increasing the availability of nitrogen and carbon in the biosphere and causing widespread biodiversity declines (Rockström et al., 2009; Elser et al., 2009; Butchart et al., 2010; Erisman et al., 2013). Critically, the ongoing human-induced increases in carbon and nitrogen are not paralleled by a proportional increase in phosphorus input. As a result, these changes are producing an unprecedented human-induced imbalance between C- N- and P stoichiometry in earth's life system (Peñuelas et al., 2012, 2013a). Here we analyse how increased C-N-P imbalances in the earth system may alter global biodiversity patterns and their effect on ecosystem functions.

Fossil fuel combustion and crop fertilization have changed the global nitrogen cycle, leading to a significant increase in atmospheric N deposition at the global scale (Vitousek et al., 1997; Rockström et al., 2009; Canfield et al., 2010; Peñuelas et al., 2013a). N inputs of anthropogenic origin into the Biosphere have been estimated in 165–259 Tg N yr⁻¹. Notably, this quantity is roughly equivalent to the total amount of N fixed in the biosphere by natural processes (Elser et al., 2009; Peñuelas et al., 2012, 2013a). Due to the continuous anthropogenic inputs of N into the system, atmospheric N deposition has continuously increased from 32 Tg N yr⁻¹ in 1860 to the current levels of 112–116 Tg yr⁻¹ (Peñuelas et al., 2012, 2013a). Both reduced and oxygenated forms of inorganic N in the atmosphere are continuously introduced in terrestrial ecosystems, mainly through dry deposition, wet deposition or cloud water deposition processes (Throop and Lerdau, 2004; Elser et al., 2009). Generally, the concentrations in N deposition of the reduced (NH_x) and oxygenated (NO_y) forms usually depend on the relative importance of agricultural and fossil fuel combustion activities at the regional scale (Throop and Lerdau, 2004; Sutton et al., 2007).

Human-induced imbalances on environmental C-N-P stoichiometry can impact biodiversity through multiple processes, including fertilization, eutrophication and acidification of terrestrial and aquatic ecosystems, increasing susceptibility to pests and environmental stresses, altering competitive and mutualistic relationships or by causing direct toxic effects on plants (Johnson, 1993; Olsson and Tyler, 2004; Elser et al., 2009; Bobbink et al., 2010; Stevens et al., 2010; Payne et al., 2013). For example, in the case of terrestrial plants increased ammonium availability can be toxic and cause very poor root and shoot development, especially in habitats with nitrate as the dominant N form (Bobbink et al., 2010). Likewise, the deposition of nitric acid frequently alters soil chemistry and leads to the depletion of essential cations (Mg, Ca, K) and can decrease soil pH and mobilize aluminum (Al) into the soil solution (Throop and Lerdau, 2004; Bobbink et al., 2010). Soil acidification in turn reduces biodiversity by producing toxicity effects due to exceedance of biological thresholds to soil pH and due to the release of toxic ions such as Al³⁺ (Bobbink et al., 2010; Jones et al., 2014). Similarly, the rates of N mineralization and nitrification tend to increase with N deposition (Throop and Lerdau 2004), but mineralization rates can also decline after soils become N saturated leading to reduced nitrification and promoting the accumulation of litter (Throop and Lerdau, 2004; Bobbink et al., 2010; Jones et al., 2014). N

deposition can result in both reduced demographic performance of plants and reduced resistance to pathogens and insect pests, and can also in turn increase leaf N content and promote herbivory (Bobbink et al., 2010). Moreover, N deposition can alter shoot/root ratios and influence the susceptibility of plants to drought and frost (Bobbink et al., 2010). Finally, changes on soil pH also influence P availability and affect plant growth (Kooijman et al., 1998; Jones et al., 2014). In sum, the available evidence highlights that multiple ecological processes have been largely impacted by increased N deposition rates and growing C-N-P imbalances.

High levels of nitrogen deposition have been reported mainly on terrestrial soils and lakes in densely populated areas of the Northern Hemisphere and several populated coasts across the globe (e.g. China, South America, North Atlantic and Baltic Sea coasts), causing important declines in biodiversity in these areas (Bobbink et al., 2010; Stevens et al., 2010; Kim et al., 2011; Payne et al., 2013). In contrast, phosphorus deposition, mainly caused by mineral aerosols (e.g. dust and wildfire ashes) but also by anthropogenic combustion that seems now to represent 30% of the global atmospheric P source (Wang et al., 2014), has been globally quantified in about 3–4 Tg P yr⁻¹ (Wang et al., 2014). These quantities are roughly one order of magnitude smaller than global nitrogen deposition. Phosphorus fertilizers are less volatile and are not widely distributed by large-scale deposition processes, being mainly transported to nearby ecosystems after their application (Peñuelas et al., 2013a). Therefore, major phosphorus fertilizer impacts have been mainly concentrated in some estuarine areas and in soils and streams located nearby intensively fertilized areas (Peñuelas et al., 2009, 2013a).

During the XXI century current high levels of nitrogen deposition in populated temperate regions of the Northern Hemisphere are expected to expand into tropical regions (Peñuelas et al., 2013a). Tilman et al. (2001) predicted a further 2.4- to 2.7-fold increase in agriculturally driven eutrophication with N and P by the year 2050. These global changes in N and P availability and in N:P ratio could alter the capacity of the biosphere to fix carbon and global nutrient cycling dynamics (Hessen et al., 2004). By the end of the 21st century, for example, recent biogeochemical modelling analyses suggest, that phosphorus and nitrogen availability could still limit the projected increase in carbon storage in response to increasing atmospheric CO₂ concentrations (Peñuelas et al., 2013).

The reported increased C-N-P imbalances are promoting shifts on both terrestrial and marine biodiversity (Bobbink et al., 2010; Peñuelas et al., 2012, 2013a). However, it is important to bear in mind that biodiversity gradients are tightly associated with changes in the spatial distribution of major functional groups (e.g. Carnicer and Díaz-Delgado 2008; Kissling et al., 2011; Weber and Deutch 2010; Stefanescu et al., 2011; Carnicer et al., 2013; Coll et al., 2013; Barton et al., 2013; Carnicer et al., 2014a). Crucially, these groups have contrasting stoichiometric and functional traits, and may in turn influence the rates of ecosystem processes and nutrient cycling, therefore producing reciprocal feedbacks among biodiversity composition, stoichiometry and ecosystem dynamics (Hessen et al., 2004; Weber and Deutch, 2010, 2012). Nowadays, a large number of studies highlight the need to account for the interactions between biodiversity, species' functional traits, stoichiometry, nutrient cycling dynamics and ecosystem functions (Schulze and Mooney 1993; Naeem et al., 1994, 1995, 2009; Tilman 1997; Chapin et al., 2000; Kinzig et al., 2001; Hessen et al., 2004;

Hooper et al., 2005; Loreau 2010; Butchart et al., 2010; Carnicer et al., 2012; Barton et al., 2013; Erisman et al., 2013). Moreover, evolutionary processes and phenotypically plastic responses need to be integrated also in the study of coupled feedbacks between biodiversity, nutrient cycling dynamics and global C-N-P imbalances (e.g. Elser et al., 2000b). To effectively integrate stoichiometry in global biodiversity analyses, the quantification of stoichiometric traits across several taxonomic and trophic groups will be possibly required. Although major axes of stoichiometric variation have been quantified in some groups like plants, marine bacteria and phytoplankton (Wright et al., 2004; Litchman and Klausmeier, 2008; Lauro et al., 2009; Reich, 2014), we still lack a precise description of the patterns of variation in stoichiometric traits in other taxonomic groups.

The consequences of increased C-N-P imbalances on the reciprocal feedbacks between biodiversity, ecosystem properties and nutrient cycling remain, though, largely uncertain. To explore how increased C-N-P imbalances in the earth system may alter global biodiversity, we develop the following objectives: 1) to briefly enumerate and overview the main hypotheses explaining inter-specific differences in C-N-P content; 2) to synthesize the major axes of variation observed in inter-specific comparisons of stoichiometric and functional traits in diverse taxonomic groups; 3) to review the global-scale gradients in C-N-P stoichiometry of major taxonomic and functional groups and explore how they may evolve in response to major global change drivers; and 4) to analyse the major interactions between biodiversity and ecosystem functions that may occur in the face of the increased C-N-P imbalances. Below we devote a section each to these four objectives.

1 Biodiversity and inter-specific differences in C-N-P content

The impacts of increased global C-N-P imbalances on biodiversity will depend on the specific traits of each taxon (Elser et al., 1996; Hessen et al., 2004; Carnicer et al., 2012). For example, variation in species' C-N-P stoichiometry has been significantly linked to organism growth rate (Elser et al., 1996; Sterner and Elser, 2002), body mass and allometry (Elser et al., 1996; Vanni et al., 2002; Woods et al., 2003, 2004; Mulder and Elser, 2009), taxonomic, phylogenetic and trophic group (Fagan et al., 2002; Hambäck et al., 2009; González et al., 2011), ontogenetic stage (Elser et al., 1996; Sterner and Elser, 2002), environment seasonality and the associated demand for storage in life history style (Hood and Sterner, 2010), investments in reproduction (Ventura and Catalan, 2005; Fujita et al., 2013), structural tissues and differential tissue allocation (Elser et al., 1996; Vanni et al., 2002; Woods et al., 2004; González et al., 2011) and genome and cell size (Hessen et al., 2010) (Table 1). Apart from all these species-specific factors, environmental factors also co-determine species stoichiometry. These environmental factors are diverse and include temperature (Woods et al., 2003; Reich and Oleksyn, 2004; Sun et al., 2013), substrate age (Walker and Syers, 1976; Reich and Oleksyn, 2004) and resource stoichiometry (Woods et al., 2002; Schade et al., 2003; Hessen et al., 2004; Small and Pringle, 2010). Overall, the available evidence supports that species-specific C-N-P stoichiometry is determined by multiple traits and environmental factors (Table 1). In spite of this overwhelming complexity of factors, both experimental and theoretical evidence suggests that species are adapted to species-specific optimal environmental C-N-P ratios (reviewed in Ågren et al., 2012).

2 Trait continua, stoichiometry and major inter-specific axes of phenotypic variation

Diverse stoichiometric and life history traits have been measured across many species allowing comparative approaches at the inter-specific level. These analyses revealed the existence of adaptive trait continua, that is, suites of traits that tend to co-vary along a main axis of variation at the inter-specific level in plants (Grime et al., 1997; Wright et al., 2004; Chave et al., 2009; Peñuelas et al., 2010; Donovan et al., 2011; Carnicer et al., 2014b), mammals (Bielby et al., 2007), birds (Sæther et al., 2011), fishes (Jeschke and Kokko, 2009), phytoplankton (Litchman and Klausmeier, 2008), marine bacteria (Lauro et al., 2009) and butterflies (Carnicer et al., 2012, 2013a). These continua often range from specialized to more generalist species and/or from slow to fast life strategies (Wright *et al.*, 2004; Bielby *et al.*, 2007; Sæther *et al.*, 2011; Carnicer et al. 2012, 2013a). Trait continua quantify and summarize life history, functional trait and stoichiometric variation at the inter-specific level in multi-specific assemblages. It has been suggested that the mechanistic origin of these taxon-specific trait continua may rely on the evolutionary emergence of contrasting stoichiometric and life-history strategies that, in particular ecological contexts, maximize fitness by acquiring a different set of traits allowing for sustained population performance (Carnicer et al 2012, 2013a). Therefore, trait continua synthesise the observed phenotypic space for a given taxonomic group in local, regional or global assemblages.

The variation in stoichiometric traits along these major functional trait axes (i.e. variation of C-N-P tissue content, C/N/P ratios) is relatively well described in some groups like plants (Wright et al., 2004; Reich, 2014), marine bacteria (Lauro *et al.*, 2009) and some groups of phytoplankton (Litchman and Klausmeier, 2008). In contrast, for many terrestrial heterotroph groups (e.g. primary consumers, predators and detritivores) the inter-specific variation in C-N-P tissue content remains yet poorly quantified (but see Fagan et al., 2002; Denno and Fagan, 2003; Fagan and Denno, 2004; Woods et al., 2003, 2004; Martinson et al., 2008; Mulder and Elser, 2009; Bishop et al., 2010; Hämbäck et al., 2009; González et al., 2011; Lemoine et al., 2014). As a general rule, available studies suggest that there is a significant decrease in P content with body size in most heterotroph groups (Woods et al., 2004; Hämbäck et al., 2009; González et al., 2011). In addition, contrasting N, P values have been reported between primary consumers and higher trophic levels in some taxonomic groups (Fagan et al., 2002; González et al., 2011; but see Woods et al., 2004). Likewise, significant differences in body N and P contents are observed between major insect orders. For example, Lepidoptera show the highest potential for P limitation because they have the lowest N and highest P concentrations when compared with other insect orders (Fagan et al., 2002; Woods et al., 2004). P limitation significantly affects many aspects of insect performance, like survival, development, growth rate, body size and sexual and oviposition behavior (reviewed in Tao and Hunter, 2012). In contrast, other orders such as Hemiptera are considered to be mainly N limited. Like in the case of phosphorus, nitrogen limitation often significantly determines insect demographic performance and improved performance of herbivorous insects has been observed after increased nitrogen deposition (Throop and Lerdau, 2004). This may be expected considering that insect body N concentrations are on average 10 times higher than those of their host plants (Tao and Hunter 2012). In addition,

recent studies highlight that species-specific demands for nutrients and the defensive responses of host plants combine to determine the responses of herbivores to P availability under N deposition (Tao and Hunter 2012).

Across multiple trophic levels, deciphering the relationships between major axes of variation in stoichiometric and functional traits emerges as a new research challenge. For example, a major axis of trait variation has been recently described in Mediterranean and temperate butterflies in Europe (Carnicer et al. 2012, 2013a; Dapporto and Dennis, 2013). In this group, traits and species-specific habitat measures covary along a main axis, ranging from multivoltine trophic generalists with high dispersal capacity to univoltine (i.e. one generation per year), trophic specialist species with low dispersal capacity (table 2). This trait continuum is closely associated with the observed distributions of butterfly species along an altitudinal species richness gradient (Figure 1, and see Carnicer et al 2012, 2013a). In addition, the position of species along the trait continuum is significantly associated with inter-specific differences in patterns of spatial genetic variability (F_{ST} and genetic distances), population responses to the impacts of global change and local turnover dynamics (Figure 1, Carnicer et al 2012, 2013a). However, the putative relationships of this trait continuum with stoichiometric traits in other trophic levels remains largely unexplored. As highlighted in Figure 2, major axes of phenotypic trait variation in butterflies can be significantly associated with leaf stoichiometric variation at lower trophic levels (host plants). Notably, leaf P and N concentration are two traits integrated in the leaf economics spectrum (Wright et al., 2004), a major axis of phenotypic variation between terrestrial plant species. Overall, Figure 2 illustrates that, across trophic levels, significant relationships hold between major life history axes (PCA 1) and stoichiometric traits (leaf N and P concentration). These results suggest that the consideration of stoichiometric and functional traits across multiple trophic levels might allow a better understanding of the structure, dynamics and stoichiometric constraints operating in plant-insect food webs.

3 Global gradients in organism C-N-P stoichiometry

Large-scale gradients of both nutrient availability in the environment and organism C-N-P tissue concentration have been reported for several groups (Reich and Oleksyn, 2004; Lambers et al., 2007; Sardans et al 2013; Daines et al 2014). For example, global-scale gradients in C-N-P tissue concentration and C-N-P ratios have been reported in plants, marine bacteria, phytoplankton, insects, mycorrhiza activity and plant litter (Reich and Oleksyn, 2004; Lambers et al., 2007; Manzoni et al., 2008; Sun et al., 2013; Sardans et al., 2013; Daines et al., 2014). In marine ecosystems, lower organism N/P and C/P ratios are observed at high latitudes, in cold nutrient-rich environments, whereas higher C/N/P ratios dominate at low latitudes. High-latitude marine environments experience low temperatures and high nutrient concentrations, are often iron-limited and also experience seasonal blooms and limitation of phytoplankton growth by light availability (Weber and Deutch, 2010, 2012; Moore et al., 2013; Martiny et al., 2013; Daines et al., 2014). The opposite conditions (warm, oligotrophic, widespread N-limitation and P co-limitation in some localities) are generally observed at low latitudes and subtropical gyres. In contrast, equatorial regions are characterized by intermediate temperatures and nutrient concentrations due to upwelling processes (Martiny et al., 2013; Daines et al., 2014). These large-scale gradients in

temperature and nutrient availability are in turn associated with gradients in species' stoichiometric values. For example, Martiny et al. (2013) reported C-N-P ratios of 195:28:1 in warm, nutrient-depleted low latitude gyres, 137:18:1 in warm, nutrient-rich upwelling zones and 78:13:1 in cold, nutrient rich high-latitude regions. The taxonomic composition of a community also significantly influences its elemental stoichiometry (Elser et al., 2000; Sterner and Elser, 2002). For example, communities dominated by diatoms have a lower N/P and C/P ratio and are more common in cold and nutrient-rich environments, located at high latitudes (Martiny et al., 2013). In contrast, communities located in subtropical oligotrophic gyres are dominated by N₂-fixing cyanobacteria and other diazotrophs and, as a result, have higher C/P and N/P ratios and smaller sizes (Martiny et al., 2013; Barton et al., 2013). N/P ratios of phytoplankton show both significant differences between different phylogenetic groups and substantial intra-specific variation due to local acclimation and phenotypic plasticity (Weber and Deutch, 2010). In line with this, phytoplankton N/P ratios often depart from the Redfield ratio (16:1; Redfield, 1934), and observed inter-specific differences in N/P ratios span more than one order of magnitude (Weber and Deutch, 2010).

Several studies have analysed the stoichiometry of primary and secondary consumers in marine and freshwater food webs (Elser and Hassett, 1994; Dobberfuhl and Elser, 2000; Vanni et al., 2002). These studies report significant differences in C-N-P content between autotroph and heterotrophs that in turn influence nutrient recycling rates and productivity (Elser and Urabe, 1999; Vanni et al., 2002; Hessen et al., 2004). Herbivores tend to have higher N and P contents relative to C (Elser et al., 2000a). Stoichiometric differences between trophic levels are in turn associated with different stoichiometric plasticity between primary consumers (more plastic) and secondary consumers (less stoichiometric plasticity) (Hessen et al., 2004; Persson et al., 2010). Some pioneering studies have also quantified the stoichiometry of detritivore and benthic groups (Cross et al., 2003; Martinson et al., 2008; Alves et al., 2010). The future distribution of the diverse marine taxonomic, trophic and functional groups in the face of global change and increased C-N-P imbalance remain yet largely uncertain. Global change model projections for the oceans mostly predict greater stratification of the water column, weaker nutrient delivery to the surface and acidification (Sarmiento et al., 2004; Caldeira and Wickett, 2005; Barton et al., 2013). This may possibly expand the oligotrophic areas and facilitate the expansion of communities dominated by smaller phytoplankton, mainly dominated by N₂-fixing cyanobacteria, other heterotrophic bacteria and generalist mixotrophs (bacteria that combine autotrophic and heterotrophic nutrition), small-sized zooplankton (Barton et al., 2013), and, if increased overfishing persists, gelatinous zooplankton (Richardson et al., 2009; Condon et al., 2012).

In the case of terrestrial plants, Reich and Oleksyn (2004) have reported a significant latitudinal increase in both leaf P and N concentration and a latitudinal decrease in N/P ratio. Similarly, Yuan et al (2011) reported latitudinal gradients for N and P in root tissues. Plant functional types (i.e. ruderals, stress-tolerants, competitive) significantly differ in their N, P concentration and N/P ratios (Grime, 1977). McJannet et al (1995) reported significant differences in N, P tissue concentration between plant functional strategies, with lower N, P and N/P ratios in ruderal species. Similarly, Willby et al (2001) reported that stress-tolerant plants (*S*) had consistently lower nutrient concentration and higher N/P ratios whereas ruderal plants (*R*) displayed the opposite pattern. Competitor (*C*) and competitor-stress

tolerator plants (*CS*) were intermediate to *R* and *S*. In line with this, the abundance of the different functional types of plants and mycorrhizas varies along N/P gradients, and intermediate N/P ratios are associated with an increase of the number of different strategies that coexist (Lambers et al., 2007). As a result, species richness of herbaceous plants is usually higher at intermediate N/P ratios (Fujita et al., 2013). Low N/P ratio environments tend to favour ruderal plant types, fast growing species with long roots, and species associated with N fixers. Likewise, intermediate N/P ratios and high local productivity are often associated with a predominance of competitor plant types (Fujita et al., 2013). In other words, species with resource-acquisitive traits, such as high leaf N and P concentrations, high SLA and short leaf lifespan reach higher abundances or occur more frequently in sites with higher nutrient and/or water availability (Adler et al., 2013). Finally, oligotrophic and high N/P ratio environments favour slow-growing species, and stress-tolerant plant types (*S*) with specialized P uptake traits like cluster roots, arbuscular mycorrhizae or high phosphatase activity (Lambers et al., 2007; Fujita et al., 2013). For example, the numbers of stress-tolerant and endangered species is higher at high N/P ratios (Fujita et al., 2013) and in low fertilized sites (Bobbink et al., 2010). These species are characterized by specific suites of traits, such as small investment in sexual reproduction, low seed number and seed investment, late start of flowering, short flowering period, perennial form, vegetative reproduction, low specific leaf area (SLA), high leaf dry matter content, low canopy height and low or absent association with N fixers. Crucially, plants can invest a high percentage of total phosphorus in reproduction (50-60%) (Fujita et al., 2013 and cites there in) and this results in significantly reduced investment in plant reproductive organs in phosphorus-limited environments with high N/P ratios (Fujita et al., 2013). In trees, deciduous species have higher leaf N and P than evergreens with similar leaf lifespan (Reich and Oleksyn, 2004). Deciduous trees make up a greater fraction of all species in temperate than in tropical zones thus contributing to higher leaf N and P in temperate forests (Reich and Oleksyn, 2004).

The response of plant functional groups to increased global C-N-P imbalance has been explored in diverse experimental studies (Silvertown et al., 2006; Bobbink et al., 2010). Available empirical evidence suggests different demographic responses between plant functional groups to increased imbalance in C-N-P supply. For example, long-term plant fertilization experiments report increases in the abundance of grasses, and significant reductions of the cover of legumes and broadleaved herbs (Silvertown, 2006). Similarly, in a wide range of arctic, alpine and temperate ecosystems, lichens, mosses, and epiphytic species tend to be the most sensitive elements of ecosystems to increased N availability and deposition (reviewed in Bobbink et al., 2010). In contrast, in several terrestrial ecosystems grasses and sedges are often benefited from increased N deposition and altered C/N/P ratios (Bobbink et al., 2010).

In contrast to aquatic communities and terrestrial plant communities, large-scale gradients of N, P tissue concentration in terrestrial primary and secondary consumers remain yet poorly quantified (Bertram et al., 2008; Hambäck et al., 2009; El-Sabaawi et al., 2012; Sun et al., 2013). The same applies to the stoichiometric differences in N, P concentration between major terrestrial groups of primary consumers, predators and detritivores (Fagan et al., 2002;

Denno and Fagan, 2003; Woods et al., 2003, 2004; Martinson et al., 2008; Mulder and Elser, 2009; Bishop et al., 2010; González et al., 2011; Lemoine et al., 2014).

In plants, aquatic communities, and secondary consumers the available empirical evidence suggests that several hypotheses jointly contribute to explain large-scale trends in N, P tissue content. Firstly, high nitrogen and phosphorus concentration may be adaptive at low temperatures (temperature–physiology hypothesis; Körner et al., 1986; Woods et al., 2003; Reich and Oleksyn, 2004; Table 1). Plants experimentally grown at low temperatures typically contain greater leaf N and P and this may be related to the diminished efficiency of N-rich enzymes and P-rich RNA at low temperatures (Reich and Oleksyn, 2004). The temperature–physiology hypothesis holds in diverse taxa, including both primary and secondary consumers (e.g. Woods et al. 2003, 2004, Reich and Oleksyn, 2004; Martiny et al., 2013). For example, cold-acclimated poikilotherms contain on average more nitrogen and phosphorus, protein and RNA than warm-acclimated conspecifics (Woods et al., 2003). Similarly, phytoplankton and plants show large-scale N-P gradients that have been significantly associated with spatial changes in ambient temperature (Reich and Oleksyn, 2004; Martiny et al., 2013). Secondly, large-scale gradients in N and P tissue content in terrestrial groups are also influenced by substrate age and fertility (Substrate age and substrate composition hypothesis, Reich and Oleksyn, 2004, Table 1). In terrestrial ecosystems tropical soils are on average older and more leached, and have lower fertility (Walker and Syers, 1976; Reich and Oleksyn, 2004). Similarly, while in the Mediterranean biome the soils in South Africa and Australia are geologically older and tend to be nutrient poor, in the Mediterranean basin, Chile and California soils often have higher nutrient contents (Ochoa-Hueso et al., 2011). Available evidence suggests that climate, substrate nutrient content and soil age gradients jointly contribute to the clinal variation of N and P content in organism tissues in several taxa (Reich and Oleksyn, 2004; Martiny et al., 2013). Moreover, mountain ranges and altitudinal gradients significantly influence soil nutrient content and regional variability in soil and organism tissue stoichiometry. For example, wet N deposition is often higher at high altitudes due to the increased importance of cloud water deposition, producing altitudinal gradients in N deposition (Bobbink et al., 2010). On the other hand, cold temperatures can slow down biogeochemical processes and result in decreased leaf N and P content at high latitudes (temperature–biogeochemistry hypothesis, Reich and Oleksyn, 2004). In addition, cold temperatures at high latitudes, such as arctic zones, can promote a dominance of NH_4^+ over NO_3^- in soil biogeochemistry (Bobbink et al., 2010).

In spite of all this empirical evidence describing large-scale stoichiometric gradients, the patterns for many groups and elements remain unquantified and therefore unveiled, specially at higher trophic levels.

4 Biodiversity, ecosystem function and global unbalanced C-N-P stoichiometry

Substantial loss of species richness has been reported with increased N deposition and associated C-N-P imbalances in a wide range of habitats and taxa. For example, a decrease

in plant richness has been observed in acid grasslands, sand dune and mixed grasslands, heath, bog, woodlands and forests (Stevens et al., 2004; Jones et al., 2004; 2014; Maskell et al., 2010; Dupré et al., 2010; Bobbink et al. 2010; Ceulemans, 2013). Similar trends have been observed in N-addition experiments, field surveys along N-deposition gradients and meta-analyses (Carroll et al., 2003; Stevens et al., 2004; Clark and Tilman, 2008; Dupré et al., 2010; De Schrijver et al., 2011; Isbell et al. 2013b). Crucially, a large number of studies now highlight an important role of biodiversity per se in determining basic ecosystem functions, such as productivity, nutrient cycling and decomposition rates. For example, studies highlight that loss of biodiversity can reduce biomass production efficiency, and alter nutrient cycling and decomposition rates (Tilman and Downing, 1994; Naeem et al., 1994; Tilman et al., 1996; Hector et al., 1999; Loreau et al., 2001; Reich et al., 2001; Loreau et al., 2001; Hooper et al., 2005; Cardinale et al., 2012; Reich et al., 2012). Moreover, other studies demonstrate that biodiversity can also increase the stability of ecosystem functions (Cardinale et al., 2006; Tilman et al., 2006; Hector and Bagchi, 2007; Zavaleta et al., 2010; Isbell et al., 2011; Cardinale et al., 2012; Reich et al., 2012; Sapijanskas et al., 2014). Several non-mutually exclusive mechanisms are possibly involved, for example recent studies show that biodiversity enhances ecosystem functioning by niche complementarity effects, compensatory dynamics associated with inter-specific trait differences, and phenotypically plastic responses (Loreau et al., 2010; Cardinale et al., 2012; Sapijanskas et al., 2014).

In line with all these trends, empirical studies are unveiling a key role for top predators, mega-herbivores and disturbance regimes (fire or other abrupt events) in mediating links between biodiversity and ecosystem function. For example, the loss of top predators and/or megaherbivores (and the associated trophic cascades) influence the dynamics of wildfire, carbon sequestration, invasive species, biogeochemical cycles and diseases (Schindler et al., 1997; Gill et al., 2009; Smith et al., 2010; Lavery et al., 2010; Pershing et al., 2010; Estes et al., 2011; Rule et al., 2012; Wolf et al., 2013; Doughty et al., 2013). For example, interactions between top predation, diseases, herbivory, plant communities, and fire produce large-scale changes in the structure of vegetation and associated communities (McLaren and Peterson, 1994; Crooks and Soulé, 1999; Sinclair et al., 2003; Croll et al., 2005; Holdo et al., 2009; Estes et al., 2011; Leganeux et al., 2014). Similarly, the absence of natural predators, loss of native predators and reduced top-down control facilitates the performance of invasive species (Estes et al., 2011). Of note, current biodiversity loss is characterized by the extinction of megaherbivores and top consumers and larger-bodied animals in general (Estes et al., 2011).

Increased C-N-P imbalances can substantially alter ecosystem functions and their relationships with biodiversity. For example, the C sequestration and C storage capacity of terrestrial and aquatic ecosystems depends on changes in the C-N-P stoichiometric ratios of the system components, the total supply of nutrients from external sources, and the relative distribution of C-N-P elements between system components (Hessen et al., 2004; Peñuelas et al., 2013a). On the other hand, changes in food web structure, and in the composition of herbivores and predators can also alter carbon sequestration and promote source-sink shifts (e.g. Schindler et al., 1997; Lavery et al., 2010; Pershing et al., 2010). In oceans, the sequestration of CO₂ occurs due to the under-saturation water pCO₂ with respect

to the atmosphere (the “Solubility pump”) and subsequent transport to depth waters (Hessen et al., 2004; Barton et al., 2013). Deposition of N and other macronutrients from the atmosphere may have important effects on the biological pump over long time scales. Changes in C/nutrient ratios of export organic matter and in nitrogen-fixing and denitrification processes can significantly alter C sequestration in oceans (Hessen et al., 2004; Barton et al., 2013). Moreover, biodiversity loss of top herbivores (e.g. whales) may significantly alter nutrient recycling processes, biotic pump processes and carbon uptake (Roman and McCarthy, 2010; Lavery et al., 2010; Pershing et al., 2010). At much larger temporal scales, positive feedbacks and compensatory negative feedbacks link ocean productivity, phosphorus availability, anoxia and the suppression of Organic matter-P and Fe-P burial (Handoh and Lenton, 2003). Million-year periodic changes in ocean N-P nutrient availability have been associated with major shifts on Earth biodiversity (Handoh and Lenton, 2003). In terrestrial systems, changes in litter C/N and C/P ratios determine nutrient release and immobilization, and decomposer carbon-use efficiency. Higher nitrogen and phosphorus concentrations are usually associated with more rapid decomposition rates (Manzoni et al., 2008, 2010). In addition, biodiversity loss and changes in the structure food webs can significantly influence decomposition processes and alter litter C-N-P ratios (Frank and Groffman, 1998; Mulder and Elser, 2009; Cardinale et al., 2012).

Overall, all this empirical evidence suggests that human-induced global C-N-P imbalances may produce multiple interactions and feedbacks between biodiversity and basic ecosystem functions. During the next decades, ecosystem functions will simultaneously respond to increased C-N-P imbalances and global warming, changes in the geographic distribution of functional groups, invasive species, the loss of top predators and mega-bervivores, altered disturbance regimes and habitat destruction and alteration, among other drivers (Peñuelas and Carnicer 2010, Carnicer and Peñuelas 2012, Peñuelas et al., 2013b). Moreover, recent assesments suggest that the impacts of biodiversity loss on ecosystem function are of comparable magnitude to the impacts of drought, climate warming, ozone, acidification, elevated CO₂, herbivory, fire and pollution (Tilman et al., 2012; Hooper et al., 2012).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

The adaptive trait continuum in Mediterranean butterflies. This functional trait continuum is described by the scores along the PCA axis 1 of 169 butterfly species (see Table 2, Carnicer et al 2013a and supplementary methods for further details). A) Observed distribution of major functional groups along an altitudinal gradient (modified from Stefanescu et al 2011). S: total butterfly species richness, Disp4: species richness of highly dispersive species; Disp3: species richness of high-medium dispersive species; Disp2: species richness of medium-low dispersive species; Disp1: species richness of low dispersive species. B)

Observed relationship of the adaptive trait continuum (PCA) with genetic variability (F_{ST}).
C) Observed relationship of the adaptive trait continuum (PCA) with regional population trends. Population trends were estimated as the slope of log-linear regression of abundances from the period 1994-2008 using TRIM software and were available for 78 species.

Butterfly functional trait continuum (PCA)

Figure 2.

Observed relationships between the adaptive trait continuum of Mediterranean butterflies (PCA) and A) leaf P content; B) Leaf N content of the host plants. See supplementary methods for further details.

Table 1

A non-exhaustive summary of the different hypotheses associated with large-scale gradients in species' stoichiometry.

Hypothesis	Description	References
Optimality, fitness maximisation and trade-offs between diverse life history, functional, stoichiometric and biochemical traits.	Fitness maximisation, trade-offs and the operation of natural selection drives the evolution of stoichiometric traits. The evolution of metabolic networks is constrained by elementary mass balance and thermodynamic laws	Parker and Maynard Smith, 1990; Klausmeier et al., 2004; Orth et al., 2010; Loladze and Elser, 2011; Daines et al., 2014
Growth rate hypothesis	Differences in organism C-N-P stoichiometry reflect increased allocation to P-rich ribosomal RNA at higher growth rates	Elser et al. 1996; Sterner and Elser, 2002; Loladze and Elser, 2011
Substrate age hypothesis	Tropical soils are often older, more leached, and have lower fertility, which can lead to reduced organism N and P with increased temperature across geographic gradients	Walker and Syers, 1976; Reich and Oleksyn, 2004
Temperature–plant physiology hypothesis	Plants grown at low temperatures develop greater leaf N and P content, to offset reduced rates of biochemical reactions caused by the diminished efficiency of N-rich enzymes and P-rich RNA	Woods et al., 2003; Reich and Oleksyn, 2004
Endothermy	Nutritional requirements of endotherms and ectotherms deviate largely and significantly affect whole organism stoichiometry	Klaassen and Nolet, 2008; Wilkinson and Ruxton, 2013
Temperature–biogeochemistry hypothesis	Low temperatures depress decomposition and mineralization of organic matter, reduce the availability of N and P, and significantly alter the stoichiometry of species	Reich and Oleksyn, 2004
Trophic position, Herbivory	Trophic position is associated with significant changes in C-N-P stoichiometry. Heterotrophs are often less rich in C than autotrophs and need to excrete/egest excess C, and this may come at a considerable metabolic cost	Elser et al., 1996; Fagan et al., 2002; Urabe et al., 2002; Hall et al., 2007; Daines et al., 2014
Taxonomic composition, evolutionary constraints and niche conservatism	Systematic differences in macronutrient composition (C-N-P) are phylogenetically conserved	Quigg et al., 2003; Woods et al., 2003, 2004
Regional differences in the species composition	Regional differences in the species composition of the plankton community drive the N/P ratio of biological nutrient removal across geographic gradients	Weber and Deutsch, 2010
Body mass and allometry	RNA tissue content, structural tissues and organism N/P ratios show allometric relationships that are determined by species-specific evolutionary processes and the emergence of contrasting life history strategies.	Peters, 1983; Elser, 1996; Sterner and Elser, 2002; Mulder and Elser, 2009
Ontogenetic stage	Ontogenetic changes are associated with changes in biochemical and cellular composition and other allocation decisions, producing changes in body N/P ratio and C-N-P stoichiometry.	Elser et al., 1996; Sterner and Elser, 2002
Structural material and differential allocation on tissues	Tissues significantly differ in nutrient composition. Inter- and intra-specific differences in allocation and tissue structures motivate significant changes in body C-N-P stoichiometry	Elser et al., 1996; Vanni et al., 2002
Differential investments in basic life-history functions (reproduction, storage, defense)	Differential investments in basic life-history functions (reproduction, storage, defense) alter body stoichiometry	Ventura and Catalan, 2005; Tao et al., 2010.
Active regulation of nutrient uptake, excretion, N ₂ fixation, reabsorption	Diverse physiological processes actively regulate body nutrient content and determine stoichiometry	Sterner and Elser, 2002; Sardans et al., 2012ab; Sardans and Peñuelas, 2012

Hypothesis	Description	References
Species-specific P and N storage strategies	Species develop evolutionary strategies and adaptations to store limiting resources, affecting in turn body stoichiometry	Martin and van Mooy, 2012; Daines et al., 2014
Resource supply stoichiometry	Resource supply stoichiometry affects the stoichiometric composition of consumers through diverse metabolic and ecophysiological processes, phenotypically plastic responses and long-term adaptive responses	Elser et al., 1996; Sterner et al., 1997; 1998; Hillebrand and Kahlert, 2001; Sterner and Elser, 2002; Woods et al., 2002; Schade et al., 2003; Klausmeier et al., 2004; Elser et al., 2006; Acquisti et al., 2009; Small and Pringle, 2010; Frost et al., 2010.
Genome and cell size	Genome and cell size affect multiple traits and the elemental composition of whole cells and organisms	Hessen et al., 2010; Kozłowski et al., 2003
Stoichiometric plasticity and stoichiometric homeostasis	Phenotypically plastic responses and regulatory physiological and biochemical processes can modify organism C-N-P stoichiometry	Hessen et al., 2004; Persson et al., 2010
Spatiotemporal gradients in conditions and resources (light, nutrients, rainfall, Fe, Si, other conditions and resources)	The spatiotemporal variation of conditions and resources significantly influences organism stoichiometry	Urabe and Sterner, 1996; Sterner et al., 1997, 1998; Klausmeier et al., 2004; Diehl 2007; Martiny et al., 2013; Barton et al., 2013
Topographic gradients associated with changes in N deposition, gradients in temperature and rainfall and other factors	Topography correlates with the clinal variation of environmental conditions, resources and ecological processes that induce changes in organism stoichiometry	Bobbink et al., 2010
Environmental filtering	The demographic performance and local persistence of populations depend on trait-environment interactions. These interactions filter some species and can influence the observed stoichiometric patterns at the species or community level.	Carnicer et al., 2008; Carnicer et al., 2012; Daines et al., 2014
Long-term periodic variations in nutrient cycling dynamics	Long-term periodic variations in nutrient cycling dynamics at geological time-scales alter Earth diversity, and the evolution of species' stoichiometry.	Tyrrell 1999; Lenton and Watson, 2000; Handoh and Lenton, 2003; Lenton and Klausmeier, 2007
Biogeochemical niche	Pant species occupy different biogeochemical niches, and differ significantly in key physiological, structural and stoichiometric traits	Peñuelas et al., 2008, 2010
Species richness	Species richness and functional groups richness affect community stoichiometry, and alter C/P and N/P ratios. Community composition affects the biochemical niche of species across functional groups	Abbas et al. 2013; Urbina et al., 2014

Table 2

Summary of the PCA analysis for species-specific traits (number of host-plants, dispersal capacity and flight period length) and habitat variables (habitat aridity breadth, habitat winter temperature breadth) for 169 Butterflies in Catalonia, Spain. A major axis of life history variation was observed, ranging from multivoltine trophic generalists with high dispersal capacity to univoltine (i.e. one generation per year), trophic specialist species with low dispersal capacity (see supplementary methods for further details). The values for the factors (habitat aridity breadth, habitat winter temperature breadth, number of host-plants, dispersal capacity, flight period length) are the loadings on PCA axis 1.

	PCA 1
Eigenvalue	2.97
Explained variance	59.49
Habitat aridity breadth	0.50
Habitat winter temperature breadth	0.48
Number of host-plants	0.37
Dispersal capacity	0.42
Flight-period length	0.45