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From atoms to ecosystems: elementome diversity meets ecosystem functioning

Authors: Marcos Fernández-Martínez^{*1,2,3}.

Affiliation:

¹ Research group PLECO (Plants and Ecosystems), Department of Biology, University of Antwerp, 2610 Wilrijk, Belgium.

² CREAF, E08193 Bellaterra (Cerdanyola del Vallès), Catalonia, Spain

³ BEECA-UB, Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, E08028 Barcelona, Catalonia, Spain

***Correspondence to:** M. Fernández-Martínez, m.fernandez@creaf.uab.cat

ORCID: <https://orcid.org/0000-0002-5661-3610>

Twitter: @Burriach

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28 **Summary**

29 The elemental composition of plants (the elementome) is a reliable indicator of their
30 functional traits and the ecological strategies that they follow, and thus represents a good
31 predictor of how ecosystems work. Biodiversity and, especially, functional diversity are
32 also widely recognised as important drivers of ecosystem functioning, mainly because of
33 niche partitioning amongst different species. I here review evidence indicating that plant
34 elementomes relate to their ecological niches, and how plant elemental concentrations
35 may shift in response to abiotic and biotic drivers. I propose the use of ecosystem
36 elementome diversity as a universal metric to compare ecosystems and investigate
37 diversity-ecosystem functioning relationships. Future research using this promising novel
38 approach will bring together elementomes, diversity and ecosystem functioning.

39 **Keywords:** stoichiometry, ecological niche, biogeochemistry, functional traits,
40 competition, nutrients

Introduction

The elemental composition of matter determines its physical and chemical properties. Living matter, mainly composed of carbon (C), oxygen (O), hydrogen, nitrogen (N) and phosphorus (P), is not an exception to this rule. Like the genome, the *elementome*, defined as the concentration of elements within organisms (Peñuelas *et al.*, 2019), is the quintessence of biological systems. Not surprisingly, the elemental composition and stoichiometry (i.e., the ratio of elemental concentrations, such as N:P) of organisms have been shown to be excellent predictors of their ancestry, their functional traits and the ecological strategies they follow (Wright *et al.*, 2004; Peñuelas *et al.*, 2019; Sardans *et al.*, 2021; Fernández-Martínez *et al.*, 2021a). Therefore, two organisms presenting very different elementomes will, most likely, occupy different ecological niches. Assessing ecological niches amongst organisms is an important feature for ecological research, because one of the main mechanisms behind the positive relationship between diversity and ecosystem functioning is niche partitioning (Cardinale, 2011) – this is that different organisms use a different set of resources within the ecosystem.

In this review, I compile evidence on how plant elementomes depend on their functional traits and habitats, and how they can be defined. Later, I review the role of plasticity on the elemental composition of plants, ecosystems and their functioning. Finally, I propose the use of *elementome diversity* and *distance* as universal tools to assess functional diversity, competition and global change impacts on ecosystem functioning.

II. Elementome ecology: niches, evolution and plasticity

Specificity of elementomes: the case of C:N:P stoichiometry

Since the early stages of life, organisms have evolved to adapt to new colonisable environments and coexist with other organisms. Thus, the large diversity of forms and functions evolved have generated a large diversity of elementomes. The elemental composition of plants can be determined by different analytical methods, such as isotope-ratio mass spectrometry (IRMS), providing concentrations of C and N, and their isotopic signal (i.e., $\delta^{13}\text{C}$ and $\delta^{15}\text{C}$) and inductively coupled plasma mass spectrometry (ICP-MS), that can provide the concentration of a large number of elements, including trace elements. By comparing the C:N:P ratio across organisms, directly derived from differences in their elementomes, we can get an overview of how species-specific elementomes (Sardans *et al.*, 2021; Fernández-Martínez *et al.*, 2021b) are related to their traits and habitats (Wright *et al.*, 2004; Peñuelas *et al.*, 2019). In general terms, plant elementomes increase C with respect to N and P as organisms get bigger and develop complex structures (**Figure 1, Table 1**).

Analysing the elementomes of morphologically simple plants is methodologically easy, but it can be challenging for complex organisms (e.g., trees) if the aim is to capture the composition of *their entire organism* and allow a fair comparison with simpler plants. Comparisons amongst complex plants are usually based on the elemental composition of their leaves because they are the photosynthetically active part of the plants, where most of the metabolic processes take place, and are easy to sample. However, plant-leaf elementomes reveal stoichiometric ratios that are far from the average C:N:P ratios of the entire biomass in some species (Balboa-Murias *et al.*, 2006).

To estimate the elementome of big organisms it is necessary to sample all different organs of the plant (e.g., roots, stems, leaves), estimate each organ's biomass using allometric equations or similar methods, and then calculate an overall concentration for each element. To achieve a community-level elementome, the concentration of each element would be the mean of its concentration weighted by the biomass of each species within the community. Once this exercise has been made, estimates clearly reflect the vast investment in C-rich structures (wood) in trees compared to that of phytoplankton, bryophytes, grasses or even shrubs, and denote clear differences between the functional traits and ecological niches of these organisms (**Table 1**).

Moreover, the presence of determined elementomes in an ecosystem could indicate the existence of competitive (i.e., similar elementomes) and/or facilitating interactions amongst species (e.g., epiphytes growing in trees, shade tolerant plants in the understory) and different successional stages. These comparisons based on C:N:P stoichiometry, however, have been made only for simplicity purposes, following (Elser *et al.*, 2000). To achieve a clear picture of elementome differences amongst organisms we must consider the differences in their elemental concentrations because very high N:P values may be the result of high N or low P concentrations.

Adaptive value of elementomes

Phylogenetic analyses have shown that plant functional traits, such as defence or reproduction, have co-evolved with the elemental composition of organisms following an adaptive rather than a random model of evolution (Fernández-Martínez *et al.*, 2018, 2019; Bai *et al.*, 2019). Consequently, elementomes have been repeatedly shown to be phylogenetically conserved (Sardans *et al.*, 2021; Fernández-Martínez *et al.*, 2021b), further indicating the adaptive value of maintaining a particular elemental composition for each species: their *biogeochemical niche* (Peñuelas *et al.*, 2019). The concentrations of C, N and P are, by far, the most commonly used to study organism features because of their strong involvement in metabolic processes (Sterner & Elser, 2002). However, a

three-dimensional elementome may be missing key information that would otherwise have been provided by additional elements (Kaspari, 2021). Recent studies have found that the concentration of elements such as K, Mg, Ca, and S, have also been conserved through evolutionary history and, thus, they should have co-evolved with several functional traits (Bai *et al.*, 2019; Sardans *et al.*, 2021; Fernández-Martínez *et al.*, 2021b).

Elementomes beyond C, N and P

Micronutrients and trace elements are essential to regulate vital plant functions such as photosynthesis and chlorophyll production (Mg, Fe), drought tolerance (K), defence (Si) or reproduction (Zn) (Couturier *et al.*, 2013; Sardans & Peñuelas, 2015; Fernández-Martínez *et al.*, 2017; Fernández Honaine *et al.*, 2021) and, hence, different concentrations denote differences in plant traits and functions (Kaspari, 2021). Concentrations of trace elements may also indicate hyperaccumulation and/or hypertolerance of heavy metals (e.g., As, Cd, Ni) (Reeves *et al.*, 2018). Consequently, recent literature has shown that analysing additional elements, together with N and P, improves the prediction of ecosystem functioning and the definition of species-specific elementomes compared to using only N and P (Huang *et al.*, 2019; Ågren & Weih, 2020; Hofmann *et al.*, 2021; Fernández-Martínez *et al.*, 2021b).

Moreover, stable isotopes can also provide valuable information regarding plant traits and functions. $\delta^{13}\text{C}$ can be used to differentiate between sources of CO_2 use in freshwater macrophytes (Maberly *et al.*, 2015) and water-use efficiency in terrestrial plants (Ding *et al.*, 2021), while differences in $\delta^{15}\text{N}$ can be used to infer contrasting sources of N use (Qian *et al.*, 2021). Similarly, $\delta^{18}\text{O}$ isotopes have been used to assess the hydrological niche of coexisting plants (Ding *et al.*, 2021). A good estimation of the elementome will thus depend on a trade-off between maximising the information included and reducing the potential noise generated by each additional element. One way to deal with this trade-off, while losing the minimum information as possible, is to perform a dimensionality reduction analysis such as a principal components analysis (Peñuelas *et al.*, 2019; Sardans *et al.*, 2021). The suitable dimensionality of an elementome will thus depend on the biological function under study.

Elemental plasticity: abiotic and biotic factors

For an organism to be and function as a determined organism it has to maintain its elementome within certain thresholds. This homeostatic regulation is evidenced by the larger variability in the concentration of elements amongst species compared to that within individuals of the same species (Sardans *et al.*, 2021) and lies behind the foundation of the *biogeochemical niche*. Plasticity, however, is also an important attribute

of plant elementomes, shifting in response to biotic and abiotic changes within the limits of their biogeochemical niche. Hence, although species elemental concentrations are usually well correlated with environmental gradients (Bai *et al.*, 2019; Fernández-Martínez *et al.*, 2021b) changes in community-level elementomes are expected to be larger due to changes in the community assembly than due to the elementome plasticity of the species.

Altered global biogeochemical cycles are changing the elemental composition of organisms and ecosystems, both directly and indirectly (**Figure 2**). The alteration of those cycles have increased the availability of nutrients for plants, creating nutrient imbalances (Peñuelas *et al.*, 2020b) that could hinder ecosystem functioning (Fernández-Martínez *et al.*, 2020). Increasing atmospheric CO₂ concentrations have been shown to reduce the concentration of N and P in trees (Peñuelas *et al.*, 2020a) potentially constraining the CO₂ fertilisation effect globally (Wang *et al.*, 2020). Grazing, fertilisation and increased atmospheric N deposition are also known to alter plant elementomes (Mao *et al.*, 2018; Du & Gao, 2021; Vallicrosa *et al.*, 2021). These changes in nutrient availability have also been related to biodiversity loss and species replacement, further modifying how ecosystems work (Soons *et al.*, 2017). On top of that, the alteration of the C cycle is increasing global temperatures and precipitation patterns, which can directly alter plant elementomes (Vallicrosa *et al.*, 2021) and ecosystem biodiversity.

On the other hand, elementome differences amongst species increase with their likelihood of coexistence, suggesting that communities are assembled in a way that minimises competition and/or that species tend to differentiate their niches in order to reduce interspecific competition (Peñuelas *et al.*, 2019; Fernández-Martínez *et al.*, 2021b). Compared to monocultures, plants growing in diverse communities change their elemental compositions, to either reduce or increase N and P concentrations depending on the species (Guiz *et al.*, 2016, 2018; Zhu *et al.*, 2020; Wu *et al.*, 2020). The suggested mechanisms behind those elemental shifts (e.g., favouring niche partitioning, reduction of soil nutrients, competition for light forcing physiological changes to increase C-rich structures) indicate that competition is an important driver of elementome plasticity.

III. Elements, diversity and ecosystem functioning

Climate and community-weighted elementome means (**Figure 3a**) have been proven to be very useful to understand ecosystem functioning (Craven *et al.*, 2018; Fernández-Martínez *et al.*, 2020). Similarly, literature shows that biodiversity, and particularly functional diversity, increases productivity and stability of ecosystems under natural and

experimental conditions (Liang *et al.*, 2016; Craven *et al.*, 2018) through *selection* and *complementarity* effects (Cardinale, 2011). The former is based on an increased probability of having species with a strong effect on ecosystem functioning (e.g., very productive) and the latter is based on different species having *contrasting ecological niches*. As mentioned above, elementomes are an excellent proxy for both plant productivity and their ecological niches. However, despite the potential of elementomes to define traits and niches they have never been used to assess ecosystem diversity nor as a proxy of functional diversity – apart from including N and P within a larger set of traits (Craven *et al.*, 2018). I here propose the use of *elementome diversity* as a measure of functional diversity and *elementome distance* as a measure of competition between organisms and temporal changes in plant and ecosystem functioning.

Elementome diversity and distance

Elementome diversity (ED) can be estimated by means of the *elementome dissimilarity index* for a given a community formed by S species for which their relative abundance is p_i and their concentration of E elements is known, similarly to state-of-the-art functional diversity indices (Villéger *et al.*, 2008). ED is then estimated as the sum of all pair-wise elementome Euclidean distances between species (D_{ij}) weighted by the minimum relative abundance of the pair of species ($\min(p_i, p_j)$). Finally, the sum of all elementome distances is divided by the number of elements used (E) so the metric is comparable across metrics calculated with different elementome dimensionality:

$$ED = \frac{\sum_{i=1}^{S-1} \sum_{j=i+1}^S D_{ij} \times \min(p_i, p_j)}{E}$$

ED correlates well with other indices of species and functional diversity and so it is expected to present similar relationships with ecosystem functioning to those reported for these other metrics (**Figure 3**). Depending on the research question, though, ED should be calculated over different compartments of the ecosystem (e.g., autotrophs, decomposers). From a mathematical point of view, ED increases with species diversity and elementome distance between species, as long as species diversity and elementome distance amongst species are both different from 0 (**Figure 3e**). This property ensures that estimates of ED comprise both ecological features: diversity and elementome distance amongst species.

Measures of ED have three main advantages over traditional indices of diversity, such as species, functional or phylogenetic diversity metrics, when investigating how diversity relates to ecosystem functioning: *i*) given that ED is based on elementomes, it comprises multiple functional traits of the organisms, which in practice makes it a functional diversity

index. In a way, ED may include *hidden functional diversity* derived from traits typically overlooked by traditional metrics (e.g., stinging hairs of *Urtica dioica*, rich in Si and useful to avoid herbivores). Additionally, functional diversity indices are expected to relate to ecosystem functioning better than species diversity indices (Díaz & Cabido, 2001). *ii*) The comparison of ED is universal across all ecosystem types and can include all living organisms, because they are all composed of the same elements. This is hardly the case when using functional traits: several tree traits are missing in herbs (e.g., wood density), and differences become even larger when comparing more functionally distant organisms (e.g., fungi, animals and plants). Additionally, measuring some frequently used functional traits (e.g., photosynthesis, respiration) can be more resource consuming (time, equipment) than analysing elementomes (with the limitation of big roots). *iii*) Although two phylogenetically close organisms are expected to be functionally closer, measures of phylogenetic diversity may not properly capture functional diversity under strong cases of convergent evolution whereas ED would reflect those functional differences independently of their ancestry. These advantages highlight the potential of ED to study diversity and ecosystem functioning from a holistic perspective that can integrate a very large array of living organisms.

On the other hand, ED could also be used as a measure of the strength of competition between plants if all species are randomly distributed in space (i.e., the lower ED, the stronger the competition because species occupy the same niche). Otherwise, ED could be multiplied by a coefficient of spatial aggregation (<1 when aggregation occurs) or, ideally, elementome distances could be calculated for neighbouring plants within a determined radius of influence to assess competition amongst individuals. Additionally, elementome distances could be used to monitor shifts in elementomes related to environmental changes (e.g., altered nutrient availability, climate or community composition) at the individual, population or community scales. Increasing elementome distances in plants or communities could be related to changes in plant performance or ecosystem functioning (e.g., increased growth for individual plants or gross primary production for ecosystems), and even changes in the community assemblage as discussed in **section II**. Obtaining long time series of elementomes could thus be used as a tool for monitoring ecosystem functioning and the impacts of global change on Earth's biosphere.

IV. Conclusions

A large body of evidence suggests that the elemental composition of organisms define their ecological niches and how their ecosystems work, and that elements other than C,

N and P should be used in order capture the diversity of traits between them. Changes in plant elementomes due to changes in biotic and abiotic conditions can also help us monitor how global change impacts ecosystems and their functioning. A focus on elementome diversity and distance looks like a promising approach to study ecosystem functioning under global change.

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Data availability

The code supporting the findings of this study is freely available at Figshare: <https://doi.org/10.6084/m9.figshare.14748261.v2>.

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415 **Competing interests**

416 The author declares no competing interests.

Figures

Figure 1. Elemental singularities. Several examples of organisms with very characteristic elemental concentrations for particular elements. Arrows indicate anomalously high or low concentrations of a given element relative to other plants. For marine plankton and *Quercus robur*, numbers indicate their C:N:P atomic ratio. Picture credits: *Salicornia europaea* by FortBienVert, *Urtica dioica* by Peter O'Connor and *Alyssum murale* by Matt Lavin (CC BY-SA 2.0). *Quercus robur* by Gikü (public domain). *Fontinalis antipyretica* by Jordi Corbera.

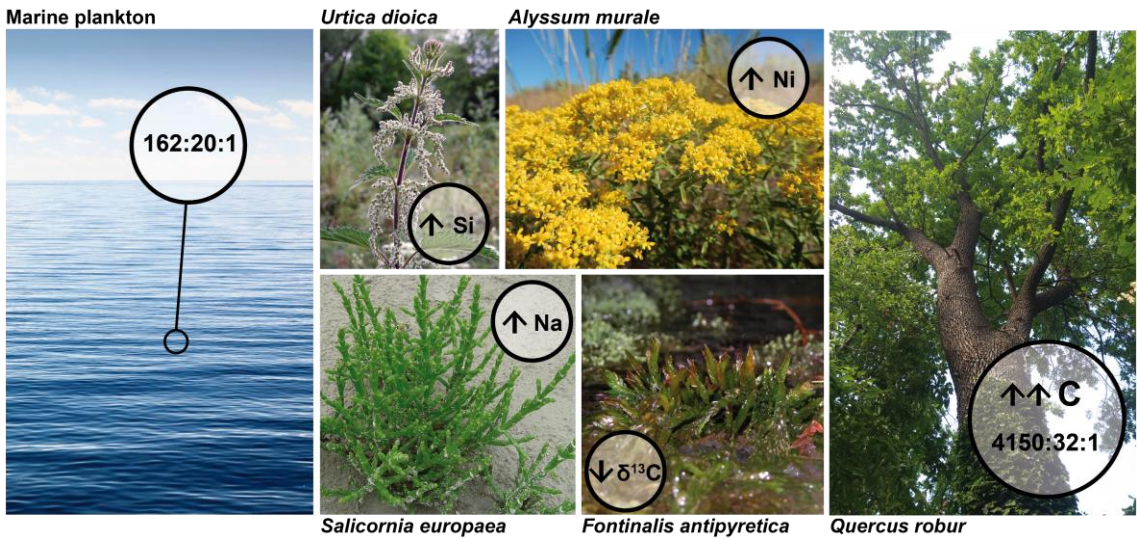


Figure 2. Impacts of altered biogeochemical cycles on plant elementomes. Fossil fuel burning and the use of fertilisers are the main contributing factors to changing global biogeochemical cycles. Altered biogeochemical cycles change plant elementomes directly by altering the environmental availability of nutrients (a) which, in turn, can modify the composition of the community and lead to loss of biodiversity (b) and changes in microclimatic conditions (c). Global warming (c) changes the environmental conditions for plants, leading to physiological changes such as increased sclerophylly, should climate become drier (i.e., in Mediterranean climates). Further changes in community composition and biodiversity loss take place if the species cannot withstand these new environmental conditions (b), hence creating a feedback loop because of altered nutrient uptake rates (a). Additional changes in elemental composition to those caused by (a) and (c) can then occur by altered competitive interactions amongst the new or fewer species present in the community. The mechanisms responsible for those elemental shifts are highlighted in the yellow box (differences in nutrient uptake, community composition, competition and environmental constraints). Further details and references can be found in section *Elemental plasticity: abiotic and biotic factors*. The size of the C, N and P circles indicate an arbitrary concentration of elements. Blue arrows indicate direct effects. Pattern vector created by pch.vector - www.freepik.com.

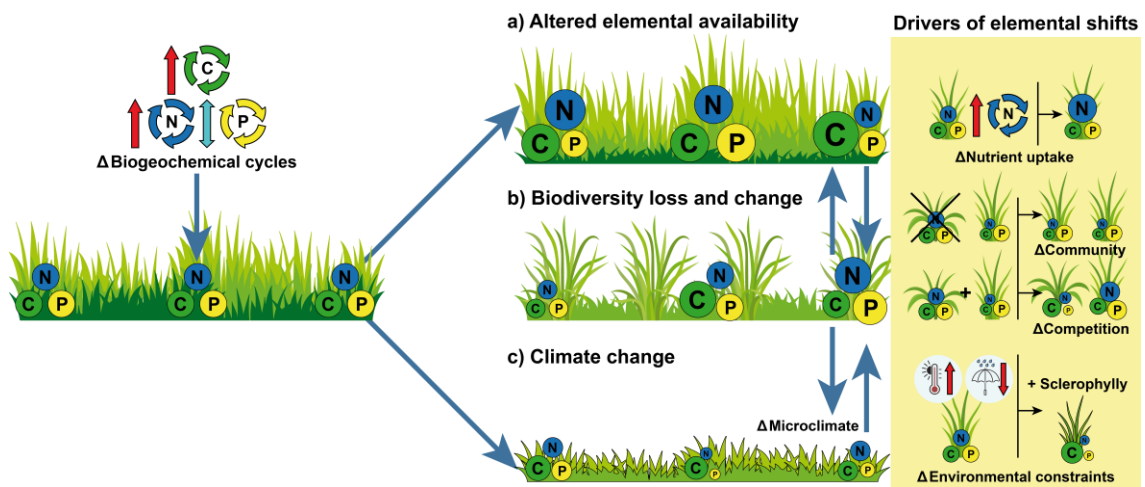
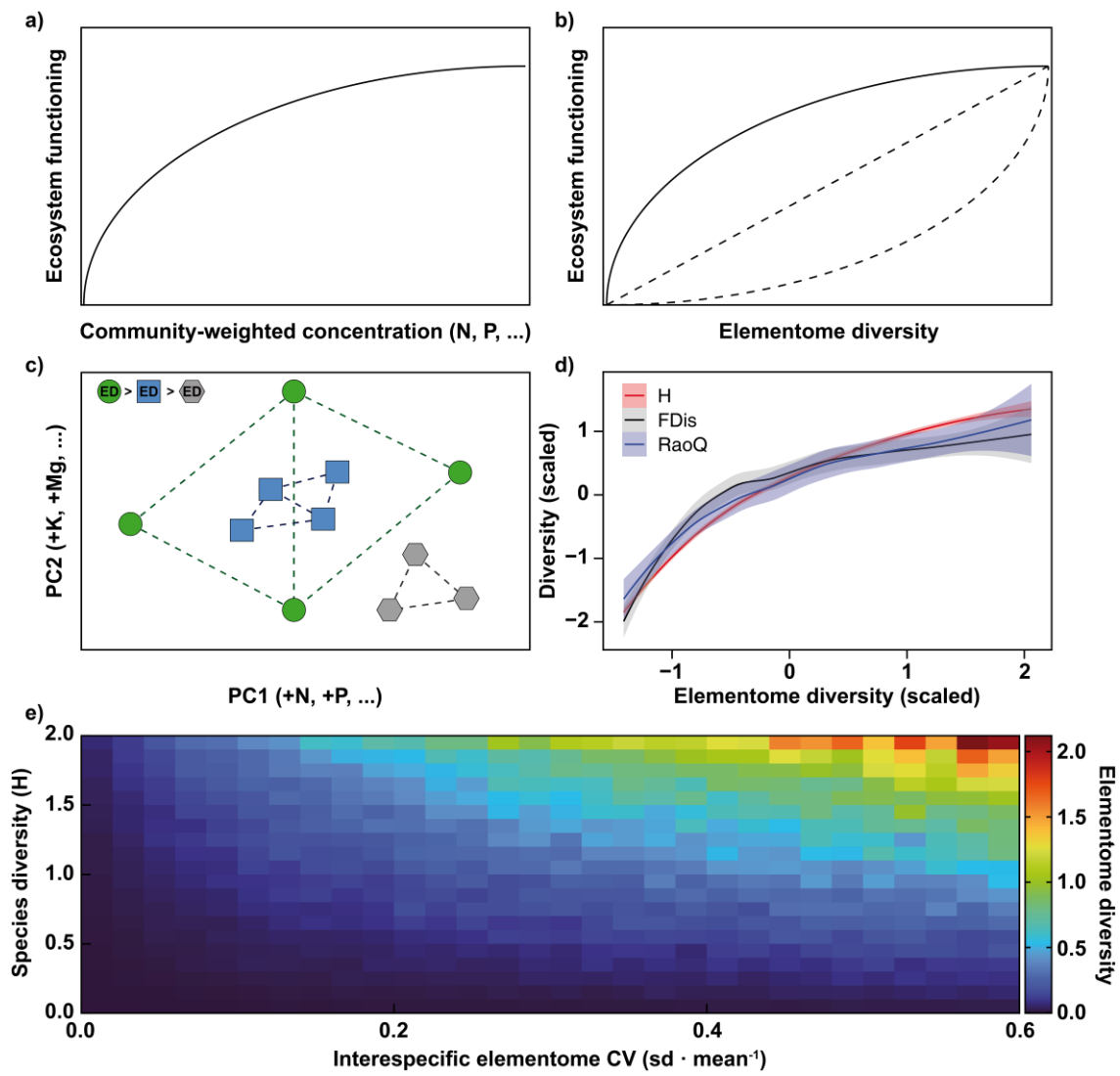


Figure 3. Plant elemental concentration and elementome diversity. The elemental concentration of nutrients generally increases ecosystem functioning (a), following a pattern of *diminishing returns on investment* (i.e., when nutrient concentrations are high, factors other than nutrients limit ecosystem functioning). Elementome diversity is expected to be similarly related to ecosystem functioning (b) as all available niches become progressively occupied, potentially, with smaller and less productive organisms (e.g., epiphytes). Other relationships (dashed lines) could also emerge when comparing different successional stages due to the appearance of plants with large contributions on ecosystem functioning (e.g., trees). Panel c) shows communities containing three and four different species. Despite having the same number of species, the green community has higher elementome diversity than the blue one because of a larger elemental difference amongst its species. The grey community shows the minimum elementome diversity, because of having only three species and them being very similar. Panel d) shows the relationship between elementome diversity and Shannon's diversity (H) and two indices of functional diversity, functional dispersion (FDis) and Rao's Q from a simulation of 100 communities containing a random assemblage of eight species with contrasting elementomes. Panel e) shows how elemental diversity increases as a function of Shannon's H and interspecific variability in elementomes, measured as the coefficient of variation ($sd \cdot mean^{-1}$) in elemental concentrations amongst species. Code to perform simulations in panels d) and e) is available at Figshare: <https://doi.org/10.6084/m9.figshare.14748261.v2>.

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Table 1. Atomic C:N:P stoichiometry of different organisms in contrasting habitats. Examples are meant to be a brief overview of the differences between organisms in relation with their traits and habitats rather than an exhaustive literature review. Values indicate means or median estimates for the group, depending on the centrality measure provided by the reference. Organisms are ordered by C:P ratio.

C:N:P	Organism	Structure	Habitat	Climate/region	Reference
106:16:1	Marine plankton	Whole organism	Ocean	Global	1
110:16:1	Phytoplankton	Whole organism	Diverse	Global	2
145:8:1	Bryophytes	Whole organism	Springs	Mediterranean	3
162:22:1	Marine plankton	Whole organism	Ocean	Global	4
215:23:1	Filamentous green algae	Whole organism	Lake	Antarctica	5
256:27:1	Plants	Leaf	Freshwater	Global	6
435:20:1	Angiosperms	Leaf	Marine	Global	2
500:24:1	Angiosperms	Leaf	Freshwater	Global	2
511:13:1	Grasses, weeds (grazed)	Whole organism	Alpine meadow	Tibetan Plateau	7
591:17:1	Bryophytes	Whole organism	Freshwater	Antarctica	5
660:24:1	Bryophytes	Whole organism	Epiphytic	Subtropical	8
799:27:1	Plants	Leaf	Terrestrial	Global	6
800:49:1	Macroalgae	Whole organism	Ocean	Global	2
878:18:1	Bryophytes	Whole organism	Soil	Subalpine	9
964:29:1	Bryophytes	Whole organism	Soil	Antarctica	5
1334:28:1	Trees	Leaf	Terrestrial	Global	10
1396:20:1	Grasses, weeds	Whole organism	Alpine meadow	Tibetan Plateau	7
1802:32:1	Lichens	Whole organism	Epiphytic	Subtropical	8
2340:26:1	Lichens	Whole organism	Soil	Antarctica	5
3686:25:1	<i>Quercus glauca</i>	Aboveground biomass	Terrestrial	Temperate	11
3989:08:1	<i>Pinus radiata</i>	Aboveground biomass	Terrestrial	Temperate	12
4150:32:1	<i>Quercus robur</i>	Whole organism	Terrestrial	Temperate	13
5507:463:1	Cyanobacterial mats	Whole organism	Freshwater	Antarctica	5
8380:40:1	Rainforest	Whole trees	Terrestrial	Temperate	14

References: 1. Redfield, 1934; 2. Duarte, 1992; 3. Fernández-Martínez *et al.*, 2021; 4. Martiny *et al.*, 2014; 5. Frias *et al.*, 2013; 6. Elser *et al.*, 2000; 7. Du & Gao 2021; 8. Huang *et al.*, 2019; 9. Wang *et al.*, 2019; 10. McGroddy *et al.*, 2004; 11. Baek *et al.*, 2020; 12. Garrett *et al.*, 2021; 13. Balboa-Murias *et al.*, 2006. 14. Perez-Quezada *et al.*, 2021.