



**HAL**  
open science

## The bioelements, the elementome, and the biogeochemical niche

Josep Penuelas, Marcos Fernández-martínez, Philippe Ciais, David Jou, Shilong Piao, Michael Obersteiner, Sara Vicca, Ivan Janssens, Jordi Sardans

► **To cite this version:**

Josep Penuelas, Marcos Fernández-martínez, Philippe Ciais, David Jou, Shilong Piao, et al.. The bioelements, the elementome, and the biogeochemical niche. *Ecology*, 2019, 100 (5), pp.e02652. 10.1002/ecy.2652 . hal-02899791

**HAL Id: hal-02899791**

**<https://hal.science/hal-02899791>**

Submitted on 2 Jul 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



# CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

*Ecology*, 100(5), 2019, e02652  
© 2019 by the Ecological Society of America

## The bioelements, the elementome, and the biogeochemical niche

JOSEP PEÑUELAS,<sup>1,2,8</sup> MARCOS FERNÁNDEZ-MARTÍNEZ,<sup>2,3</sup> PHILIPPE CIAIS,<sup>4</sup> DAVID JOU,<sup>5</sup> SHILONG PIAO,<sup>6</sup>  
MICHAEL OBERSTEINER,<sup>7</sup> SARA VICCA,<sup>3</sup> IVAN A. JANSSENS,<sup>3</sup> AND JORDI SARDANS<sup>1,2</sup>

<sup>1</sup>CSIC, Global Ecology Unit CREAM-CSIC-UAB, Bellaterra 08193 Spain

<sup>2</sup>CREAF, Cerdanyola del Valles 08193 Spain

<sup>3</sup>Research Group Plants and Ecosystems (PLECO), Department of Biology, University of Antwerp, Wilrijk B-2610 Belgium

<sup>4</sup>Laboratoire des Sciences du Climat et de l'Environnement, IPSL, Gif-sur-Yvette 91191 France

<sup>5</sup>Department of Physics, Universitat Autònoma de Barcelona, Bellaterra 08193 Spain

<sup>6</sup>Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing 100871 China

<sup>7</sup>International Institute for Applied Systems Analysis (IIASA), Ecosystems Services and Management, Schlossplatz 1, Laxenburg A-2361 Austria

*Citation:* Peñuelas, J., M. Fernández-Martínez, P. Ciais, D. Jou, S. Piao, M. Obersteiner, S. Vicca, I. A. Janssens, and J. Sardans. 2019. The bioelements, the elementome, and the biogeochemical niche. *Ecology* 100(5):e02652. 10.1002/ecy.2652

**Abstract.** Every living creature on Earth is made of atoms of the various bioelements that are harnessed in the construction of molecules, tissues, organisms, and communities, as we know them. Organisms need these bioelements in specific quantities and proportions to survive and grow. Distinct species have different functions and life strategies, and have therefore developed distinct structures and adopted a certain combination of metabolic and physiological processes. Each species is thus also expected to have different requirements for each bioelement. We therefore propose that a “biogeochemical niche” can be associated with the classical ecological niche of each species. We show from field data examples that a biogeochemical niche is characterized by a particular elementome defined as the content of all (or at least most) bioelements. The differences in elementome among species are a function of taxonomy and phylogenetic distance, sympatry (the bioelemental compositions should differ more among coexisting than among non-coexisting species to avoid competitive pressure), and homeostasis with a continuum between high homeostasis/low plasticity and low homeostasis/high plasticity. This proposed biogeochemical niche hypothesis has the advantage relative to other associated theoretical niche hypotheses that it can be easily characterized by actual quantification of a measurable trait: the elementome of a given organism or a community, being potentially applicable across taxa and habitats. The changes in bioelemental availability can determine genotypic selection and therefore have a feedback on ecosystem function and organization, and, at the end, become another driving factor of the evolution of life and the environment.

**Key words:** *bioelements; biogeochemical niche; ecological niche; ecosystem function and organization; elementome; evolution; phylogenetic distance; plasticity; sympatry.*

### THE ELEMENTS OF LIFE AND THE CONSTRUCTION OF MOLECULES, TISSUES, ORGANISMS, AND COMMUNITIES

All living beings are made of atoms of various bioelements (elements used by living organisms). The most common bioelements are hydrogen (H) 59%, oxygen (O) 24%, carbon (C) 11%, nitrogen (N) 4%, phosphorus (P)

1%, and sulfur (S) 0.1–1% (percentages are of the total number of atoms in organisms; Slade 2006). C, H, and O are the basis of organismic structure, i.e., water and primary structural molecules, whereas N, P, and S enter in the various biomolecules allowing biochemical reactions. C, H, and O from CO<sub>2</sub> and H<sub>2</sub>O are converted into the skeleton of all types of organic molecules by photo- and chemosynthesis. The molecular structures that control life processes (e.g., RUBISCO or chlorophyll), that carry information (e.g., DNA and RNA), and that control the storage and release of energy when and where necessary

Manuscript received 10 October 2018; revised 26 December 2018; accepted 16 January 2019. Corresponding Editor: Diane S. Srivastava.

<sup>8</sup>E-mail: josep.penuelas@uab.cat

(e.g., ATP and NAD) all incorporate N, P, and, in lower amounts, S.

These six bioelements, however, are not the only bioelements that have important roles in organisms (Slade 2006). Other bioelements, normally present in low concentrations such as potassium (K), magnesium (Mg), iron (Fe), calcium (Ca), molybdenum (Mo), manganese (Mn), and zinc (Zn) have functions that are more specific. They are cofactors in catalytic reactions in several biochemical and physiological processes. For example, in plants, K, Mg, Fe, S, Ca, and Zn are involved in photosynthesis, respiration, regulation of ion balance in chloroplasts and vacuoles, transport of sugar into the phloem, secondary metabolism, maintenance of internal cellular osmotic or pH equilibria and balances, and strategies for stomatal control and avoidance of water stress (Knight et al. 1991, Bourgis et al. 1999, Shaul 2002, Tripler et al. 2006, Peñuelas and Sardans 2009, Naples and Fisk 2010, Baribault et al. 2012, Rivas-Ubach et al. 2012, Peñuelas et al. 2013, Sardans and

Peñuelas 2015). All these bioelements thus contribute essentially to organismic functions, albeit to different degrees (Fig. 1).

The concentrations and ratios of C, N and P have been the basis of ecological stoichiometry (Elser et al. 2000a,b, 2001, Sardans et al. 2015, 2016a,b). However, to link bioelemental composition and stoichiometry with ecological traits in all types of organisms and communities will thus require information about bioelemental composition beyond the C:N:P concentrations and ratios (Peñuelas and Sardans 2009). The other bioelements such as S, K, Ca, or Mg are also crucial and can be limiting in some ecosystems (Naples and Fisk 2010, Baribault et al. 2012, Lapeis et al. 2013). These other bioelements have been introduced in ecological stoichiometric studies to link the elemental composition of individuals and species with their ecological traits, such as drought resistance (related to K), light environment (related to Mg), or the levels of N and S deposition (related to K, Ca, Mg, and S; Sardans et al. 2011,

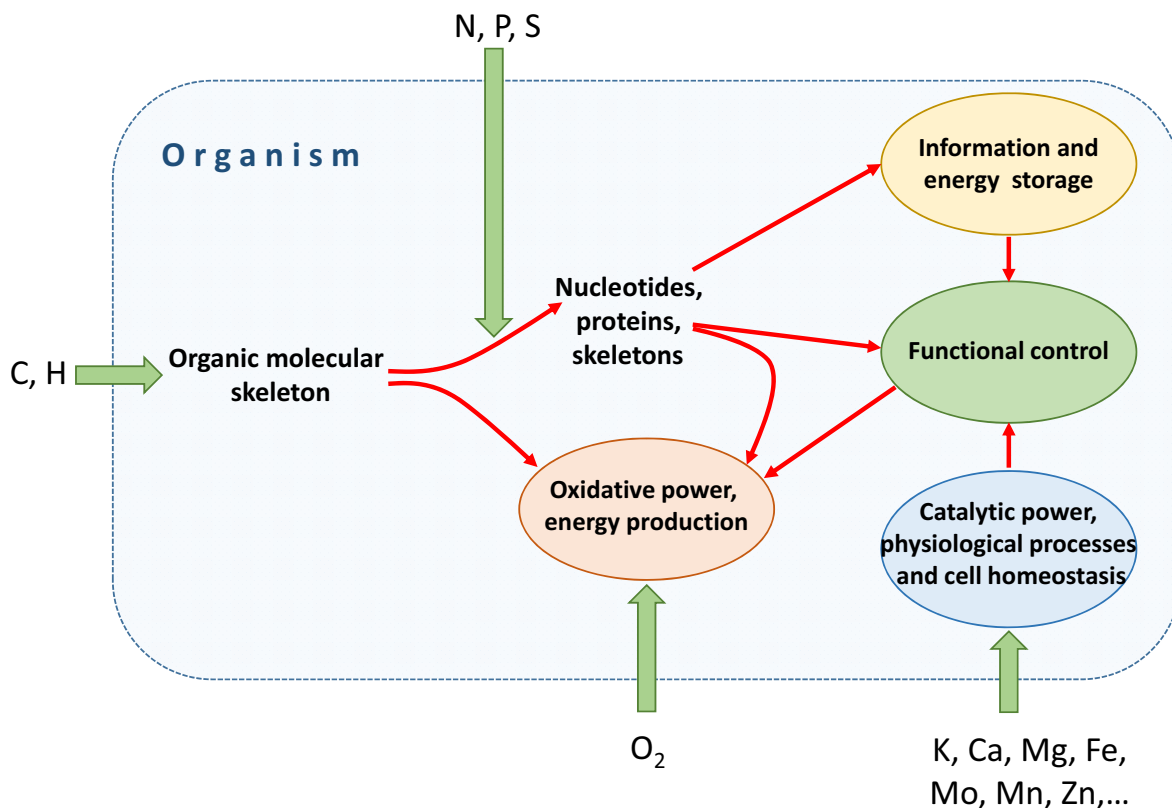


FIG. 1. Schematic of the use of bioelements by organism in different functions. C, H, and O are the basis of organismic structure, whereas N, P, and S enter in the various biomolecules allowing biochemical reactions. The molecules that control life processes (e.g., RUBISCO or chlorophyll), that carry information (e.g., DNA and RNA), and that control the storage and release of energy when and where necessary (e.g., ATP and NAD) all incorporate N, P, and, in lower amounts, S. Other bioelements normally present in low concentrations such as potassium (K), magnesium (Mg), iron (Fe), calcium (Ca), molybdenum (Mo), manganese (Mn), and zinc (Zn) are cofactors in catalytic reactions in several biochemical and physiological processes including, for example, photosynthesis, respiration, or cellular ion balance. The arrows indicate the processes in which each bioelement is involved. Green arrows indicate the main organismal functions to which each bioelement contributes. The red arrows indicate the relationships of the different bio-molecules with basic organismal structures and functions.

2012a, 2015). All of these bioelements should thus be considered in ecological stoichiometric studies.

ELEMENTOME AND BIOGEOCHEMICAL NICHE

Species use these bioelements to different degrees based on their ecological strategy (example for plants in Fig. 2). Classic Hutchinson’s (1957) description of species niche has been largely applied to the main taxa from the point of view of distinct species in a site position in an “n-dimensional hypervolume” formed by the values of determined environmental variables and/or organism traits. For instance, plant species have been classified in a hypervolume formed by three axes, i.e., corresponding to Grime’s three strategies: competitor, stress tolerant, and ruderal (Grime 1977). In animals, the species-specific niche has been determined and located in functions of hypervolumes for *n* axes of different values of energy expenditure (Wilson et al. 2011), distinct diet sources (Bearhop et al. 2004, Araujo et al. 2007), or different elemental composition (González et al. 2017, González et al. 2018). In microbial communities, genotype-niches have also been described in function of the different availabilities of different nutrients (Pereira and Berry 2017) or as a function of the values of diverse functional traits (Lennon et al. 2012) thus describing multivariant spaces with a determined combination of nutrients availability or functional traits where a determined genotype can exist. Any living species should thus tend to optimize its overall function within a determined space within this volume generated by a combination of these

axes describing strategies or biotic and/or abiotic variables while avoiding the overlap with other coexisting species. Following this niche approach, we can hypothesize that distinct species have different functions and life strategies and have therefore developed distinct structures and adopted a certain combination of metabolic and physiological processes. Therefore, each species (of all taxa types) also has different requirements for each bioelement, and should thus tend to have its own elemental composition (Kattge et al. 2011, Yu et al. 2011, Sardans and Peñuelas 2013, 2014, Sardans et al. 2015, Pierce et al. 2016, Bartrons et al. 2018).

We postulate that the more functionally separated two species are, the more different the content of bioelements should be. This led us to propose a “biogeochemical niche” (BN) defined as the multidimensional space defined by the concentrations of bioelements in individuals of a given species (Peñuelas et al. 2008). This BN has been used in the recent years by other authors such as González et al. (2017) who proposed the “multidimensional stoichiometric niche” as the specific position of different taxonomic/trophic groups in the three-dimensional space determined by C, N, and P, and other elements as additional axes in their application of the BN to animals (Gonzalez et al. 2018), as previously proposed for plants by Peñuelas et al. (2008), and for plants and animals together by Bartrons et al. (2018). BN is thus based on the species-specific needs and use of bioelements in different amounts and proportions resulting from the organismic structure and function in the given abiotic and biotic environmental space where the

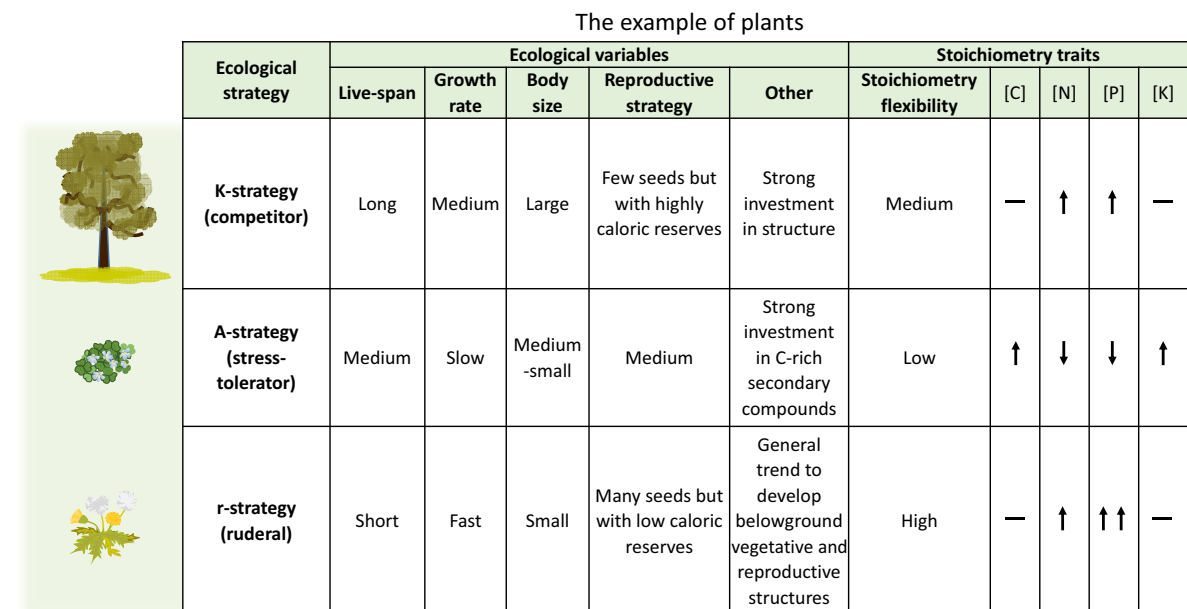


Fig. 2. The example of plants. Hypothesized asymmetric uses of bioelements in evolution, depending on the ecological strategy of each species. Vertical arrows indicate low or high concentration values (double arrows indicate especially high values). Dashes indicate not clear patterns. There is a different use of all these elements depending on the ecological strategy of each species (Grime 1977).

species has evolved (Peñuelas et al. 2008, 2010). Each species should thus have an optimal (at maximum fitness) equilibrium of bioelemental composition, resulting from its functional and structural adaptations, equivalent to the optimum “elemental phenotype” (Jeyasingh et al. 2014). Thus the BN represents the species-specific strategies of growth and resource uptake and the differences in soil-space occupation.

We propose that the processes underlying this species-specific elementome and the BN are based on three basic complementary rules (Fig. 3). First, distinct taxonomic groups exhibit different elementomes, with larger differences as taxonomic distance and evolutionary time increase. Second, at equilibrium, coexisting species tend to have distinct elementomes to minimize competitive pressure. Third, trade-offs between adaptation to being competitive in a stable environment vs. being successful in more fluctuating environments cause homeostasis and plasticity differences between species in a continuum of strategies. The BN distances among species should thus be a function of taxonomic difference, sympatry (coexistence), and homeostasis/plasticity and sympatry (Fig. 3). The BN of taxon *i* is assumed to be the result of its taxonomical evolutionary determination and its capacity to respond to changes in external conditions, which is also partly taxonomically determined. External changes include nutrient availability (including the level of atmospheric CO<sub>2</sub>), changes in growing season duration,

disturbance regimes, and, on longer time scales, changes in soil properties. This capacity to respond to environmental changes is, in turn, a function of taxonomy, sympatry, and homeostasis:

$$\begin{aligned}
 BN_i &= BN \text{ of } taxa_i = \text{Elementome}_{i1-n} \\
 &= (C : N : P : K : S : Mg : Ca : \dots)_{i1-n} \\
 &= BN_{tax_i} + \frac{\partial BN_{tax_i}}{\partial Env} = BN_{tax_i} \\
 &+ f(Tax_i, Symp_i, Hom_i)
 \end{aligned} \tag{1}$$

where

BN<sub>tax<sub>*i*</sub></sub> is the biogeochemical niche explained by taxonomy of taxon *i* (measured in *n* individuals of taxon *i*). An *n*-dimensional hypervolume describes the fundamental BN of a species. The domain of this hypervolume function is restricted to a finite region corresponding to the possible values of bioelemental combinations:

$$\begin{aligned}
 \frac{\partial BN_{tax_i}}{\partial Env} &= \text{Changes in } BN_{tax_i} \text{ of } taxa_i \\
 &\text{explained by environmental changes}
 \end{aligned}$$

tax<sub>*i*</sub> is the taxonomy of taxon *i*, symp<sub>*i*</sub> is the sympatry of taxon *i* with other competing taxa (*j*), and hom<sub>*i*</sub> is the elemental homeostasis-plasticity of the taxon *i*

$$\begin{aligned}
 BN_i &= BN \text{ of } taxa_i = \text{Elementome}_{i1-n} = (C : N : P : K : S : Mg : Ca : \dots)_{i1-n} = BN_{tax_i} + \frac{\partial BN_{tax_i}}{\partial Env} = BN_{tax_i} + f(Tax_i, Symp_i, Hom_i) \\
 BN_j &= BN \text{ tax}_j = \text{Elementome}_{j1-n} = (C : N : P : K : S : Mg : Ca \dots)_j \\
 BN_j &= BN_{tax_j} + \frac{\partial BN_{tax_j}}{\partial Env} = BN_{tax_j} + f(Tax_j, Symp_j, Hom_j) \\
 \Delta BN_{i-j} &= (BN_{tax_i} - BN_{tax_j}) + \frac{\partial BN_{tax_i} - \partial BN_{tax_j}}{\partial Env} = (BN_{tax_i} - BN_{tax_j}) + [f(Tax_i, Symp_i, Hom_i) - f(Tax_j, Symp_j, Hom_j)]
 \end{aligned}$$

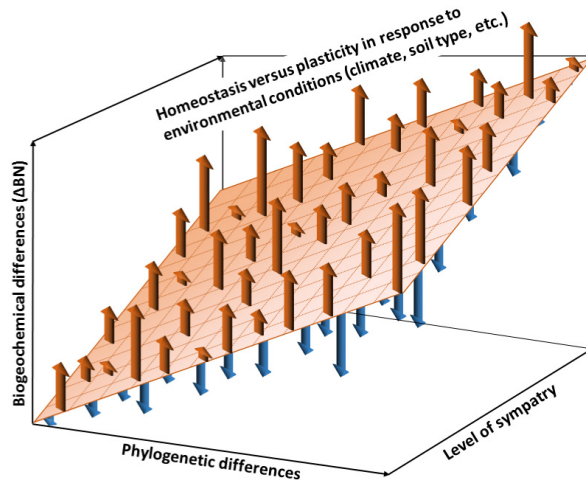


FIG. 3. Theoretical distribution of the biogeochemical differences between species as a function of (1) the taxonomic and phylogenetic distances between them, (2) the level of sympatry (overlap frequency in their corresponding areas of distribution) and (3) the homeostatic or flexible response to current environmental conditions (e.g., climate, soil traits). The surface represents the biogeochemical distance resulting from phylogenetic distance and level of sympatry, and the brown and blue arrows the positive and negative residuals of the biogeochemical niche (BN) distance induced by variable current environmental conditions (e.g., climate, soil traits, neighbors).

$$\text{BN}_j = \text{BN tax}_j = \text{Elementome}_{j1-n} = (\text{C} : \text{N} : \text{P} : \text{K} : \text{S} : \text{Mg} : \text{Ca} \dots)_j$$

$$\text{BN}_j = \text{BNtax}_j + \frac{\partial \text{BNtax}_j}{\partial \text{Env}} = \text{BNtax}_{j1-n} + f(\text{Tax}_j, \text{Symp}_j, \text{Hom}_j) \quad (2)$$

The BN distance between tax  $i$  and  $j$ ,  $\Delta \text{BN}_{i-j}$ , will be

$$\Delta \text{BN}_{i-j} = (\text{BNtax}_i - \text{BNtax}_j) + \frac{\partial \text{BNtax}_i - \partial \text{BNtax}_j}{\partial \text{Env}}$$

$$= (\text{BNtax}_i - \text{BNtax}_j) + [f(\text{Tax}_i, \text{Symp}_i, \text{Hom}_i) - f(\text{Tax}_j, \text{Symp}_j, \text{Hom}_j)] \quad (3)$$

The segregation of the BNs of the dominant species of a holm-oak evergreen Mediterranean forest (Fig. 4a) and their displacement when exposed to drought in a climatic field experiment (Fig. 4b) constitute a consistent confirmation of these two first BN rules. Very similar results for segregation and displacement were found using different calculation approaches, from the additional use of ratios as explanatory variables to the use of discriminant and other multivariate analyses (Appendix S1: Fig. S1). Pairs of species with more overlap in their distributions had greater differences in their BNs as estimated from PCA scores (PCA based on N, P,

K, S, Ca, and Mg concentrations) in a set of the 12 most representative Mediterranean tree species of South Europe (Fig. 4c), confirming the third rule. The BN hypothesis is an extension of the ecological niche concept (Schoener 1989) to the bioelemental components of life. The BN aims to establish the morphological and functional “adaptation” to the abiotic and biotic traits that define the niche of each species-genotype from simple determination of the elemental composition. It is based on the different contribution of each bioelement to the different organismal functions and structures. Its main advantage over other theoretical classical niche concepts is that it can be characterized by the measurable bioelemental composition, the elementome, of the organism, species, community, or even biome (Fig. 5). This BN measurement is not biased by the most abundant bioelements since the analysis is conducted for a multivariate space defined by the standardized elemental concentrations (Figs. 4 and 6).

The quantitative BN framework can then be used to improve projections of how species will respond to environmental changes, provided elementome homeostasis/plasticity (Hom) on a given time horizon is known. This Hom can be defined, for example, as the coefficient of variance of the scores for the different individuals of a species in the PCA. It results from both intraspecific variation and phenotypic individual responses. These two responses can be differentiated when the hypervolume occupied by the individuals of one species is compared with the hypervolume generated after changing

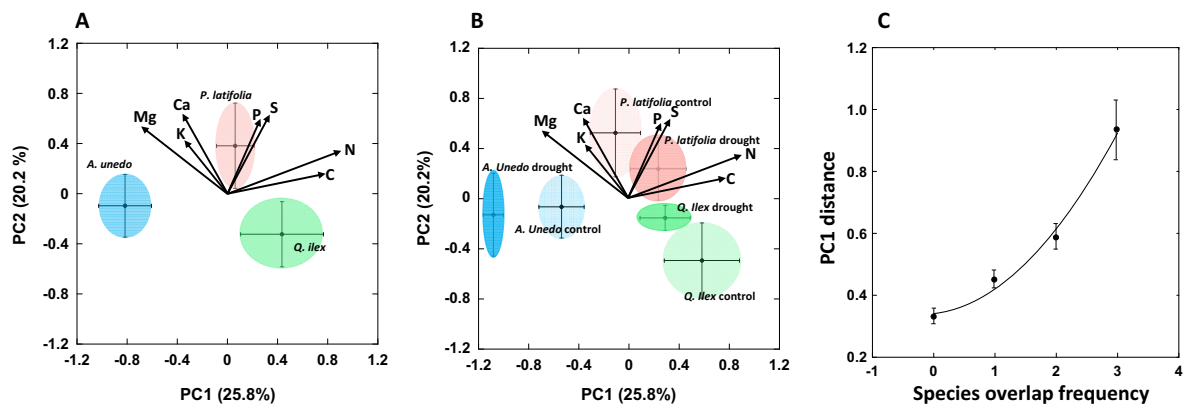


FIG. 4. (A) Biogeochemical niche segregation among coexisting plant species. We analyzed the foliar elementomes of the three dominant trees (*Quercus ilex*, *Arbutus unedo*, and *Phillyrea latifolia*) in a field experiment of climatic manipulation in an evergreen Mediterranean forest in the Prades Mountains (Catalonia). We plotted the plant scores for the first two principal components of the principal component analysis (PCA) conducted with foliar N, P, K, S, Ca, Mg concentrations as variables. (B) Shifts in biogeochemical niche in a drought experiment. The mean  $\pm$  confidence intervals (95%), represented by the ellipses of the species  $\times$  climate interaction groups are depicted in the plot thus comparing control plants to those submitted to a decrease of 20% of water availability during 6 yr in field conditions. The other PCAs (from PC3 to PC7) and the corresponding other axes are now shown in the Appendix S1: Table S1. (C) Score distances for PC1 of the PCA of the foliar stoichiometry (foliar N, P, K, S, Ca, and Mg concentrations and their ratios) in a set of the 12 most representative Mediterranean species of South Europe as a function of the frequency of pairwise species overlap (coincidence in the same community): six broadleaf species (*Quercus ilex*, *Q. faginea*, *Q. pyrenaica*, *Q. suber*, *Castanea sativa*, and *Eucalyptus globulus*) and six needleleaf species (*Pinus halepensis*, *P. pinaster*, *P. nigra*, *P. pinea*, *Juniperus oxycedrus*, and *J. thurifera*). Numbers represent 0, no overlap; 1, occasional overlap; 2, moderate overlap; 3, frequent overlap. Based on Rivas-Martínez et al. (2001), De Bolos and Vigo (2001), CREA, Catalonia cover map, (2013) and Folch et al. (1984).

the environmental conditions, for instance in experiments in field conditions where environmental conditions are changed.

BN aims to refocus the use of the hypervolume in ecological niche studies. An  $n$ -dimensional hypervolume was originally proposed by Hutchinson (1957) and defined as a subset of the space, i.e., an  $n$ -dimensional geometrical shape, to describe the fundamental niche of a species. Hutchinson suggested that the axes correspond to requirements of the species (e.g., light, temperature, food size) and that the boundaries of the shape indicate the conditions that permit the growth and reproduction of the individuals of a species. This description of the species niche has been widely used and discussed (Chase and Leibold 2003, Begon et al. 2006, Colwell and Rangel 2009, Holt 2009, Peterson 2011). There is now a growing set of statistical methods to operate this hypothesis of species niche with data (Blonder 2017). BN should be a tool to detect the niche shifts at short-, medium- and long-term scales in response to all type of environmental changes (drought, species invasion, pests, new biotic relationships, etc.). The mathematical description of each specific BN position in a multi-space as a function of the concentrations of several bioelements can be done by using essential multivariate statistical analyses such as principal components analyses (PCA) or functional/general discriminant analysis (F/GDA; Sardans et al. 2015, Urbina et al. 2017), or other analyses such as kernel density estimation, support vector machine, Bayesian ellipse, etc. (Blonder 2017). BN distances and the level of overlap/separation among different groups can be computed with the score means (centroids) of the main axes (in the PCAs; Fig. 4, Appendix S1: Fig. S1) or with squared Mahalanobis distances (in the discriminant analyses; Appendix S1: Fig. S2). These metrics provide numerical evidences of the “distances” between the BN of different species and of the BN displacement (if any) when comparing the BN of different populations of the same species along space or time. Correlations between matrices provide a way of comparing the distances between hypervolumes, for instance the correlation matrix of the genome differences or of the differences in some ecological or eco-physiological variables in a particular set of species with the corresponding correlation matrix of the BN distances of the same set of species. Statistical tests such as Mantel tests (Mantel 1967) can be used with this aim. All these mathematical tools to estimate the BN allow all levels of comparisons, from species (Sardans et al. 2015) to different taxa and trophic groups (Bartrons et al. 2018), also including the comparison of different populations of the same species growing under distinct environmental conditions (Urbina et al. 2015, 2017).

These studies have shown the facility and consistency in the use of different types of multivariate analyses to detect the BN in spatial and temporal gradients/scales.

Moreover, the different levels of homeostasis/plasticity of different studied groups can be calculated by the area/volume in that the individuals of each group are spread in the multidimensional space generated. The temporal shifts of the BN of a species or populations of one species can also be calculated and thus their evolution can be followed. BN also allows the description and quantification of niche appearance (i.e., when new species colonize the ecosystem), expansion, contraction, and extinction. Therefore, BN constitutes a quantifiable tool to detect, quantify and thus better comprehend the mechanisms and processes underlying community evolution and species turnover (Fig. 7). Niche construction vs niche expansion or niche contraction vs niche extinction are apparently difficult to differentiate because of their similar outcomes, and niche contraction (and extinction) could be the result of environmental filtering, whereas niche expansion could be due to addition of species to a community. Phenomena within the niche theory such as niche convergence (Pianka et al. 2017) can be followed by monitoring the species BN hyper-dimension along spatial and temporal gradients and focusing on the changes in the level of overlap/distance in their BN.

#### EVIDENCE FROM OBSERVATIONAL DATA

##### *Taxonomy*

The BN hypothesis is supported by strong evidence in recent studies. Observational data (Sardans and Peñuelas 2014, Bartrons et al. 2018) provide evidence that plant and animal species have their own elementome, their own BN. For example, different groups of species in distinct climatic biomes have different foliar bioelemental compositions and stoichiometries (Sardans and Peñuelas 2014, Sardans et al. 2015, 2016a,b, Sardans et al. 2017). Foliar bioelemental composition of forest tree species, for example, has been positively correlated with phylogenetic distance between taxa at different geographic extents, from local to continental (Sardans et al. 2014, 2015, 2016a,b). Bioelemental composition and stoichiometry thus tend to differ more between phylogenetically distant than between phylogenetically close tree species (Sardans and Peñuelas 2014, Sardans et al. 2014, 2015, 2016a,b). These positive correlations between elemental composition differences and phylogenetic distances have been also observed in animals (Gonzalez et al. 2018) in a further demonstration of the first process underlying the BN hypothesis. The stoichiometry of an individual under a given climatic and edaphic condition is determined in part by the uptake and the efficiency with which the individual uses each bioelement, all of which depend on the trade-offs among the various individual functions that maximize individual fitness under that specific climatic situation. Each species and taxon have its own space in the two-dimensional plot formed by the first two components of the PCA of individual composition (N, P, S, K, Ca, and Mg

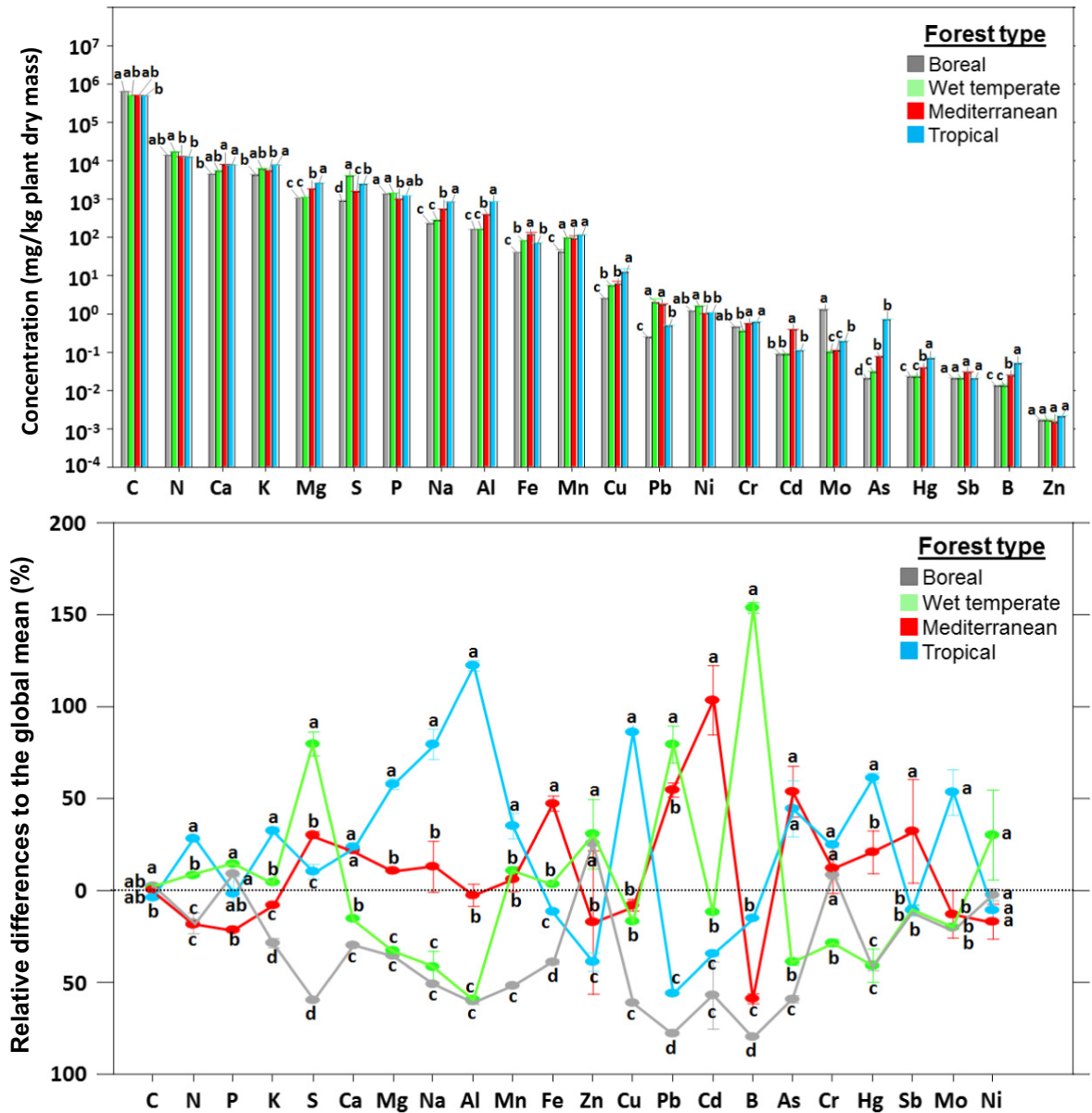


FIG. 5. Elementome, full spectrum of bioelemental content, of boreal, wet temperate, Mediterranean and tropical forests. (A) Elementomes calculated from web of science data incorporated to our GEU-CREAF data set (boreal forest, 473 sites and 1,890 trees; wet temperate forests, 2,882 sites and 12,665 trees; Mediterranean forests, 2,001 sites and 2,901 trees; tropical wet forest, 1,100 sites and 1,821 trees). The values in panel B show the difference of each forest type relative to the global mean ( $\pm$ SE). We have used data from the main available databases (e.g., TRY and ICP forest) and from an exhaustive search for woody plants from non-manipulated areas in WEB of Science. Different letters indicate significant differences ( $P < 0.05$ ).

concentrations and their ratios; see example in Fig. 4a and see Appendix S1: Table S1 for the scores of additional PCs).

*Sympatry*

Larger differences in the stoichiometry of foliar composition among sympatric than allopatric species have recently been reported both in plant communities

(Sardans et al. 2015, 2016a,b) and in animal communities (Gonzalez et al. 2018) as implied in the third process involved in the BN. The overlapping frequency of all pairwise comparisons among many tree species is correlated with the elementome distances of the corresponding tree pairs (Fig. 4c; Sardans et al. 2015), thus supporting this third process. Different grass and shrub species growing under different climatic conditions in communities with distinct species compositions maintain



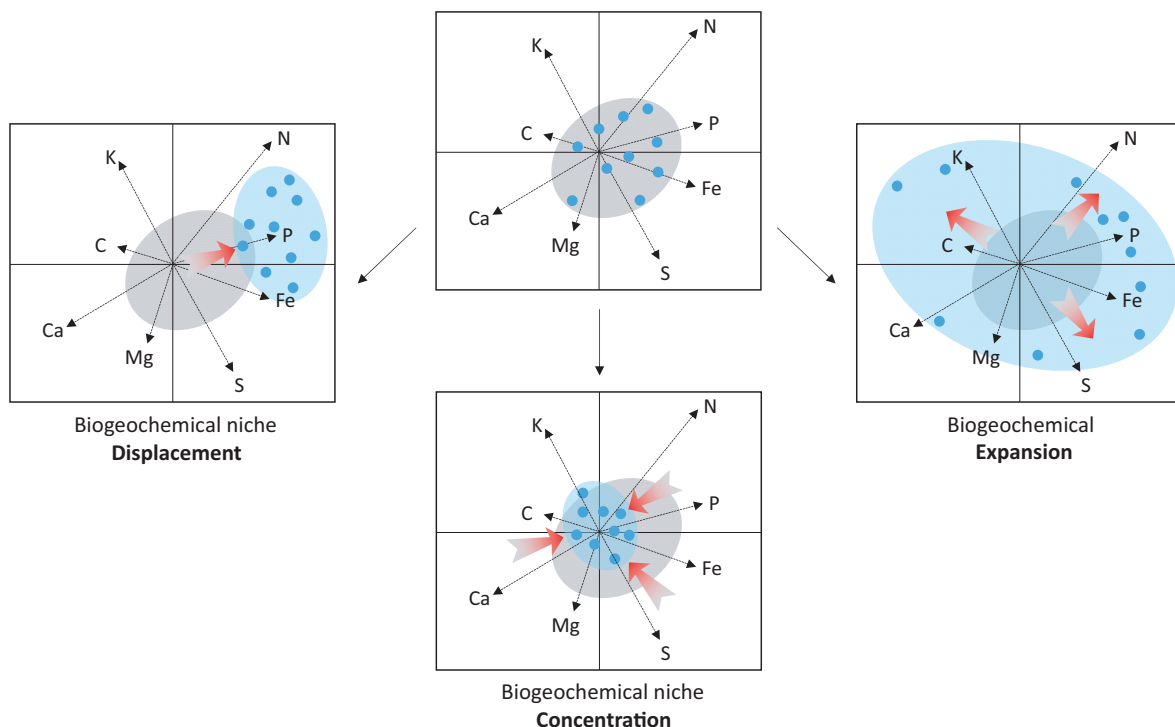


FIG. 6. Three possible biogeochemical niche responses to short-term changes in the environmental conditions: contraction, expansion, or displacement. Blue dots represent individuals of a species, gray and blue ellipses represent the initial and final BN space.

distinct species-specific foliar compositions, although there may be displacement, expansion or concentration of the biogeochemical space occupied (Fig. 6) depending on the coexisting species (Urbina et al. 2015, 2017). The species bioelemental composition changes in parallel with the shifts of environmental conditions, in accordance with the new optimal functions that require new proportional use of different bioelements. Contraction, expansion, and displacement in the short term would thus be complemented by construction (allopatric speciation), extinction, segregation, and equalization in the long-term both for estenoic (narrow range of ecological and environmental conditions) and euroic (wide range) niches (Fig. 7).

In-depth investigation of these processes constitutes a challenge for ecologists. Some studies have already demonstrated different biogeochemical niche space (euroic-estenoic) among different coexisting species-genotypes in plants (Sardans et al. 2015, Urbina et al. 2015, 2017), animals (González et al. 2017, 2018, Bartrons et al. 2018) and microbes (Pereira and Berry 2017). Other studies have observed how the same species displaced their biogeochemical niche depending on the intraspecific and intraspecific competition (Urbina et al. 2015, 2017, Sardans et al. 2016a,b). However, observational field studies along successional stages and field manipulation studies of biotic (introducing new species, changes in density, and so on), and abiotic (changing

climate conditions or nutrient availability) factors in conjunction with similar studies in greenhouse, microcosm, and mesocosm conditions would be necessary to further test the consistency of the new holistic view of ecosystem processes provided by the BN.

#### *Homeostasis/plasticity*

Changes in environmental supply (for example soil or water bioelemental composition) can affect the bioelemental composition of organisms, as observed in microbes (Frenken et al. 2017) and plants (He et al. 2016, Salvagiotti et al. 2017). A trade-off between adaptations to be competitive in stable environments vs. being successful in less stable environments should underpin the differences in the continuum of homeostasis-plasticity strategies in bioelemental composition and stoichiometry among individuals, species and communities (Figs. 3, 4b). Higher N and P concentrations and lower N:P ratios coincide with higher stoichiometric plasticity in opportunistic (r-strategy) than in competitor (K-strategy) plant species (Yu et al. 2011). Climate can also account for some of the variability in the bioelemental composition of plant tissues at intra- and interspecific levels (Sardans et al. 2015, Sardans et al. 2016, Zhang et al. 2012) indirectly through climate controls on bioelemental availability and directly as a forcing of traits linked to the elementome. Environments with

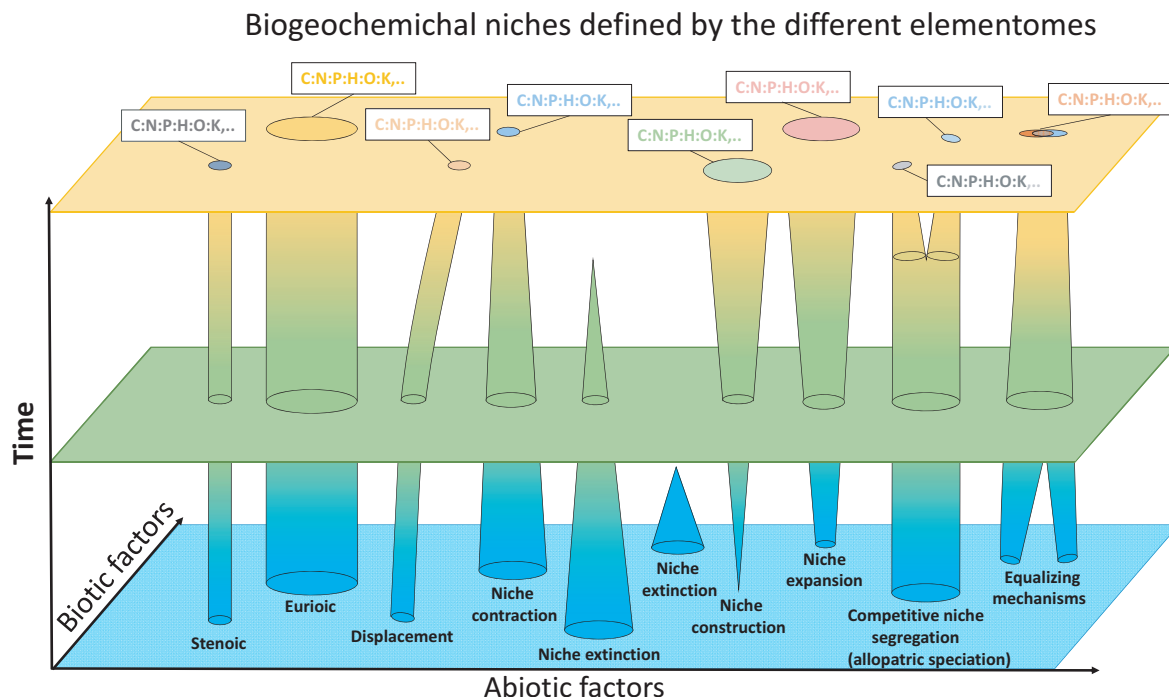


Fig. 7. Possible responses of species biogeochemical niches to long-term changes in the abiotic and biotic environmental conditions (possible evolutionary changes in the elementome of a species). We hypothesize that each species has an optimal function related with its niche traits and thus an optimal content of bioelements. Species have an optimal function related with its niche traits and thus an optimal content of bioelements. The species content of bioelements changes in parallel with the species niche shifts according with the new optimal functions for the new environmental conditions. Contraction, expansion, and displacement are here complemented by construction (allopatric speciation), extinction, segregation, and equalization at the long-term both for estenoic (narrow range of ecological and environmental conditions) and eurioic (wide range) niches. The communities resulting of interactions with changing abiotic and biotic conditions are even more capable to adjust their stoichiometry than single species to new nutrient supply and stoichiometrical conditions. Each particular niche constitutes a singular functional and physical position in the ecosystem that can vary with time in response to changes in abiotic variables (climate, perturbations such as volcanic eruptions, etc.) and to changes in the impacts and feed-backs of the other organisms living in it (biotic factors). In this context, each niche should determine a specific and particular content of different bioelements in each moment. This should also determine a singular elementome accompanying the niche characteristics of each genotype and species at both micro- and macro-evolutionary time-scales.

fluctuating nutrient availabilities relative to the species' lifetime would have to favor organisms with greater stoichiometric plasticity. Stoichiometric plasticity tends to decrease in response to fertilization as environmental nutrient richness increases, in both terrestrial and aquatic systems (Sistla et al. 2015), thus suggesting a different position in the homeostatic-plasticity continuum between species in nutrient-rich vs. nutrient-poor environments. The BN hypothesis allows to detect the plasticity at two levels: at the individual level (phenotypic plasticity) by showing how its individual elemental composition can vary when environmental conditions shift, and at the intraspecific level as a result of intraspecific variability (individual genotypic differences, different ontogenic stage, sex differences, and so on) in elemental composition of a set of individuals of the same species living under the same environmental conditions. This dual source of variability due to natural intra-population variability and to individual capacity to shift BN in response to environmental changes can be at least

partially detected experimentally with multivariate analyses working with populations of the same genotype growing in different environmental conditions across space or time.

#### *Evolutionary change*

Species have stoichiometric strategies to adapt to heterogeneous environments (Sun et al. 2017) and are able to adapt their elemental compositions to those of the media after several generations (Turner et al. 2017). The stoichiometry of phytoplankton appears to reflect oceanic stoichiometry over geological timescales, providing even stronger support to this link between organisms' composition and media nutrients availability (Quigg et al. 2003, Reinhard et al. 2017). Other studies of terrestrial ecosystems found that microbial community N:P ratios were correlated with plant-community and soil N:P ratios (Kerckhoff and Enquist 2006, Cleveland and Liptzin 2007). Close relationships between

microbial and soil C:N ratios across a soil C:N gradient have been also observed, e.g., in Scandinavian boreal forests (Högberg et al. 2006). Evidence suggests that variation in the environmental supply of P affects the expression of highly conserved genes (e.g., those of the phosphate-transporter system) and that the acquisition, assimilation, and allocation of P is genetically variable (Jeyasingh and Weider 2007). Transcriptomic studies of algae (Grossman 2000), microbes (Baek and Lee 2007), terrestrial plants (Morcuende et al. 2007), and more recently herbivores (Jeyasingh et al. 2011) have also reported that the availability of P influences genetic expression. Such effects of the supply of P should impinge on fitness and drive evolutionary change. Jeyasingh et al. (2009) observed that genetic variation in phosphoglucose isomerase (Pg) indicated that Pg heterozygotes of *Daphnia pulicaria* outcompeted Pg homozygotes under conditions of low C:P ratios, whereas the opposite was observed under conditions of high C:P ratios.

Availability and stoichiometry of bioelements can determine transcriptional expression and metabolomic structure (Rivas-Ubach et al. 2012) and phenotypic selection (Chowdhury et al. 2015), and can affect genomes and thereby become evolutionary drivers for organisms and ecosystems on the longest timescales (Acquisti et al. 2009). For example, the mechanisms controlling P acquisition are genetically variable, and the expression of the genes involved is strongly affected by its environmental supply (Grossman 2000, Jeyasingh and Weider 2007, Jeyasingh et al. 2011, 2014). Selection in environments with very low N availability can even favor new genes richer in N-poor nucleotides (Acquisti et al. 2009). Evolution could also be controlled by directly affecting the quality of matter, e.g., different N:P ratios available to genomes for the optimal allocation of N and P to DNA/RNA for maximizing fitness (Sardans et al. 2012b).

#### *BN of communities*

Communities should be more capable to adjust their stoichiometry to additional nutrient inputs and varying stoichiometrical conditions than single species (Danger et al. 2008). A simple and comprehensive example, only considering N and P concentrations and stoichiometry, can be observed when P is added to a freshwater community. In such a case, a shift in community composition typically occurs in favor of N-fixing organisms with a posterior cascade of composition changes towards a new equilibrium in community composition (Davidson and Howarth 2007). Environmental changes (anthropogenic or natural) such as perturbations or shifts in climate, N deposition, species invasion, or the increase in atmospheric CO<sub>2</sub> can probably generate changes in the availability of various nutrients. Species of the target community can then adapt, depending on their phenotypic flexibility. For example, species with a BN better

adapted to new environmental conditions can be favored under large long-term loadings of N by N deposition, but species less well adapted can disappear. Species can also turnover, when possible, with the entrance of new species with traits better adapted to life in the newly generated niches (with different optimal elemental compositions). This sequence of events has been observed in several field studies where shifts in the elemental composition of the media (water or soil) due to changing conditions (anthropogenic or natural) have been translated into changes in the species composition of species of the community (Sterner and Elser 2002). The species with more favorable elemental compositions gain then importance and/or there is species turnover (Novotny et al. 2007, Yu et al. 2011, Poxleitner et al. 2016, Du 2017). Changes in N:P have been related to substantial changes in species composition of plant communities (Peñuelas et al. 2013) and changes in P loads to adjusted C:P ratios in zooplankton communities (Teurlinx et al., 2017).

#### FEEDBACKS ON ENVIRONMENT

The relationships between evolution and the bioelemental composition of ecosystems are bidirectional, because nutrient supply can affect evolutionary processes, while the changes imposed by evolutionary processes can also affect nutrient supply (Durston and El-Sabaawi 2017). As a result, ocean and soil stoichiometries may have been also partly controlled by organisms over long time scales (Tyrrell 1999, Lenton and Klausmeier 2007, Hatton et al. 2015, Zederer et al. 2017).

The strongest support of Redfield ratio comes from the fact that the N:P ratio in the open sea areas of all major oceans is remarkably similar to the N:P ratio of plankton (16:1). This is due to the residence time of N and P in the ocean (104 years) relative to the ocean's circulation time (103 years; Falkowski and Davis 2004). However, in addition to the geochemical causes, biological processes are also underlying Redfield ratios. N<sub>2</sub> fixation can play an important role in ocean N:P ratio homeostasis (Tyrrell 1999, Lenton and Watson 2000, Ganeshram et al. 2002, Kenesi et al. 2009). When ocean N:P ratios fall too low, nitrogen fixation increases by augmenting the biomass of N<sub>2</sub>-fixers and when these N<sub>2</sub>-fixers decompose or are eaten, their N rich organic matter turns to dissolved ammonium and nitrate in the water increasing water N:P ratios. Conversely, when the ratio rises too high, N<sub>2</sub> fixation inputs decrease by P limitation of N<sub>2</sub>-fixation, thus restoring lower water N:P ratio. This process would confer to P primary control of ocean production (Tyrrell 1999, Lenton and Klausmeier 2007).

Soil elemental composition is also controlled by the species of plants (Zederer et al. 2017), the soil microbiota (Hartman et al. 2017), and the interactions between plants and soil fungal communities. For example, *Quercus* species control nutrient dynamics by

determining the composition and activity of the forest floor fungal community (Chávez-Vergara et al. 2016) and the litter type (Hatton et al. 2015). Conifers acidifying soil to reduce soil nutrient availabilities (base cations and P) to outcompete species with a different BN provide another consistent example.

We should thus expect a constant feedback between organisms and their environment. Understanding the processes underlying species shifts in bioelemental composition and their genetic basis will help us understand the responses of organisms to environmental changes (Yamamichi et al. 2015, Leal et al. 2017) and in turn the effects of organisms on ecosystem functioning and services (Frisch et al. 2014, Leal et al. 2017). We are currently still moving towards understanding and identifying the feedbacks between species evolution and shifts in the bioelemental composition of ecosystems and how these feedbacks interact and determine ecosystem and evolutionary processes. Available data seem to indicate that the long-term availability and use of bioelements can determine individual selection and therefore ecosystem function and organization and evolution of life.

#### THE BIOGEOCHEMICAL NICHE HYPOTHESIS AND RELATED APPROACHES

Functional traits such as leaf mass area, seed size or plant height have been also used to build hypervolumes to identify species-specific niche (Violle and Jiang 2009, Lamanna et al. 2014, Violle et al. 2014). However, taxonomical groups (e.g., animals, plants, fungi) have different functional traits, preventing the use of these approaches to different taxonomy clades. Instead, all the organisms, independently of their taxonomical groups, are constituted by the same basic bio-elements, thus providing a general and easy to measure variable, the elementome, with which to establish the species-specific niche in plants (Sardans et al. 2015), in animals (González et al. 2017), and in sets of plants and animals analyzed altogether (Bartrons et al. 2018). The use of organismal elemental stoichiometry has been proven to be related to the species functional traits in aquatic and terrestrial ecosystems (Sardans et al. 2012c, Peñuelas et al. 2013, Meunier et al. 2017). This also allows us to establish relationships between observed shifts in ecosystem N:P medium (water or soil) with the shift in species dominance or community and/or in trophic web composition and structure.

We first defined the BN in 2008 for plant communities (Peñuelas et al. 2008) and we have since then developed it in several papers (Peñuelas et al. 2008, Sardans and Peñuelas 2014, Frisch et al. 2014, Sardans et al. 2015, Sardans et al. 2016, Urbina et al. 2017). Other groups have also used this approach (De and Bhattacharyya 2009, Menge and Hedin 2009, Chimphango et al. 2015, Zamora et al. 2017), obtaining results that have provided solid experimental consistency to BN hypothesis. The BN that we define as species elemental composition is wide in scope and simple in determination, and reflects

the structure and function of each species-genotype resulting from its unique evolutionary history (Sardans et al. 2008a,b,c 2015, Urbina et al. 2017).

BN aimed to progress beyond the classical ecological stoichiometric studies (Elser et al. 2000a,b, 2009, 2010, Sterner and Elser 2002, Elser and Kyle 2009, Rivas-Ubach et al. 2012, Sardans et al. 2012b). These ecological stoichiometric studies have linked several important ecosystem processes with ecosystem and organismal C:N:P ratios. Several organismal functions and responses to environmental shifts, though, cannot be explained only by the changes in these three main bioelements (Sardans et al. 2012b,c). As stated above, other bioelements (such as K, S, Ca, Mg, and Fe) are needed in ecological stoichiometric studies to provide more complete and global information correlating shifts in organismal elemental composition with changes in organismal morphology and function in response to environmental conditions (Peñuelas et al. 2008, Peñuelas and Sardans 2009, Sardans and Peñuelas 2014, Sardans et al. 2015). The BN hypothesis is thus based on the entire elemental composition or at least on the composition of as many elements as possible. The BN hypothesis has afterwards also been used to refer to the concentrations and availabilities of nutrients in soil or water that favor or determine the corresponding spatial occupation by a species or taxon (De and Bhattacharyya 2009, Menge and Hedin 2009, Chimphango et al. 2015, Zamora et al. 2017).

A similar hypothesis of a “multidimensional stoichiometric niche” was recently introduced by Gonzalez et al. (2018). These authors defined a “multidimensional stoichiometric niche” for taxonomic/trophic groups as their position in the three-dimensional space determined by C, N, and P following Peñuelas et al. (2008). González et al. (2017) also interestingly opened the possibility to incorporate more elements, and also element fluxes and transformation rates as additional axes. In their studies, Gonzalez et al. (2018) proved the suitability of this approach for animals. This “multidimensional stoichiometric niche” also tried to incorporate rates of nutrient cycling, but these are much more difficult to quantify than elemental concentrations and ratios. Thus, according with the observations in plants, animals, microbes, and also in combination of different taxa altogether (animals and plants; Peñuelas et al. 2008, Sardans et al. 2015, González et al. 2017, Bartrons et al. 2018), the BN multidimensional space proposed here should allow the establishment and quantification of the links between the species BN distances and their taxonomic/phylogenetic distances and between homeostatic capacities and sympatries, and thus to provide information on species/taxa evolutionary processes. The BN thus also aims to refocus the use of the hypervolume in ecological and evolutionary niche studies as discussed above in the section of “Elementome and Biogeochemical Niche”.

Another similar approach to BN, ionomics, i.e., the profiles of mineral elements in plants, has been proposed mostly focused on the genetics of plant mineral nutrition. Ionomics analyzes the elemental composition of

organisms in relation to soil concentrations of nutrients and trace elements and also plant functional traits (Salt et al. 2008, Buescher et al. 2010, Baxter et al. 2012, Huang and Salt 2016). Ionomics is mostly used to study the content of bioelements with electrical charge, mostly absorbed from soils, and mostly within a context of the impact on plant health, food quality and/or identification of hyper-accumulation species. It comes from the confluence of metabolomics and plant nutrition (Salt et al. 2008) that, with the incorporation of modern analytical platforms such as ICP techniques, allows us to determine most elements altogether. The fusion of this information with bioinformatics and genetic tools, such as genomic sequencing, allows the identification of the genes that control uptake, storage, and use of soil nutrients and trace elements in plants (Baxter et al. 2012, Lowry et al. 2012). This further allows us to analyze the effects of genes and environment on plant nutrition (Neugebauer et al. 2008, Buescher et al. 2010, Lowry et al. 2012) and plant physiological status (Baxter et al. 2008). BN instead considers all, or as many as possible, bioelements, i.e., also including those such as C or N that are initially from atmospheric, not ionic, forms (e.g., N comes mainly from atmospheric N<sub>2</sub>; nitrates are rare in bedrock). BN focuses on organisms and on the total elemental composition and stoichiometry as a proxy of their optimal function and morphology, whereas ionomics focuses on the composition of the medium (soil) to describe different ionic niches in the abiotic dimension of an ecosystem. Ionomics has aimed to explain shifts in ionic composition by identifying specific genes and their control in changing environmental conditions, thus providing knowledge and information to improve the nutrition of crop species. BN is instead based on the idea that the entire genome of each genotype/species determines species-specific functionality and morphology (more distinct as genomic differences increase) and thus a distinct use of different bioelements, which in turn contribute asymmetrically to different functions and morphological structures. BN can thus be used without knowing about the control of gene expression or about gene function. Moreover, whereas ionomic approach has been developed for plants, BN is developed to be equally applicable to all type of taxa.

Even though these ionomic studies are mostly agriculturally oriented, and thus the link with the classical theory of ecological niche is not specifically considered, they are consistent with the BN hypothesis, at least at the level to correlate elemental composition with phylogenetic distance. They constitute strong evidence in favor of BN consistency and constitute a very interesting contribution to the BN.

#### CONCLUDING SUMMARY AND PERSPECTIVES

Here we propose a BN of genotypes/species/communities that should provide an improved and quantifiable

proxy of the general ecological niche. The BN is characterized by a particular hypervolume of their individual elementomes based on their specific needs and use of bioelements in different amounts and proportions for their structure and functioning. Several organismal structures and functions and the responses to environmental shifts cannot be explained only by the changes in the three main bioelements, C, N and P. We propose that other bioelements such as K, S, Ca, Mg, Fe, Mn, and Mo, among others, must be incorporated to fully describe the BN. The BN extends the classical ecological niche concept but has the advantage that it can be easily, directly and quantitatively analyzed.

The biogeochemical distances, i.e., the differences in elementome, among species, are a function of taxonomy (phylogenetic distance), sympatry (the bioelemental compositions should differ more among coexisting than among non-coexisting species to avoid competitive pressure), and homeostasis (within the continuum between high homeostasis/low plasticity and low homeostasis/high plasticity). Further studies are warranted to discern the ecological and evolutionary processes involved in the BN of all types of individuals, taxa, and ecosystems. The changes in bioelemental availability and use at long timescales should determine phenotypic selection and therefore also ecosystem function and organization, and, at the end, the evolution of life and the environment.

#### ACKNOWLEDGMENTS

The authors would like to acknowledge the financial support from the European Research Council Synergy grant ERC-SyG-2013-610028 IMBALANCE-P, the Spanish Government grant CGL2016-79835-P, and the Catalan Government grant SGR 2017-1005.

#### LITERATURE CITED

- Acquisti, C., J. J. Elser, and S. Kumar. 2009. Ecological nitrogen limitation shapes the DNA composition of plant genomes. *Molecular Biology and Evolution* 26:953–956.
- Araujo, M. S., D. I. Bolnick, G. Machado, A. A. Giaretta, and S. F. dos Reis. 2007. Using d<sup>13</sup>C stable isotopes to quantify individual-level diet variation. *Oecologia* 152:643–654.
- Baek, J. H., and S. Lee. 2007. Transcriptome analysis of phosphate starvation response in. *Journal of Microbiological Biotechnology* 17:244–252.
- Baribault, T., R. Kobe, and A. Finley. 2012. Tropical tree growth is correlated with soil phosphorus, potassium, and calcium, though not for legumes. *Ecological Monograph* 82:189–203.
- Bartrons, M., J. Sardans, D. Hoekman, and J. Peñuelas. 2018. Trophic transfer from aquatic to terrestrial ecosystems: a test of the biogeochemical niche hypothesis. *Ecosphere* 9:e02338.
- Baxter, I. R., O. Vitek, B. Lahner, B. Muthukumar, M. Borghi, J. Morrissey, M. L. Guerinot, and D. E. Salt. 2008. The leaf ionome as a multivariable system to detect a plant's physiological status. *Proceedings of the National Academy of Sciences USA* 105:12081–12086.
- Baxter, I., C. Hermans, B. Lahner, E. Yakubova, M. Tikhonova, N. Verbruggen, D. Y. Chao, and D. E. Salt. 2012.

- Biodiversity of mineral nutrient and trace element accumulation in *Arabidopsis thaliana*. *PLoS ONE* 7:e35121.
- Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. MacLeod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73:1007–1012.
- Begon, M., C. R. Colin, and J. L. Harper. 2006. *Ecology: from individuals to ecosystems*. Wiley-Blackwell, Oxford, England.
- Blonder, B. 2017. Hypervolume concepts in niche- and trait-based ecology. *Ecography* 41:1441–1445.
- Bourgis, F., et al. 1999. S-methylmethionine plays a major role in phloem sulfur transport and is synthesized by a novel type of methyltransferase. *Plant Cell* 11:1485–1498.
- Buescher, E., et al. 2010. Natural genetic variation in selected populations of *Arabidopsis thaliana* is associated with ionic differences. *PLoS ONE* 5:e11081.
- Chase, J. M. and M. A. Leibold. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago, Chicago, Illinois, USA.
- Chávez-Vergara, B., et al. 2016. *Quercus* species control nutrients dynamics by determining the composition and activity of the forest floor fungal community. *Soil Biology and Biochemistry* 98:186–195.
- Chimphango, S. B. M., G. Potgieter, and M. D. Cramer. 2015. Differentiation of the biogeochemical niches of legumes and non-legumes in the Cape Floristic Region of South Africa. *Plant Ecology* 216:1583–1595.
- Chowdhury, P. R., et al. 2015. Differential transcriptomic responses of ancient and modern *Daphnia* genotypes to phosphorus supply. *Molecular Ecology* 24:123–135.
- Cleveland, C. C., and D. Liptzin. 2007. C:N: P stoichiometry in soil: Is there a 'Redfield ratio' for the microbial biomass? *Biogeochemistry* 85:235–252.
- Colwell, R. K., and T. F. Rangel. 2009. Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences USA* 106:19651–19658.
- Danger, M., T. Daufresne, F. Lucas, S. Pissard, and G. Lacroix. 2008. Does Liebig's law of the minimum scale up from species to communities? *Oikos* 117:1741–1751.
- Davidson, E. A. W., and R. Howarth. 2007. Nutrients in synergy. *Nature* 449:1000–1003.
- De, C., and S. Bhattacharyya. 2009. First record of the Recent—subRecent diatomaceous earth from the Gangetic alluvial floodplains of. *Current Science* 96:967–973.
- De Bolos, O., and J. Vigo. 2001. *Flora dels Països Catalans (I-IV)*, Editorial Barcino, Barcelona, Spain.
- Du, E. 2017. Integrating species composition and leaf nitrogen content to indicate effects of nitrogen deposition. *Environmental Pollution* 221:392–397.
- Durston, D., and R. El-Sabaawi. 2017. Bony traits and genetics drive intraspecific variation in vertebrate elemental composition. *Functional Ecology* 31:2128–2137.
- Elser, J. J., and M. Kyle. 2009. Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition. *Ecology* 90:3062–3073.
- Elser, J. J., et al. 2000a. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408:578–580.
- Elser, J. J., et al. 2000b. Pelagic C:N: P stoichiometry in a eutrophic lake: Responses to a whole-lake food-web manipulation. *Ecosystems* 3:293–307.
- Elser, J. J., K. Hayakawa, and J. Urabe. 2001. Nutrient limitation reduces food quality for zooplankton: *Daphnia* response to seston Phosphorus enrichment. *Ecology* 82:898–903.
- Elser, J. J., et al. 2009. Shifts in Lake N: P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science* 326:835–837.
- Elser, J. J., et al. 2010. Atmospheric nitrogen deposition is associated with elevated phosphorus limitation of lake zooplankton. *Ecological Letters* 13:1256–1261.
- Falkowski, P. G., and C. S. Davis. 2004. Natural proportions. Redfield ratios: the uniformity of elemental ratios in the oceans and the life they contain underpins our understanding of marine biogeochemistry. *Nature* 431:131.
- Folch, R., T. Franquesa, and J. M. Camarasa. 1984. *Vegetació*. Page 404 in *Fundació Enciclopèdia Catalana*, editor. *Història Natural dels Països Catalans (VII)*. Fundació Enciclopèdia Catalana, Barcelona.
- Frerken, T., et al. 2017. Changes in N: P supply ratios affect the ecological stoichiometry of a toxic cyanobacterium and its fungal parasite. *Frontiers in Microbiology* 8:1–11.
- Frisch, D., et al. 2014. A millennial-scale chronicle of evolutionary responses to cultural eutrophication in *Daphnia*. *Ecology Letters* 17:360–368.
- Ganeshram, R. S., T. F. Pedersen, S. E. Calvert, and R. Francois. 2002. Reduced nitrogen fixation in the glacial ocean inferred from changes in marine nitrogen and phosphorus inventories. *Nature* 415:156–159.
- González, A. L., R. Cérèghino, O. Dézerald, V. F. Farjalla, C. Leroy, B. A. Richardson, M. J. Richardson, G. Q. Romero, and D. S. Srivastava. 2018. Ecological mechanisms and phylogeny shape invertebrate stoichiometry: A test using detritus-based communities across Central and South America. *Functional Ecology* 32:2448–2463.
- González, A. L., O. Dézerald, P. A. Marquet, G. Q. Romero, and D. S. Srivastava. 2017. The multidimensional stoichiometric niche. *Frontiers in Ecology and Evolution* 5:1–17.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Grossman, A. 2000. Acclimation of *Chlamydomonas reinhardtii* to its nutrient environment. *Protist* 151:201–224.
- Hartman, W. H., R. Ye, W. R. Horwath, and S. G. A. Tringe. 2017. Genomic perspective on stoichiometric regulation of soil carbon cycling. *ISME Journal* 11:2652–2665.
- Hatton, P. J., C. Castanha, M. S. Torn, and J. A. Bird. 2015. Litter type control on soil C and N stabilization dynamics in a temperate forest. *Global Change Biology* 21:1358–1367.
- He, M., et al. 2016. Influence of life form, taxonomy, climate, and soil properties on shoot and root concentrations of 11 elements in herbaceous plants in a temperate desert. *Plant and Soil* 398:339–350.
- Högberg, M. N., D. D. Myrold, R. Giesler, and P. Högberg. 2006. Contrasting patterns of soil N-cycling in model ecosystems of Fennoscandian boreal forests. *Oecologia* 147:96–107.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences USA* 106:19659–19665.
- Huang, X. Y., and D. E. Salt. 2016. Plant Ionomics: From elemental profiling to environmental adaptation. *Molecular Plant* 9:787–797.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- Jeyasingh, P. D., and L. J. Weider. 2007. Fundamental links between genes and elements: Evolutionary implications of ecological stoichiometry. *Molecular Ecology* 16:4649–4661.
- Jeyasingh, P. D., L. J. Weider, and R. W. Sterner. 2009. Genetically-based trade-offs in response to stoichiometric food quality influence competition in a keystone aquatic herbivore. *Ecological Letters* 12:1229–1237.
- Jeyasingh, P. D., et al. 2011. How do consumers deal with stoichiometric constraints? Lessons from functional genomics using *Daphnia pulex*. *Molecular Ecology* 20:2341–2352.

- Jeyasingh, P. D., R. D. Cothran, and M. Tobler. 2014. Testing the ecological consequences of evolutionary change using elements. *Ecology and Evolution* 4:528–538.
- Kattge, J., et al. 2011. TRY—a global database of plant traits. *Global Change Biology* 17:2905–2935.
- Kenesi, G., H. M. Shafik, A. W. Kovács, S. Herodek, and M. Présing. 2009. Effect of nitrogen forms on growth, cell composition and N<sub>2</sub> fixation of *Cylindrospermopsis raciborskii* in phosphorus-limited chemostat cultures. *Hydrobiologia* 623:191–202.
- Kerkhoff, A. J., and B. J. Enquist. 2006. Ecosystem allometry: The scaling of nutrient stocks and primary productivity across plant communities. *Ecological Letters* 9:419–427.
- Knight, M. R., A. K. Campbell, S. M. Smith, and A. J. Trevas. 1991. Transgenic plant aequorin reports the effects of touch and cold-shock and elicitors on cytoplasmic calcium. *Nature* 352:524–526.
- Lamanna, C. B., et al. 2014. Functional trait species and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences USA* 111:13745–13750.
- Lapenis, A. G., G. B. Lawrence, A. Heim, C. Zheng, and W. Shortle. 2013. Climate warming shifts carbon allocation from stemwood to roots in calcium-depleted spruce forests. *Global Biogeochemical Cycles* 27:101–107.
- Leal, M. C., O. Seehausen, and B. Matthews. 2017. The ecology and evolution of stoichiometric phenotypes. *Trends in Ecology and Evolution* 32:108–117.
- Lennon, J. T., Z. T. Aanderud, B. K. Lehmkuhl, and D. R. Schoolmaster, Jr. 2012. Mapping the niche space of soil microorganisms using taxonomy and traits. *Ecology* 93:1867–1879.
- Lenton, T. M., and C. Klausmeier. 2007. Biotic stoichiometric controls on the deep ocean N: P ratio. *Biogeosciences* 4:353–367.
- Lenton, T. M., and A. J. Watson. 2000. Redfield revisited: 1. Regulation of nitrate, phosphate, and oxygen in the ocean. *Global Biogeochemical Cycles* 14:225–248.
- Lowry, D. B., C. C. Sheng, Z. Zhu, T. E. Juenger, B. Lahner, D. E. Salt, and J. H. Willis. 2012. Mapping of ionomic traits in *Mimulus guttatus* reveals Mo and Cd QTLs that colocalize with MOT1 homologues. *PLoS ONE* 7:art e30730.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209–220.
- Menge, D. N. L., and L. O. Hedin. 2009. Nitrogen fixation in different biogeochemical niches along a 120 000-year chronosequence in New Zealand. *Ecology* 90:2190–2201.
- Meunier, C. L., M. Boersma, R. El-Sabaawi, H. M. Halvorson, E. M. Herstoff, D. B. Van de Waal, and R. J. Vogt. 2017. From elements to function: toward unifying ecological stoichiometry and trait-based Ecology. *Frontiers in Environmental Science* 5:Art 18.
- Morcuende, R., et al. 2007. Genome-wide reprogramming of metabolism and regulatory networks of *Arabidopsis* in response to phosphorus. *Plant, Cell and Environment* 30:85–112.
- Naples, B. K., and M. C. Fisk. 2010. Belowground insights into nutrient limitation in northern hardwood forests. *Biogeochemistry* 97:109–121.
- Neugebauer, K., M. R. Broadley, H. A. El-Serehy, T. S. George, J. W. McNicol, M. F. Moraew, and P. J. White. 2008. Variation in the Angiosperm Ionome. *Physiologia Plantarum* 163:1–17.
- Novotny, A. M., et al. 2007. Stoichiometric response of nitrogen-fixing and non-fixing dicots to manipulations of CO<sub>2</sub>, nitrogen, and diversity. *Oecologia* 151:687–696.
- Peñuelas, J., and J. Sardans. 2009. Elementary factors. *Nature* 460:803–804.
- Peñuelas, J., J. Sardans, R. Ogaya, and M. Estiarte. 2008. Nutrient stoichiometric relations and biogeochemical niche in coexisting plant species: Effect of simulated climate change. *Polish Journal of Ecology* 56:613–622.
- Peñuelas, J., et al. 2010. Faster returns on ‘leaf economics’ and different biogeochemical niche in invasive compared with native plant species. *Global Change Biology* 16:2171–2185.
- Peñuelas, J., et al. 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Global Change Biology* 19:2303–2338.
- Pereira, F. C., and D. Berry. 2017. Microbial nutrient niches in the gut. *Environmental Microbiology* 19:1366–1378.
- Peterson, A. T. 2011. Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography* 38:817–827.
- Pianka, E. R., L. J. Vitt, N. Pelegrin, D. B. Fitzgerald, and K. O. Winemiller. 2017. Toward a periodic table on niches, or exploring the lizard niche hypervolume. *American Naturalist* 190:601–616.
- Pierce, S. D., et al. 2016. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology* 31:444–457.
- Poxleitner, M., G. Trommer, P. Lorenz, and H. Stibor. 2016. The effect of increased nitrogen load on phytoplankton in a phosphorus-limited lake. *Freshwater Biology* 61:1966–1980.
- Quigg, A., et al. 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. *Nature* 425:291–294.
- Reinhard, C. T., et al. 2017. Evolution of the global phosphorus cycle. *Nature* 541:386–389.
- Rivas-Martínez, S., F. Fernández-González, J. Loidi, M. Lousa, and A. Penas. 2001. Syntaxonomical Checklist of vascular plant communities of Spain and Portugal to association level. *Itineraria Geobotany* 14:5–341.
- Rivas-Ubach, A., J. Sardans, M. Perez-Trujillo, M. Estiarte, and J. Peñuelas. 2012. Strong relationship between elemental stoichiometry and metabolome in plants. *Proceedings of the National Academy of Sciences USA* 109:4181–4186.
- Salt, D. E., I. Baxter, and B. Lahner. 2008. Ionomics and the study of plant ionome. *Annual Review of Plant Biology* 59:709–733.
- Salviagotti, F., et al. 2017. N:P: S stoichiometry in grains and physiological attributes associated with grain yield in maize as affected by phosphorus and sulfur nutrition. *Field Crop Research* 203:128–138.
- Sardans, J., R. Alonso, J. Carnicer, M. Fernandez-Martinez, M. G. Vivanco, and J. Peñuelas. 2016a. Factors influencing the foliar elemental composition and stoichiometry in forest trees in Spain. *Perspectives Plant Ecology, Evolution and Systematics* 18:52–69.
- Sardans, J., O. Grau, H. Y. H. Chen, I. A. Janssens, P. Ciais, S. Piao, and J. Peñuelas. 2017. Changes in nutrient concentrations of leaves and roots in response to global change factors. *Global Change Biology* 23:3849–3856.
- Sardans, J., I. A. Janssens, R. Alonso, S. D. Veresoglou, M. C. Rillig, T. G. M. Sanders, J. Carnicer, I. Filella, G. Farré-Armengol, and J. Peñuelas. 2015. Foliar elemental composition of European forest tree species results from evolutionary traits and the present environmental and competitive conditions. *Global Ecology and Biogeography* 24:240–255.
- Sardans, J., and J. Peñuelas. 2013. Tree growth changes with climate and forest type are associated with relative allocation of nutrients, especially phosphorus, to leaves and wood. *Global Ecology and Biogeography* 22:494–507.
- Sardans, J., and J. Peñuelas. 2014. Climate and taxonomy underlie different elemental concentrations and stoichiometries of forest species: The optimum ‘biogeochemical niche’. *Plant Ecology* 215:441–455.

- Sardans, J., and J. Peñuelas. 2015. Potassium: a neglected nutrient in global change. *Global Ecology and Biogeography* 24:261–275.
- Sardans, J., J. Peñuelas, M. Coll, J. Vayreda, and A. Rivas-Ubach. 2012a. Stoichiometry of potassium is largely determined by water availability and growth in Catalanian forests. *Functional Ecology* 26:1077–1089.
- Sardans, J., J. Peñuelas, and M. Estiarte. 2008a. Changes in soil enzymes related to C and N cycle and in soil C and N content under prolonged warming and drought in a Mediterranean shrubland. *Applied Soil Ecology* 39:223–235.
- Sardans, J., J. Peñuelas, M. Estiarte, and P. Prieto. 2008b. Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland. *Global Change Biology* 14:2304–2316.
- Sardans, J., J. Peñuelas, and R. Ogaya. 2008c. Drought-induced changes in C and N stoichiometry in a *Quercus ilex* Mediterranean Forest. *Forest Science* 54:513–522.
- Sardans, J., A. Rivas-Ubach, and J. Peñuelas. 2011. Factors affecting nutrient concentration and stoichiometry of forest trees in Catalonia (NE Spain). *Forest Ecology and Management* 262:2024–2034.
- Sardans, J., A. Rivas-Ubach, and J. Peñuelas. 2012b. The elemental stoichiometry of aquatic and terrestrial ecosystems and its relationships with organismic lifestyle and ecosystem structure and function: a review and perspectives. *Biogeochemistry* 111:1–39.
- Sardans, J., A. Rivas-Ubach, and J. Peñuelas. 2012c. The C:N:P stoichiometry of organisms and ecosystems in a changing world: a review and perspectives. *Perspectives in Plant Ecology Evolution and Systematics* 14:33–47.
- Sardans, J., et al. 2016b. Foliar and soil concentrations and stoichiometry of nitrogen and phosphorus across European *Pinus sylvestris* forests: relationships with climate, N deposition and tree growth. *Functional Ecology* 16:676–689.
- Schoener, T. W. 1989. *The Ecological Niche*. Pages 79–114. *The Contribution of Ecology to an Understanding of the Natural World*. Blackwell Scientific, Oxford, England.
- Shaul, O. 2002. Magnesium transport and function in plants: the tip of the iceberg. *BioMetals* 15:309–323.
- Sistla, S. A., A. P. Appling, A. M. Lewandowska, B. N. Taylor, and A. A. Wolf. 2015. Stoichiometric flexibility in response to fertilization along gradients of environmental and organismal nutrient richness. *Oikos* 124:949–959.
- Slade, S. 2006. *Elements in living organisms*. The Rosen Publishing Group, New York, USA.
- Sturner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, New Jersey, USA. pp 464.
- Sun, L., et al. 2017. Leaf elemental stoichiometry of *Tamarix* Lour. species in relation to geographic, climatic, soil, and genetic components in China. *Ecological Engineering* 106:448–457.
- Teurlinckx, S., M. Velthuis, D. Seroka, L. Govaert, E. van Donk, D. S. B. Van der Waal, and S. A. Declerk. 2017. Species sorting and stoichiometric plasticity control community C:P ratio of first-order aquatic consumers. *Ecology Letters* 20(6): 751–760.
- Tripler, C. E., S. S. Kaushal, G. E. Likens, and M. Todd Walter. 2006. Patterns in potassium dynamics in forest ecosystems. *Ecological Letters* 9:451–466.
- Turner, C. B., B. D. Wade, J. R. Meyer, B. Sommerfeld, and R. E. Lenski. 2017. Evolution of organismal stoichiometry in a long-term experiment with *Escherichia coli*. *Royal Society Open Science* 4:170497.
- Tyrrell, T. 1999. The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature* 400: 525–530.
- Urbina, I., J. Sardans, C. Beierkuhnlein, A. Jentsch, S. Backhaus, K. Grant, J. Kreyling, and J. Peñuelas. 2015. Shifts in the elemental composition of plants during a very severe drought. *Environmental and Experimental Botany* 111:63–73.
- Urbina, I., J. Sardans, O. Grau, C. Beierkuhnlein, A. Jentsch, J. Kreyling, and J. Peñuelas. 2017. Plant community composition affects the species biogeochemical niche. *Ecosphere* 8: e01801.1.
- Violle, C., and L. Jiang. 2009. Towards a trait-based quantification of species niche. *Journal of Plant Ecology* 2:87–93.
- Violle, C., P. B. Reich, S. W. Pacala, B. Enquist, and J. Kattge. 2014. The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences USA* 11:13690–13696.
- Wilson, R. P., C. R. McMahon, C. R. Quintana, E. Frere, A. Scolare, G. C. Hays, and C. J. A. Bradshaw. 2011. N-dimensional animal energetic niches clarify behavioural options in a variable marine environment. *Journal of Experimental Biology* 214:646–656.
- Yamamichi, M., C. L. Meunier, A. Peace, C. Prater, and M. A. Rúa. 2015. Rapid evolution of a consumer stoichiometric trait destabilizes consumer-producer dynamics. *Oikos* 124:960–969.
- Yu, Q., J. J. Elser, N. He, H. Wu, Q. Chen, G. Zhang, and X. Han. 2011. Stoichiometry homeostasis of vascular plants in the inner Mongolia grassland. *Oecologia* 166:1–10.
- Zamora, P. B., M. B. Cardenas, R. Lloren, and F. P. Siringan. 2017. Seawater-groundwater mixing in and fluxes from coastal sediment overlying discrete fresh seepage zones: a modeling study. *Journal of Geophysical Research Oceans* 122:6565–6582.
- Zederer, D. P., U. Talkner, M. Spohn, and R. G. Joergensen. 2017. Microbial biomass phosphorus and C/N/P stoichiometry in forest floor and A horizons as affected by tree species. *Soil Biology and Biochemistry* 111:166–175.
- Zhang, S. B., J. L. Zhang, J. W. F. Slik, and K. F. Cao. 2012. Leaf element concentrations of terrestrial plants across China are influenced by taxonomy and the environment. *Global Ecology and Biogeography* 21:809–818.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2652/supinfo>