1 **The bioelements, the elementome and the "biogeochemical niche".**

2 Josep Peñuelas[1,2*], Marcos Fernández-Martínez[2,3], Philippe Ciais[4], David Jou[5], Shilong Piao[6],

3 Michael Obersteiner[7], Sara Vicca[3], Ivan A. Janssens[3], Jordi Sardans[1,2]

5 [1] CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra, 08193 Catalonia, Spain.

6 [2] CREAF, Cerdanyola del Valles, 08193 Catalonia, Spain.

7 [3] Research Group Plants and Ecosystems (PLECO), Department of Biology, University of

8 Antwerp, B-2610 Wilrijk, Belgium.

9 [4] Laboratoire des Sciences du Climat et de l'Environnement, IPSL, 91191 Gif-sur-Yvette,

10 France.

11 [5] Department of Physics. Universitat Autònoma de Barcelona, Bellaterra, 08193 Catalonia,

12 Spain.

13 [6] Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences,

14 Peking University, Beijing 100871, China.

15 [7] International Institute for Applied Systems Analysis (IIASA), Ecosystems Services and

16 Management, Schlossplatz 1, A-2361 Laxenburg, Austria.

17 * Corresponding author:
18 Josep Peñuelas, CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra, 08193 Catalonia, Spain
19 and CREAF, Cerdanyola del Valles, 08193 Catalonia, Spain. E-mail: josep.penuelas@uab.cat
20

21 Running Head: **Elementome and biogeochemical niche.**

22

23

24

28

29

30

31

32   **Abstract**

33   Every living creature on Earth is made of atoms of the various bioelements that are harnessed in

34   the construction of molecules, tissues, organisms and communities, as we know them. Organisms

35   need these bioelements in specific quantities and proportions to survive and grow. Distinct

36   species have different functions and life strategies, and have therefore developed distinct

37   structures and adopted a certain combination of metabolic and physiological processes. Each

38   species is thus also expected to have different requirements for each bioelement. We therefore

39   propose that a "biogeochemical niche" can be associated with the classical ecological niche of

40   each species. We show from field data examples that a biogeochemical niche is characterized by

41   a particular elementome defined as the content of all (or at least most) bioelements. The

42   differences in elementome among species are a function of taxonomy and phylogenetic distance,

43   sympatry (the bioelemental compositions should differ more among coexisting than among non-

44   coexisting species to avoid competitive pressure), and homeostasis with a continuum between

45   high homeostasis/low plasticity and low homeostasis/high plasticity. This proposed

46   biogeochemical niche hypothesis has the advantage relative to other associated theoretical niche

47 hypotheses that it can be easily characterized by actual quantification of a measurable trait: the

48 elementome of a given organism or a community, being potentially applicable across taxa and

49 habitats. The changes in bioelemental availability can determine genotypic selection and

50 therefore have a feedback on ecosystem function and organization, and, at the end, become

51 another driving factor of the evolution of life and the environment.

52

53

54

55

56 **1. The elements of life and the construction of molecules, tissues, organisms and**

57 **communities**

58 All living beings are made of atoms of various bioelements (elements used by living organisms).

59 The most common bioelements are: hydrogen (H) 59%, oxygen (O) 24%, carbon (C) 11%,

60 nitrogen (N) 4%, phosphorus (P) 1% and sulfur (S) 0.1-1% (percentages of total number of

61 atoms in organisms) (Slade 2006). C, H, and O are the basis of organismic structure, i.e. water

62 and primary structural molecules, whereas N, P and S enter in the various biomolecules allowing

63 biochemical reactions. C, H and O from CO_2 and H_2O are converted into the skeleton of all types

64 of organic molecules by photo- and chemosynthesis. The molecular structures that control life

65 processes (e.g. RUBISCO or chlorophyll), that carry information (e.g. DNA and RNA), and that

66 control the storage and release of energy when and where necessary (e.g. ATP and NAD) all

67 incorporate N, P and in lower amounts S.

68   These six bioelements, however, are not the only bioelements that have important roles in

69   organisms (Slade, 2006). Other bioelements, normally present in low concentrations such as

70   potassium (K), magnesium (Mg), iron (Fe), calcium (Ca), molybdenum (Mo), manganese (Mn)

71   and zinc (Zn) have functions that are more specific. They are cofactors in catalytic reactions in

72   several biochemical and physiological processes. For example, in plants, K, Mg, Fe, S, Ca, and

73   Zn are involved in photosynthesis, respiration, regulation of ion balance in chloroplasts and

74   vacuoles, transport of sugar into the phloem, secondary metabolism, maintenance of internal

75   cellular osmotic or pH equilibria and balances, and strategies for stomatal control and avoidance

76   of water stress (Knight et al. 1991, Bourgis et al. 1999, Shaul 2002, Tripler et al. 2006, Peñuelas

77   and Sardans 2009, Baribault et al. 2012, Naples and Fisk 2010, Rivas-Ubach et al. 2012,

78   Peñuelas et al. 2013, Sardans and Peñuelas 2015). All these bioelements thus contribute

79   essentially to organismic functions, albeit to different degrees (Figure 1).

80   The concentrations and ratios of C, N and P have been the basis of ecological

81   stoichiometry (Elser et al. 2000a,b, 2001, Sardans et al. 2015, 2016). However, to link

82   bioelemental composition and stoichiometry with ecological traits in all types of organisms and

83   communities will thus require information about bioelemental composition beyond the C:N:P

84   concentrations and ratios (Peñuelas and Sardans 2009). The other bioelements such as S, K, Ca

85   or Mg are also crucial and can be limiting in some ecosystems (Naples and Fisk 2010, Baribault

86   et al. 2012, Lapenis et al. 2013). These other bioelements have been introduced in ecological

87   stoichiometric studies to link the elemental composition of individuals and species with their

88   ecological traits, such as drought resistance (related to K), light environment (related to Mg) or

89   the levels of N and S deposition (related to K, Ca, Mg and S) (Sardans et al., 2011;2012a;

4

90   Sardans et al., 2015). All these bioelements should thus be considered in ecological

91   stoichiometric studies.

92

2. Elementome and biogeochemical niche.

94   Species use these bioelements to different degrees based on their ecological strategy (example

95   for plants in Figure 2). Classic Hutchinson's (1957) description of species niche has been largely

96   applied to the main taxa from a point-of-view of distinct species in a site position in a "n-

97   dimensional hypervolume" formed by the values of determined environmental variables and/or

98   organisms traits. For instance, plant species have been classified in a hypervolume formed by

99   three axes, i.e. corresponding to Grime's 3 strategies: competitor, stress-tolerant and ruderal

100   (Grime 1977). In animals, the species-specific niche has been determined and located in

101   function of hypervolumes for n-axis of different values of energy expenditure (Wilson et al.,

102   2011), distinct diet sources (Araujo et al., 2007; Bearhop et al., 2004) or different elemental

103   composition (González et al., 2017, 2018). In microbial communities, genotype-niches have also

104   been described in function of the different availabilities of different nutrients (Pereira and Berry,

105   2017) or as a function of the values of diverse functional traits (Lennon et al., 2012) thus

106   describing multivariant spaces with a determined combination of nutrients availability or

107   functional traits where a determined genotype can exist. Any living species should thus tend to

108   optimize its overall function within a determined and space within this volume generated by a

109   combination of these axes describing strategies or biotic and/or abiotic variables while avoiding

110   the overlap with other coexisting species. Following these niche approach, we can hypothesize

111   that distinct species have different functions and life strategies and have therefore developed

112   distinct structures and adopted a certain combination of metabolic and physiological processes.

5

113   Therefore, each species (of all taxa types) also has different requirements for each bioelement,

114   and should thus tend to have its own elemental composition (Yu et al. 2011; Kattge et al. 2011;

115   Sardans and Peñuelas 2013, 2014; Sardans et al. 2015; Pierce et al. 2016; Bartrons et al., 2018).

116   We postulate that the more functionally separated two species are, the more different the

117   content of bioelements should be. This led us to propose a "biogeochemical niche" (BN) defined

118   as the multidimensional space defined by the concentrations of bioelements in individuals of a

119   given species (Peñuelas et al., 2008). This BN has been used in the recent years by other authors

120   such as Gonzalez et al. (2017) who proposed the "multidimensional stoichiometric niche" as the

121   specific position of different taxonomic/trophic groups in the three-dimensional space

122   determined by C, N, and P, and other elements as additional axes in their application of the BN

123   to animals (Gonzalez et al., 2018), as previously proposed for plants by Peñuelas et al. (2008),

124   and for plants and animals together by Bartrons et al (2018). BN is thus based on the species-

125   specific needs and use of bioelements in different amounts and proportions resulting from the

126   organismic structure and function in the given abiotic and biotic environmental space where the

127   species has evolved (Peñuelas et al. 2008, 2010). Each species should thus have an optimal (at

128   maximum fitness) equilibrium of bioelemental composition, resulting from its functional and

129   structural adaptations, equivalent to the optimum "elemental phenotype" (Jeyasingh et al., 2014).

130   The BN represents thus the species-specific strategies of growth and resource uptake and the

131   differences in soil-space occupation.

132   We propose that the processes underlying this species-specific elementome and the BN

133   are based on three basic complementary rules (Figures 3). First, distinct taxonomic groups

134   exhibit different elementomes, with larger differences as taxonomic distance and evolutionary

135   time increase. Second, at equilibrium, coexisting species tend to have distinct elementomes to

6

136   minimize competitive pressure. Third, trade-offs between adaptation to being competitive in a

137   stable environment versus being successful in more fluctuating environments cause homeostasis

138   and plasticity differences between species in a continuum of strategies. The BN distances among

139   species should thus be a function of taxonomic difference, sympatry (coexistence), and

140   homeostasis/plasticity and sympatry (Figure 3). The BN of taxa i is assumed to be the result of

141   its taxonomical evolutionary determination and its capacity to respond to changes in external

142   conditions, which is also partly taxonomically-determined. External changes include nutrient

143   availability (including the level of atmospheric CO_2), changes in growing season duration,

144   disturbance regimes, and, on longer time scales, changes in soil properties. This capacity to

145   respond to environmental changes is, in turn, a function of taxonomy, sympatry, and

146   homeostasis:

147   $\qquad BN_i = BN \text{ of taxa}_i = Elementome_{i1-n} = (C: N: P: K: S: Mg: Ca: ...)_{i1-n} = BNtax_i +$

148   $\frac{\partial BNtax_i}{\partial Env} = BNtax_i + f(Tax_i, \ Symp_i, Hom_i)$ $\qquad\qquad\qquad\qquad$ (Eq. 1)

149   where:

150   $\qquad BNtax_i =$ Biogeochemical niche explained by taxonomy of taxa i (measured in n

151   individuals of taxa i). A n-dimensional hypervolume describes the fundamental BN of a species.

152   The domain of this hypervolume function is restricted to a finite region corresponding to the

153   possible values of bioelemental combinations.

154   $\qquad \frac{\partial BNtax_i}{\partial Env} =$ Changes in $BNtax_i$ of taxa i explained by environmental changes

155   $\qquad tax_i =$ taxonomy of taxa i; $Symp_i$ sympatry of taxa i with other competing taxa (j), and

156   $Hom_i =$ elemental homeostasis-plasticity of the taxa i

7

157     $BN_j = BN\ taxa_{j\ =}\ Elementome_{j1-n} = (C: N: P: K: S: Mg: Ca \dots)_j$

158     $BN_j = BNtax_j + \frac{\partial BNtax_j}{\partial Env} = BNtax_{j1-n} + f(Tax_j, Symp_j, Hom_j)$ (Eq. 2)

159   The BN distance between taxa i and j, ΔBN_{i-j}, will be:

160     $\Delta BN_{i-j} = (BNtax_i - BNtax_j) + \frac{\partial BN_{taxi} - \partial BN_{taxj}}{\partial Env} = (BNtax_i - BNtax_j) +$

161     $[f(Tax_i,\ Symp_i, Hom_i) - f(Tax_j, Symp_j, Hom_j)$ (Eq. 3)

162   The segregation of the BNs of the dominant species of a holm-oak evergreen

163   Mediterranean forest (Figure 4a) and their displacement when exposed to drought in a climatic

164   field experiment (Figure 4b) constitute a consistent confirmation of these two first BN rules.

165   Very similar results for segregation and displacement were found using different calculation

166   approaches, from the additional use of ratios as explanatory variables to the use of discriminant

167   and other multivariate analyses (Appendix S1: Fig. S1). Pairs of species with more overlap in

168   their distributions had greater differences in their BNs as estimated from PCA scores (PCA based

169   on N,P, K, S, Ca and Mg concentrations) in a set of the 12 most representative Mediterranean

170   tree species of South Europe (Figure 4c), confirming the third rule. The BN hypothesis is an

171   extension of the ecological niche concept (Schoener 1986) to the bioelemental components of

172   life. The BN aims to establish the morphological and functional "adaptation" to the abiotic and

173   biotic traits that define the niche of each species-genotype from simple determination of the

174   elemental composition. It is based on the different contribution of each bioelement to the

175   different organismal functions and structures. Its main advantage over other theoretical classical

176   niche concepts is that it can be characterized by the measurable bioelemental composition, the

177   elementome, of the organism, species, community or even biome (Figure 5). This BN

178   measurement is not biased by the most abundant bioelements since the analysis is conducted for

179   a multivariate space defined by the standardized elemental concentrations (Figures 4 and 6).

180   The quantitative BN framework can then be used to improve projections of how species

181   will respond to environmental changes, provided elementome homeostasis/plasticity (Hom) on a

182   given time horizon is known. This Hom can be defined for example as the coefficient of variance

183   of the scores for the different individuals of a species in the PCA. It results from both

184   intraspecific variation and phenotypic individual responses. These two responses can be

185   differentiated when the hypervolume occupied by the individuals of one species is compared

186   with the hypervolume generated after changing the environmental conditions, for instance in

187   experiments in field conditions where environmental conditions are changed.

188   BN aims to refocus the use of the hypervolume in ecological niche studies. A n-

189   dimensional hypervolume was originally proposed by Hutchinson (1957) and defined as a subset

190   of the space, i.e. an n-dimensional geometrical shape, to describe the fundamental niche of a

191   species. Hutchinson suggested that the axes correspond to requirements of the species (e.g. light,

192   temperature, food size) and that the boundaries of the shape indicate the conditions that permit

193   the growth and reproduction of the individuals of a species. This description of the species niche

194   has been widely used and discussed (Begon et al, 2006 Chase and Leibold 2003, Colwell and

195   Rangel 2009, Holt 2009, Peterson et al 2011). There is now a growing set of statistical methods

196   to operate this hypothesis of species niche with data (Blonder 2017). BN should be a tool to

197   detect the niche shifts at short-, medium- and long-term scales in response to all type of

198   environmental changes (drought, species invasion, pests, new biotic relationships, etc.). The

199   mathematical description of each specific BN position in a multi-space in function of the

200   concentrations of several bioelements can be done by using essential multivariate statistical

201 analyses such as principal components analyses (PCA) or functional/general discriminant

202 analysis (F/GDA) (Sardans et al. 2015; Urbina et al. 2017), or other analyses such as kernel

203 density estimation, support vector machine, Bayesian ellipse, etc. (Blonder 2017). BN distances

204 and the level of overlap/separation among different groups can be computed with the score

205 means (centroids) of the main axes (in the PCAs; Figure 4, Appendix S1, Fig. S1) or with

206 squared Mahalanobis distances (in the discriminant analyses; Appendix S1: Fig. S2). These

207 metrics provide numerical evidences of the "distances" between the BN of different species and

208 of the BN displacement (if any) when comparing the BN of different populations of the same

209 species along space or time. Correlations between matrices provide a way of comparing the

210 distances between hypervolumes, for instance the correlation matrix of the genome differences

211 or of the differences in some ecological or ecophysiological variables in a particular set of

212 species with the corresponding correlation matrix of the BN distances of the same set of species.

213 Statistical tests such as Mantel tests (Mantel, 1967) can be used with this aim. All these

214 mathematical tools to estimate the BN allow all levels of comparisons, from species (Sardans et

215 al. 2015) to different taxa and trophic groups (Bartrons et al. 2018), also including the

216 comparison of different populations of the same species growing under distinct environmental

217 conditions (Urbina et al., 2015, 2017).

218 These studies have shown the facility and consistency in the use of different types of

219 multivariate analyses to detect the BN in spatial and temporal gradients/scales. Moreover, the

220 different levels of homeostasis/plasticity of different studied groups can be calculated by the

221 area/volume in that the individuals of each group are spread in the multidimensional space

222 generated. The temporal shifts of the BN of a species or populations of one species can also be

223 calculated and thus their evolution can be followed. BN also allows the description and

224 quantification of niche appearance (i.e. when new species colonize the ecosystem), expansion,

225 contraction, and extinction. Therefore, BN constitutes a quantifiable tool to detect, quantify and

226 thus better comprehend the mechanisms and processes underlying community evolution and

227 species turn-over (Figure 7). Niche construction vs niche expansion or niche contraction vs niche

228 extinction are apparently difficult to differentiate because of their similar outcomes, and niche

229 contraction (and extinction) could be the result of environmental filtering, whereas niche

230 expansion could be due to addition of species to a community. Phenomena within the niche

231 theory such as niche convergence (Pianka et al., 2017) can be followed by monitoring the species

232 BN hyper-dimension along spatial and temporal gradients and focusing on the changes in the

233 level of overlap/distance in their BN.

234

235 **3. Evidence from observational data**

236 3.1- Taxonomy

237 The BN hypothesis is supported by strong evidence in recent studies. Observational data

238 (Sardans and Peñuelas 2014; Bartrons et al., 2018) provide evidence that plant and animal

239 species have their own elementome, their own BN. For example, different groups of species in

240 distinct climatic biomes have different foliar bioelemental compositions and stoichiometries

241 (Sardans et al. 2014, 2015, 2016). Foliar bioelemental composition of forest tree species, for

242 example, has been positively correlated with phylogenetic distance between taxa at different

243 geographic extents, from local to continental (Sardans et al. 2014, 2015, 2016). Bioelemental

244 composition and stoichiometry thus tend to differ more between phylogenetically distant than

245 between phylogenetically close tree species (Sardans and Peñuelas 2014, Sardans et al. 2015,

246 2016). These positive correlations between elemental composition differences and phylogenetic

247 distances have been also observed in animals (Gonzalez et al. 2018) in a further demonstration of

248 the first process underlying the BN hypothesis. The stoichiometry of an individual under a given

249 climatic and edaphic condition is determined in part by the uptake and the efficiency with which

250 the individual uses each bioelement, all of which depend on the trade-offs among the various

251 individual functions that maximize individual fitness under that specific climatic situation. Each

252 species and taxon have its own space in the two-dimensional plot formed by the two first

253 components of the PCA of individual composition (N, P, S, K, Ca and Mg concentrations and

254 their ratios) (See example in Figure 4A and see Appendix S1: Table S1 for the scores of

255 additional PCs).

256

257 3.2- Sympatry

258 Larger differences in the stoichiometry of foliar composition among sympatric than allopatric

259 species have recently been reported both in plant communities (Sardans et al. 2015, 2016) and in

260 animal communities (González et al., 2018) as implied in the third process involved in the BN.

261 The overlapping frequency of all pairwise comparisons among many tree species is correlated

262 with the elementome distances of the corresponding tree pairs (Figure 4c) (Sardans et al. 2015),

263 thus supporting this third process. Different grass and shrub species growing under different

264 climatic conditions in communities with distinct species compositions maintain distinct species-

265 specific foliar compositions, although there may be displacement, expansion or concentration of

266 the biogeochemical space occupied (Figure 6) depending on the coexisting species (Urbina et al.

267 2015, 2017). The species bioelemental composition changes in parallel with the shifts of

268 environmental conditions, in accordance with the new optimal functions that require new

269 proportional use of different bioelements. Contraction, expansion, and displacement at the short-

270   term would thus be complemented by construction (allopatric speciation), extinction,

271   segregation, and equalization at the long-term both for estenoic (narrow range of ecological and

272   environmental conditions) and euroic (wide range) niches (Figure 7).

273   In-depth investigation of these processes constitutes a challenge for ecologists. Some

274   studies have already demonstrated different biogeochemical niche space (euroic-estenoic) among

275   different coexisting species-genotypes in plants (Urbina et al., 2015, 2017, Sardans et al., 2015),

276   animals (González et al., 2017, 2018; Bartrons et al., 2018) and microbes (Pereira and Berry,

277   2017). Other studies have observed how the same species displaced their biogeochemical niche

278   depending on the intraspecific and intraspecific competition (Urbina et al., 2015, 2017; Sardans

279   et al., 2016). However, observational field studies along successional stages, field manipulation

280   studies of biotic (introducing new species, changes in density,..), and abiotic (changing climate

281   conditions or nutrient availability) followed along time with similar studies in greenhouse,

282   micro- and mesocosm conditions would be necessary to further test the consistency of the new

283   holistic view of ecosystem processes provided by the BN.

284

285

286   3.3- Homeostasis/Plasticity

287   Changes in environmental supply (for example soil or water bioelemental composition) can

288   affect the bioelemental composition of organisms, as observed in microbes (Frenken et al 2017)

289   and plants (He et al. 2016, Salvagiotti et al. 2017). A trade-off between adaptations to be

290   competitive in stable environments versus being successful in less stable environments should

291   underpin the differences in the continuum of homeostasis-plasticity strategies in bioelemental

292   composition and stoichiometry among individuals, species and communities (Figure 3, Figure

293   4B). Higher N and P concentrations and lower N:P ratios coincide with higher stoichiometric

294   plasticity in opportunistic (r-strategy) than in competitor (K-strategy) plant species (Yu et al.

295   2011). Climate can also account for some of the variability in the bioelemental composition of

296   plant tissues at intra- and interspecific levels (Sardans et al. 2015, 2016, Zhang et al. 2012)

297   indirectly though climate controls on bioelemental availability and directly as a forcing of traits

298   linked to the elementome. Environments with fluctuating nutrient availabilities relative to the

299   species' lifetime would have to favor organisms with greater stoichiometric plasticity.

300   Stoichiometric plasticity tends to decrease in response to fertilization as environmental nutrient

301   richness increases, in both terrestrial and aquatic systems (Sistla et al. 2015), thus suggesting a

302   different position in the homeostatic-plasticity continuum between species in nutrient-rich versus

303   nutrient-poor environments. The BN hypothesis allows to detect the plasticity at two levels: at

304   the individual level (phenotypic plasticity) by showing how its individual elemental composition

305   can vary when environmental conditions shift, and at the intraspecific level as a result of

306   intraspecific variability (individual genotypic differences, different ontogenic stage, distinct

307   sex,..) in elemental composition of a set of individuals of the same species living under the same

308   environmental conditions. This dual source of variability due to natural intra-population

309   variability and to individual capacity to shift BN in response to environmental changes can be at

310   least partially detected experimentally with multivariate analyses working with populations of

311   the same genotype growing in different environmental conditions across space or time.

312

313   3.4 Evolutionary change

314   Species have stoichiometric strategies to adapt to heterogeneous environments (Sun et al. 2017)

315   and are able to adapt their elemental compositions to those of the media after several generations

14

316 (Turner et al. 2017). The stoichiometry of phytoplankton appears to reflect oceanic stoichiometry

317 over geological timescales, providing even stronger support to this link between organisms'

318 composition and media nutrients availability (Quigg et al. 2003; Reinhard et al. 2017). Other

319 studies of terrestrial ecosystems found that microbial community N:P ratios were correlated with

320 plant-community and soil N:P ratios (Kerkhoff and Enquist 2006, Cleveland and Liptzin 2007).

321 Close relationships between microbial and soil C:N ratios across a soil C:N gradient have been

322 also observed, e.g. in Scandinavian boreal forests (Högberg et al. 2006). Evidence suggests that

323 variation in the environmental supply of P affects the expression of highly conserved genes (e.g.

324 those of the phosphate-transporter system) and that the acquisition, assimilation and allocation of

325 P is genetically variable (Jeyasingh and Weider 2007). Transcriptomic studies of algae

326 (Grossman 2000), microbes (Baek and Lee 2007), terrestrial plants (Morcuende et al. 2007) and

327 more recently herbivores (Jeyasingh et al. 2011) have also reported that the availability of P

328 influences genetic expression. Such effects of the supply of P should impinge on fitness and

329 drive evolutionary change. Jeyasingh et al. (2009) observed that genetic variation in

330 phosphoglucose isomerase (Pg) indicated that Pg heterozygotes of *Daphnia pulicaria*

331 outcompeted Pg homozygotes under conditions of low C:P ratios, whereas the opposite was

332 observed under conditions of high C:P ratios.

333   Availability and stoichiometry of bioelements can determine transcriptional expression

334 and metabolomic structure (Rivas-Ubach et al. 2012) and phenotypic selection (Chowdhury et al.

335 2015), and can affect genomes and thereby become evolutionary drivers for organisms and

336 ecosystems on the longest timescales (Acquisti et al. 2009). For example, the mechanisms

337 controlling P acquisition are genetically variable, and the expression of the genes involved is

338 strongly affected by its environmental supply (Grossman 2000, Jeyasingh and Weider 2007,

339   Jeyasingh et al. 2011, 2014). Selection in environments with very low N availability can even

340   favor new genes richer in N-poor nucleotides (Acquist et al. 2009). Evolution could also be

341   controlled by directly affecting the quality of matter, e.g. different N:P ratios available to

342   genomes for the optimal allocation of N and P to DNA/RNA for maximizing fitness (Sardans et

343   al., 2012b).

344

345   3.5 BN of communities

346   Communities should be more capable to adjust their stoichiometry to additional nutrient inputs

347   and varying stoichiometrical conditions than single species (Danger et al. 2008). A simple and

348   comprehensive example, only considering N and P concentrations and stoichiometry, can be

349   observed when P is added to a freshwater community. In such a case, a shift in community

350   composition typically occurs in favor of N-fixing organisms with a posterior cascade of

351   composition changes towards a new equilibrium in community composition (Davidson et al.

352   2007). Environmental changes (anthropogenic or natural) such as perturbations or shifts in

353   climate, N deposition, species invasion or the increase in atmospheric CO_2 can probably generate

354   changes in the availability of various nutrients. Species of the target community can then adapt,

355   depending on their phenotypic flexibility. For example, species with a BN better adapted to new

356   environmental conditions can be favored under large long-term loadings of N by N deposition,

357   but species less well adapted can disappear. Species can also turnover, when possible, with the

358   entrance of new species with traits better adapted to life in the newly generated niches (with

359   different optimal elemental compositions). This sequence of events has been observed in several

360   field studies where shifts in the elemental composition of the media (water or soil) due to

361   changing conditions (anthropogenic or natural) have been translated into changes in the species

362 composition of species of the community (Sterner and Elser, 2002). The species with more

363 favorable elemental compositions gain then importance and/or there is species turnover

364 (Novotny et al. 2007; Yu et al. 2011, Poxleitner et al. 2016, Du 2017). Changes in N:P have ben

365 related to substantial changes in species composition of plant communities (Peñuelas et al 2013)

366 and changes in P loads to adjusted C:P ratios in zooplankton communities (Teurlink et al., 2017).

367

4- Feedbacks on environment

369 The relationships between evolution and the bioelemental composition of ecosystems are

370 bidirectional, because nutrient supply can affect evolutionary processes, while the changes

371 imposed by evolutionary processes can also affect nutrient supply (Durston and El-Sabaawi

372 2017). As a result, ocean and soil stoichiometries may have been also partly controlled by

373 organisms over long time scales (Tyrrell 1999, Lenton and Klausmeier 2007, Hatton et al. 2015,

374 Zederer et al. 2017).

375 The strongest support of Redfield ratio comes from the fact that the N:P ratio in the open

376 sea areas of all major oceans is remarkably similar to the N:P ratio of plankton (16:1). This is

377 due to the residence time of N and P in the ocean (104 years) relative to the ocean's circulation

378 time (103 years) (Falkowski and Davis 2004). However, in addition to the geochemical causes,

379 biological processes are also underlying Redfield ratios. N_2 fixation can play an important role in

380 ocean N:P ratio homeostasis (Tyrrell 1999, Lenton and Watson 2000, Ganeshram et al. 2002,

381 Kenesi et al. 2009). When ocean N:P ratios fall too low, nitrogen fixation increases by

382 augmenting the biomass of N_2-fixers and when these N_2-fixers decompose or are eaten, their N

383 rich organic matter turns to dissolved ammonium and nitrate in the water increasing water N:P

384 ratios. Conversely, when the ratio rises too high, N_2 fixation inputs decrease by P limitation of

385 N_2-fixation, thus restoring lower water N:P ratio. This process would confer to P primary control

386 of ocean production (Tyrrell 1999, Lenton and Klausmeier 2007).

387   Soil elemental composition is also controlled by the species of plants (Zederer et al.

388 2017), the soil microbiota (Hartman et al. 2017), and the interactions between plants and soil

389 fungal communities. For example, *Quercus* species control nutrient dynamics by determining the

390 composition and activity of the forest floor fungal community (Chávez-Vergara et al. 2016) and

391 the litter type (Hatton et al. 2015). Conifers acidifying soil to reduce soil nutrient availabilities

392 (base cations and P) to outcompete species with a different BN provide another consistent

393 example.

394   We should thus expect a constant feedback between organisms and their environment.

395 Understanding the processes underlying species shifts in bioelemental composition and their

396 genetic basis will help us understand the responses of organisms to environmental changes

397 (Yamamichi et al. 2015, Leal et al. 2017) and in turn the effects of organisms on ecosystem

398 functioning and services (Frisch et al. 2014, Leal et al. 2017). We are currently still moving

399 towards understanding and identifying the feedbacks between species evolution and shifts in the

400 bioelemental composition of ecosystems and how these feedbacks interact and determine

401 ecosystem and evolutionary processes. Available data seems to indicate that the long-term

402 availability and use of bioelements can determine individual selection and therefore ecosystem

403 function and organization and evolution of life.

404

405 **5- The biogeochemical niche hypothesis and related approaches**

406 Functional traits such as leaf mass area, seed size or plant height have been also used to build

407 hypervolumes to identify species-specific niche (Violle and Jiang, 2009; Violle et al., 2014;

408 Lamanna et al., 2014). However, taxonomical groups (e.g. animals, plants, fungi,..) have

409 different functional traits, preventing the use of these approaches to different taxonomy clades.

410 Instead, all the organisms, independently of their taxonomical groups, are constituted by the

411 same basic bio-elements, thus providing a general and easy to measure variable, the elementome,

412 with which to establish the species-specific niche in plants (Sardans et al., 2015), in animals

413 (Gonzalez et al., 2017) and in sets of plants and animals analyzed altogether (Bartrons et al.,

414 2018). The use of organismal elemental stoichiometry has been proven to be related to the

415 species functional traits in aquatic and terrestrial ecosystems (Meunier et al., 2017, Sardans et al.

416 2012c, Peñuelas et al. 2013). This also allows us to establish relationships between observed

417 shifts in ecosystem N:P medium (water or soil) with the shift in species dominance or

418 community and/or in trophic web composition and structure.

419   We first defined the BN in 2008 for plant communities (Peñuelas et al. 2008) and we

420 have since then developed it in several papers (Peñuelas et al. 2008, Sardans and Peñuelas 2014,

421 Frisch et al. 2014, Sardans et al. 2015, 2016, Urbina et al. 2017). Other groups have also used

422 this approach (De and Bhattacharyya 2009, Menge and Hedin 2009, Chimphango et al. 2015,

423 Zamora et al. 2017), obtaining results that have provided solid experimental consistency to BN

424 hypothesis. The BN that we define as species elemental composition is wide in scope and simple

425 in determination, and reflects the structure and function of each species-genotype resulting from

426 its unique evolutionary history (Sardans et al. 2008, 2015, Urbina et al. 2017).

427   BN aimed to progress beyond the classical ecological stoichiometric studies (Elser et al.

428 2000a,b, Sterner and Elser 2002, Elser and Kyle 2009, Elser et al. 2009, 2010, Rivas-Ubach et al.

429   2012, Sardans et al. 2012b). These ecological stoichiometric studies have linked several

430   important ecosystem processes with ecosystem and organismal C:N:P ratios. Several organismal

431   functions and responses to environmental shifts, though, cannot be explained only by the

432   changes in these three main bioelements (Sardans et al. 2012b,c). As stated above, other

433   bioelements (such as K, S, Ca, Mg and Fe) are needed in ecological stoichiometric studies to

434   provide more complete and global information correlating shifts in organismal elemental

435   composition with changes in organismal morphology and function in response to environmental

436   conditions (Peñuelas et al. 2008, Peñuelas and Sardans 2009, Sardans and Peñuelas 2014,

437   Sardans et al. 2015). The BN hypothesis is thus based on the entire elemental composition or at

438   least on the composition of as many elements as possible. The BN hypothesis has afterwards also

439   been used to refer to the concentrations and availabilities of nutrients in soil or water that favor

440   or determine the corresponding spatial occupation by a species or taxon (De and Bhattacharyya

441   2009, Menge and Hedin 2009, Chimphango et al. 2015, Zamora et al. 2017).

442   A similar hypothesis of a "multidimensional stoichiometric niche" was recently

443   introduced by Gonzalez et al. (2017). These authors defined a "multidimensional stoichiometric

444   niche" for taxonomic/trophic groups as their position in the three-dimensional space determined

445   by C, N, and P following Peñuelas et al. (2008). Gonzalez et al (2017) also interestingly opened

446   the possibility to incorporate more elements, and also element fluxes and transformation rates as

447   additional axes. In their studies, Gonzalez et al. (2017, 2018) proved the suitability of this

448   approach for animals. This "multidimensional stoichiometric niche" also tried to incorporate

449   rates of nutrient cycling, but these are much more difficult to quantify than elemental

450   concentrations and ratios. Thus, according with the observations in plants, animals, microbes,

451   and also in combination of different taxa altogether (animals and plants) (Peñuelas et al., 2008;

20

452   Sardans et al., 2015; González et al., 2017; Bartrons et al., 2008), the BN multidimensional space

453   proposed here should allow the establishment and quantification of the links between the species

454   BN distances and their taxonomic/phylogenetic distances and between homeostatic capacities

455   and sympatries, and thus to provide information on species/taxa evolutionary processes. The BN

456   thus also aims to refocus the use of the hypervolume in ecological and evolutionary niche studies

457   as discussed above in section 2.

458   Another similar approach to BN, ionomics, i.e. the profiles of mineral elements in plants,

459   has been proposed mostly focused on the genetics of plant mineral nutrition. Ionomics analyzes

460   the elemental composition of organisms in relation to soil concentrations of nutrients and trace

461   elements and also plant functional traits (Salt et al., 2008; Buescher et al., 2010; Baxter et al.,

462   2012; Huang and Salt, 2016). Ionomics is mostly used to study the content of bioelements with

463   electrical charge, mostly absorbed from soils, and mostly within a context of the impact on plant

464   health, food quality and/or identification of hyper-accumulation species. It comes from the

465   confluence of metabolomics and plant nutrition (Salt et al., 2008) that, with the incorporation of

466   modern analytical platforms such as ICP techniques, allows to determine most elements

467   altogether. The fusion of this information with bioinformatics and genetic tools, such as genomic

468   sequencing, allows the identification of the genes that control uptake, storage, and use of soil

469   nutrients and trace elements in plants (Baxter et al., 2012; Lowry et al., 2012). This further

470   allows to analyze the effects of genes and environment on plant nutrition (Buescher, et al., 2010;

471   Lowry et al., 2012; Neugebauer et al., 2018) and plant physiological status (Baxter et al., 2008).

472   BN instead considers all, or as many as possible, bioelements, i.e. also including those such as C

473   or N that are initially from atmospheric, not ionic, forms (e.g. N comes mainly from atmospheric

474   N_2; nitrates are rare in bedrock). BN focuses on organisms and on the total elemental

475   composition and stoichiometry as a proxy of their optimal function and morphology, whereas

476   ionomics focuses on the composition of the medium (soil) to describe different ionomic niches in

477   the abiotic dimension of an ecosystem. Ionomics has aimed to explain shifts in ionic composition

478   by identifying specific genes and their control in changing environmental conditions, thus

479   providing knowledge and information to improve the nutrition of crop species. BN is instead

480   based on the idea that the entire genome of each genotype/species determines species-specific

481   functionality and morphology (more distinct as genomic differences increase) and thus a distinct

482   use of different bioelements, which in turn contribute asymmetrically to different functions and

483   morphological structures. BN can thus be used without knowing about the control of gene

484   expression or about gene function. Moreover, whereas ionomic approach has been developed for

485   plants, BN is developed to be equally applicable to all type of taxa.

486   Even though these ionomic studies are mostly agriculturally oriented, and thus the link

487   with the classical theory of ecological niche is not specifically considered, they are consistent

488   with the BN hypothesis, at least at the level to correlate elemental composition with phylogenetic

489   distance. They constitute strong evidence in favor of BN consistency and constitute a very

490   interesting contribution to the BN.

491   7. **Concluding summary and perspectives**

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

493   quantifiable proxy of the general ecological niche. The BN is characterized by a particular

494   hypervolume of their individual elementomes based on their specific needs and use of

495   bioelements in different amounts and proportions for their structure and functioning. Several

496   organismal structures and functions and the responses to environmental shifts cannot be

497   explained only by the changes in the three main bioelements, C, N and P. We propose that other

498   bioelements such as K, S, Ca, Mg, Fe, Mn and Mo, among others, must be incorporated to fully

499   describe the BN. The BN extends the classical ecological niche concept but has the advantage

500   that it can be easily, directly and quantitatively analyzed.

501   The biogeochemical distances, i.e. the differences in elementome, among species, are a function

502   of taxonomy (phylogenetic distance), sympatry (the bioelemental compositions should differ

503   more among coexisting than among non-coexisting species to avoid competitive pressure), and

504   homeostasis (within the continuum between high homeostasis/low plasticity and low

505   homeostasis/high plasticity). Further studies are warranted to discern the ecological and

506   evolutionary processes involved in the BN of all types of individuals, taxa and ecosystems. The

507   changes in bioelemental availability and use at long timescales should determine phenotypic

508   selection and therefore also ecosystem function and organization, and, at the end, the evolution

509   of life and the environment.

510

516

517   **References**

518   Acquisti, C., J. J. Elser, and S. Kumar. 2009. Ecological nitrogen limitation shapes the DNA

519   composition of plant genomes. Molecular Biology and Evolution 26:953–956.

520   Araujo, M. S., D. I. Bolnick, G. Machado, A. A. Giaretta, and S. F. dos Reis. 2007. Using d13C

521   stable isotopes to quantify individual-level diet variation. Oecologia 152:643–654.

522   Baek, J. H. and S. Lee. 2007. Transcriptome Analysis of Phosphate Starvation Response in.

523   Journal of Microbiological Biotechnology 17:244–252.

524   Baribault, T., R. Kobe, and A. Finley. 2012. Tropical tree growth is correlated with soil

525   phosphorus, potassium, and calcium, though not for legumes. Ecological Monograph

526   82**:**189–203.

527   Bartrons, M., J. Sardans, D. Hoekman, and J. Peñuelas. 2018. Trophic transfer from aquatic to

528   terrestrial ecosystems: a test of the biogeochemical niche hypothesis. Ecosphere 9:e02338.

529   Baxter, I.R., O. Vitek, B. Lahner, B. Muthukumar, M. Borghi, J. Morrissey, M. L.Guerinot, and

530   D. E. Salt. 2008. The leaf ionome as a multivariable system to detect a plant's

531   physiological status. Proceedings of the National Academy of Sciences, USA 105:12081-

532   12086.

533   Baxter, I., C. Hermans, B. Lahner, E. Yakubova, M. Tikhonova, N. Verbruggen, D. Y. Chao,

534   and D. E. Salt. 2012. Biodiversity of mineral nutrient and trace element accumulation in

535   *Arabidopsis thaliana*. PlosOne 7:e35121.

536   Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. MacLeod. 2004. Determining

537   trophic niche width: a novel approach using stable isotope analysis. Journal of Animal

538   Ecology 73:1007–1012.

539   Begon, M. et al. 2006. Ecology: from individuals to ecosystems. – Blackwell.

540   Blonder, B. 2017. Hypervolume concepts in niche- and trait-based ecology. Ecography 41, 1441-

541   1445.

542   Bourgis, F. et al. 1999. S-methylmethionine plays a major role in phloem sulfur transport and is

543   synthesized by a novel type of methyltransferase. Plant Cell 11**:**1485–1498.

544   Buescher, E., T. Achberger, I. Amusan, A. Giannini, C. Oschsenfeld, A. Rus, B. Lahner, O.

545   Hoekenga, E. Yakubova, J. F. Harper, JM. L. Guerinot, M. Zhang, D. E. Salt, and I. R.

546   Baxter, I.R. 2010. Natural genetic variation in selected populations of Arabidopsis thaliana

547   is associated with ionomic differences. PlosOne:art 211081.

548   Chase, J. M. and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary

549   approaches. – University of Chicago Press.

550   Chávez-Vergara, B. et al. 2016. Quercus species control nutrients dynamics by determining the

551   composition and activity of the forest floor fungal community. Soil Biology and

552   Biochemistry 98:186–195.

553   Chimphango, S. B. M., G. Potgieter, and M. D. 2015. Cramer, M. D. Differentiation of the

554   biogeochemical niches of legumes and non-legumes in the Cape Floristic Region of South

555   Africa. Plant Ecology 216:1583–1595.

556   Chowdhury, P. R. et al. 2015. Differential transcriptomic responses of ancient and modern

557   Daphnia genotypes to phosphorus supply. Molecular Ecology 24:123–135 (2015).

558   Cleveland, C. C. and D. Liptzin. 2007. C:N:P stoichiometry in soil: Is there a 'Redfield ratio' for

559   the microbial biomass? Biogeochemistry 85:235–252.

560   Colwell, R. K. and T. F. Rangel. 2009. Hutchinson's duality: the once and future niche.

561   Proceedings of the National Academy of Sciences USA 106:19651–19658.

562   Danger, M., T. Daufresne, F. Lucas, S, Pissard, and G. Lacroix. 2008. Does Liebig's law of the

563   minimum scale up from species to communities? Oikos 117:1741–1751.

564   Davidson, E. A. W., and R. Howarth. (2007) Nutrients in synergy. Nature 449:1000–1003.

565   De, C., and S. Bhattacharyya. 2009. First record of the Recent − subRecent diatomaceous earth

566   from the Gangetic alluvial floodplains of. Current Science 96:967–973.

567 De Bolos, O., and J. Vigo. 2001. In: Barcino (Ed.), Flora dels Països Catalans (I-IV), Barcelona.

568 Du, E. 2017. Integrating species composition and leaf nitrogen content to indicate effects of

569   nitrogen deposition. Environmental Pollution 221:392–397.

570 Durston, D., El-Sabaawi, R. (2017) Bony traits and genetics drive intraspecific variation in

571   vertebrate elemental composition. Functional Ecology 31, 2128-2137.

572 Elser, J. J., K. Hayakawa, and J. Urabe. 2001. Nutrient limitation reduces food quality for

573   zooplankton: Daphnia response to seston Phosphorus enrichment. Ecology 82**:** 898–903.

574 Elser, J. J. et al. 2000a. Nutritional constraints in terretrial and freshwater food webs. Nature

575   **408:**578–580.

576 Elser, J. J. et al. 2000b. Pelagic C:N:P stoichiometry in a eutrophied lake: Responses to a whole-

577   lake food-web manipulation. Ecosystems 3:293–307.

578 Elser, J. J. et al. 2009. Shifts in Lake N:P Stoichiometry and Nutrient Limitation Driven by

579   Atmospheric Nitrogen Deposition. Science 326:835–837.

580 Elser, J. J., and M. Kyle, M. 2009. Nutrient availability and phytoplankton nutrient limitation

581   across\ra gradient of atmospheric nitrogen deposition. Ecology 90:3062–3073 .

582 Elser, J. J. et al. 2010. Atmospheric nitrogen deposition is associated with elevated phosphorus

583   limitation of lake zooplankton. Ecological Letters 13**:** 1256–1261.

584 Falkowski, P. G. and C. S. Davis. 2004. Natural proportions. Redfield ratios: the uniformity of

585   elemental ratios in the oceans and the life they contain underpins our understanding of

586   marine biogeochemistry. Nature 431**:** 131.

587 Folk, R., T. Franquesa, and J. M. Camarasa. 1984. Vegetació. In: Història Natural

588   PaïsosCatalans (VII). Fundació Enciclopèdia Catalana, Barcelona.

589 Frenken, T. et al. 2017. Changes in N:P supply ratios affect the ecological stoichiometry of a

590   toxic cyanobacterium and its fungal parasite. Frontieres in Microbiology 8:1–11.

591 Frisch, D. et al. 2014. A millennial-scale chronicle of evolutionary responses to cultural

592   eutrophication in Daphnia. Ecology Letters 17**:** 360–368.

593 Ganeshram, R. S., T. F. Pedersen, S. E. Calvert, and R. Francois.2002. Reduced nitrogen fixation

594   in the glacial ocean inferred\rfrom changes in marine nitrogen and

595   phosphorus\rinventories. Nature 415:156–159.

596 González, A. L., O. Dézerald, P. A. Marquet, G. Q. Romero, and D. S. Srivastava. 2017. The

597   Multidimensional Stoichiometric Niche. Frontiers in Ecology and Evolution 5:1–17.

598 Gonzalez, A.L., Céréghino, R., Dézerald, O., Farjalla, V.F., Leroy, C., Richardson, B.A.,

599   Richardson, M.J., Romero, G.Q., Srivastava, D.S. 2018. Ecological mechanisms and

600   phylogeny shape invertebrate stoichiometry: A test using detritus-based communities

601   across Central and South America. Functional Ecology, 32, 2448-2463.

602 Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its

603   relevance to ecological and evolutionary theory. American Naturalist 111:1169–1194.

604 Grossman, A. 2000. Acclimation of Chlamydomonas reinhardtii to its Nutrient Environment.

605   Protist 151:201–224.

606 Hartman, W. H., R. Ye, W. R. Horwath, and S. G. A. Tringe 2017. genomic perspective on

607   stoichiometric regulation of soil carbon cycling. ISME Journal:2652–2665.

608 Hatton, P. J., C. Castanha, M. S. Torn, and J. A. Bird. 2015. Litter type control on soil C and N

609   stabilization dynamics in a temperate forest. Global Change Biology 21:1358–1367.

610 He, M. et al. 2016. Influence of life form, taxonomy, climate, and soil properties on shoot and

611   root concentrations of 11 elements in herbaceous plants in a temperate desert. Plant Soil

27

612   398:339–350.

613   Högberg, M. N., D. D. Myrold, R. Giesler, and P. Högberg. 2006. Contrasting patterns of soil

614   N-cycling in model ecosystems of Fennoscandian boreal forests. Oecologia 147:96–107.

615   Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and

616   evolutionary perspectives. Proceedings of the National Academy of Sciences USA 106:

617   19659–19665.

618   Huang, X. Y., and D. E. Salt. 2016. Plant Ionomics: From elemental profiling to environmental

619   adaptation. Molecular Plant 9:787-797.

620   Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative

621   Biology 22:415-427.

622   Jeyasingh, P. D., and L. J. Weider. 2007. Fundamental links between genes and elements:

623   Evolutionary implications of ecological stoichiometry. Moecular Ecology 16:4649–4661.

624   Jeyasingh, P. D. et al. 2011. How do consumers deal with stoichiometric constraints? Lessons

625   from functional genomics using Daphnia pulex. Molecular Ecology 20:2341–2352.

626   Jeyasingh, P. D., L. J. Weider, and R. W. Sterner. 2009. Genetically-based trade-offs in response

627   to stoichiometric food quality influence competition in a keystone aquatic herbivore.

628   Ecological Letters 12**:**1229–1237.

629   Jeyasingh, P. D., R. D. Cothran, and M. Tobler. 2014. Testing the ecological consequences of

630   evolutionary change using elements. Ecology and Evolution 4:528-538.

631   Kattge J., Díaz S., Lavorel S., Prentice I.C., Leadley P., Bönish G., Garnier E., Westoby M., et

632   al., . 2011. TRY - a global database of plant traits. Global Change Biology 17: 2905-2935.

633   Kenesi, G., H. M. Shafik, A. W. Kovács, S. Herodek, and m. Présing. 2009. Effect of nitrogen

634   forms on growth, cell composition and N_2 fixation of Cylindrospermopsis raciborskii in

635   phosphorus-limited chemostat cultures. Hydrobiologia 623:191–202.

636 Kerkhoff, A. J. and B. J. Enquist. 2006.Ecosystem allometry: The scaling of nutrient stocks and

637   primary productivity across plant communities. Ecological Letters 9**:**419–427.

638 Knight, M. R., A. K. Campbell, S. M. Smith, A. J. Trewasvas. 1991. Transgenic plant aequorin

639   reports the effeccts of touch and cold-shock and elicitors on cytoplasmic calcium. Nature

640   352:524–526.

641 Lapenis, A. G., G. B. Lawrence, A. Heim, C. Zheng, and W. Shortle (2013) Climate warming

642   shifts carbon allocation from stemwood to roots in calcium-depleted spruce forests. Global

643   Biogeochemical Cycles 27:101–107.

644 Lamanna, C., B. Blonder, C., Violle, N.J.B., Kraft, B., Sandel, I., Simova, J.C.., Donoghue, J.C.,

645   Svenning, J.C., McGill, B.J., Boyle, B., Buzzard, V., Dollins, P.M.., Jorgensen, A.,

646   Marcuse-Kubitza, N., Moureta-Holme, P.K.., Peet, W.H., Piel, J., Regetz, M., Schlidhauer,

647   N., Spencer, B., Thiers, S.K.., Wilser, S.K., and B.J. Enquist. 2014. Fungtional trait species

648   and the latitudinal diversity gradient. Proceedings of the National Academy of Sciences

649   USA 111:13745-13750.

650 Leal, M. C., O. Seehausen, O., and B. Matthews. 2017. The Ecology and Evolution of

651   Stoichiometric Phenotypes. Trends in Ecology and Evolution 32:108–117.

652 Lennon, J.T., Aanderud, Z.T., Lehmkuhl, B.K., Schoolmaster, D.R.Jr. 2012. Mapping the niche

653   space of soil microorganisms using taxonomy and traits. Ecology 93, 1867-1879.

654 Lenton, T. M., and A. J. Watson. 2000. Redfield revisited: 1. Regulation of nitrate, phosphate,

655   and oxygen in the ocean. Global Biogeochemical Cycles 14:225–248.

656 Lenton, T. M., and C. Klausmeier. 2007. Biotic stoichiometric controls on the deep ocean N : P

657   ratio. Biogeosciences 4**:**353–367.

658   Lowry, D. B., C. C. Sheng, Z. Zhu, T. E. Juenger, B. Lahner, D. E. Salt, and J. H. Willis. 2012.

659   Mapping of ionomic traits in Mimulus guttatus reveals Mo and Cd QTLs that colocalize

660   with MOT1 homologues. PlosOne 7:art e30730.

661   Mantel, N. 1967. The detection of disease clustering and a generalized regression approach.

662   Cancer Research 27, 209-220.

663   Menge, D. N. L. and L. O. Hedin. 2009. Nitrogen fixation in different biogeochemical niches

664   along a 120 000-year chronosequence in New Zealand. Ecology 90:2190–2201.

665   Meunier, C. L., M. Boersma, R. El-Sabaawi, H. M. Halvorson, E. M. Herstoff, D. B. Van de

666   Waal, and R. J. Vogt, 2017. From elements to function: toward unifying ecological

667   stoichiometr and trait-based Ecology. Frontieres in Environmental Science 5:Art 18.

668   Morcuende, R. et al. 2007. Genome-wide reprogramming of metabolism and regulatory

669   networks of Arabidopsis in response to phosphorus. Plant, Cell Environment 30:85–112.

670   Naples, B. K., and M. C. Fisk. 2010. Belowground insights into nutrient limitation in northern

671   hardwood forests. Biogeochemistry 97**:**109–121.

672   Neugebauer, K., M. R. Broadley, H. A. El-Serehy, T. S. George, J. W. McNicol, M. F. Moraew,

673   and P. J. White. 2008. Variation in the Angiosperm Ionome. Physiologia Plantarum 1–17.

674   Novotny, A. M. et al. 2007. Stoichiometric response of nitrogen-fixing and non-fixing dicots to

675   manipulations of CO_2, nitrogen, and diversity. Oecologia 151:687–696.

676   Peñuelas, J. et al. 2013. Evidence of current impact of climate change on life: A walk from genes

677   to the biosphere. Global Change Biology 19:2303–2338.

678   Peñuelas, J., and J. Sardans. 2009. Elementary factors. Nature 460:803–804 (2009).

679   Peñuelas, J. et al. 2010. Faster returns on 'leaf economics' and different biogeochemical niche in

680   invasive compared with native plant species. Global Change Biology 16:2171–2185.

681   Peñuelas, J., J. Sardans, R. Ogaya, and M. Estiarte. 2008. Nutrient stoichiometric relations and

682   biogeochemical niche in coexisting plant species: Effect of simulated climate change.

683   Polish Journal of Ecology 56**:**613–622 (2008).

684   Pereira, F.C., Berry, D. 2017. Microbial nutrient niches in the gut. Environmental Microbiology,

685   19, 1366-1378.

686   Peterson, A. T. 2011. Ecological niche conservatism: a time-structured review of evidence.

687   Journal of Biogeography 38:817-827.

688   Pianka E. R., L.J. Vitt, N. Pelegrin, D.B. Fitzgerald, and K.O. Winemiller. 2017. Toward a

689   periodic table on niches, or exploring the lizard niche hypervolume. The American

690   Naturalist 2017. Toward a Periodic Table of Niches, or Exploring the Lizard Niche

691   Hypervolume. The American Naturalist 190:601-616.

692   Pierce, S., D. Negreiros, B. E. L. Cerabolini, J. Kattge, S. Díaz, M. Kleyer, B., Shiply, S. J.

693   Wright, et al. 2016. A global method for calculating plant CSR ecological strategies

694   applied across biomes world-wide. Functional Ecology 31:444-457.

695   Poxleitner, M., G. Trommer, P. Lorenz, and H. Stibor. 2016. The effect of increased nitrogen

696   load on phytoplankton in a phosphorus-limited lake. Freshwater Biology 61**:**1966–1980.

697   Quigg, A. et al. 2003. The evolutionary inheritance of elemental stoichiometry in marine

698   phytoplankton. Nature 425:291–294.

699   Rivas-Ubach, A., J. Sardans, M. Perez-Trujillo, M. Estiarte, and J. Peñuelas. 2012. Strong

700   relationship between elemental stoichiometry and metabolome in plants. Proceedings of

701   the National Academy of Sciences USA 109:4181–4186.

702   Rivas-Martínez, S., F. Fernández-González, J. Loidi, M. Lousa, and A. Penas. 2001.

703   Syntaxonomical Checklist of vascular plant communities of Spain and Portugal to

704   association level. Itinera Geobotany 14, 5–341.

705   Reinhard, C. T. et al. 2017.Evolution of the global phosphorus cycle. Nature 541:386–389.

706   Salt, D. E., I. Baxter, and B. Lahner. 2008. Ionomics and the study of plant ionome. Annual

707   Review of Plant Biology 59:709-733.

708   Salvagiotti, F. et al. 2017. N:P:S stoichiometry in grains and physiological attributes associated

709   with grain yield in maize as affected by phosphorus and sulfur nutrition. Field Crop

710   Research 203:128–138.

711   Sardans J., J., Peñuelas, and M. Estiarte. 2008a. Changes in soil enzymes related to C and N

712   cycle and in soil C and N content under prolonged warming and drought in a

713   Mediterranean shrubland. Applied Soil Ecology 39: 223-235.

714   Sardans J., J. Peñuelas, M. Estiarte and P. Prieto. 2008b. Warming and drought alter C and N

715   concentration, allocation and accumulation in a Mediterranean shrubland. Global Change

716   Biology 14: 2304-2316.

717   Sardans J., J. Peñuelas, and R. Ogaya. 2008c. Drought-Induced Changes in C and N

718   Stoichiometry in a *Quercus ilex* Mediterranean Forest. Forest Science 54: 513-522.

719   Sardans, J., and J. Peñuels. 2013. Tree growth changes with climate and forest type are

720   associated with relative allocation of nutrients, especially phosphorus, to leaves and wood.

721   Global Ecology and Biogeography 22:494-507.

722   Sardans, J., and J.Peñuelas. 2014. Climate and taxonomy underlie different elemental

723   concentrations and stoichiometries of forest species: The optimum 'biogeochemical niche'.

724   Plant Ecology 215:441–455.

725   Sardans J., Peñuelas J. 2015. Potassium: a neglected nutrient in global change. Global Ecology

726   and Biogeography 24:261-275.

727   Sardans, J., O. Grau, H.Y.H. Chen, I.A. Janssens, P. Ciais, S. Piao, and J. Peñuelas. 2017.

728   Changes in nutrient concentrations of leaves and roots in response to global change

729   factors. Global Change Biology 23:3849-3856.

730   Sardans, J. et al. 2016. Foliar and soil concentrations and stoichiometry of nitrogen and

731   phosphorous across European Pinus sylvestris forests: Relationships with climate, N

732   deposition and tree growth. Functional Ecology 16:676-689.

733   Sardans, J., A. Rivas-Ubach, and J. Peñuelas. 2011. Factors affecting nutrient concentration and

734   stoichiometry of forest trees in Catalonia (NE Spain). Forest Ecology and Management

735   262:2024-2034.

736   Sardans, J., R. Alonso, J. Carnicer, M. Fernandez-Martinez, M. G. Vivanco, and J. Peñuelas.

737   2016. Factors influencing the foliar elemental composition and stoichiometry in forest trees

738   in Spain. Perspectives Plant Ecology, Evolution and Systematics 18:52–69.

739   Sardans, J., I. A. Janssens, R. Alonso, S. D. Veresoglou, M. C. Rillig, T. G. M. Sanders, J.

740   Carnicer, I. Filella, G. Farré-Armengol, and J. Peñuelas. 2015. Foliar elemental

741   composition of European forest tree species results from evolutionary traits and the present

742   environmental and competitive conditions. Global Ecology and Biogeography 24**:**240–255.

743   Sardans J., Peñuelas J., Coll M., Vayreda J., Rivas-Ubach A. 2012a. Stoichiometry of potassium

744   is largely determined by water availability and growth in Catalonian forests. Functional

745   Ecology 26: 1077-1089.

746   Sardans, J., A. Rivas-Ubach, and J. Penuelas. 2012b. The elemental stoichiometry of aquatic and

747   terrestrial ecosystems and its relationships with organismic lifestyle and ecosystem

748   structure and function: A review and perspectives. Biogeochemistry 111:1–39.

749   Sardans, J., A. Rivas-Ubach, and J. Peñuelas. 2012c. The C:N:P stoichiometry of organisms and

750   ecosystems in a changing world: A review and perspectives. Perspectuives in Plant

751   Ecology Evolution and Systematics 14:33–47.

752   Schoener, T. W. 1986. in Ecological concepts: the contribution of ecology to an understanding

753   on the natural word (ed. Cherret, J. M.) (Cambridge, Blackwell Scientific Publications,

754   1986). doi:10.1126/science.232.4746.113-a

755   Shaul, O. 2002. Magnesium transport and function in plants: the tip of the iceberg. BioMetals

756   15:309–323.

757   Sistla, S. A., A. P. Appling, A. M. Lewandowska, B. N. Taylor, and A. A. Wolf. 2015.

758   Stoichiometric flexibility in response to fertilization along gradients of environmental and

759   organismal nutrient richness. Oikos 124**:** 949–959.

760   Slade, S. 2006. Elements in living organisms. (The Rosen publishing Group, 2006).

761   Sterner, R. W.., and J. J. Elser. 2002. Ecological Stoichiometry: The Biology of Elements from

762   Molecules to the Biosphere.

763   Sun, L. et al. 2017. Leaf elemental stoichiometry of Tamarix Lour. species in relation to

764   geographic, climatic, soil, and genetic components in China. Ecological Enginnering

765   106:448–457.

766   Tripler, C. E. S. S. Kaushal, G. E. Likens, and M. Todd Walter. 2006. Patterns in potassium

767   dynamics in forest ecosystems. Ecological Letters 9:451–466.

768   Turner, C. B., B. D. Wade, J. R. Meyer, B. Sommerfeld, and R. E. Lenski 2017. Evolution of

769   organismal stoichiometry in a long-term experiment with Escherichia coli. Royal Society

770   Open Science 4:170497.

771   Tyrrell, T. 1999. The relative in inluences of nitrogen and phosphorus on oceanic primary

772   production. Nature 400:525–530.

773   Urbina I., Sardans J., C. Beierkuhnlein, A. Jentsch, S. Backhaus, K. Grant, J. Kreyling J., and J.

774   Peñuelas. 2015. Shifts in the elemental composition of plants during a very severe drought.

775   Environmental and Experimental Botany 111:63-73.

776   Urbina, I., J. Sardans, O. Grau, C. Beierkuhnlein, A. Jentsch, J. Kreyling, and J. Peñuelas. 2017.

777   Plant community composition affects the species biogeochemical niche. Ecosphere

778   8:e01801.1

779   Violle, C., and L. Jiang. 2009. Towards a trait-based quantification of species niche. Journal of

780   Plant Ecology 2:87-93

781   Violle, C., P. B. Reich, S. W. Pacala, B. Enquist, and J. Kattge. 2014. The emergence and

782   promise of functional biogeography. Proceedings of the National Academy of Sciences

783   USA 11:13690-13696.

784   Wilson, R.P., McMahon, C.R., Quintana, C.R., Frere, E., Scolare, A., Hays, G.C., Bradshow,

785   C.J.A. 2011. N-dimensional animal energetic niches clarify behavioural options in a

786   variable marine Environmental. Journal of Experimental Biology 214, 646-656.

787   Yamamichi, M., and C. L. Meunier, A. Peace, C. Prater, and M. A. Rúa. 2015.. Rapid evolution

788   of a consumer stoichiometric trait destabilizes consumer-producer dynamics. Oikos

789   124:960–969.

790   Yu, Q., J. J. Elser, N. He, H. Wu, Q. Chen, G. Zhang, and X. Han. 2011. Stoichiometry

791   homeostasis of vascular plants in the inner Mongolia grassland. Oecologia 166:1–10.

792   Zamora, P. B., M. B. Cardenas, R. Lloren, and F. P. Siringan. 2017. Seawater-groundwater

793   mixing in and fluxes from coastal sediment oberlying discrete fresh seepage zones: a

794   modeling study. Journal of Geophysical Research Oceans 122:6565–6582.

795   Zederer, D. P., U. Talkner, M. Spohn, and R. G. Joergensen. 2017. Microbial biomass

796   phosphorus and C/N/P stoichiometry in forest floor and A horizons as affected by tree

797   species. Soil Biology and Biochemistry 111:166–175.
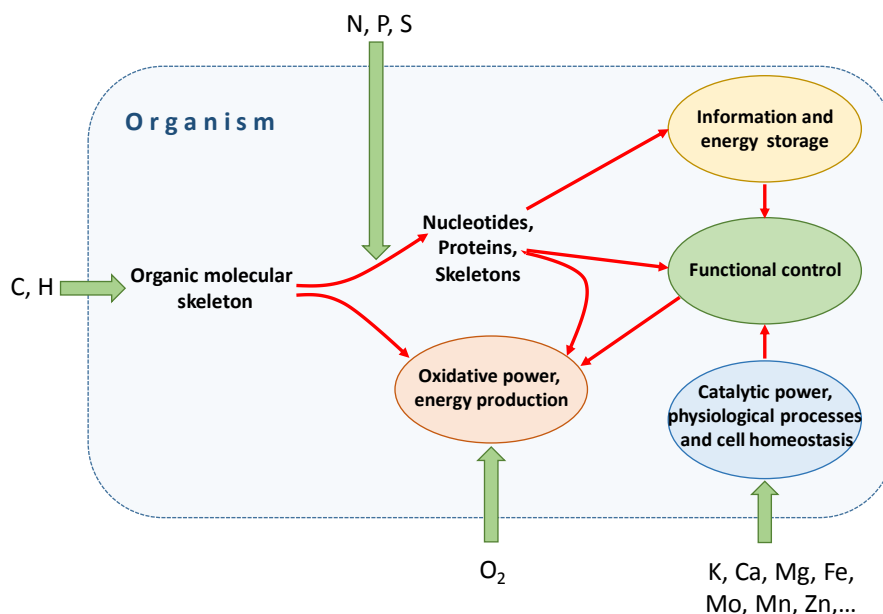
798   Zhang, S. B., J. L. Zhang, J. W. F. Slik, and K. F. Cao. 2012. Leaf element concentrations of

799   terrestrial plants across China are influenced by taxonomy and the environment. Global

800   Ecology and Biogeography 21: 809–818.

801

802

803
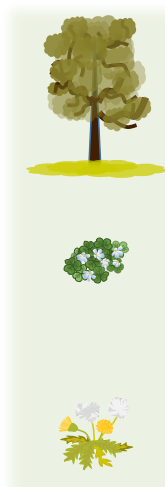
Figure captions

806 Figure 1. Schematic of the use of bioelements by organism in different functions. C, H, and O

807 are the basis of organismic structure, whereas N, P and S enter in the various biomolecules

808 allowing biochemical reactions. The molecules that control life processes (e.g. RUBISCO or

809 chlorophyll), that carry information (e.g. DNA and RNA), and that control the storage and

810 release of energy when and where necessary (e.g. ATP and NAD) all incorporate N, P and in

811 lower amounts S. Other bioelements, normally present in low concentrations such as potassium

812 (K), magnesium (Mg), iron (Fe), calcium (Ca), molybdenum (Mo), manganese (Mn) and zinc

813 (Zn) are cofactors in catalytic reactions in several biochemical and physiological processes

814 including for example photosynthesis, respiration, or cellular ion balance. The arrows indicate

815 the processes in which each bioelement is involved. Green arrows indicate the main organismal

816 functions to which each bioelement contributes. The red arrows indicate the relationships of the

817 different bio-molecules with basic organismal structures and functions.

The example of plants

Ecological strategy	Ecological variables					Stoichiometry traits				
	Live-span	Growth rate	Body size	Reproductive strategy	Other	Stoichiometry flexibility	[C]	[N]	[P]	[K]
K-strategy (competitor)	Long	Medium	Large	Few seeds but with highly caloric reserves	Strong investment in structure	Medium	—	↑	↑	—
A-strategy (stress-tolerator)	Medium	Slow	Medium-small	Medium	Strong investment in C-rich secondary compounds	Low	↑	↓	↓	↑
r-strategy (ruderal)	Short	Fast	Small	Many seeds but with low caloric reserves	General trend to develop belowground vegetative & reproductive structures	High	—	↑	↑↑	—

Figure 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).

$$BN_i = BN \text{ of } taxa_i = Elementome_{i1-n} = (C:N:P:K:S:Mg:Ca:\dots)_{i1-n} = BNtax_i + \frac{\partial BNtax_i}{\partial Env} = BNtax_i + f(Tax_i, Symp_i, Hom_i)$$

$$BN_j = BN \ taxa_{j=} Elementome_{j1-n} = (C:N:P:K:S:Mg:Ca\dots)_j$$

$$BN_j = BNtax_j + \frac{\partial BNtax_j}{\partial Env} = BNtax_{j1-n} + f(Tax_j, Symp_j, Hom_j)$$

$$\Delta BN_{i-j} = (BNtax_i - BNtax_j) + \frac{\partial BN_{taxi} - \partial BN_{taxj}}{\partial Env} = (BNtax_i - BNtax_j) + [f(Tax_i, Symp_i, Hom_i) - f(Tax_j, Symp_j, Hom_j)]$$

825
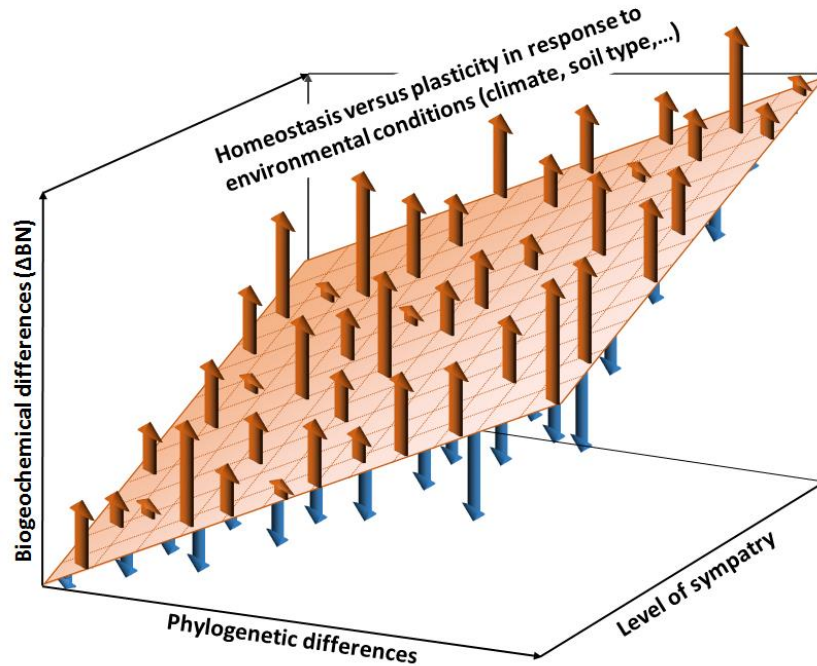
Figure 3. Theoretical distribution of the biogeochemical differences between species as a

function of (1) the taxonomic and phylogenetic distances between them, (2) the level of

sympatry (overlap frequency in their corresponding areas of distribution) and of (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 BN

distance induced by variable current environmental conditions (e.g. climate, soil traits,

neighbors).

834

835
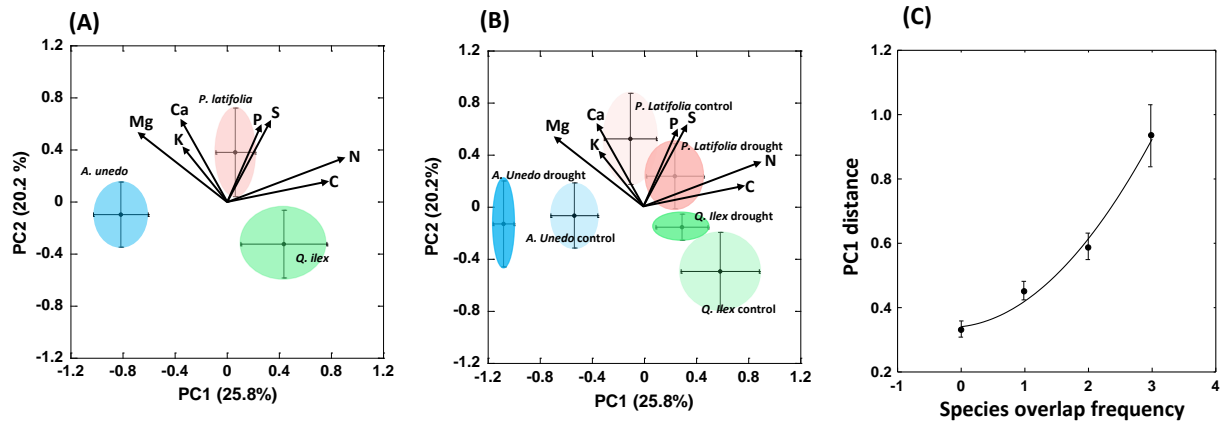
Figure 4. (A) Biogeochemical niche segregation among coexisting plant species. We analyzed

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 ± confidence intervals (95%, represented by the ellipses) of the species × climate

interaction groups are depicted in the plot thus comparing control plants to those submitted to a

decrease of 20 % of water availability during six years 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*). 0, no overlap; 1, occasional overlap; 2,

moderate overlap; 3, frequent overlap. Based on Rivas-Martinez et al. (2001) De Bolos and Vigo

853   (2001), CREAF, Catalonia cover map, (2013) and Folk et al. (1984).

854
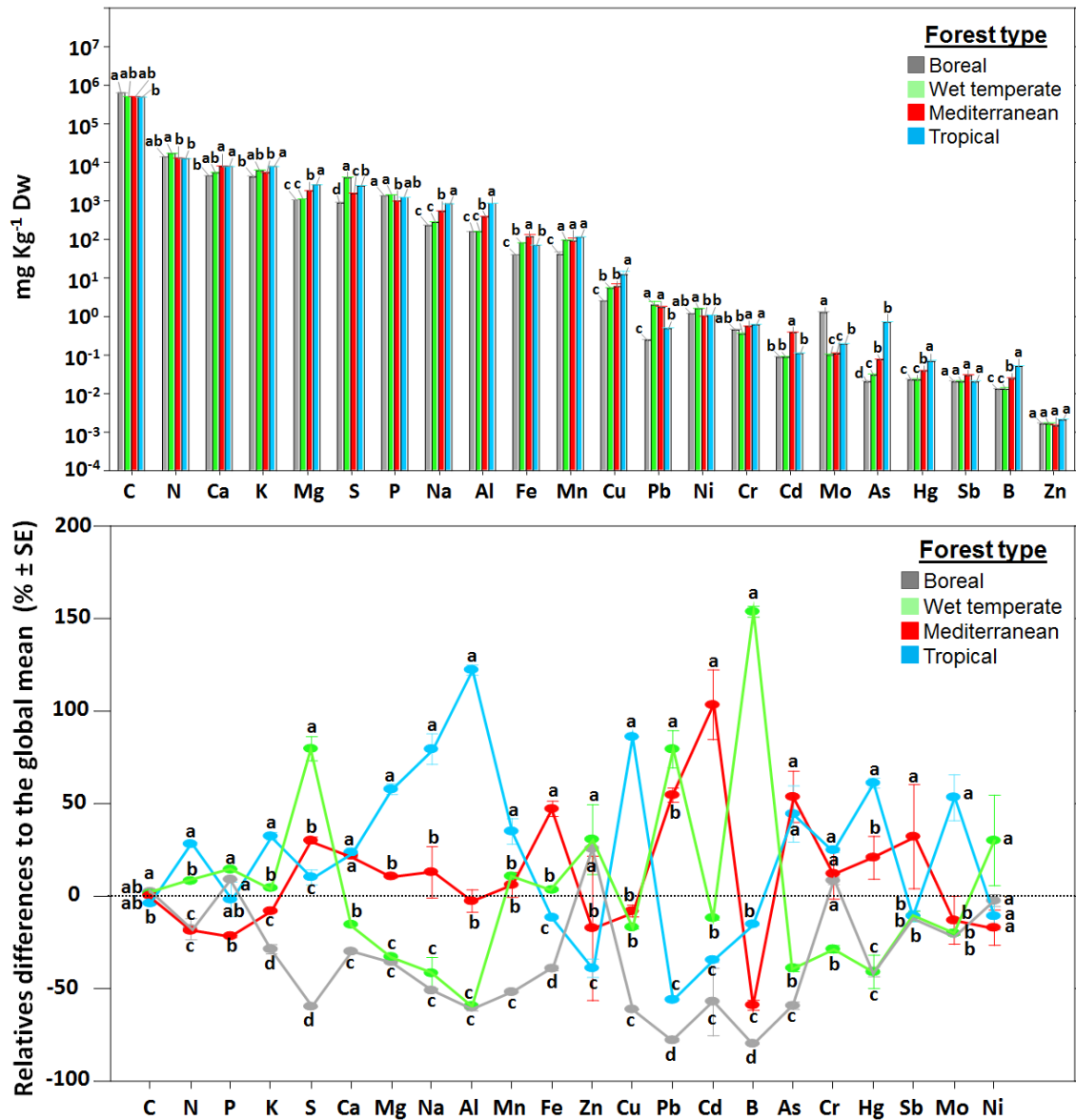
855

856   Figure 5. Elementome, full spectrum of bioelemental content, of boreal, wet temperate,

857   Mediterranean and tropical forests. (A) Elementomes calculated from web of science data

858   incorporated to our GEU-CREAF dataset (Boreal forest: 473 sites and 1890 trees; Wet temperate

859   forests: 2882 sites and 12665 trees; Mediterranean forests: 2001 sites and 2901 trees; Tropical

860   wet forest: 1100 sites and 1821 trees). The values in plot B show the difference of each forest

861   type relative to the global mean (% ± SE). We have used data from the main available data bases

862   (e.g. TRY and ICP forest) and from an exhaustive search for woody plants from non-

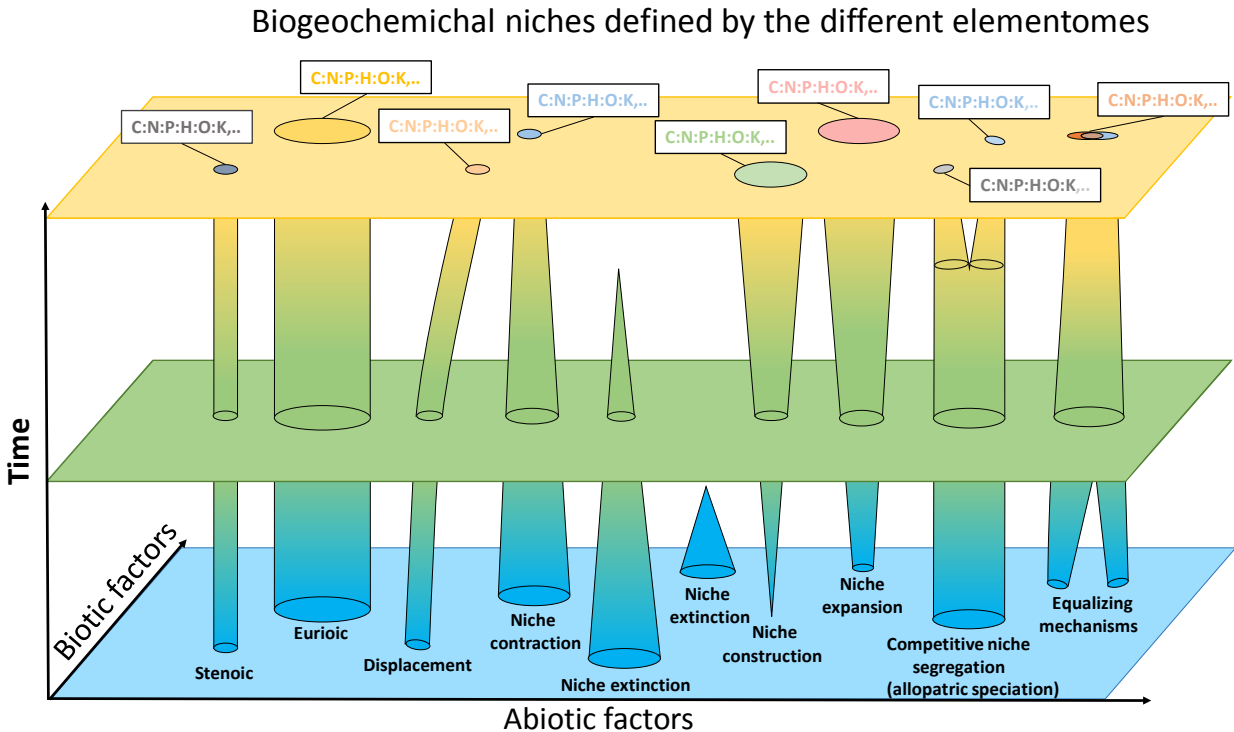863   manipulated areas in WEB of Science

864
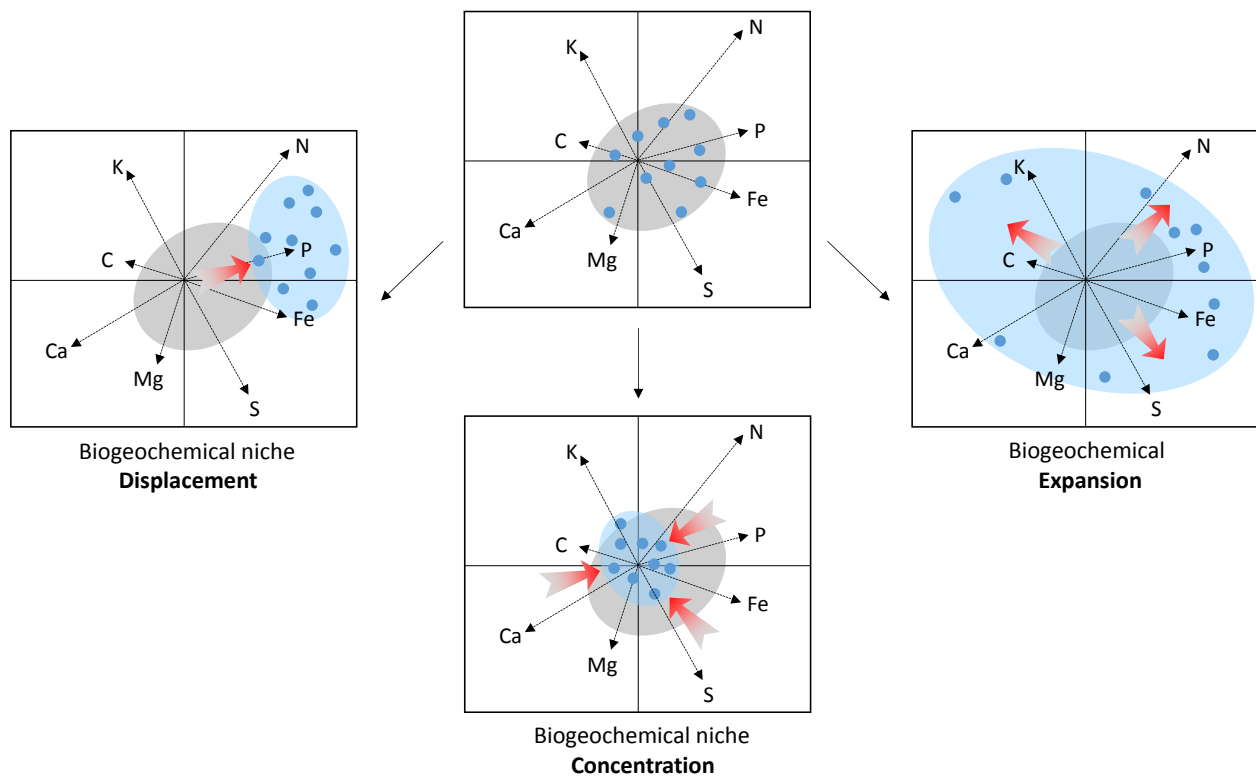
865

866   Figure 6. Three possible biogeochemical niche responses to short-term changes in the

867   environmental conditions: Contraction, Expansion or Displacement. Blue dots represent

868   individuals of a species, grey and blue ellipses represent the initial and final BN space.

869

Figure 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 euroic (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

883   and physical position in the ecosystem that can vary with time in response to changes in abiotic

884   variables (climate, perturbations such as volcanic eruptions, etc.) and to changes in the impacts

885   and feed-backs of the other organisms living in it (biotic factors). In this context, each niche

886   should determine a specific and particular content of different bioelements in each moment. This

887   should also determine a singular elementome accompanying the niche characteristics of each

888   genotype and species at both micro- and macro-evolutionary timescales.