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Bryophyte C:N:P stoichiometry, biogeochemical niches, and elementome plasticity driven by environment and coexistence

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Abstract

Ecological stoichiometry and studies of biogeochemical niches have mainly focused on plankton and vascular plants, but the phenotypically closest modern relatives of early plants, bryophytes, have been largely neglected. We analysed C:N:P stoichiometries and elemental compositions (K, Na, Mg, Ca, S, Fe) of 35 widely distributed bryophyte species inhabiting springs. We estimated bryophyte C:N:P ratios and their biogeochemical niches, investigated how elementomes respond to the environment, and determined whether they tend to diverge more for coexisting than non-coexisting individuals and species. The median C:N:P was 145:8:1, intermediate between Redfield's ratio for marine plankton and those for vascular plants. Biogeochemical niches were differentiated amongst species and were phylogenetically conserved. Differences in individual and species-specific elementomes increased with coexistence between species. Our results provide an evolutionary bridge between the ecological stoichiometries of algae and vascular plants and suggest that differences in elementomes could be used to understand community assemblages and functional diversity.

Keywords: Elemental composition, mosses, liverworts, nitrogen, phosphorus, niche partitioning.

Introduction

The elemental composition and stoichiometry of organisms strongly determine their functional traits and thus their interaction with the environment (Sterner & Elser 2002; Peñuelas *et al.* 2019). Many studies have successfully associated the concentrations of carbon (C), nitrogen (N), and phosphorus (P) and stoichiometric ratios (C:N, C:P, and N:P) of organisms with the functioning of marine, freshwater, and terrestrial ecosystems (Redfield 1934; Güsewell & Koerselman 2002; Sterner & Elser 2002; Wright *et al.* 2004; Güsewell 2004; McGroddy *et al.* 2004; Rivas-Ubach *et al.* 2012; Sardans *et al.* 2012; Gargallo-Garriga *et al.* 2014; Fernández-Martínez *et al.* 2018, 2019b). Differences in the elemental composition of organisms, including C, N and P as well as many other elements such as K, Na, Mg, Ca, S and Fe, represent different proportions of biomolecules such as proteins, sugars, and lipids, contrasting metabolic and functional features, and trophic levels and thus underlie differences in the *ecological niches* that they occupy (Elser *et al.* 1996; Sterner & Elser 2002; Peñuelas *et al.* 2008, 2010, 2019; Sardans *et al.* 2012; Sardans & Peñuelas 2014).

The homeostatic regulation of the concentrations of elements in an individual (i.e., the *elementome* (Peñuelas *et al.* 2019)) is expected to some extent in most types of organisms; the variability of C, N, and P concentrations has been reported to be higher amongst species than within species (Hessen *et al.* 2013; Sardans *et al.* 2015; Urbina *et al.* 2017). Homeostatic control is generally stronger in heterotrophs than autotrophs (Hessen *et al.* 2013). Instead, some taxa such as chlorophytes totally lack homeostatic control (Persson *et al.* 2010; Hessen *et al.* 2013). Additionally, different elements may present different levels of homeostatic control depending on whether they are macronutrients, essential micronutrients or trace elements (Karimi & Folt 2006). The concept of the homeostatic regulation of elementomes of individuals and species is the foundation of the *biogeochemical niche* (also called *multidimensional stoichiometric niche* (González *et al.* 2017)), defined as the *n*-dimensional space occupied by the characteristic concentrations of elements of individuals of a species (Peñuelas *et al.* 2008, 2010; Sardans *et al.* 2021). An elementome will be further or closer to the optimal species-specific biogeochemical niche depending on environmental conditions, the developmental stage of the organism and the balance between elementome plasticity and homeostatic regulation. The evolutionary histories of species have been repeatedly associated with differences in elemental composition amongst species (Sardans *et al.* 2015, 2021; Bai *et al.* 2019; Fernández-Martínez *et al.* 2019b), further indicating the adaptive value of biogeochemical niches.

Differences in biogeochemical niches amongst species require different adaptations to take up, use, retain, and release elements after differences in environmental elemental availability have been accounted for (Güsewell 2004). We therefore hypothesised that two coexisting species would be more likely to compete for the same resources, and in the same proportions, if their biogeochemical niches were very similar and strongly homeostatic (i.e., showing no plasticity; with a limited ability to shift to avoid competition). Organisms in biological systems should thus tend towards diverse communities of biogeochemical niches in order to optimise the use of environmental resources by *niche partitioning* (Loreau & de Mazancourt 2013). The foliar elementomes of 12 coexisting Mediterranean tree species have, accordingly, been reported to be more different than those of non-coexisting species (Peñuelas *et al.* 2019). This finding is crucial, because strong evidence that competition between organisms decreases with the distance between their elementomes could lead to new research and methodologies for studying community assemblages (e.g. why some combinations of species are more likely than others) and functional diversity across ecosystems. Evidence supporting this hypothesis, however, is still scarce, and it has not yet been tested on the elementomes of entire organisms. Bryophytes are thus excellent subjects for studying the ramifications of the biogeochemical niche hypothesis.

Bryophytes were the first plants to colonise and spread on land, evolving from freshwater algae between the Cambrian and Ordovician eras, 470–515 million years ago (Renzaglia *et al.* 2007; Morris *et al.* 2018; Harris *et al.* 2020). Modern bryophytes, and particularly the aquatic and semi-aquatic ones, are thus amongst the phenotypically closest relatives of the first colonisers of land and amongst the oldest living terrestrial plants. They are also much simpler than vascular plants and are extremely sensitive to environmental conditions due to their lack of true roots and thick cuticles (Porley & Hodgetts 2005), excellent qualities for testing ecological theories. The field of ecological stoichiometry has studied a wide array of organisms, including marine and freshwater plankton, other animals, and vascular plants (including grasses and trees)(Redfield 1934; Goldman *et al.* 1979; Elser 2000; McGroddy *et al.* 2004; Reich *et al.* 2010). Bryophytes, however, have been largely overlooked even though they are the evolutionary link between algae and vascular plants (but see (Steinman 1994; Christmas & Whitton 1998; Waite & Sack 2011; Huang *et al.* 2019) where only a few species were studied and reference (Wang *et al.* 2019) were 22 species were analysed). From a practical point of view, bryophytes, like algae, have the advantage that analyses of their elemental composition represent the entire organism, allowing a better representation of the elementome, in contrast with vascular plants for which only the elemental composition of leaves is usually analysed (Kattge *et al.* 2011; Sardans *et al.* 2016b).

Our main aims to fill in these gaps were thus to: *i*) first determine the average C:N:P ratio for bryophytes for comparison to those previously estimated for marine plankton (Redfield's ratio (Redfield 1934)) and vascular plants, *ii*) then investigate the environmental and phylogenetic controls of bryophyte elementomes by studying their C:N:P stoichiometry and the elemental concentrations of C, N, P, K, Na, Ca, Mg, S, and Fe, and *iii*) finally to estimate the biogeochemical niches for the most common bryophyte species inhabiting Mediterranean springs and to test whether coexisting individuals and species tend to differentiate their elementomes more than individuals and species that do not coexist. We hypothesised that: *i*) bryophyte C:N:P stoichiometric ratios will lie between those reported for marine plankton and those of vascular plants, *ii*) evolutionary history, as well as current environmental variables, explain a considerable amount of the variability in the elementomes of the bryophyte species, *iii*) bryophyte biogeochemical niches differ between species and that differences between individual elementomes or species biogeochemical niches tend to be larger between coexisting individuals or species.

We thus analysed the elementomes of 35 aquatic and semi-aquatic (hygrophytic) species of bryophytes inhabiting springs distributed across large gradients of water chemical composition, climate, and altitude as a proxy for exposure to ultraviolet (UV) light. Differences in climate have been identified as one of the reasons for differences in the elemental composition amongst plants because of physiological changes such as growth rates and stress adaptations (Sardans *et al.* 2016a, 2021). Water chemistry, and especially water electrical conductivity, have been previously identified as key environmental variables accounting for the traits of bryophytes (Fernández-Martínez *et al.* 2019) and their distributions (Bes *et al.* 2018; Fernández-Martínez *et al.* 2020). Given that bryophytes absorb nutrients through all their tissues (Porley & Hodgetts 2005), nutrients dissolved in water should be one of the main sources of elements for these bryophytes. UV radiation, however, reduces bryophyte performance, such as photosynthetic rates and chlorophyll concentrations (Martínez-Abaigar *et al.* 2006) and could thus be also affecting bryophyte elemental composition. Our results will help us to understand the ecological stoichiometric transitions between marine and freshwater ecosystems, plankton, and vascular plants.

Methods

Experimental design: field and laboratory analyses

We surveyed a total of 363 Mediterranean springs (i.e. 363 independent bryophyte communities) distributed across Catalonia (northeastern Iberian Peninsula, **Figure S1**) from which we collected a sample of all aquatic and semi-aquatic bryophyte species (i.e. hygrophytic species (Dierssen 2001)) in direct contact with the spring water (Bes *et al.* 2018; Fernández-Martínez *et al.* 2019). Studied bryophytes coexist in dense and heterogeneous patches formed by several species competing for space and resources (i.e., some species often grow on top of other species, so interaction between species is ensured). Samples were stored dry after the species were identified. We then selected a subset of 253 bryophyte specimens with large enough samples to analyse their elemental compositions (see below). The subset comprised 35 species (29 mosses and six liverworts) from 163 springs along large gradients of climate and water chemistry (Fernández-Martínez *et al.* 2019a). The species were representative of a very broad geographic area due to the large climatic and hydrochemical gradients sampled, with some species distributed across the entire Northern Hemisphere (see GBIF records: www.gbif.org).

We submerged the samples in a solution of acetic acid at pH 2.7 to remove incrustations of $CaCO_3$ prior to the elemental analyses. The samples were then thoroughly rinsed with distilled water, dried at 60 °C for 48 h, and ground to a powder with a mortar and pestle using liquid nitrogen. The C and N concentrations in the bryophytes were analysed by Isotope Ratio Mass Spectrometry (IRMS) using a Flash EA1112 and TC/EA coupled to a Delta C stable-isotope mass spectrometer through a ConFlo III interface (Thermo Finnigan, Thermo Electron Corporation, Bremen, Germany). Bryophyte concentrations of P, K, Na, K, Mg, Ca, S, and Fe were determined by inductively coupled plasma mass/optical emission spectrophotometry (ELAN 600 and Optima 8300, respectively, Perkin Elmer, Waltham, Massachusetts, USA). Before the analyses, the samples were digested overnight at 90 °C in a 2:1 nitric acid:hydrogen peroxide solution. These analyses were carried out at the Scientific and Technical Centers of the University of Barcelona.

All springs drained water from natural aquifers, so the chemical features of the water were constant over time. None of our springs drained treated water. Water flows constantly throughout the year, so the bryophytes were in continuous contact with the spring water. Interruptions in water flow, however, may occasionally occur during winter when some springs freeze or in summer because of intense drought.

We measured the electrical conductivity and pH of the water in each spring using a combined pH and conductivity meter (Hanna Instruments, Woonsocket, Rhode Island, USA). A sample of water was collected to measure the concentrations of ions and elements. We used ion chromatography to determine Cl^-, SO_4^{2-}, NH_4^+, NO_3^-, Na^+, K^+, Mg^{2+}, and Ca^{2+} concentrations. The NH_4^+ concentrations in our springs were all below detectable limits (<0.1 μeq L^{-1}). Phosphate (PO_4^{3-}) was analysed colorimetrically as described by Murphy and Riley (Murphy & Riley 1962). Fe was determined using inductively coupled plasma/mass spectrometry. Further details of the analyses of water chemistry are provided in reference (Fernández-Martínez *et al.* 2019a). We also recorded the geographic coordinates of the springs using a GPS device to extract the altitude and mean monthly temperature and precipitation from the Climatic Atlas of Catalonia (Pons 1996; Ninyerola *et al.* 2000). Mean annual temperature was calculated as the average of monthly mean temperatures. We also estimated annual water availability as the annual sum of monthly precipitation minus evapotranspiration (estimated using Hargreaves' equation (Hargreaves 1994)). A Mediterranean climate dominates the study area, but mean annual precipitation (approximately 550–1200 mm), mean annual temperature (approximately 4–16 °C), and seasonality vary greatly between regions of the study area (Martín-Vide 1992; Fernández-Martínez *et al.* 2019).

Statistical analyses

Effect of the environment on bryophyte elementomes

We first tested the effects of water chemistry (electrical conductivity and dissolved elements), climate (mean annual temperature and water availability), and altitude (as a proxy for the intensity of UV light) on bryophyte elemental composition and stoichiometry. We fitted three mixed multivariate and phylogenetically informed models using a Bayesian framework and the R (R Core Team 2019) *brms* package (Bürkner 2017, 2018). *i*) In the first model, we used C:N, C:P, and N:P molar ratios as response variables and NO_3^- and PO_4^{3-} concentrations, water electrical conductivity, mean annual temperature, annual water availability, and altitude as explanatory variables. This model was also used to estimate the overall bryophyte C:N:P stoichiometry based on its posterior distributions. *ii*) The second model included the concentrations of the main macronutrients (C, N, P, and K) as response variables and the same predictors described in the first model plus the water concentration of dissolved K^+ to test its relationship with bryophyte K concentration. *iii*) The third model included Na, Mg, Ca, S, and Fe concentrations as response variables and all predictors described in the first model plus the concentrations of the corresponding elements dissolved in water for each response variable (Na^+, Mg^{2+}, Ca^{2+}, SO_4^{2-}, and total Fe). Additional models were also fitted to investigate the scaling relationship between the C, N, and P concentrations.

All three models were fitted using a log-normal distribution for the response variables, with species as a random factor and controlled for phylogenetic effects using the consensus phylogenetic tree provided in reference (Fernández-Martínez *et al.* 2019). All predictors were standardised (mean=0, SD=1), and the concentrations of water ions were also log-transformed before standardisation. Priors used followed a normal distribution (0, 2) for beta estimates of the predictors and a *t*-student distribution (3, 0, 5) for the intercept, random and phylogenetic effects, and the residuals. The probability of direction (PD) and Bayes factors (BFs) were estimated for all predictors as an estimation of the relevance of the explanatory variables. PD and BFs were based on the null hypothesis that mean = 0, using the functions *p_direction* and *bayesfactor_parameters* from the *bayestestR* package (Makowski *et al.* 2019), respectively. Conditional effects plots were used to visualise the relationships between the response and predictor variables using the *conditional_effects* function in *brms*. We also tested how phylogenetic uncertainty could condition our results by fitting all three models using a random subset of 100 molecular phylogenetic trees of the sample of 1000 trees with similar posterior probabilities estimated in reference (Fernández-Martínez *et al.* 2019) and using default flat priors in *brms* to reduce calculation times. Our results using the consensus phylogeny compared to using 100 trees were identical, but the phylogenetic and interspecific effects shown here correspond to the models using 100 trees, estimated as intraclass correlation coefficients (see **Model summaries** in **Supplementary information**). We discarded seven of the 253 bryophyte samples with data for elemental composition (two for clear outliers for P concentration and five for a lack of measurements of either water NO_3, PO_4^{3-}, or Fe concentration) for the final data set contained 246 bryophyte samples.

Estimating biogeochemical niches

We selected the 13 bryophyte species for which four or more replicates were available to estimate the biogeochemical niches for each species. Given that these 13 species were not present in all springs studied, this analysis included 145 springs. We then performed two principal component analyses (PCAs), one for the elementomes and one for the environmental variables, and extracted the first three axes (PC1, PC2, and PC3) for each. The elementome PCA included all log-transformed and standardised stoichiometric molar ratios and elements used in the previous section (i.e. C:N, C:P, N:P, C, N, P, K, Na, Mg, Ca, S, and Fe). The environmental PCA included all log-transformed and standardised concentrations of water nutrients (NO_3, PO_4^{3-}, K^+, Na^+, Mg^{2+}, Ca^{2+}, SO_4^{2+}, and Fe), the NO_3^-:PO_4^{3-} mass ratio, and the standardised mean annual temperature, annual water availability, and altitude. We then fitted a model similar to those described in the previous section, with species as a random factor, the use of equal priors, and the estimates of the PD and BF metrics. Elementome PC1, PC2, and PC3 were the response variables following a normal distribution, and environmental PC1, PC2, and PC3 were the predictors. The biogeochemical niche of each species was estimated as the posterior distribution of the mean of elementome PC1, PC2, and PC3 after accounting for environmental variability. We used density and 3D plots based on the full posterior distributions of the model to visualise differences in biogeochemical niches amongst species.

We assessed the phylogenetic signal of the biogeochemical niches by again fitting the previous model, including phylogenetic correction and estimation of the intraclass correlation. We assessed the effects of phylogenetic uncertainty in our results by repeating the same model for 100 randomly selected trees, as in the previous section. The results were almost identical.

Testing differences in elementomes amongst coexisting species

We performed two separate analyses to test the hypothesis that coexisting species and individuals tend to increase the differences in their elementomes. The first analysis was aimed at testing whether elementome differences between samples from different species living in the same spring were larger than between non-coexisting samples of the same species. To test that, we used our data set of 246 individual elementomes to calculate all pair-wise log-transformed elementome Euclidean distances (*vegdist* function, *vegan* R package (Oksanen *et al.* 2014)) between samples using all stoichiometric ratios and elements used in the previous sections and recorded whether or not they coexisted in the same spring. We also calculated the Euclidean distances in the log-transformed concentrations of water ions and the environmental variables to control for environmental effects on the elementomes. We then selected the comparisons between species for which five or more replicates for coexistence were available. The remaining combinations were between *Apopellia endiviifolia* and *Conocephalum conicum* (12 comparisons from specimens coexisting in the same spring, 492 comparisons from different springs), *Apopellia endiviifolia and Oxyrrhynchium speciosum* (5, 475), *Conocephalum conicum and Plagiomnium undulatum* (5, 415), and *Cratoneuron filicinum* and *Platyhypnidium riparioides* (5, 355). We then fitted a linear mixed model in which the response variable was the Euclidean distance between elementomes of two samples (log-normal distribution), the predictors were the log-transformed Euclidean distances between environmental variables for these two samples, a factor indicating whether or not they coexisted in the same spring, and the two species to be compared as the random effect (the four levels described above).

The second analysis was aimed at testing whether elementome differences between species that coexist frequently are larger than between species that coexist rarely. To test that, we first calculated the median log-transformed elementomes and environmental variables for all species in our data set. We then calculated the Euclidean distances for the elementomes and environmental conditions between all pairs of species and used the full survey of bryophyte communities (363 springs) to estimate the absolute (number of springs) and relative (number of springs in which they coexisted divided by the number springs where species were found) coexistence between pairs of species (only those species present in five or more springs were used). We then fitted a linear model in which the response variable was the Euclidean distance between a pair of species, following a log-normal distribution, and the predictors were the log-transformed Euclidean distances in the environmental variables and the log-transformed relative coexistence. The model was weighted by the absolute frequency of coexistence to give more weight to pair-wise comparisons for which more observations were available. Comparisons between pairs of species that did not coexist in any spring were removed from the analysis to avoid confounding effects in the analyses: species with very different ecological requirements or legacy effects on their current distribution.

Results

Bryophyte C:N:P stoichiometry and scaling relationships

Our results indicated that the median C:N:P stoichiometry of bryophytes, on a molar basis, was $145^{[55\text{-}460]}$:$8^{[4\text{-}19]}$:1 (95% credible intervals between brackets), and the median C:N ratio was $18^{[12\text{-}27]}$:1, although considerable variation amongst species was found (**Figure 1a**). The scaling of N and P indicated that the increase in P was accompanied by a much lower proportional increase in N (**Figure 1b**, scaling slope of $0.19^{[0.15\text{-}0.24]}$ N vs. P). We found no evidence supporting a scaling relationship between C and N nor between C and P (see **Model summaries, Supplementary Information**).

Environmental and phylogenetic controls of bryophyte elementomes

All three stoichiometric ratios (C:N, C:P, and N:P) tended to be lower in bryophytes living in springs with high NO_3^- and PO_4^{3-}, but evidence supporting these findings was weak (**Figure 2**). Annual water availability was negatively correlated with C:P and N:P and weakly with C:N, and altitude was positively correlated with C:N and, to a much lower degree, with C:P and N:P. The variance (R^2) explained by the models was low for C:N (0.34) and very low for C:P (0.10) and N:P (0.07), and the median phylogenetic signal (Pagel's λ: ranging from 0, indicating no phylogenetic signal, to 1 perfect Brownian motion trajectory) ranged from 0.34 to 0.45. Hence, the variability was lower within than amongst species for all three ratios.

Most elements and their ions dissolved in the water were positively correlated with the bryophyte concentrations, except for C (for which dissolved organic C was not available), K, and S (**Figures 2, S2, and S3**). Bryophyte C and K concentrations were not consistently linked to any of the environmental variables, and S concentrations were only negatively correlated with altitude (**Figure S4**). Our models performed better for concentrations of N and P, explaining 47% of their variance in both cases. Both N and P were positively correlated with both NO_3^- and PO_4^{3-} and tended to increase with increasing water availability and decreasing altitude (**Figures S2 and S4**). High concentrations of Na were more likely in springs with low electrical conductivity and high concentrations of PO_4^{3-}; Ca had the opposite behaviour. The concentrations of Mg were also higher in springs with low electrical conductivity, similar to Na. The median phylogenetic signal estimated for most elements ranged from 0.17 (S) to 0.65 (Mg). All elements varied less within than between species.

Bryophyte biogeochemical niches and differences in elementomes between coexisting species

We estimated three-dimensional biogeochemical niches while controlling for environmental variability using a mixed model, with the three first axes of a PCA of all C:N:P stoichiometric ratios and elements as the response variables and the first three axes of all environmental variables previously used as the predictors (see **Methods, models 5 and 6 in Model summaries, Supplementary Information**). Our analyses indicated that most species had specific elementomes, i.e. they had species-specific biogeochemical niches when the distributions did not overlap for, at least, one of the three axes (**Figure 3, S5** and interactive 3D plot in **Online Materials 1** or https://rpubs.com/mfernandez/bbn**)**. The model explained 38, 23, and 25% of the variability in elementome PC1, PC2, and PC3, with median phylogenetic signals of 0.78, 0.45, and 0.37, respectively. Again, the variability was much lower within than amongst species for all three axes.

We found evidence indicating that the elementomes differed more between individuals of different species coexisting in the same spring than in different springs when environmental differences were taken into account (BF=2.5, i.e. H_1 (slope ≠ 0) is 2.5 times more likely than H_0 (slope = 0), **see Model 7 in Model summaries, Supplementary Information**). Similarly, we found very strong evidence

(BF=1.1×10^{11}), indicating that pair-wise differences in median elementomes between species were larger for pairs of species that often coexist compared to those that rarely live together (low coexistence) (**Figure 4**). Again, these results emerged when the differences in environmental requirements were taken into account (**Model 8 in Model summaries, Supplementary Information)**.

Discussion

C:N:P stoichiometry: from plankton to vascular plants

Our estimate of C:N:P stoichiometry for hygrophytic bryophytes (142:8:1, **Figure 1a**) was closer to the traditional and revised Redfield's ratios (106:16:1 (Redfield 1934) and 162:22:1 (Martiny *et al.* 2014), respectively) for marine plankton than for benthic marine plants (550:30:1 (Atkinson & Smith 1983)) and terrestrial vascular plants (799:27:1 (Elser *et al.* 2000)), or tree leaves (1334:28:1 (McGroddy *et al.* 2004)). However, our estimate was remarkably similar to those previously reported for the liverwort *Porella pinnata* (Steinman 1994) and close to those reported for other bryophytes (Christmas & Whitton 1998; Waite & Sack 2011; Huang *et al.* 2019), except for reference (Wang *et al.* 2019) presenting considerably higher C:N, C:P and N:P stoichiometric ratios. We estimated a median C:N ratio of 18:1 for bryophytes, similar to those for marine plants (20:1), but lower than tree leaves (44:1) and vascular plants (32:1) (Elser *et al.* 2000). An evolutionary gradient of C:N:P stoichiometry may thus follow the colonisation of land plants. P availability is much lower in marine ecosystems than terrestrial and freshwater environments, constraining P uptake by autotrophs while N is relatively abundant and a weak limiting factor in marine ecosystems (Margalef 1997; Wu *et al.* 2000; Patey *et al.* 2008). Bryophytes, however, evolved thicker C structures compared to phytoplankton. These environmental and morphological differences are represented by the similar C:P but lower N:P ratios of bryophytes compared to marine plankton probably because bryophytes had access to weathering P from rocks, much richer in P than marine ecosystems (Wu *et al.* 2000; Patey *et al.* 2008; Porder & Ramachandran

2013). C-rich structures (e.g. cellulose and lignin) are instead still less abundant in bryophytes than vascular plants, accounting for the much lower C:P and C:N ratios in bryophytes. Our results thus suggest a potential intermediate evolutionary step that further supports the hypothesis that the evolution of the stoichiometry of terrestrial plants has favoured C over N and P (Elser *et al.* 2000).

Our analyses indicated that N and P were positively correlated, with a proportionately lower increase in N as P increased (scaling slope 0.19 for N vs. P, **Figure 1b**). This estimate is much lower than those across phytoplankton and freshwater and terrestrial bryophytes and vascular plants (Duarte 1992; Güsewell 2004; Reich *et al.* 2010; Sardans *et al.* 2016b; Wang *et al.* 2019) but is similar to those reported across forests (1.12, (McGroddy *et al.* 2004)) and agrees with all of them on the lower proportional increase in N relative to P. We did not observe a scaling relationship between C and P nor between C and N, similar to previous analyses conducted with freshwater angiosperms for C versus N and P and for macroalgae and seagrasses for P and C (Duarte 1992). C, N, and P have previously been found to positively correlate in trees and phytoplankton, but no scaling relationships between C and P have been reported for freshwater angiosperms, macroalgae, or seagrasses (Duarte 1992; McGroddy *et al.* 2004), similar to our findings. C and N, and C and P may thus only be correlated across some groups of organisms, especially in non-freshwater environments, but N and P may be universally correlated across autotrophs. The tight correlation between N and P results from N being used to produce proteins, and proteins being synthesised by P-rich ribosomes (Ågren 2004). Hence, high protein synthesis, related to high N concentrations, cannot occur without a proportional increase in P.

Evidence for bryophyte homeostatic regulation and biogeochemical niches

Our results provide evidence suggesting that bryophytes can homeostatically regulate their elemental composition and stoichiometry, allowing the definition of differentiated biogeochemical niches amongst species. The biogeochemical niches of *Didymodon* *tophaceus* and *Eucladium verticillatum*, two phylogenetically close species with very similar ecological requirements and functional traits (Fernández-Martínez *et al.* 2019) but different biogeochemical niches, is a particularly interesting case (**Figure 3**). Elementome variability was higher amongst than within species (across sites), and the relationships between the environmental availability of elements and their concentrations in bryophytes were relatively low (all log-log slopes were well below 0.4, see **Model summaries** in **Supplementary Material**), providing evidence that suggests homeostatic regulation and diversification of the biogeochemical niche with speciation. Additionally, bryophyte macronutrients (e.g., N, P) were less correlated to water nutrient availability than micronutrients, suggesting a stronger homeostatic control for macro- than for micronutrients (Karimi & Folt 2006). Most models, nonetheless, explained only a small proportion of the variance of bryophyte elemental composition, indicating that other important predictors may be missing, such as different forms of elements dissolved in water (e.g., NH_4^+, NO_2^-), the chemistry of the substrate where bryophytes are attached, atmospheric pollution or more detailed climate variables (e.g., microclimate).

The phylogenetic signal for C:N:P stoichiometry and most elements was also lower than that often reported in studies using a wide array of vascular plants (Fernández-Martínez *et al.* 2018, 2019b) but was similar to those studies using fewer species (Penuelas *et al.* 2011; Sardans *et al.* 2015; Bai *et al.* 2019). Instead, the conservatism of the biogeochemical niche (especially PC1, being mainly positively related to C, C:N, N:P and C:P and negatively related to all macro- and micronutrients except C and Ca, **Figure 3, Figure S5**) was remarkably high ($\lambda=0.78^{[0.25-0.94]}$) supporting the biogeochemical niche hypothesis (Peñuelas *et al.* 2019; Sardans *et al.* 2021). This result is very interesting considering the high genetic diversity of bryophytes (Wyatt *et al.* 1989), despite their small genomes (Bainard *et al.* 2019), even in the absence of sexual reproduction (Karlin *et al.* 2012). Bryophytes also lack thick cuticles and true roots, so they are very sensitive to environmental variability (Porley & Hodgetts 2005), and potentially more than vascular plants. They can also accumulate large quantities of trace elements present in their environment (Tyler 1990; Zechmeister *et al.* 2003), directly modifying their elementomes. All these features of bryophytes should, a priori, impede finding well-defined biogeochemical niches for bryophytes, relative to vascular plants, due to their expected higher elementome variability. We thus hypothesise that differences in biogeochemical niches amongst species would be larger for vascular plants than for bryophytes when entire organisms are analysed.

Elementome distance as a potential measure of competition between organisms

We found evidence supporting our initial hypothesis that elementomes would tend to differ more for individuals and species that coexist than for those that do not coexist when environmental differences are taken into account (**Figure 4**). Most of the studied bryophytes here grow in dense and heterogeneous patches formed by several species competing for space and resources. Similar functional traits between species may be due to similar nutrient and environmental needs and thus similar elementomes (Peñuelas *et al.* 2019). Competition for resources between organisms under these circumstances would then be high compared to a situation in which functional traits, environmental requirements, and elementomes differ, thus leading to *niche partitioning* (Loreau & de Mazancourt 2013). The proposed mechanism, of course, should not only apply to bryophytes but is also expected to be a universal pattern across organisms of all kinds.

From our findings we hypothesise that we can estimate functional diversity in a community as the average distance or the variability amongst the elementomes of the various component organisms. A similar and promising approach would be to use hypervolumes (Blonder 2018; Carvalho & Cardoso 2020) to estimate species biogeochemical niches or community elementomes. Then, the shared hypervolume between two or more species could be estimated as a theoretical measure of competition. The size of the hypervolume of community elementomes could also potentially be a good indicator of competition within the community given a number of species. Overall, these measures of niche overlap could help us to better understand community assemblages, competitive and mutualistic interactions between species, and the relationships between biodiversity, nutrient availability, and productivity in ecosystems.

Data availability statement

Data supporting the findings of this study are available at FigShare: https://doi.org/10.6084/m9.figshare.13691878.v2.

Code availability statement

Code to perform the analyses supporting the findings of this study is available at FigShare: https://doi.org/10.6084/m9.figshare.13691878.v2.

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Competing interests

The authors declare no competing interests.

Figures

Figure 1. Bryophyte C:N:P stoichiometry and N:P scaling relationship. a) A sample of 5000 randomly selected posterior ratios within the 2.5 and 97.5% quantiles for C:P and N:P coloured following C:N ratios (gradient colour bar). Black dots indicate average (± 95% credible intervals, CIs) ratios for each species. Red isoclines indicate the density of the distribution of the points. Red dashed lines indicate the average bryophyte C:N:P ratio (145:8:1). b) Scaling relationship between N and P concentrations. The shaded area corresponds to the 95% CI of the slope. The inverse scaling relationship in panel b (P vs. N) is $1.12^{[0.85\text{-}1.39]}$. See **models 1 and 2** in **Model summaries, Supplementary Information**, for further details. BF: Bayes factor.

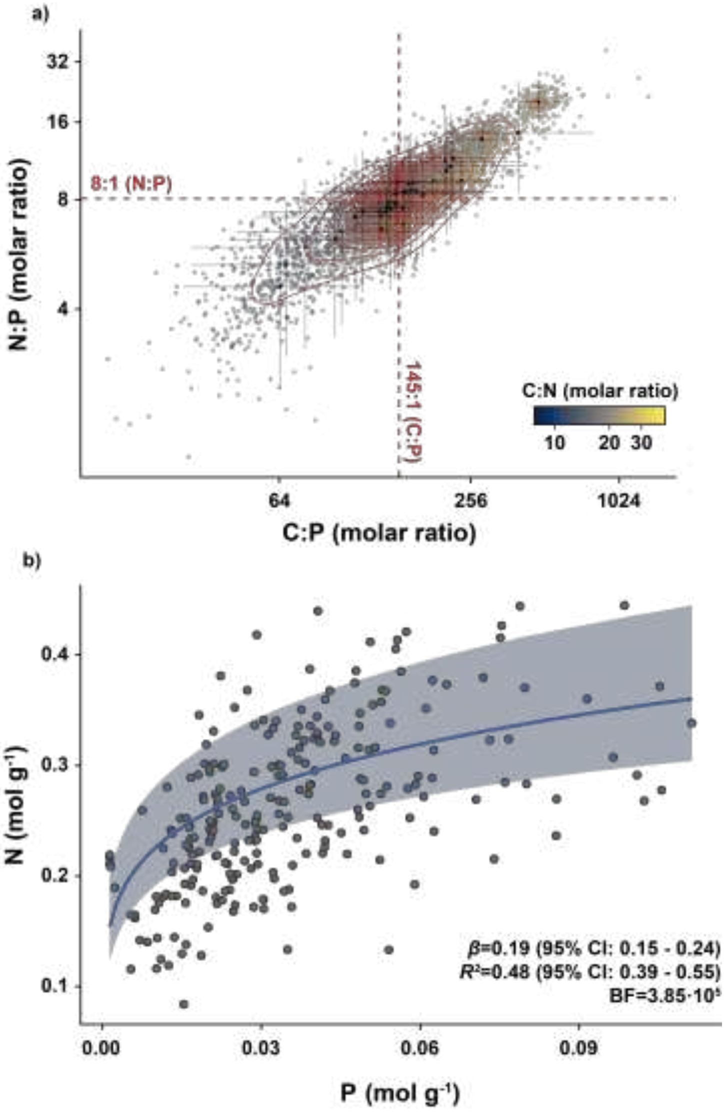


Figure 2. Heat map of the relationships of bryophyte elemental composition (columns) with water chemistry, climate, and altitude (rows) of the springs. Colours indicate the probability of direction (PD) of the posterior distributions of the relationship between pairs of variables, where red and blue indicate positive and negative relationships, respectively. Black dots indicate Bayes factors >1. The row *Concentration in water* refers to the concentration of each element in the spring water (note that for N and P this row equals rows NO_3^- and PO_4^{3-}, respectively). The amount of variance explained (R^2, blue) and the phylogenetic signal (Pagel's λ, red) and 95% credible intervals are shown in the bottom panel. See **models 1, 3, and 4** in **Model summaries, Supplementary Information**, for further details.

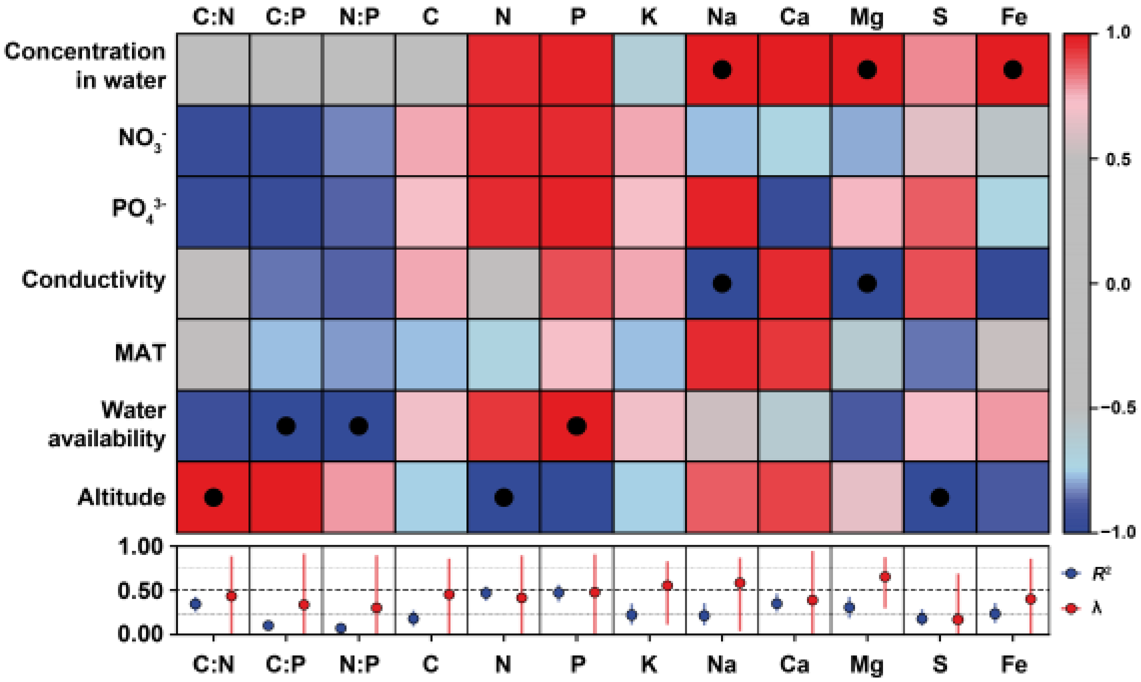


Figure 3. Biogeochemical niches of 13 bryophyte species estimated using a reduced multivariate space of three axes of a principal component analysis. Density plots indicate the entire posterior distributions for the average PC1, PC2, and PC3 axes for each species, ordered by their evolutionary history (phylogenetic tree on the left). Species-specific biogeochemical niches are found when the distributions do not overlap for, at least, one of the three axes. Only species for which four or more replicates were available were used in this analysis. The percentage of variance of the elementomes retained by the axes is shown in parentheses (see **section 5 and model 6** in **Model summaries, Supplementary Information**). An interactive 3D plot of the biogeochemical niches is available in **Online Materials 1** or https://rpubs.com/mfernandez/bbn.

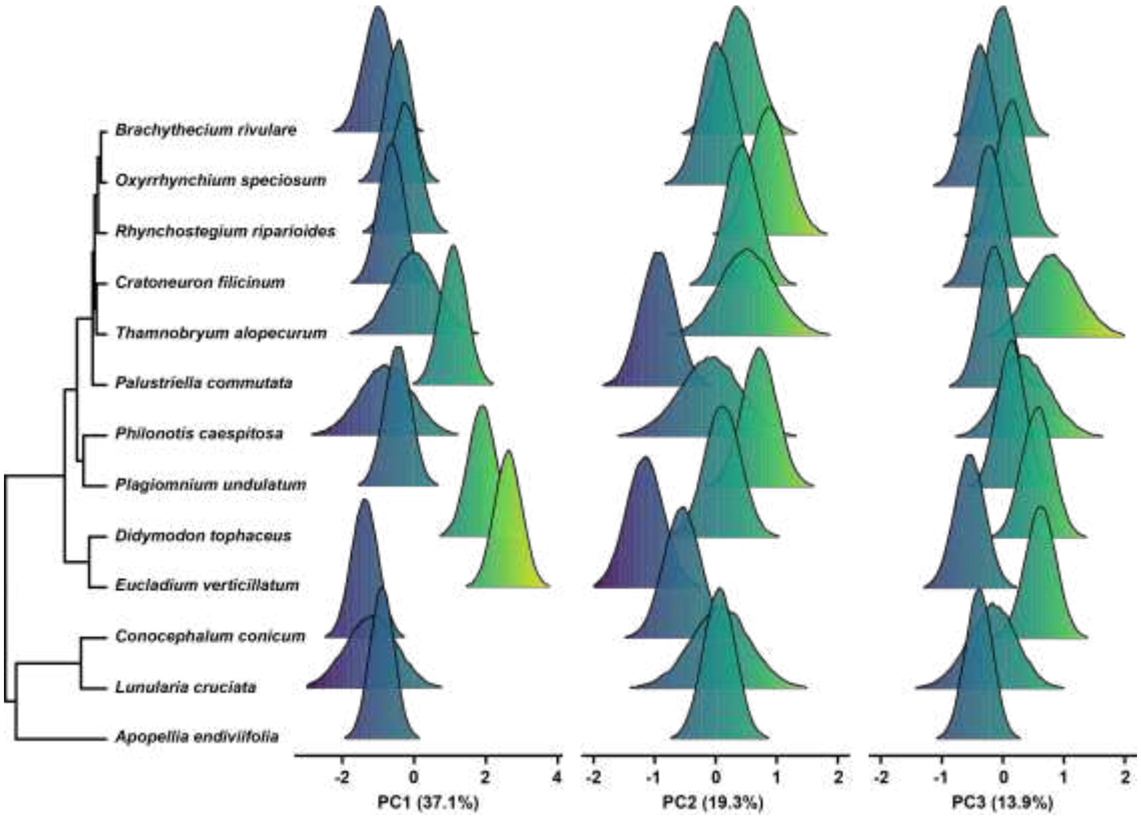
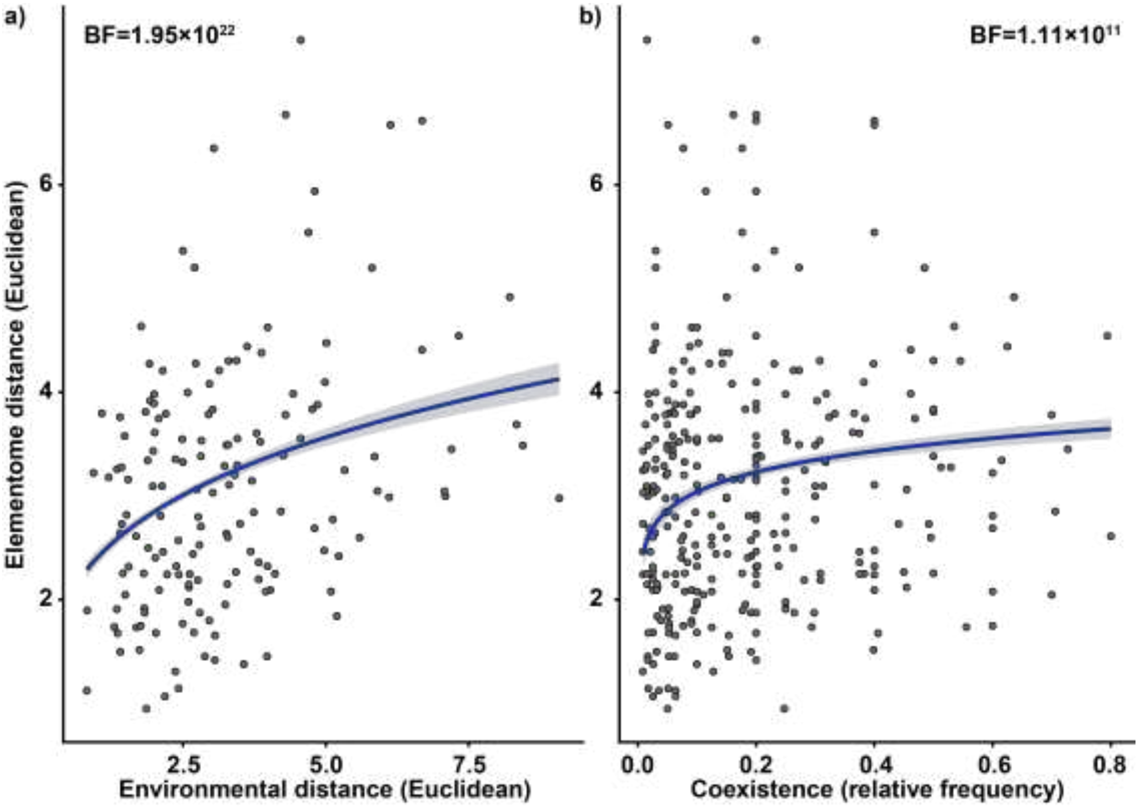
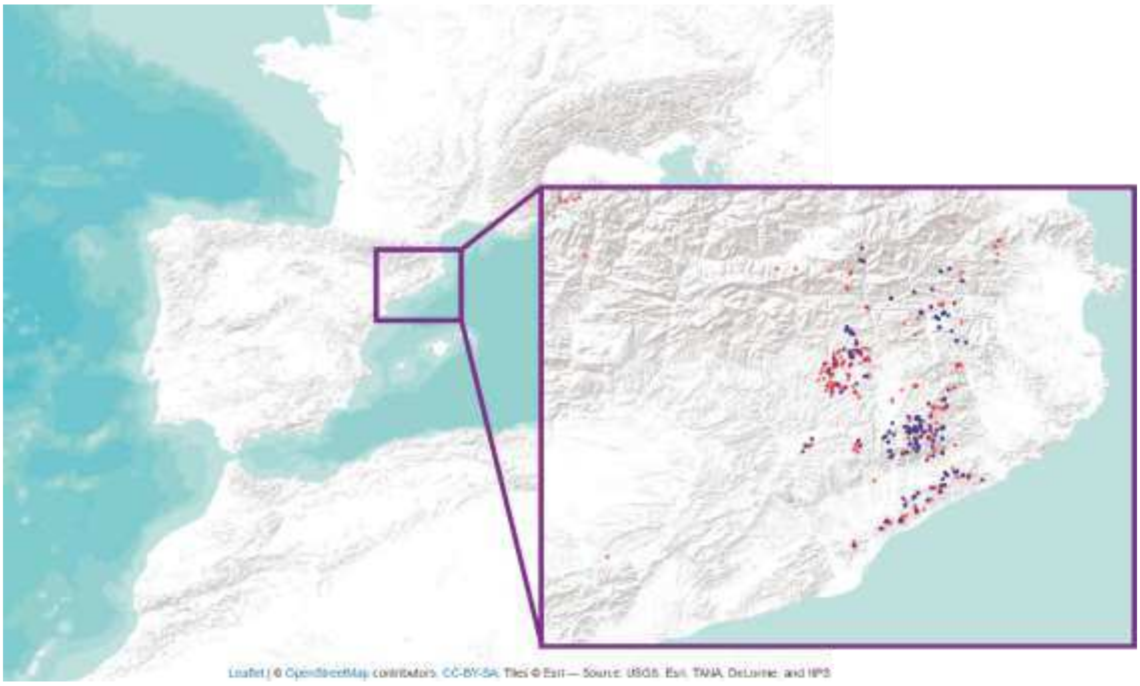


Figure 4. Conditional effect plots showing the increases in distance between average species elementomes (pairs of species) as a function of a) environmental distance and b) frequency of coexistence. Only species in ≥5 springs were used in this analysis. The sum of springs in which each pair of species was found was used as weights in the model. Comparisons between species that were never found in the same spring were not included to avoid comparing species with non-overlapping environmental niches. Shaded bands correspond to the 2.5-97.5% posterior credible intervals of the slopes (see **model 8** in **Model summaries, Supplementary Information**). BF: Bayes factor.



Supplementary material

Figure S1. Map of the locations of the springs. Red dots indicate sampled springs, and blue dots indicate springs from which the elementomes of bryophytes were analysed.



Leaflet | © OpenStreetMap contributors, CC-BY-SA, Tiles © Esri — Source: USGS, Esri, TANA, DeLorme, and NPS

Figure S2. Conditional effect plots of the estimated relationships between bryophyte N and P concentrations with water nitrate and phosphate concentrations and altitude. Shaded bands correspond to the 2.5-97.5% posterior credible intervals of the slopes. Dashed lines indicate Bayes factors (BFs, against slope = 0) <1. BFs for panels a, b, c, d, e, and f were 0.04, 0.03, 7.45, 0.11, 0.10, and 0.40, respectively. Probability of direction (PD) was >0.95 for all cases except for panel a (PD=0.9479), (see **Figure 2** and **model 3** in **Model summaries**, **Supplementary Information**).

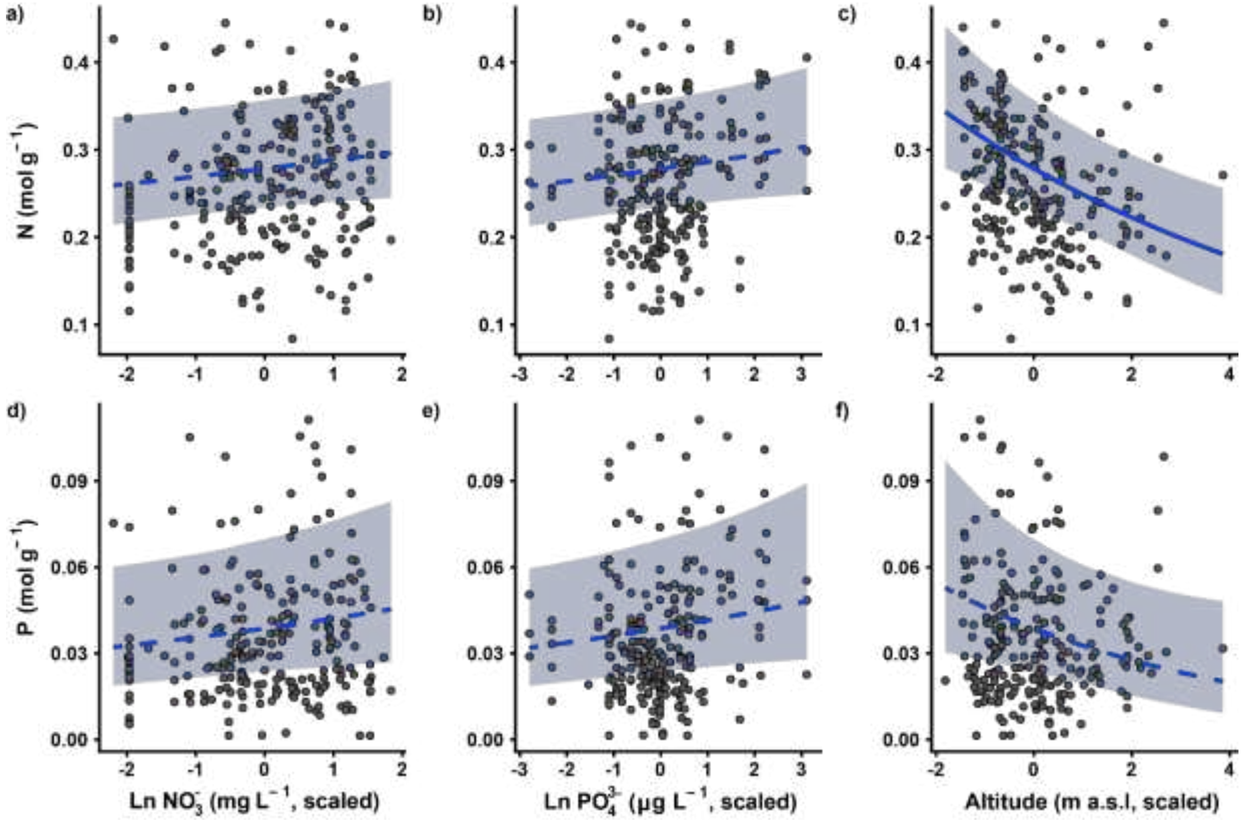


Figure S3. **Conditional effect plots of the estimated relationships between bryophyte and water Na, Ca, Mg, and Fe concentrations.** Shaded bands correspond to the 2.5-97.5% posterior credible intervals of the slopes. Dashed lines indicate Bayes factors (against slope = 0) <1. BFs for panels a, b, c, and d were 11.58, 0.93, 2.33 and 5.45, respectively. The probability of direction was >0.99 for all cases (see **Figure 2** and **model 4** in **Model summaries**, **Supplementary Information**).

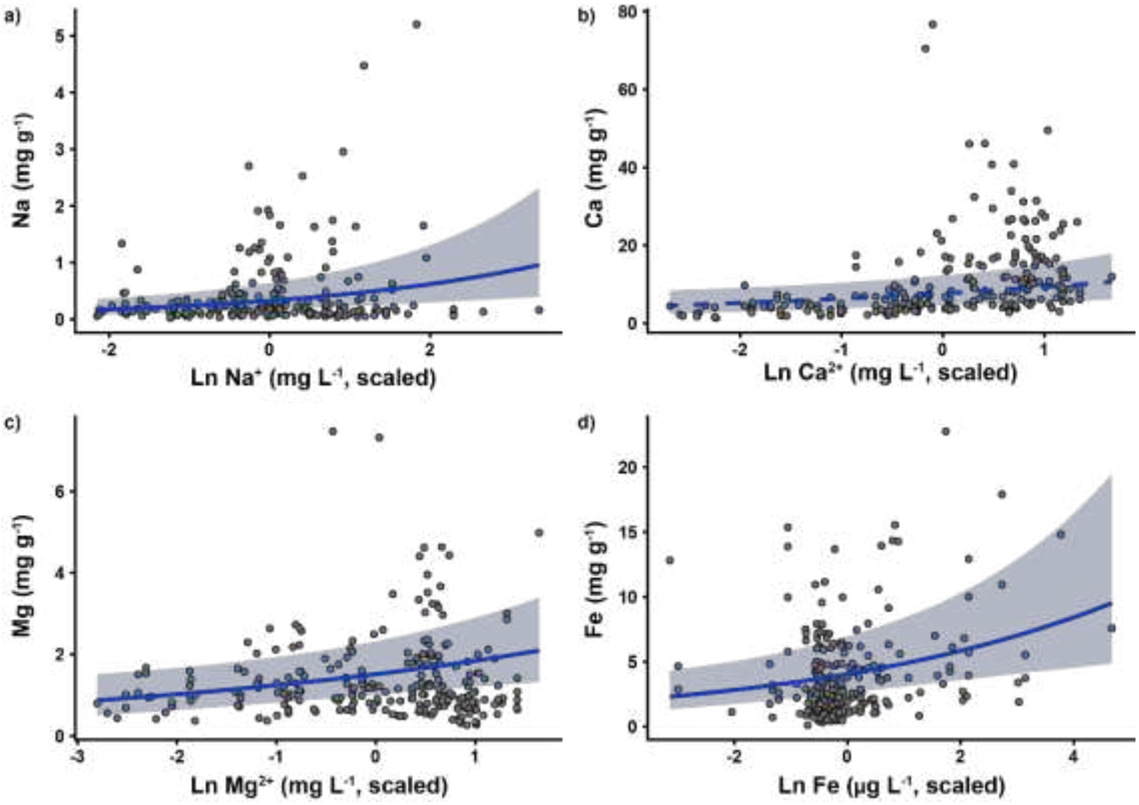


Figure S4. Conditional effect plots of the estimated relationships between bryophyte P, Na, S, and Mg concentrations and environmental variables. Shaded bands correspond to the 2.5-97.5% posterior credible intervals of the slopes. Bayes factors (against slope = 0) for panels a, b, c, and d were, 3.54, 7.04, 6.84 and 2.19, respectively. Probability of direction was >0.99 for all cases (see **models 3** and **4** in **Model summaries**, **Supplementary Information**).

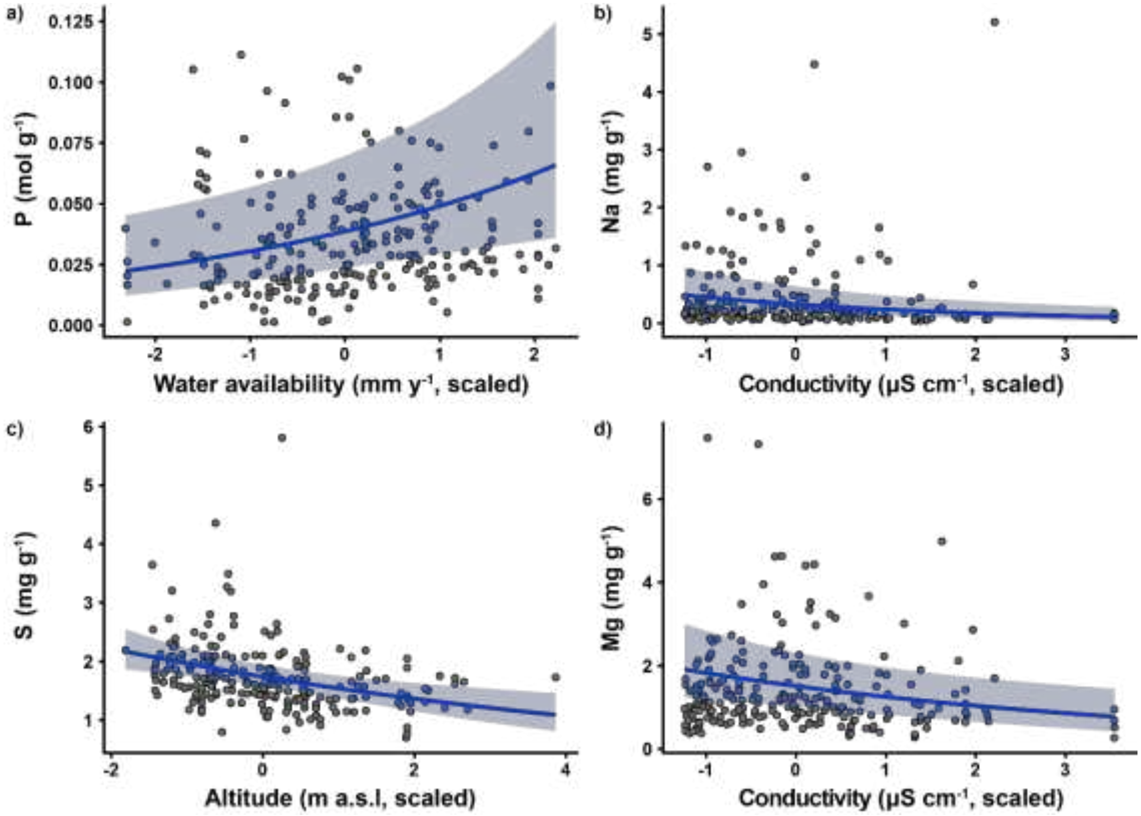
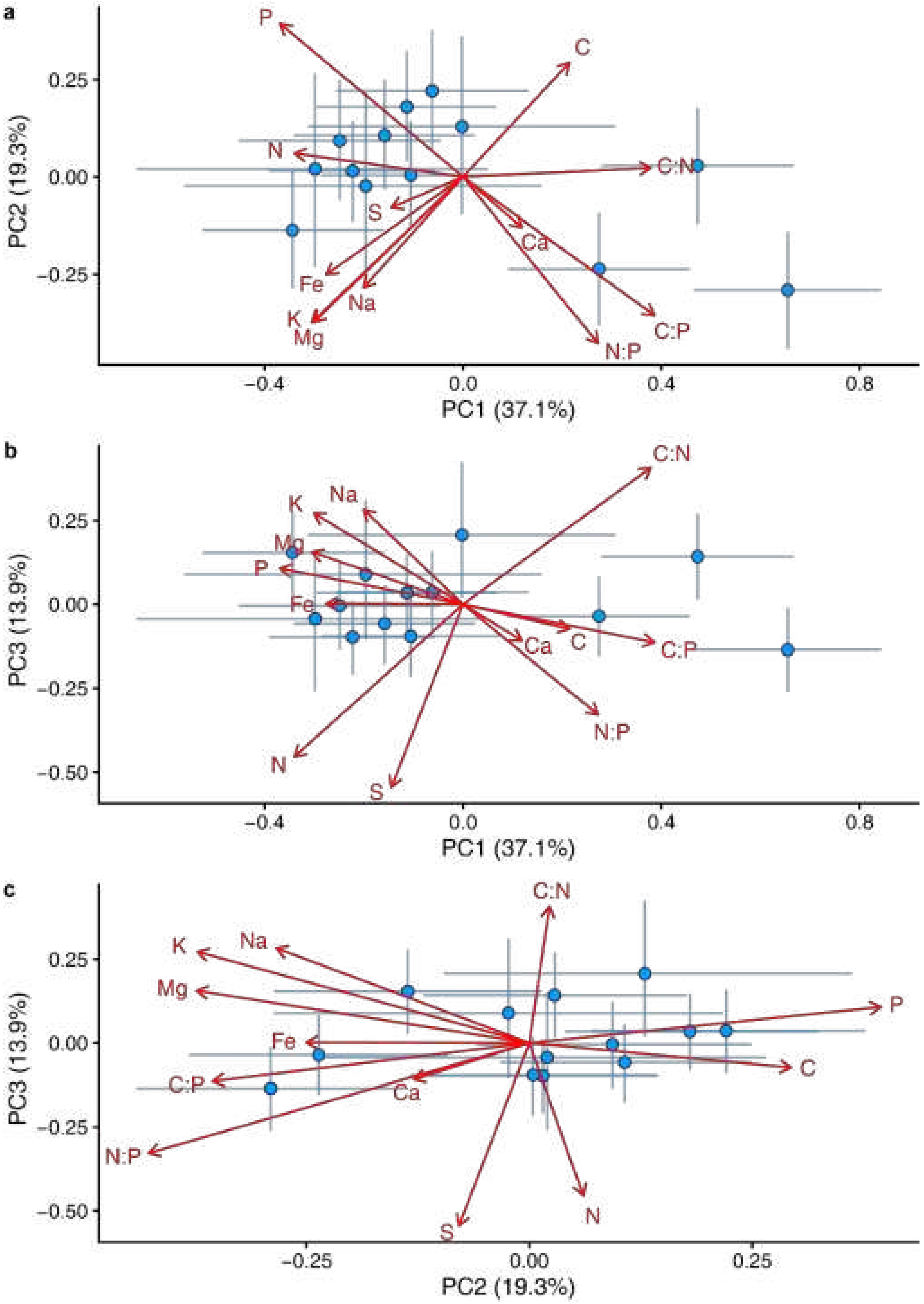


Figure S5. Biplots showing loadings and median scores per species of the principal components analysis used to estimate biogeochemical niches. Red arrows indicate factor loadings and blue dots the median scores per species. Blue lines indicate the 95% credible interval for the median of each species. The percentage of variance of the elementomes retained by the axes is shown in parentheses (see **section 5 and model 6** in **Model summaries, Supplementary Information**).



Model summaries

1. C:N, C:P, N:P model

Formulas:

cn.mol ~ no3 + po4 + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)

cp.mol ~ no3 + po4 + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)

np.mol ~ no3 + po4 + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)

Data: data (Number of observations: 246)

Samples: 40 chains, each with iter = 3000; warmup = 1000; thin = 1; total post-warmup samples = 80000

```
Group-Level Effects:
~species (Number of levels: 35)
                                      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(cnmol_Intercept)                       0.16      0.06     0.04     0.27 1.01     6823     9147
sd(cpmol_Intercept)                       0.39      0.14     0.04     0.64 1.01     3039     2884
sd(npmol_Intercept)                       0.30      0.11     0.03     0.48 1.01     3250     3476
cor(cnmol_Intercept, cpmol_Intercept)     0.63      0.28    -0.21     0.93 1.00    10024     6420
cor(cnmol_Intercept, npmol_Intercept)     0.32      0.36    -0.63     0.82 1.01     6681     5405
cor(cpmol_Intercept, npmol_Intercept)     0.79      0.29    -0.20     0.99 1.01     4833     4024

~phylo (Number of levels: 35)
                                      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(cnmol_Intercept)                       0.31      0.20     0.02     0.77 1.01     5191    13335
```

sd(cpmol_Intercept)	0.66	0.56	0.02	2.05	1.01	2816	4704
sd(npmol_Intercept)	0.50	0.45	0.02	1.65	1.01	2978	4568
cor(cnmol_Intercept, cpmol_Intercept)	0.39	0.47	-0.71	0.96	1.00	10154	33987
cor(cnmol_Intercept, npmol_Intercept)	0.13	0.50	-0.84	0.91	1.00	9955	28654
cor(cpmol_Intercept, npmol_Intercept)	0.44	0.50	-0.73	0.99	1.01	4415	13023

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	PD	pval	BF
cnmol_Intercept	2.85	0.11	2.61	3.03	1.00	23503	22105	1.0000	0.0000	5.70E+13
cpmol_Intercept	4.96	0.24	4.41	5.41	1.00	18737	10134	1.0000	0.0000	1.24E+08
npmol_Intercept	2.11	0.19	1.69	2.49	1.00	21399	9624	1.0000	0.0000	4943
cnmol_no3	-0.03	0.02	-0.07	0.01	1.00	94877	65204	0.9474	0.1053	0.04
cnmol_po4	-0.03	0.02	-0.06	0.01	1.00	124852	62861	0.9421	0.1158	0.03
cnmol_conductivity	0.00	0.03	-0.05	0.05	1.00	81467	62898	0.5026	0.9949	0.01
cnmol_MAT	0.00	0.03	-0.07	0.07	1.00	80715	63708	0.5013	0.9974	0.02
cnmol_WA	-0.05	0.03	-0.11	0.02	1.00	84712	61832	0.9293	0.1414	0.05
cnmol_altitude	0.10	0.03	0.04	0.17	1.00	71281	63054	0.9986	0.0029	1.69
cpmol_no3	-0.07	0.05	-0.17	0.02	1.00	102358	65357	0.9408	0.1185	0.08
cpmol_po4	-0.06	0.04	-0.14	0.01	1.00	124014	62164	0.9511	0.0978	0.08
cpmol_conductivity	-0.06	0.06	-0.17	0.05	1.00	77207	62631	0.8468	0.3065	0.05
cpmol_MAT	-0.06	0.08	-0.21	0.09	1.00	77728	61905	0.7754	0.4492	0.05
cpmol_WA	-0.23	0.08	-0.38	-0.08	1.00	85907	62622	0.9986	0.0027	3.17
cpmol_altitude	0.16	0.08	0.01	0.32	1.00	67463	61335	0.9805	0.0389	0.34
npmol_no3	-0.04	0.04	-0.12	0.04	1.00	99538	64488	0.8333	0.3333	0.03
npmol_po4	-0.04	0.03	-0.11	0.03	1.00	124634	61660	0.8631	0.2738	0.03
npmol_conductivity	-0.06	0.05	-0.16	0.04	1.00	79788	65008	0.8759	0.2483	0.05
npmol_MAT	-0.06	0.07	-0.19	0.08	1.00	78040	63447	0.8020	0.3961	0.05
npmol_WA	-0.18	0.07	-0.31	-0.05	1.00	85829	61016	0.9958	0.0084	1.15
npmol_altitude	0.06	0.07	-0.08	0.20	1.00	69908	60688	0.7950	0.4101	0.05

```
Family Specific Parameters:
                  Estimate  Est.Error  l-95% CI  u-95% CI  Rhat  Bulk_ESS  Tail_ESS
sigma_cnmol           0.25       0.01      0.22      0.27  1.00     84974     57500
sigma_cpmol           0.57       0.03      0.52      0.63  1.00    110651     60434
sigma_npmol           0.51       0.02      0.47      0.56  1.00    118402     59345
```

Effect of phylogeny (λ), intraspecific variability, and residuals (inter-class correlations):

```
Hypothesis     Estimate  Est.Error  CI.Lower  CI.Upper  Evid.Ratio  Post.Prob  Star
λ.cn               0.43       0.27      0.00      0.88        0.42       0.30  *
species.cn         0.20       0.14      0.01      0.50        0.41       0.29  *
residuals.cn       0.37       0.17      0.09      0.69        0.00       0.00  *
λ.cp               0.33       0.29      0.00      0.91        0.81       0.45  *
species.cp         0.25       0.15      0.00      0.53        0.64       0.39  *
residuals.cp       0.41       0.17      0.08      0.69        0.00       0.00  *
λ.np               0.30       0.28      0.00      0.90        0.96       0.49  *
species.np         0.21       0.12      0.00      0.45        0.78       0.44  *
residuals.np       0.49       0.19      0.10      0.77        0.00       0.00  *
```

Variance explained:

```
        Estimate  Est.Error  Q2.5  Q97.5
cnmol       0.34       0.04  0.26   0.43
cpmol       0.10       0.03  0.06   0.16
npmol       0.07       0.02  0.04   0.12
```

2. CNP scaling models

2.1. C to N scaling

Family: lognormal, Links: mu = identity; sigma = identity

Formula: c.mol ~ log(n.mol) + (1 | p | gen_spec) + (1 | q | phylo)

Data: data (Number of observations: 246)

Samples: 20 chains, each with iter = 2000; warmup = 1000; thin = 1; total post-warmup samples = 20000

Group-Level Effects:

~gen_spec (Number of levels: 35)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.02	0.01	0.00	0.05	1.01	3068	5300

~phylo (Number of levels: 35)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.07	0.05	0.00	0.18	1.01	3085	7026

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	BF	PD	Pval
Intercept	1.54	0.03	1.47	1.61	1.00	17064	13272	2.63E+32	1	0
logn.mol	-0.01	0.02	-0.05	0.03	1.00	25055	15552	0.01	0.7259	0.5482

Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	0.08	0.00	0.07	0.09	1.00	26528	14941

Effect of phylogeny (λ), intraspecific variability, and residuals (inter-class correlations):

Hypothesis	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
species	0.07	0.07	0.00	0.24	4.15	0.81	*
λ	0.40	0.26	0.00	0.85	0.45	0.31	*
residuals	0.53	0.22	0.15	0.9	0	0	*

Variance explained:

	Estimate	Est.Error	Q2.5	Q97.5
R2	0.15	0.05	0.07	0.25

2.2. C to P scaling

Family: lognormal, Links: mu = identity; sigma = identity

Formula: c.mol ~ log(p.mol) + (1 | p | gen_spec) + (1 | q | phylo)

Data: data (Number of observations: 246)

Samples: 20 chains, each with iter = 2000; warmup = 1000; thin = 1; total post-warmup samples = 20000

Group-Level Effects:

~gen_spec (Number of levels: 35)

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
sd(Intercept)	0.03	0.01	0.00	0.05	1.00	3028	4050

~phylo (Number of levels: 35)

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
sd(Intercept)	0.08	0.05	0.00	0.19	1.01	2963	6287

Population-Level Effects:

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**	**BF**	**PD**	**Pval**
Intercept	1.51	0.04	1.43	1.58	1.00	15253	12751	4.40E+32	1	0
logp.mol	-0.01	0.01	-0.03	0.00	1.00	20624	14721	0.02	0.9545	0.091

Family Specific Parameters:

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
sigma	0.08	0.00	0.07	0.08	1.00	21950	14905

Effect of phylogeny (λ), intraspecific variability, and residuals (inter-class correlations):

Hypothesis	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
species	0.09	0.08	0.00	0.29	2.77	0.74	*
λ	0.40	0.27	0.00	0.86	0.52	0.34	*
residuals	0.52	0.22	0.13	0.88	0	0	*

Variance explained:

	Estimate	Est.Error	Q2.5	Q97.5
R2	0.17	0.05	0.08	0.27

2.3. N to P scaling

Family: lognormal, Links: mu = identity; sigma = identity

Formula: n.mol ~ log(p.mol) + (1 | p | species) + (1 | q | phylo)

Data: data (Number of observations: 246)

Samples: 20 chains, each with iter = 2000; warmup = 1000; thin = 1; total post-warmup samples = 20000

Group-Level Effects:

~species (Number of levels: 35)

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
sd(Intercept)	0.10	0.04	0.01	0.18	1.00	3925	3242

~phylo (Number of levels: 35)

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
sd(Intercept)	0.29	0.15	0.04	0.64	1.00	3692	4903

Population-Level Effects:

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**	**BF**	**PD**	**Pval**
Intercept	-0.61	0.12	-0.85	-0.37	1.00	16275	13097	29.81	1.000	1.00E-04
Log p.mol	0.19	0.02	0.15	0.24	1.00	29506	16276	3.85E+05	1.000	0.00E+00

Family Specific Parameters:

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
sigma	0.22	0.01	0.20	0.24	1.00	24921	15325

Effect of phylogeny (λ), intraspecific variability, and residuals (inter-class correlations):

Hypothesis	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
species	0.09	0.09	0.00	0.32	1.67	0.63	*
λ	0.53	0.24	0.02	0.89	0.16	0.13	*
residuals	0.37	0.18	0.10	0.76	0.00	0.00	*

Variance explained:

	Estimate	Est.Error	Q2.5	Q97.5
R2	0.48	0.04	0.39	0.55

3. C, N, P and K model

Family: MV(lognormal, lognormal, lognormal, lognormal)

Links: mu = identity; sigma = identity

Formulas:

c.mol ~ no3 + po4 + k + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)

n.mol ~ no3 + po4 + k + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)

p.mol ~ no3 + po4 + k + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)

K ~ no3 + po4 + k + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)

Data: data (Number of observations: 246)

Samples: 30 chains, each with iter = 2500; warmup = 1000; thin = 1; total post-warmup samples = 45000

```
Group-Level Effects:
~species (Number of levels: 35)
                                     Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(cmol_Intercept)                       0.02      0.01     0.00     0.05 1.00     8090    10185
sd(nmol_Intercept)                       0.18      0.05     0.07     0.29 1.00     6100     4581
sd(pmol_Intercept)                       0.40      0.13     0.12     0.65 1.00     5587     4574
sd(K_Intercept)                          0.13      0.10     0.00     0.38 1.00    15040    20336
cor(cmol_Intercept,nmol_Intercept)       0.28      0.37    -0.56     0.86 1.00     5442     7190
cor(cmol_Intercept,pmol_Intercept)       0.36      0.36    -0.50     0.89 1.00     6119     7680
cor(nmol_Intercept,pmol_Intercept)       0.68      0.23     0.07     0.94 1.00     8505     6713
cor(cmol_Intercept,K_Intercept)         -0.04      0.44    -0.81     0.79 1.00    38987    33917
cor(nmol_Intercept,K_Intercept)          0.03      0.43    -0.78     0.80 1.00    46726    35634
cor(pmol_Intercept,K_Intercept)          0.05      0.43    -0.78     0.81 1.00    37962    38071

~phylo (Number of levels: 35)
                                     Estimate Est.Error l-95% CI u-95% CI       Rhat  Bulk_ESS Tail_ESS
sd(cmol_Intercept)                       0.08      0.05     0.01          0.19   1.00     7927    12778
sd(nmol_Intercept)                       0.29      0.20     0.01          0.79   1.01     5012     6354
sd(pmol_Intercept)                       0.81      0.51     0.05          1.97   1.01     5098     7640
sd(K_Intercept)                          0.96      0.35     0.31          1.72   1.00    17988    11251
cor(cmol_Intercept,nmol_Intercept)      -0.05      0.44    -0.82          0.76   1.00    17376    27496
cor(cmol_Intercept,pmol_Intercept)       0.03      0.43    -0.79          0.78   1.00    14426    25576
cor(nmol_Intercept,pmol_Intercept)       0.35      0.43    -0.62          0.94   1.00     8373    19419
cor(cmol_Intercept,K_Intercept)         -0.06      0.38    -0.77          0.68   1.00    19012    25650
cor(nmol_Intercept,K_Intercept)          0.16      0.41    -0.68          0.84   1.00    13106    20450
cor(pmol_Intercept,K_Intercept)          0.31      0.38    -0.55          0.89   1.00    17999    21690
```

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	pd	pval	BF
cmol_Intercept	1.55	0.03	1.50	1.60	1.00	20552	24283	1.0000	0.0000	1.46E+38
nmol_Intercept	-1.29	0.10	-1.48	-1.06	1.00	16869	15095	1.0000	0.0000	95714
pmol_Intercept	-3.40	0.26	-3.90	-2.82	1.00	18767	17922	1.0000	0.0000	1574833
K_Intercept	0.07	0.27	-0.46	0.61	1.00	27941	28992	0.5982	0.8036	0.05
cmol_no3	0.01	0.01	-0.01	0.02	1.00	58708	37168	0.7746	0.4509	0.00
cmol_po4	0.00	0.01	-0.01	0.01	1.00	80062	34915	0.7181	0.5638	0.00
cmol_k	0.00	0.01	-0.02	0.01	1.00	54255	36539	0.6410	0.7180	0.00
cmol_conductivity	0.01	0.01	-0.01	0.02	1.00	54866	38173	0.7735	0.4530	0.01
cmol_MAT	-0.01	0.01	-0.03	0.01	1.00	52976	35570	0.7784	0.4432	0.01
cmol_WA	0.01	0.01	-0.02	0.03	1.00	50377	37077	0.6803	0.6394	0.01
cmol_altitude	-0.01	0.01	-0.03	0.01	1.00	48030	35455	0.7546	0.4909	0.01
nmol_no3	0.03	0.02	-0.01	0.07	1.00	52813	37102	0.9479	0.1042	0.04
nmol_po4	0.03	0.02	0.00	0.06	1.00	72579	36475	0.9548	0.0905	0.03
nmol_k	0.02	0.02	-0.03	0.06	1.00	48540	37942	0.7595	0.4811	0.01
nmol_conductivity	0.00	0.02	-0.05	0.05	1.00	51910	37001	0.5059	0.9882	0.01
nmol_MAT	-0.02	0.03	-0.08	0.05	1.00	48629	36952	0.7028	0.5944	0.02
nmol_WA	0.05	0.03	-0.02	0.11	1.00	49194	37141	0.9299	0.1402	0.05
nmol_altitude	-0.11	0.03	-0.18	-0.05	1.00	48478	35491	0.9996	0.0007	7.45
pmol_no3	0.08	0.05	-0.01	0.18	1.00	53355	37265	0.9563	0.0875	0.11
pmol_po4	0.07	0.04	-0.01	0.15	1.00	71316	36684	0.9616	0.0767	0.10
pmol_k	-0.01	0.06	-0.12	0.10	1.00	48022	36796	0.5392	0.9217	0.03
pmol_conductivity	0.08	0.06	-0.05	0.20	1.00	50504	37236	0.8924	0.2152	0.07
pmol_MAT	0.04	0.08	-0.11	0.20	1.00	46967	35941	0.7109	0.5782	0.05
pmol_WA	0.24	0.08	0.08	0.39	1.00	47441	36194	0.9986	0.0028	3.54
pmol_altitude	-0.17	0.08	-0.32	-0.02	1.00	48008	36459	0.9837	0.0327	0.40
K_no3	-0.09	0.07	-0.22	0.04	1.00	56891	36583	0.9088	0.1824	0.08
K_po4	-0.03	0.06	-0.14	0.08	1.00	69824	35004	0.6934	0.6131	0.03

K_k	-0.02	0.08	-0.17	0.14	1.00	47846	36014	0.5926	0.8148	0.04
K_conductivity	-0.11	0.09	-0.27	0.06	1.00	49053	36396	0.8910	0.2181	0.09
K_MAT	0.10	0.11	-0.12	0.31	1.00	47486	35708	0.8124	0.3751	0.08
K_WA	-0.01	0.11	-0.23	0.21	1.00	44804	36369	0.5350	0.9299	0.06
K_altitude	0.00	0.11	-0.21	0.21	1.00	47742	36690	0.5006	0.9988	0.05

Family Specific Parameters:

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
sigma_cmol	0.08	0.00	0.07	0.09	1.00	61174	34454
sigma_nmol	0.22	0.01	0.20	0.25	1.00	57882	33098
sigma_pmol	0.56	0.03	0.51	0.62	1.00	67550	34341
sigma_K	0.80	0.04	0.73	0.88	1.00	73209	34501

Effect of phylogeny (λ), intraspecific variability, and residuals (inter-class correlations):

Hypothesis	**Estimate**	**Est.Error**	**CI.Lower**	**CI.Upper**	**Evid.Ratio**	**Post.Prob**	**Star**
λ.cmol	0.45	0.25	0.01	0.86	0.32	0.24	*
species.cmol	0.07	0.07	0.00	0.25	3.77	0.79	*
residuals.cmol	0.48	0.21	0.13	0.87	0.00	0.00	*
λ.nmol	0.41	0.28	0.00	0.89	0.49	0.33	*
species.nmol	0.25	0.15	0.02	0.56	0.18	0.16	*
residuals.nmol	0.34	0.15	0.08	0.64	0.00	0.00	*
λ.pmol	0.48	0.28	0.00	0.91	0.36	0.27	*
species.pmol	0.20	0.14	0.01	0.52	0.38	0.27	*
residuals.pmol	0.32	0.16	0.08	0.64	0.00	0.00	*
λ.K	0.55	0.18	0.11	0.83	0.06	0.06	*
species.K	0.02	0.04	0.00	0.13	24.21	0.96	*
residuals.K	0.43	0.16	0.17	0.79	0.00	0.00	*

Variance explained:

	Estimate	Est.Error	Q2.5	Q97.5
cmol	0.18	0.05	0.09	0.27
nmol	0.47	0.04	0.38	0.54
pmol	0.47	0.05	0.37	0.56
K	0.22	0.06	0.11	0.35

4. Na, Ca, Mg, S and Fe model

Family: MV (lognormal, lognormal, lognormal, lognormal, lognormal)

Links: mu = identity; sigma = identity

Formulas:

Ca. ~ no3 + po4 + ca + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)
Mg. ~ no3 + po4 + mg + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)
Na. ~ no3 + po4 + na + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)
S. ~ no3 + po4 + s + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)
Fe. ~ no3 + po4 + fe + conductivity + MAT + WA + altitude + (1 | p | species) + (1 | q | phylo)

Data: data (Number of observations: 245)

Samples: 50 chains, each with iter = 2000; warmup = 1000; thin = 1; total post-warmup samples = 50000

```
Group-Level Effects:
~species (Number of levels: 35)
                               Estimate  Est.Error  l-95% CI  u-95% CI  Rhat  Bulk_ESS  Tail_ESS
sd(Ca_Intercept)                   0.46       0.13      0.18      0.72  1.00      6785      3794
sd(Mg_Intercept)                   0.11       0.08      0.00      0.31  1.00     10920     17515
sd(Na_Intercept)                   0.22       0.15      0.01      0.54  1.00      9584     21042
sd(S_Intercept)                    0.07       0.05      0.00      0.20  1.01      9010     18754
sd(Fe_Intercept)                   0.27       0.13      0.02      0.53  1.01      9588     13321
cor(Ca_Intercept,Mg_Intercept)     0.03       0.38     -0.70      0.73  1.00     49202     37490
cor(Ca_Intercept,Na_Intercept)    -0.06       0.37     -0.73      0.66  1.00     42652     35428
cor(Mg_Intercept,Na_Intercept)     0.15       0.42     -0.69      0.84  1.00     18948     32165
cor(Ca_Intercept,S_Intercept)     -0.07       0.36     -0.72      0.65  1.00     43459     34077
cor(Mg_Intercept,S_Intercept)     -0.01       0.40     -0.75      0.74  1.00     25628     34915
cor(Na_Intercept,S_Intercept)      0.03       0.39     -0.72      0.75  1.00     29981     37235
cor(Ca_Intercept,Fe_Intercept)    -0.17       0.33     -0.74      0.54  1.00     31798     27757
cor(Mg_Intercept,Fe_Intercept)     0.20       0.40     -0.65      0.84  1.00     15161     25707
cor(Na_Intercept,Fe_Intercept)    -0.16       0.39     -0.81      0.65  1.00     23855     32801
cor(S_Intercept,Fe_Intercept)      0.06       0.38     -0.69      0.75  1.00     33574     40610
```

~phylo (Number of levels: 35)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Ca_Intercept)	0.65	0.58	0.02	2.22	1.01	5543	4812
sd(Mg_Intercept)	0.76	0.25	0.35	1.33	1.00	16970	14387
sd(Na_Intercept)	1.15	0.49	0.19	2.19	1.00	11188	10137
sd(S_Intercept)	0.12	0.11	0.00	0.41	1.00	18203	24486
sd(Fe_Intercept)	0.71	0.50	0.03	1.84	1.00	9905	21005
cor(Ca_Intercept,Mg_Intercept)	0.10	0.38	-0.66	0.77	1.00	13647	23134
cor(Ca_Intercept,Na_Intercept)	0.09	0.40	-0.69	0.79	1.00	15412	25892
cor(Mg_Intercept,Na_Intercept)	0.47	0.30	-0.23	0.90	1.00	24089	26878
cor(Ca_Intercept,S_Intercept)	-0.03	0.41	-0.78	0.75	1.00	51219	37553
cor(Mg_Intercept,S_Intercept)	-0.03	0.39	-0.75	0.71	1.00	52841	39739
cor(Na_Intercept,S_Intercept)	-0.02	0.40	-0.76	0.74	1.00	48442	43120
cor(Ca_Intercept,Fe_Intercept)	-0.08	0.41	-0.80	0.71	1.00	24363	32842
cor(Mg_Intercept,Fe_Intercept)	0.17	0.36	-0.58	0.78	1.00	35163	37601
cor(Na_Intercept,Fe_Intercept)	-0.11	0.39	-0.77	0.68	1.00	30354	37521
cor(S_Intercept,Fe_Intercept)	0.05	0.41	-0.73	0.79	1.00	35808	41944

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	PD	Pval	BF
Ca_Intercept	1.89	0.24	1.40	2.37	1.00	22186	16954	1.0000	0.0000	245.17
Mg_Intercept	0.29	0.21	-0.12	0.71	1.00	22710	29781	0.9271	0.1457	0.12
Na_Intercept	-1.49	0.32	-2.14	-0.82	1.00	26618	29143	0.9998	0.0003	48.97
S_Intercept	0.52	0.05	0.42	0.63	1.00	26674	25090	1.0000	0.0001	242.02
Fe_Intercept	1.11	0.24	0.65	1.63	1.00	27999	26850	0.9996	0.0008	35.20
Ca_no3	-0.03	0.05	-0.12	0.06	1.00	63750	40969	0.7393	0.5215	0.03
Ca_po4	-0.06	0.04	-0.14	0.01	1.00	77512	37815	0.9531	0.0938	0.08
Ca_ca	0.19	0.08	0.04	0.35	1.00	39714	39415	0.9936	0.0127	0.93
Ca_conductivity	0.11	0.07	-0.03	0.25	1.00	45897	41159	0.9447	0.1106	0.13
Ca_MAT	0.12	0.08	-0.05	0.28	1.00	50223	40206	0.9236	0.1529	0.11
Ca_WA	-0.02	0.08	-0.18	0.13	1.00	44217	38065	0.6105	0.7790	0.04
Ca_altitude	0.10	0.08	-0.05	0.25	1.00	54448	39577	0.9038	0.1925	0.09
Mg_no3	-0.04	0.04	-0.12	0.05	1.00	59407	41240	0.7974	0.4051	0.03
Mg_po4	0.02	0.03	-0.04	0.09	1.00	84662	38164	0.7540	0.4920	0.02
Mg_mg	0.20	0.07	0.06	0.33	1.00	51216	40914	0.9982	0.0036	2.33
Mg_conductivity	-0.19	0.06	-0.31	-0.06	1.00	48428	41404	0.9981	0.0039	2.19
Mg_MAT	-0.02	0.07	-0.16	0.11	1.00	58809	38926	0.6157	0.7686	0.04
Mg_WA	-0.09	0.07	-0.22	0.05	1.00	53561	39806	0.8896	0.2208	0.07
Mg_altitude	0.03	0.07	-0.12	0.17	1.00	48238	38474	0.6434	0.7132	0.04
Na_no3	-0.06	0.07	-0.20	0.09	1.00	70144	39222	0.7768	0.4464	0.05
Na_po4	0.11	0.06	0.00	0.23	1.00	83795	37308	0.9720	0.0560	0.18
Na_na	0.32	0.09	0.14	0.50	1.00	56017	41122	0.9996	0.0007	11.58
Na_conductivity	-0.31	0.10	-0.51	-0.12	1.00	49098	42119	0.9991	0.0018	7.04
Na_MAT	0.19	0.11	-0.03	0.42	1.00	60729	39031	0.9565	0.0870	0.24
Na_WA	0.02	0.12	-0.21	0.24	1.00	63093	39997	0.5502	0.8995	0.06
Na_altitude	0.14	0.12	-0.10	0.38	1.00	47895	39459	0.8724	0.2552	0.12
S_no3	0.01	0.02	-0.04	0.05	1.00	68603	40329	0.6237	0.7525	0.01

S_po4	0.02	0.02	-0.01	0.05	1.00	86881	38829	0.8736	0.2528	0.02
S_s	0.03	0.03	-0.04	0.10	1.00	54444	38708	0.8129	0.3742	0.02
S_conductivity	0.04	0.03	-0.02	0.10	1.00	54021	40655	0.8880	0.2241	0.03
S_MAT	-0.03	0.03	-0.10	0.03	1.00	55077	39376	0.8459	0.3083	0.03
S_WA	0.02	0.03	-0.04	0.09	1.00	64948	36169	0.7386	0.5228	0.02
S_altitude	-0.12	0.04	-0.19	-0.05	1.00	49690	40297	0.9998	0.0004	6.84
Fe_no3	-0.01	0.07	-0.14	0.12	1.00	54764	42304	0.5460	0.9079	0.03
Fe_po4	-0.03	0.05	-0.14	0.07	1.00	82366	37473	0.7375	0.5251	0.03
Fe_fe	0.18	0.05	0.07	0.29	1.00	74739	36939	0.9996	0.0008	5.45
Fe_conductivity	-0.14	0.08	-0.30	0.01	1.00	60659	41023	0.9684	0.0632	0.22
Fe_MAT	0.01	0.11	-0.20	0.21	1.00	53862	38811	0.5303	0.9394	0.05
Fe_WA	0.09	0.10	-0.12	0.29	1.00	61381	39730	0.7938	0.4124	0.07
Fe_altitude	-0.13	0.11	-0.35	0.08	1.00	52677	40484	0.8887	0.2226	0.11

Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma_Ca	0.54	0.03	0.49	0.59	1.00	54371	38369
sigma_Mg	0.51	0.02	0.47	0.56	1.00	71829	38862
sigma_Na	0.86	0.04	0.78	0.95	1.00	72188	39053
sigma_S	0.26	0.01	0.23	0.28	1.00	33523	33220
sigma_Fe	0.78	0.04	0.71	0.86	1.00	69656	38899

Effect of phylogeny (λ), intraspecific variability, and residuals (inter-class correlations):

	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
λ.Ca	0.387	0.307	0.001	0.944	0.660	0.3974	*
species.Ca	0.271	0.166	0.004	0.587	0.448	0.3095	*
residuals.Ca	0.342	0.176	0.046	0.667	0.003	0.0027	*
λ.Mg	0.652	0.149	0.295	0.874	0.017	0.0165	*
species.Mg	0.024	0.042	0.000	0.145	18.814	0.9495	*
residuals.Mg	0.324	0.128	0.120	0.613	0.000	0.0000	*
λ.Na	0.582	0.213	0.040	0.868	0.120	0.1069	*
species.Na	0.041	0.059	0.000	0.219	10.210	0.9108	*
residuals.Na	0.377	0.173	0.126	0.778	0.000	0.0000	*
λ.S	0.171	0.194	0.000	0.687	1.876	0.6523	*
species.S	0.079	0.093	0.000	0.339	3.735	0.7888	*
residuals.S	0.750	0.204	0.259	0.992	0.000	0.0000	*
λ.Fe	0.398	0.276	0.001	0.857	0.565	0.3611	*
species.Fe	0.081	0.078	0.000	0.274	3.354	0.7703	*
residuals.Fe	0.521	0.226	0.136	0.895	0.000	0.0000	*

Variance explained:

	Estimate	Est.Error	Q2.5	Q97.5
Ca	0.35	0.05	0.25	0.46
Mg	0.30	0.06	0.19	0.43
Na	0.21	0.06	0.10	0.35
S	0.18	0.05	0.10	0.28
Fe	0.23	0.06	0.13	0.35

5. Environmental and elementome PCAs + model

Elementome PCA (all elements and ratios logged)

Importance of components:

	PC1	PC2	PC3
Standard deviation	2.111	1.521	1.293
Proportion of Variance	0.371	0.193	0.139
Cumulative Proportion	0.371	0.564	0.703

Loadings

	PC1	PC2	PC3
c.mol	0.215	0.294	-0.073
cn.mol	0.379	0.023	0.409
n.mol	-0.340	0.060	-0.455
p.mol	-0.369	0.394	0.108
np.mol	0.272	-0.428	-0.328
cp.mol	0.386	-0.355	-0.114
K.ppm	-0.301	-0.373	0.273
Ca.ppm	0.119	-0.130	-0.109
Mg.ppm	-0.305	-0.374	0.156
Na.ppm	-0.201	-0.284	0.283
S.ppm	-0.145	-0.079	-0.546
Fe.ppm	-0.276	-0.250	0.001

Loadings (correlation with axes)

	PC1	PC2	PC3
c.mol	0.454	0.447	-0.095
cn.mol	0.800	0.034	0.528
n.mol	-0.718	0.092	-0.588
p.mol	-0.778	0.600	0.139
np.mol	0.575	-0.650	-0.424
cp.mol	0.815	-0.540	-0.147
K.ppm	-0.634	-0.567	0.353
Ca.ppm	0.252	-0.197	-0.140
Mg.ppm	-0.643	-0.568	0.202
Na.ppm	-0.424	-0.432	0.366
S.ppm	-0.306	-0.120	-0.705
Fe.ppm	-0.582	-0.381	0.002

Environmental PCA (all nutrient concentrations logged, climate not logged)

Importance of components:

	PC1	PC2	PC3
Standard deviation	2.489	1.199	1.072
Proportion of Variance	0.516	0.120	0.096
Cumulative Proportion	0.516	0.636	0.731

Loadings

	PC1	PC2	PC3
no3	0.275	-0.285	-0.274
Po4	-0.090	0.523	-0.620
Na	0.317	0.092	0.073
Ca	0.338	0.005	-0.041
K	0.280	0.123	-0.375
Mg	0.347	0.016	-0.029
so4	0.345	-0.017	-0.117
Fe	-0.040	0.413	0.532
No3:po4	0.281	-0.521	0.101
MAT	0.319	0.275	0.131
WA	-0.327	-0.138	-0.170
Altitude	-0.307	-0.290	-0.199

Loadings (correlation with axes)

	PC1	PC2	PC3
no3	0.685	-0.342	-0.293
Po4	-0.223	0.626	-0.665
Na	0.789	0.110	0.078
Ca	0.842	0.006	-0.044
K	0.698	0.147	-0.401
Mg	0.863	0.019	-0.031
so4	0.858	-0.020	-0.125
Fe	-0.099	0.495	0.570
No3:po4	0.698	-0.625	0.108
MAT	0.794	0.330	0.140
WA	-0.815	-0.166	-0.182
Altitude	-0.764	-0.348	-0.213

Model

```
Family: MV(gaussian, gaussian, gaussian)
Links: mu = identity; sigma = identity
Formulas:
pc1 ~ pc.env1 + pc.env2 + pc.env3 + (1 | p | gen_spec) + (1 | q | phylo)
pc2 ~ pc.env1 + pc.env2 + pc.env3 + (1 | p | gen_spec) + (1 | q | phylo)
pc3 ~ pc.env1 + pc.env2 + pc.env3 + (1 | p | gen_spec) + (1 | q | phylo)
Data: subdata (Number of observations: 214)
Samples: 30 chains, each with iter = 3000; warmup = 1000; thin = 1; total post-warmup samples = 60000
```

```
Group-Level Effects:
~species (Number of levels: 13)
                                 Estimate  Est.Error  l-95% CI  u-95% CI  Rhat  Bulk_ESS  Tail_ESS
sd(pc1_Intercept)                    0.54       0.43      0.02      1.60  1.00     11305     15732
sd(pc2_Intercept)                    0.67       0.30      0.08      1.32  1.00     13285     11881
sd(pc3_Intercept)                    0.56       0.24      0.11      1.09  1.00     17102     12922
cor(pc1_Intercept,pc2_Intercept)    -0.25       0.48     -0.93      0.77  1.00     13351     24540
cor(pc1_Intercept,pc3_Intercept)    -0.02       0.47     -0.86      0.84  1.00     13893     26861
cor(pc2_Intercept,pc3_Intercept)     0.22       0.40     -0.62      0.88  1.00     25901     29412
```

~phylo (Number of levels: 13)

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
sd(pc1_Intercept)	3.73	1.30	1.19	6.55	1.00	13995	9871
sd(pc2_Intercept)	1.63	1.20	0.07	4.43	1.00	11478	27581
sd(pc3_Intercept)	1.04	0.90	0.04	3.31	1.00	14088	22200
cor(pc1_Intercept,pc2_Intercept)	-0.22	0.45	-0.89	0.76	1.00	27917	36861
cor(pc1_Intercept,pc3_Intercept)	-0.03	0.47	-0.86	0.84	1.00	45699	39888
cor(pc2_Intercept,pc3_Intercept)	0.02	0.51	-0.88	0.89	1.00	34744	43732

Population-Level Effects:

	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**	**PD**	**Pval**	**BF**
pc1_Intercept	-0.40	1.03	-2.51	1.65	1.00	26617	32461	0.6656	0.6688	0.19
pc2_Intercept	-0.07	0.58	-1.35	1.09	1.00	28908	28056	0.5454	0.9093	0.08
pc3_Intercept	0.05	0.41	-0.82	0.90	1.00	31833	27000	0.5784	0.8431	0.06
pc1_pc.env1	-0.10	0.06	-0.21	0.01	1.00	83122	47599	0.9583	0.0834	0.13
pc1_pc.env2	-0.24	0.10	-0.44	-0.04	1.00	88837	45710	0.9915	0.0171	0.92
pc1_pc.env3	0.08	0.11	-0.14	0.30	1.00	93988	44774	0.7619	0.4763	0.07
pc2_pc.env1	0.00	0.05	-0.09	0.09	1.00	87548	46435	0.5373	0.9254	0.02
pc2_pc.env2	-0.01	0.08	-0.17	0.15	1.00	91490	45104	0.5414	0.9173	0.04
pc2_pc.env3	-0.15	0.09	-0.32	0.03	1.00	95312	47224	0.9499	0.1002	0.18
pc3_pc.env1	-0.17	0.04	-0.24	-0.09	1.00	88654	46051	1.0000	0.0000	158
pc3_pc.env2	-0.05	0.07	-0.18	0.08	1.00	90418	45025	0.7689	0.4622	0.04
pc3_pc.env3	0.08	0.08	-0.07	0.23	1.00	98358	45623	0.8518	0.2965	0.07

```
Family Specific Parameters:
                  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sigma_pc1             1.69      0.09     1.54     1.87 1.00    90817    45228
sigma_pc2             1.37      0.07     1.25     1.52 1.00    88866    47864
sigma_pc3             1.15      0.06     1.04     1.28 1.00    87854    45054

Residual Correlations:
                  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
rescor(pc1,pc2)       0.15      0.07     0.02     0.29 1.00    89770    45962
rescor(pc1,pc3)       0.05      0.07    -0.09     0.19 1.00    88324    47029
rescor(pc2,pc3)      -0.09      0.07    -0.22     0.05 1.00    89180    46192
```

Effect of phylogeny (λ), intraspecific variability, and residuals (inter-class correlations):

```
Hypothesis        Estimate Est.Error CI.Lower CI.Upper Evid.Ratio Post.Prob Star
λ.pc1                 0.78      0.16     0.25     0.94       0.06      0.06    *
species.pc1           0.04      0.08     0.00     0.29      13.93      0.93    *
residuals.pc1         0.18      0.11     0.05     0.47       0.00      0.00    *
λ.pc2                 0.45      0.30     0.00     0.92       0.50      0.33    *
species.pc2           0.13      0.11     0.00     0.40       1.59      0.61    *
residuals.pc2         0.42      0.23     0.07     0.83       0.00      0.00    *
λ.pc3                 0.37      0.30     0.00     0.90       0.72      0.42    *
species.pc3           0.13      0.11     0.00     0.40       1.32      0.57    *
residuals.pc3         0.50      0.24     0.09     0.88       0.00      0.00    *
```

Variance explained:

	Estimate	Est.Error	Q2.5	Q97.5
R2pc1	0.38	0.04	0.29	0.46
R2pc2	0.23	0.05	0.14	0.31
R2pc3	0.25	0.05	0.15	0.34

6. Model to estimate biogeochemical niches

Family: MV(gaussian, gaussian, gaussian)

Links: mu = identity; sigma = identity

Formulas:

pc1 ~ pc.env1 + pc.env2 + pc.env3 + (1 | p | gen_spec)

pc2 ~ pc.env1 + pc.env2 + pc.env3 + (1 | p | gen_spec)

pc3 ~ pc.env1 + pc.env2 + pc.env3 + (1 | p | gen_spec)

Data: subdata (Number of observations: 214)

Samples: 50 chains, each with iter = 2500; warmup = 1000; thin = 1; total post-warmup samples = 75000

Group-Level Effects:
~gen_spec (Number of levels: 13)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(pc1_Intercept)	1.49	0.37	0.93	2.38	1.00	24584	41590
sd(pc2_Intercept)	0.81	0.23	0.46	1.35	1.00	31450	45971
sd(pc3_Intercept)	0.61	0.20	0.30	1.08	1.00	29781	41510
cor(pc1_Intercept,pc2_Intercept)	-0.30	0.28	-0.77	0.30	1.00	32621	45924
cor(pc1_Intercept,pc3_Intercept)	-0.06	0.30	-0.62	0.53	1.00	38038	49183
cor(pc2_Intercept,pc3_Intercept)	0.16	0.31	-0.47	0.72	1.00	31906	48915

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	PD	Pval	BF
pc1_Intercept	-0.10	0.44	-0.97	0.76	1.00	17700	29139	0.5944	0.8113	0.19
pc2_Intercept	0.03	0.25	-0.46	0.53	1.00	26989	39794	0.5565	0.8869	0.11
pc3_Intercept	0.06	0.20	-0.32	0.46	1.00	34253	41575	0.6253	0.7495	0.09
pc1_pc.env1	-0.11	0.06	-0.22	0.00	1.00	85614	59530	0.9708	0.0583	0.17
pc1_pc.env2	-0.25	0.10	-0.45	-0.05	1.00	102693	57808	0.9930	0.0140	1.11
pc1_pc.env3	0.08	0.11	-0.14	0.30	1.00	99822	56971	0.7549	0.4902	0.07
pc2_pc.env1	0.00	0.04	-0.09	0.09	1.00	89172	59745	0.5083	0.9834	0.02
pc2_pc.env2	-0.01	0.08	-0.17	0.14	1.00	100192	57726	0.5704	0.8592	0.04
pc2_pc.env3	-0.15	0.09	-0.32	0.03	1.00	99350	57435	0.9432	0.1135	0.16
pc3_pc.env1	-0.16	0.04	-0.24	-0.09	1.00	92198	58823	1.0000	0.0000	104.36
pc3_pc.env2	-0.05	0.07	-0.18	0.09	1.00	101993	57758	0.7594	0.4812	0.04
pc3_pc.env3	0.08	0.08	-0.07	0.23	1.00	105484	58112	0.8532	0.2935	0.06

Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma_pc1	1.70	0.09	1.54	1.88	1.00	99797.00	57570.00
sigma_pc2	1.37	0.07	1.25	1.52	1.00	97173.00	56231.00
sigma_pc3	1.15	0.06	1.04	1.27	1.00	86979.00	54678.00

Residual Correlations:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
rescor(pc1,pc2)	0.16	0.07	0.02	0.29	1.00	94360	58425
rescor(pc1,pc3)	0.05	0.07	-0.09	0.19	1.00	95310	57546
rescor(pc2,pc3)	-0.09	0.07	-0.22	0.05	1.00	95595	56745

Inter-class correlations:

	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
species.pc1	0.427	0.114	0.227	0.669	0.000	0.0000	*
residuals.pc1	0.573	0.114	0.331	0.773	0.000	0.0000	*
species.pc2	0.257	0.104	0.097	0.499	0.000	0.0003	*
residuals.pc2	0.743	0.104	0.501	0.903	0.000	0.0000	*
species.pc3	0.219	0.107	0.061	0.473	0.020	0.0200	*
residuals.pc3	0.781	0.107	0.527	0.939	0.000	0.0000	*

Variance explained:

	Estimate	Est.Error	Q2.5	Q97.5
pc1	0.376	0.044	0.284	0.455
pc2	0.219	0.046	0.127	0.308
pc3	0.241	0.048	0.145	0.331

7. Models to test higher elementome distance between coexisting individuals

```
Family: lognormal
  Links: mu = identity; sigma = identity
Formula: dist.elem ~ log(dist.env + 0.1) + coexist + (1 | sp.vs.sp)
   Data: elemdist.dif (Number of observations: 1764)
Samples: 30 chains, each with iter = 2500; warmup = 1000; thin = 1;
         total post-warmup samples = 45000

Group-Level Effects:
~sp.vs.sp (Number of levels: 4)
                   Estimate  Est.Error  l-95% CI  u-95% CI  Rhat  Bulk_ESS  Tail_ESS
sd(Intercept)          0.31       0.25      0.10      0.97  1.00      8710     11612

Population-Level Effects:
                   Estimate  Est.Error  l-95% CI  u-95% CI  Rhat  Bulk_ESS  Tail_ESS  BF     pd      pval
Intercept              0.82       0.19      0.43      1.17  1.00     10249     10488  14.66  0.9964  0.0072
logdist.envP0.1        0.09       0.02      0.05      0.12  1.00     24363     27694   4144  1.0000  0.0000
coexist1               0.12       0.07     -0.03      0.26  1.00     24932     26690   2.50  0.9411  0.1177

Family Specific Parameters:
                   Estimate  Est.Error  l-95% CI  u-95% CI  Rhat  Bulk_ESS  Tail_ESS
sigma                  0.34       0.01      0.33      0.35  1.00     31999     26631
```

Inter-class correlations

	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
species_vs_species	0.38	0.23	0.08	0.89	0.01	0.01	*
residuals	0.62	0.23	0.11	0.92	0.03	0.03	*

	Estimate	Est.Error	Q2.5	Q97.5
R2	0.164	0.015	0.134	0.194

8. Models to test higher elementome distance between coexisting species

Family: lognormal

Links: mu = identity; sigma = identity

Formula: elem.dist | weights(abscoinc) ~ log(env.dist) + log(relcoinc)

Data: res[which(res$abscoinc != 0),] (Number of observations: 308)

Samples: 15 chains, each with iter = 2000; warmup = 1000; thin = 1; total post-warmup samples = 15000

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	BF	pd	pval
Intercept	0.96	0.02	0.92	1.00	1.00	15268	11972	1.66E+56	1.0000	0.0000
logenv.dist	0.24	0.01	0.22	0.27	1.00	14965	10955	1.95E+22	1.0000	0.0000
logrelcoinc	0.09	0.01	0.07	0.10	1.00	11509	10880	1.11E+11	1.0000	0.0000

Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	0.35	0.01	0.34	0.36	1.00	14456	10743

	Estimate	Est.Error	Q2.5	Q97.5
R2	0.15	0.01	0.12	0.17