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RESEARCH ARTICLE

High-dimensional elementomes outperform CNP models in explaining photosynthetic traits

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Abstract

1. Links between plant elementomes (i.e. the concentration of chemical elements in plant tissue) and functional traits have the potential to improve predictions of plant physiological performance and ecosystem processes, and their response to environmental change. High-dimensional plant elementomes, which encompass not only macronutrients but also micronutrients and trace elements, have been associated with various morphological and physiological plant traits, but not with photosynthetic traits.
2. We determined elementomes, comprising 21 elements and isotopic ratios of C and N, of 26 hygrophytic bryophyte species (16 mosses and 10 liverworts) in Mediterranean springs, and examined their relationship with four photosynthetic light response traits: maximum photosynthetic rates, apparent quantum yield, light compensation point and dark respiration rates.
3. Results from linear mixed effects models showed that high-dimensional elementomes are strongly associated with photosynthetic traits, explaining substantially more variance (R^2=38%–61%; 72%–85% when also including taxonomic information) than models based solely on C, N and P (R^2=6%–45% and 35%–72%, respectively). Model selection and averaging revealed that each photosynthetic light response trait was optimally modelled by a set of 8–13 elemental variables, including various macronutrients (e.g. N, S, K), micronutrients (e.g. Zn, Cu), trace elements (e.g. Ni, Co) and isotopic ratios ($\delta^{13}C$ and $\delta^{15}N$).
4. We demonstrate that plant elementomes capture key drivers of photosynthetic variation, which adds to growing evidence of strong links between elementomes and various functional traits that underpin organismal and ecosystem functioning. Our results suggest that characterising plant elementomes could contribute to improved predictions of ecosystem-scale processes such as CO_2 uptake.

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KEYWORDS
ionome, isotope ratio, liverwort, maximum photosynthetic capacity, moss, nutrient, plant traits

1 | INTRODUCTION

The concentration of chemical elements in whole organisms or specific organs such as leaves (i.e. the elementome, sometimes called the ionome) has formidable potential to improve our understanding of biotic assemblages, ecosystem functioning and their responses to environmental change (Fernández-Martínez, 2022; González et al., 2017; Neugebauer et al., 2018; Peñuelas et al., 2019). Concentrations of macronutrients such as carbon (C), nitrogen (N) and phosphorus (P), and their stoichiometric ratios, have long been associated with functional traits within ecological stoichiometry and resource economics frameworks (Díaz et al., 2016; Elser et al., 2000; Sardans et al., 2021; Wright et al., 2004). Recent research shows that considering high-dimensional elementomes, which include not only macronutrients but also micronutrients (elements required in small quantities for metabolic functions, for example, zinc [Zn], manganese [Mn]) and trace elements (elements present in very low concentrations that may or may not have biological functions or toxic effects on metabolism, e.g. lead [Pb], cadmium [Cd]) greatly improves predictions of functional traits across very different types of organisms including phytoplankton, bryophytes, herbs, trees and animals (Fernández-Martínez, Corbera, Cano-Rocabayera, Sabater, & Preece, 2021; Furey & Tilman, 2023; González et al., 2017; Hofmann et al., 2021; Peñuelas et al., 2019). This is because functional traits, such as plant water-use efficiency, reproductive effort and herbivory defence, are influenced not only by C, N and P but also by elements like potassium (K), Zn and silicon (Si), respectively (Fernández-Martínez et al., 2017; Reynolds et al., 2009; Sardans & Peñuelas, 2015). In line with this, elementomes have been found to map to functional traits and to be phylogenetically conserved (Fernández-Martínez, Preece, Corbera, Cano, Garcia-Porta, Sardans, et al., 2021; Furey & Tilman, 2023; Neugebauer et al., 2018), which has led to the prediction that different species and their functional traits occupy distinct regions in a multidimensional space defined by bio-element concentrations (i.e. the biogeochemical niche hypothesis; Peñuelas et al., 2019; Sardans et al., 2023). Therefore, assessing the association between elementomes and functional traits is a crucial first step to improve our understanding of how plant communities are structured and may drive ecosystem functioning including primary productivity, carbon cycling and nutrient fluxes.

In terrestrial ecosystems, relationships between key plant functional traits and elementomes beyond C, N and P are not well understood. In particular, links between plant elementomes and photosynthetic traits remain untested. Plant traits associated with photosynthetic capacity and efficiency are commonly evaluated through the analysis of light response curves (Marino et al., 2010; Peek et al., 2002). These photosynthetic light response traits include the light-saturated photosynthetic rate, indicating maximum photosynthetic capacity; the apparent quantum yield, representing the efficiency of light energy utilisation during photosynthesis; the light compensation point, which denotes the light intensity at which photosynthetic carbon uptake exactly balances respiratory carbon loss; and the dark respiration rate, linked to baseline energy consumption levels. These traits have been related to foliar concentrations of N and P coherent with resource economics theory: high nutrient concentrations are often associated with high values of light-saturated photosynthesis, dark respiration and apparent quantum yield, as part of resource-acquisitive trait spectra and the great contribution of N and P in the molecular structures working in these tasks (Grau-Andrés, Kardol, et al., 2022; Marino et al., 2010; Reich et al., 2008, 2009; Wright et al., 2004). However, several other elements can also regulate photosynthesis (e.g. K, magnesium [Mg], calcium [Ca], iron [Fe]; Briat et al., 2007; Hochmal et al., 2015; Tränkner et al., 2018). Additionally, the effect on photosynthesis of varying concentrations of less studied elements such as copper (Cu), Zn and Mn, which are required for electron transport, CO_2 fixation and photoprotection, and the potential detrimental effect of heavy metals (e.g. mercury [Hg], cadmium [Cd], arsenic [As]), is largely unknown (Szopiński et al., 2019; Yruela, 2013). Considering a wider range of bioelements may thus improve model predictions of photosynthetic traits compared to models including only C, N and P. Recent work has shown that foliar elementomes are associated with functional trait spectra including photosynthetic traits (Sardans et al., 2023), but associations with specific photosynthetic traits, and the relative importance of the elements comprising the elementomes, has not been investigated. Given the central role of photosynthesis in plant communities and ecosystems, assessing whether and how elementomes are associated with photosynthetic traits is key to evaluating the potential of elementomes to predict ecosystem-level processes.

Elementome research in terrestrial ecosystems has focused on vascular plants, especially tree leaves (Neugebauer et al., 2018; Sardans et al., 2023) and herbs (Furey & Tilman, 2023; Kaspari et al., 2021). Bryophytes (i.e. mosses, liverworts and hornworts) have received comparatively little attention (but see Hájek et al., 2014; Fernández-Martínez, Preece, Corbera, Cano, Garcia-Porta, Bogdziewicz, et al., 2021; Fernández-Martínez, Corbera, Cano-Rocabayera, Sabater, & Preece, 2021; Fernández-Martínez, Preece, Corbera, Cano, Garcia-Porta, Sardans, et al., 2021). This is despite their crucial roles in many ecosystems worldwide, such as forming substantial ground-layer biomass in high-latitude mires and forests (Nilsson & Wardle, 2005; Turetsky et al., 2010), regulating C and nutrient dynamics in boreal forests (Grau-Andrés, Wardle, et al., 2022; Hupperts et al., 2021) or sustaining biodiversity in Mediterranean spring-fed ecosystems (Fernández-Martínez et al., 2024). Importantly, the small size of bryophytes and their relatively simple morphology, characterised by the absence of true vascular tissues and by low differentiation of specialised tissues, facilitates establishing links between whole-plant elementomes and functional traits (Fernández-Martínez, Preece, Corbera, Cano, Garcia-Porta, Sardans, et al., 2021). Further, as the extant lineage most closely related to the first land plants, bryophytes

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can offer insights into the functional strategies that may have been important during the colonisation of land (Oliver et al., 2000), while also reflecting their own unique evolutionary trajectories. In bryophytes, various element concentrations and isotopic ratios have been related to photosynthetic light response traits. For example, light-saturated photosynthesis has been found to increase with N (Carriquí et al., 2019; Grau-Andrés, Kardol, et al., 2022) and to decrease with $\delta^{13}C$ (Grau-Andrés et al., 2022; Rice et al., 2008), but associations with other elements that may enhance photosynthesis have not been explored (e.g. with K and nickel [Ni], which regulate CO_2 diffusion and enzyme activity; Shahzad et al., 2018; Tränkner et al., 2018). Regarding elementome research, recent work has shown that elementomes are associated with morphological and reproductive traits in bryophytes (Fernández-Martínez, Corbera, Cano-Rocabayera, Sabater, & Preece, 2021; Fernández-Martínez, Preece, Corbera, Cano, Garcia-Porta, Bogdziewicz, et al., 2021). However, links between elementomes and photosynthetic light response traits, not only in bryophytes but more generally in terrestrial plants, remain unexplored.

Here, we analysed 105 bryophyte samples belonging to 16 moss and 10 liverwort species collected from semi-natural springs in mountain areas of NE Iberian Peninsula to explore whether and how elementomes drive photosynthetic light response traits. For each bryophyte individual, we measured maximum photosynthetic capacity, apparent quantum yield, light compensation point and dark respiration, as well as tissue elemental composition. We hypothesised that: (1) Bryophyte elementomes are associated with photosynthetic light response traits because elementomes have been shown to drive other functional traits in bryophytes (Fernández-Martínez, Corbera, Cano-Rocabayera, Sabater, & Preece, 2021; Fernández-Martínez, Preece, Corbera, Cano, Garcia-Porta, Bogdziewicz, et al., 2021) and vascular plants (Furey & Tilman, 2023; Sardans et al., 2023); (2) Compared to considering only C, N and P, high-dimensional elementomes are more strongly associated with photosynthetic light response traits. This has been observed for other functional traits in bryophytes, vascular plants (Furey & Tilman, 2023), and phytoplankton (Hofmann et al., 2021); (3) The optimal elemental set (i.e. the number and identity of elements that best explain trait variation) differs for each light-response trait, reflecting their diverse physiological roles (Hofmann et al., 2021; Peñuelas et al., 2019). By addressing these hypotheses, we aim to expand our understanding of elementome–functional trait relationships in terrestrial plants to include also photosynthetic light response traits, which is crucial for improving elementome-based predictions of how communities and ecosystems are structured, function and respond to environmental change.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

Bryophyte samples were collected between September and November 2020 from 51 semi-natural springs in mountain areas of Catalonia, north-eastern Iberian Peninsula, within a 50×75-km area in the region of Bages (number of springs = 6) and in the areas of Serralada Litoral Central ($N = 14$), Montseny ($N = 14$) and La Garrotxa ($N = 2$) (Appendix S1: Figure S1). Climate varies across these regions: it is sub-humid Mediterranean at Bages (averaged across springs, mean annual precipitation = 584 mm, annual temperature = 13.9°C, altitude = 260 m), humid Mediterranean at Montseny (958 mm, 9.8°C, 872 m), maritime Mediterranean at Serralada Litoral Central (762 mm, 13.4°C, 369 m) and pre-Pyreneeal at La Garrotxa (1051 mm, 13.1°C, 466 m). Climate data was obtained from the 1979 to 1999 digital Climatic Atlas of Catalonia (https://opengis.grumets.cat/acdc).

The springs were small constructions of rock and concrete with a spout that directed water from the aquifer into a sink or cistern. We sampled entire bryophyte shoots that were in direct contact with the spring water, that is, they were either submerged in water or received water splash. From each of 51 springs, we collected 1–6 bryophyte samples of different species (depending on species diversity at each spring) for a total of 105 bryophyte samples of 26 different species (16 mosses, 10 liverworts; Appendix S1: Table S1). Bryophytes are key constituents of Mediterranean spring-fed ecosystems (Fernández-Martínez et al., 2024). Groundwater-fed ecosystems have stable hydrology, hydrochemistry and microclimate (Johnson, 2025), thus minimising effects of short-term environmental variation on bryophyte physiology. Additionally, phenological changes in photosynthetic light response traits during the sampling period were likely minimal given the low growth seasonality of bryophytes (Proctor, 1990). All samples were gametophytes with a healthy appearance composed of green photosynthetic tissue with no brown, senescent tissue or sporophytes present. The large climatic and hydrochemical gradients sampled ensured that the species are representative of a wide geographical area, with some species spanning the entire Northern Hemisphere (refer to GBIF records: www.gbif.org). We did not require a permit to collect the small amount of bryophytes used in this study, as the selected species are common in the study area and had no protection status.

2.2 | Photosynthetic light response parameters

Measurements of bryophyte photosynthesis were carried out in the laboratory within 12–24 h of sample collection. To transport the samples, we used transparent plastic pots with a small amount of water from the spring. Bryophyte CO_2 exchange was measured using an infrared gas analyser (Licor 6400-XT, LI-COR, Lincoln, USA) fitted with the 6400–07 Needle Chamber adapted for bryophytes. We used two PFA tubes to secure a Teflon foil tray in the middle of the chamber, onto which the bryophytes were placed. Air with a CO_2 mixing ratio of 400 ppm was supplied to the chamber at 500 $\mu mol\,s^{-1}$. Median relative humidity in the chamber was 64.8% (interquartile range: 61.5%–68.8%). To obtain a light response curve for each bryophyte sample, we first acclimatised the bryophyte to light conditions by placing it in the chamber and running the system at 1000 $\mu mol\,m^{-2}\,s^{-1}$ of photosynthetic photon

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flux density (PPFD) and 30°C for 20 min. Immediately after, we recorded CO_2 exchange at PPFD 1000 μmol m^{-2} s^{-1} and re-wetted the sample to keep the bryophyte at optimal moisture conditions. We then measured CO_2 exchange at PPFD levels of 500, 250, 100, 50, 25 and 0 μmol m^{-2} s^{-1}. For samples with high photosynthetic rates at low PPFD values, we included an additional measurement at 10 μmol m^{-2} s^{-1} PPFD. The minimal increase in vapour pressure deficit of the cuvette air over the measuring sequence (from 1.59 kPa at PPFD = 1000 μmol m^{-2} s^{-1} to 1.69 kPa at PPFD = 0 μmol m^{-2} s^{-1}) and the absence of a general decline in net assimilation during the 4–6 min measuring period at each PPFD level indicate that the bryophytes remained well hydrated (Appendix S1: Figure S2). Finally, samples were oven-dried at 60°C for 48 h to calculate dry mass. Eighteen out of 105 samples presented calcium carbonate incrustations, likely due to precipitation of spring water Ca^{2+} due to increased water pH during photosynthesis. We put those samples in a solution of acetic acid (pH = 2.7) for up to 1 h to dissolve the incrustations, and we rinsed them with deionised water before oven-drying them, following Fernández-Martínez, Preece, Corbera, Cano, Garcia-Porta, Bogdziewicz, et al. (2021).

Photosynthetic light response parameters were calculated by fitting the Mitscherlich equation to the CO_2 flux versus PPFD data (Grau-Andrés, Kardol, et al., 2022; Marino et al., 2010), following (Peek et al., 2002):

$$y = A_{max}\left[1 - e^{-A_{qe}\,(x-LCP)}\right] \quad (1)$$

where y (CO_2 flux) and x (PPFD) are the measured variables, A_{max} is the asymptote (i.e. the light-saturated CO_2 flux or maximum rate of net photosynthesis); A_{qe} is the initial slope of the curve (i.e. the apparent quantum yield); and *LCP* is the x-intercept (i.e. the light compensation point).

Model fitting was carried out in R software version 4.3.2 (R Core Team, 2025), using the function *nls* (non-linear least squares). Dark respiration (R_{dark}) of each sample was taken as the observed CO_2 flux at PPFD = 0 μmol cm^{-2} s^{-1} (Marino et al., 2010); we multiplied this value by minus one so that larger (more positive) values indicate greater R_{dark}. Therefore, positive A_{max} indicates net CO_2 uptake by bryophytes, and positive R_{dark} indicates CO_2 efflux to the atmosphere. Photosynthetic light response parameters were expressed on a mass basis, that is, relative to the dry mass of the bryophyte sample (Waite & Sack, 2010; Wang et al., 2014). Net CO_2 uptake versus PPFD of all samples, as well as averaged model fits for each bryophyte species, are provided in Appendix S1: Figure S3.

2.3 | Chemical analysis

Since our samples were also used in a bryophyte leachate study, we calculated the total tissue elemental composition by summing the contents found in leachates and dry tissues. Bryophytes were first oven-dried at 50°C for 48 h, and leachates from each sample were extracted by mild agitation in 100 mL of distilled water for 1 h. Incrustations of $CaCO_3$ were removed from 18 samples by soaking in acetic acid (pH 2.7) for 1 h. Leachate concentrations of P, sodium (Na), K, Mg, Ca, sulfur (S), As, chromium (Cr), Ni, cobalt (Co), Fe, Cu, Mn, aluminium (Al), boron (B), Cd, Hg, Pb and Zn were determined by inductively coupled plasma–optical emission/mass spectrometry (ICP-OES/MS) (ELAN 600 and Optima 8300, Perkin Elmer, Waltham, Massachusetts, USA). There were no missing values due to detection limits for any elements, although Hg concentrations were generally low and on the lower end of the calibration curve, which likely reduced measurement accuracy for this element. Total organic C and total N were quantified using an Analytik Jena-multi N/C 3100 analyser (Jena, Germany).

Bryophytes were then dried at 60°C for 48 h and ground to a powder using a ball mill (MM400, Retsch, Germany). Elemental concentrations of C and N and the isotopic ratios $\delta^{13}C$ ($^{13}C/^{12}C$) and $\delta^{15}N$ ($^{15}N/^{14}N$) were measured by isotope ratio mass spectrometer (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 $\delta^{13}C$ and $\delta^{15}N$ can be used to infer different sources of C and N and how these nutrients are mobilized in the ecosystem (Martín et al., 2024). Concentrations of other elements were determined using ICP-OES/MS (see above). Samples were pre-digested overnight at 90°C in a 2:1 nitric acid:hydrogen peroxide solution. All analyses were carried out at the Scientific and Technical Centres of the University of Barcelona.

2.4 | Data analysis

2.4.1 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Individual	Individual	105

To determine whether the photosynthetic light response parameters A_{max}, A_{qe}, LCP and R_{dark} were associated with bryophyte phylogeny, we first averaged the values of the parameters per species and then computed the phylogenetic signal for each parameter using the function *phylosig* in the R package 'phytools' (Revell, 2012). Phylogenetic data were obtained from (Fernández-Martínez et al., 2019). Since we found no evidence of phylogenetic signal, we did not account for phylogenetic relatedness in further analyses.

We used linear mixed effects models (LMMs; function *lme* in package 'nlme'; Pinheiro et al., 2023) to analyse the response of photosynthetic light response traits to elemental concentrations and isotopic ratios of bryophyte tissue. Separate LMMs were fitted for each response variable (A_{max}, A_{qe}, LCP and R_{dark}), and all response variables were log-transformed to remove

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heteroscedasticity. Saturated LMMs included as fixed effects all measured elements and isotopic ratios, and two-way interactions between concentrations of C, N and P. We included bryophyte species identity as a random effect to account for the non-independence of samples from the same species. We carried out diagnostic tests using Cook's Distance (via the 'predictmeans' package; Luo et al., 2023), which indicated that no single sample exerted undue influence on our model estimates. To compare the performance of saturated elementomes models to simpler models, we also fitted reduced LMMs that included as fixed effects C, N, P and their two-way interactions. To test differences between mosses and liverworts, we fitted LMMs with the single fixed effect 'bryophyte type'. Simple linear regression was used to test differences among bryophyte species replicated at least three times in our dataset. Confidence intervals for the different levels of the categorical variables 'bryophyte type' and 'bryophyte species' were computed using the R package 'emmeans' (Lenth, 2024). Finally, we computed for each trait the within- and between-species variance using ANOVA. Marginal and conditional coefficients of determination (R^2) (i.e. the variance explained by the fixed effects and by the entire model, respectively) of linear mixed effects models were computed using the function *r.squaredGLMM* in the R package 'MuMIn' (Bartoń, 2023).

To evaluate the performance of different combinations of elementome variables, we carried out automated model selection using the function *dredge* in the R package 'MuMIn', specifying that coefficients are standardised, and that a likelihood-ratio based R^2 is computed. We assessed the importance of fixed effect terms in explaining A_{max}, A_{qe}, LCP and R_{dark} by performing model averaging based on Akaike's Information Criterion (AIC). To do this, we used the function *model.avg* in the package 'MuMIn' on a subset of the best models, defined as those with ΔAIC <2 relative to the top ranked model (Symonds & Moussalli, 2011). This modelling approach is appropriate for finding parsimonious predictors in high-dimensional datasets by minimising overfitting and multicollinearity and accounting for model uncertainty (Grueber et al., 2011; Symonds & Moussalli, 2011). Coefficients were computed following the full model average method, which includes all variables in every model, setting their coefficients and variances to zero when appropriate. We used the function *vif* in the package 'car' (Fox & Weisberg, 2019) to calculate variance inflation factors (VIF) for predictors retained in the best model subsets. Across the four traits, collinearity was low (mean subset VIF ranged 1.4–2.2), and variables with VIF >5 were only found in six out of 92 selected models, with negligible effects on model-averaged coefficients. To compare performance among models differing in number of fixed effect terms, we sequentially subsetted best models (ΔAIC <2) for 1–26 fixed effects terms. Finally, we used partial residual plots to visualise the relationships between photosynthetic light response traits and individual element concentrations while holding other predictors constant (R package 'visreg'; Breheny & Burchett, 2017). We used the package 'corrplot' to plot correlations among elements (Wei & Simko, 2024).

3 | RESULTS

We found large variation in photosynthetic light response traits among bryophytes: species-averaged maximum photosynthetic capacity (A_{max}) ranged from 9.4±0.9 (mean±standard error of the mean) to 115.5 nmol CO_2 $g^{-1}s^{-1}$ (single replicate when SEs are not provided), apparent quantum yield (A_{qe}) ranged from 0.008 to 0.056±0.009 nmol CO_2 g^{-1} (μmol photons m^{-2})$^{-1}$, light compensation point (LCP) ranged from 4.1±1.1 to 44.7 μmol $m^{-2}s^{-1}$ and dark respiration (R_{dark}), from 2.0±0.4 to 18.2 nmol CO_2 $g^{-1}s^{-1}$ (Appendix S1: Table S1). In species with three or more replicates, partitioning of trait variance revealed substantial within-species variation: 70% of total variance for A_{max}, 42% for A_{qe}, 86% for LCP and 72% for R_{dark}. For all four traits, we found statistically significant differences between bryophyte species ($F_{10,57}$=3.8–6.7, p<0.001), but not between mosses and liverworts ($F_{24,79}$=0.03–3.6, p>0.07) (Figure 1). There were strong correlations between traits, both positive (A_{max} with R_{dark}, R_{dark} with LCP) and negative (A_{max} with A_{qe}, A_{qe} with LCP) (Appendix S1: Figure S4). The elemental concentrations across the 105 bryophyte samples varied substantially depending on the specific element, with coefficients of variation ranging between 9% for C to 359% for Pb (Appendix S1: Table S2). Correlations among elements were generally low, but were high for Fe and Mn (Pearson's r=0.85), S and Na (r=0.75), S and K (r=0.71) and Cd and Pb (r=0.72) (Appendix S1: Figure S5).

The elemental composition of bryophyte tissue, comprising 21 elements, $\delta^{13}C$, $\delta^{15}N$ and two-way interactions between C, N and P, outperformed models including only C, N, P and their two-way interactions in explaining the variation in A_{max}, A_{qe}, LCP and R_{dark} (e.g. R^2 marginal=0.41–0.65 vs 0.06–0.45; Table 1). The best-supported models for each trait (i.e. ΔAIC <2 compared to the top-ranked model) performed substantially better, according to AIC, than models including the full elementome and better than the C, N and P models (Table 1). Change in AIC in the best-supported models as number of variables increased indicated that the dimensionality of the optimal elemental set had a median of 11 (range: 7–14) for A_{max}, 11 (9–13) for A_{qe}, 8 (6–8) for LCP and 13 (10–15) for R_{dark} (Figure 2).

The specific elements driving variation in A_{max}, A_{qe}, LCP and R_{dark} differed considerably for each trait (Figure 3; see Appendix S1: Figure S6 for results using a modified dataset with downweighed potential outliers). The most important elements for explaining variation in A_{max} were N, K and $\delta^{13}C$ (positive effect) and S (negative effect). For A_{qe}, Ni had a positive effect, while Co, N and $\delta^{15}N$ had negative effects. Models of LCP showed large positive effects of S and Co, and negative effects of K and Ni. Finally, R_{dark} responded positively to N, S, B and As, and negatively to Mg. Modelled relationships between the photosynthetic light response traits and concentrations of important elements (N, Ni, Co, S, K and B) are illustrated in Figure 4.

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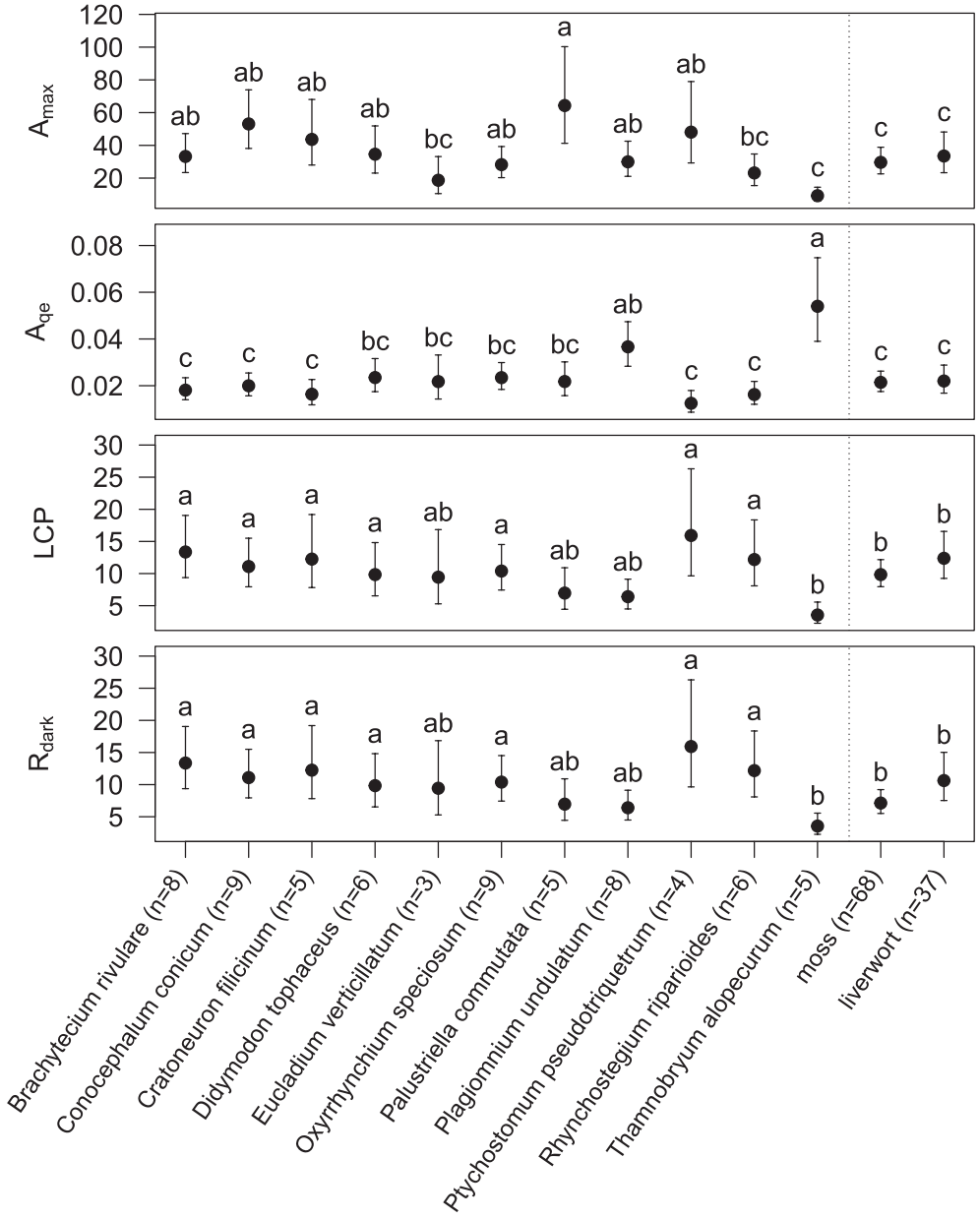

FIGURE 1 Model coefficients and 95% confidence intervals of photosynthetic parameters for (left) bryophyte species with three or more observations, and (right) bryophyte type (moss or liverwort). A_{max} is the maximum rate of net photosynthesis (in nmol CO_2 g^{-1} s^{-1}), A_{qe} is the apparent quantum yield (in nmol CO_2 g^{-1} (μmol photons m^{-2})$^{-1}$), LCP is the light compensation point (in μmol photons m^{-2} s^{-1}) and R_{dark} is dark respiration (in nmol CO_2 g^{-1} s^{-1}). Overall test statistics for species effects were $F_{10,57}=6.2$ (A_{max}), $F_{10,57}=6.7$ (A_{qe}), $F_{10,57}=3.8$ (LCP) and $F_{10,57}=5.9$ (R_{dark}). For bryophyte type, test statistics were $F_{24,79}=0.3$ (A_{max}), $F_{24,79}=0.03$ (A_{qe}), $F_{24,79}=1.7$ (LCP) and $F_{24,79}=3.6$ (R_{dark}). For species, different letters indicate statistically significant differences ($\alpha=0.05$).

4 | DISCUSSION

Plant elementomes beyond C, N and P have been linked to several functional traits (Fernández-Martínez et al., 2017; Furey & Tilman, 2023; Peñuelas et al., 2019), but links to photosynthetic traits remain largely untested. We measured photosynthetic light response traits (maximum photosynthetic rates, A_{max}; apparent quantum yield, A_{qe}; light compensation point, LCP; and dark respiration rates, R_{dark}) and elemental composition of bryophytes and found that all four photosynthetic traits were highly correlated with bryophyte elementomes. Models including 21 element concentrations, two-way interactions between C, N and P, and isotopic ratios of C and N as predictors explained a large amount of the variation in photosynthetic light response traits. These results support our first hypothesis that plant elementomes are closely linked to photosynthetic light response traits and provide novel empirical evidence that the strong relationships observed between elementomes and plant morphological and physiological traits (Fernández-Martínez, Corbera, Cano-Rocabayera, Sabater, & Preece, 2021; Sardans et al., 2023) can be extended to photosynthetic traits (Figure 4).

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TABLE 1 Second-order Akaike Information Criterion, and marginal and conditional coefficients of determination (R^2_m and R^2_c, respectively), for models of photosynthetic parameters including as fixed effects all elementomes variables (i.e. 21 elements, δ13C, δ15N, and two-way interactions between C, N and P; 'saturated model'), only C, N, P and their two-way interactions ('CNP model') and various subsets of elementome variables after a best subset selection process (i.e. ΔAIC <2; 'best subset').

	Saturated model			CNP model			Best subset		
Variables	AIC	R^2_m	R^2_c	AIC	R^2_m	R^2_c	AIC	R^2_m	R^2_c
A_{max}	138	0.56	0.86	131	0.45	0.72	108	0.50	0.83
A_{qe}	107	0.41	0.80	119	0.11	0.53	75	0.38	0.75
LCP	164	0.57	0.75	188	0.06	0.35	117	0.53	0.72
R_{dark}	138	0.65	0.87	145	0.41	0.64	106	0.61	0.85

Note: For the latter, AIC, R^2_m and R^2_c are averages of the best models. Photosynthetic parameters are maximum rate of net photosynthesis (A_{max}), apparent quantum yield (A_{qe}), light compensation point (LCP) and dark respiration (R_{dark}).

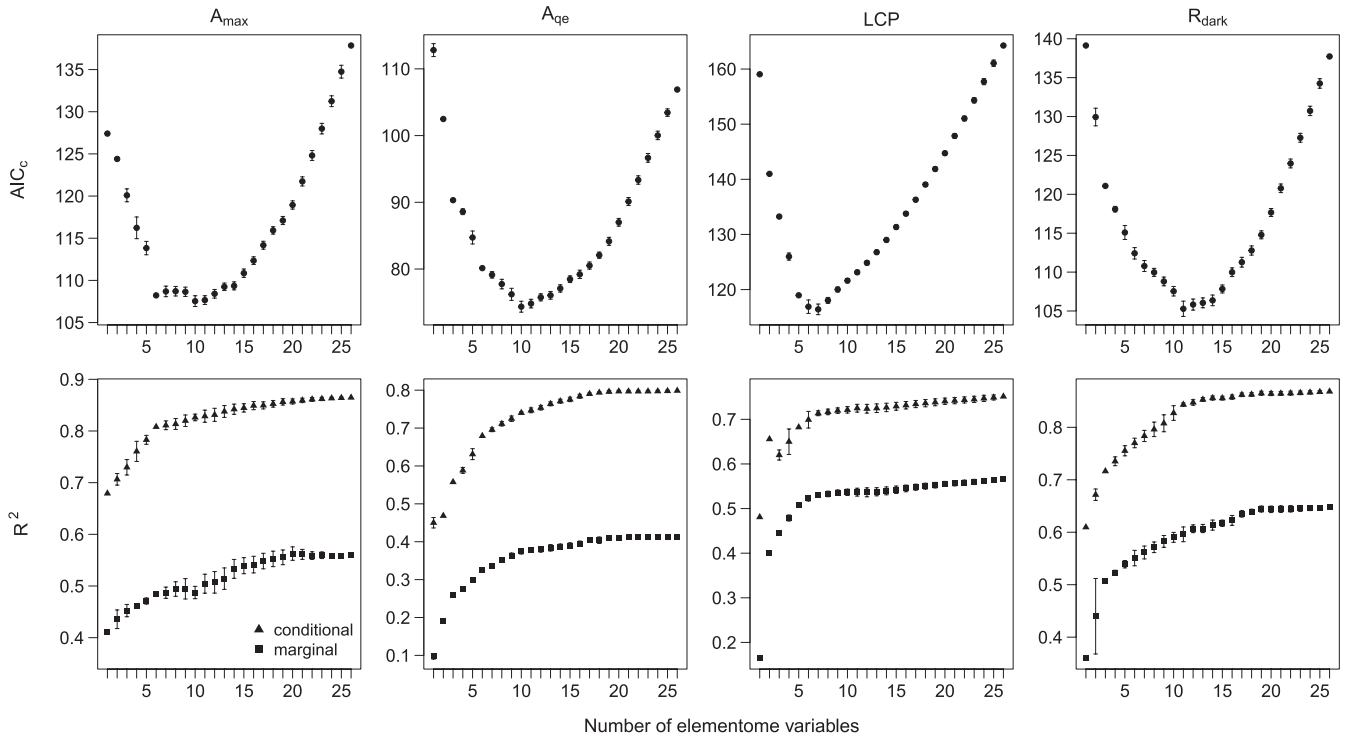

FIGURE 2 Mean ± SD (in brackets) second-order Akaike Information Criterion (top row) and marginal and conditional R^2 (bottom row) for sets of best models (i.e. ΔAIC <2) containing 1–26 fixed effect terms (selected from up to 21 element concentrations, isotopic ratios of C and N, and two-way interactions of C, N and P) for the response variables maximum rate of net photosynthesis (Amax), apparent quantum yield (Aqe), light compensation point (LCP), and dark respiration (Rdark).

4.1 | Species-specific differences in photosynthetic traits and their relationships

The substantial variation in photosynthetic light response traits among bryophyte species underscores the diversity within this group. Species-averaged A_{max} varied 12-fold, while species-averaged A_{qe}, LCP and R_{dark} varied about sevenfold. These ranges are on the higher end of those reported previously for bryophytes (Grau-Andrés, Kardol, et al., 2022; Waite & Sack, 2010; Wang et al., 2014) and may reflect the high diversity of life forms of our samples, which included pleurocarpous and acrocarpous mosses as well as leafy and thallose liverworts. Differences in photosynthetic light response traits were statistically significant across species, but not between mosses and liverworts, indicating that photosynthetic performance is more species-specific rather than being driven by broader taxonomic groupings. The average A_{max} we found (39 nmol CO_2 $g^{-1}s^{-1}$) is similar to that previously reported for diverse terrestrial bryophytes (37 nmol CO_2 $g^{-1}s^{-1}$; Perera-Castro et al., 2022) and greater than for forest and wetland mosses (11–16 nmol CO_2 $g^{-1}s^{-1}$; Wang et al., 2014, 2016; Grau-Andrés, Kardol, et al., 2022), epiphytic mosses (8 nmol CO_2 $g^{-1}s^{-1}$; Waite & Sack, 2010) and *Sphagnum* spp. (8 nmol CO_2 $g^{-1}s^{-1}$; Rice et al., 2008). Given the known trade-off between A_{max} and water retention capacity in bryophytes (Grau-Andrés et al., 2022; Rice et al., 2008), the high A_{max} of the hygrophytic bryophytes in this study could be related to

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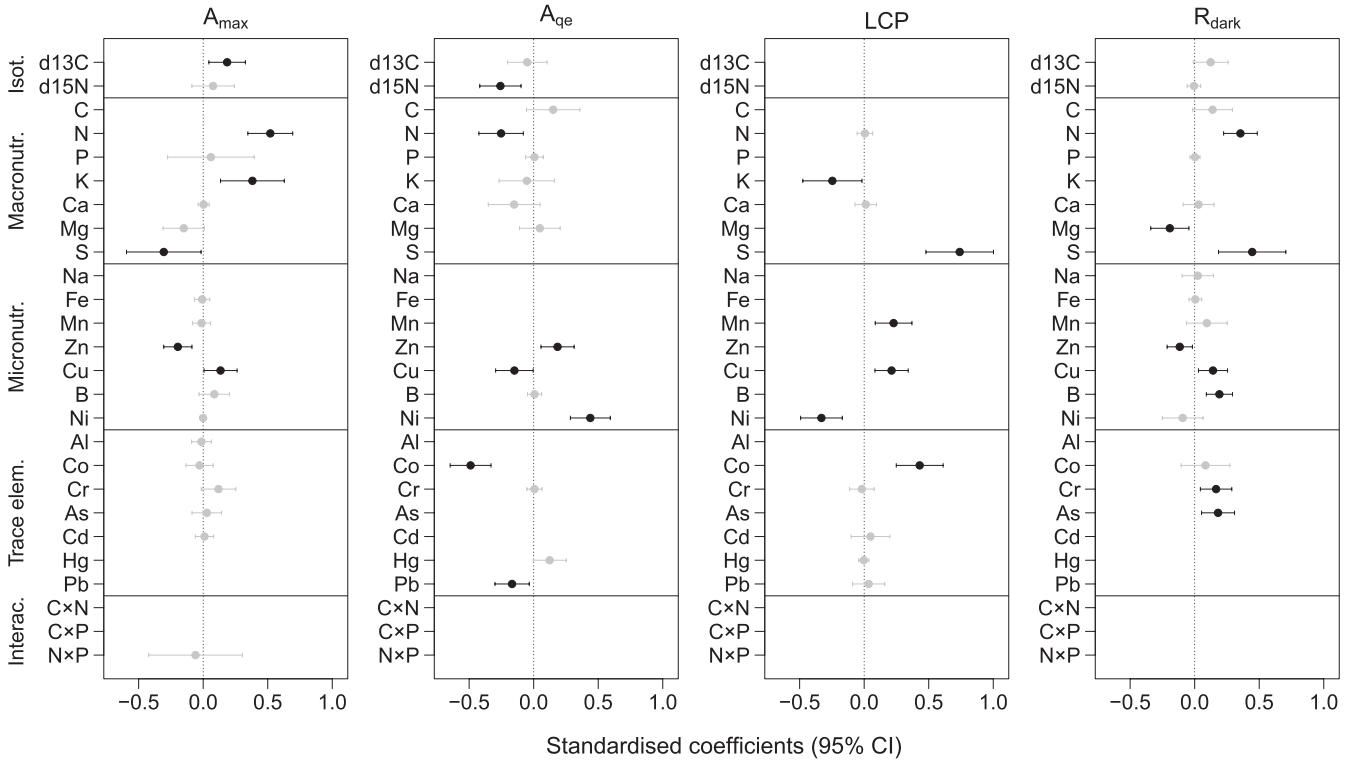

FIGURE 3 Coefficients in averaged best models (ΔAIC <2) of maximum rate of net photosynthesis (Amax), apparent quantum yield (Aqe), light compensation point (LCP), and dark respiration (Rdark). Symbols in black indicate that effects are statistically significant ($p < 0.05$), and in grey, that $p > 0.05$. Variables with no symbol were not retained in the best model subsets. Elementome variables are grouped by type: Isotopes, macronutrients, micronutrients, trace elements and interactions. Coefficients and standard errors are provided in Appendix S1: Table S3.

their lower water retention capacity compared to bryophytes from drier habitats (Deltoro et al., 1998), as underdeveloped water retention structures (e.g. thick cell walls, hyaline cells; Vitt et al., 2014) may free up resources for photosynthesis. Our results also revealed strong correlations between photosynthetic light response traits, especially between A_{max} and R_{dark}, and between A_{qe} and LCP. The positive relationship between A_{max} and R_{dark} has been observed in bryophytes (Grau-Andrés, Kardolm, et al., 2022; Laing et al., 2014) and vascular plants (Marino et al., 2010; Wright et al., 2004) and may arise because both traits are related to the plant's metabolic activity and growth potential. Regarding the negative relationship between A_{qe} and LCP, a higher A_{qe} generally leads to a lower LCP because the plant is more efficient at photosynthesising at low light levels, allowing it to compensate for respiration with less light. Overall, these results point to interconnected physiological processes governing photosynthesis in bryophytes.

4.2 | Best-performing models for explaining photosynthetic trait variation

Elemental concentrations of bryophytes in spring-fed ecosystems were broadly in line with previous bryophyte studies in Mediterranean springs (Fernández-Martínez, Preece, Corbera, Cano, Garcia-Porta, Sardans, et al., 2021) and in spring-fed fens (Hájek et al., 2014), although these studies considered only eight and six elements, respectively. Some elements (e.g. Co, B, Ni, Zn) were found in very high concentrations in a few bryophyte samples, which likely reflects large, localised chemical variation in spring water and/or substrate due to different lithologies and land uses (Martín et al., 2024). We found that models incorporating high-dimensional elementomes explained substantially more trait variation than CNP models, in line with our second hypothesis and with recent studies on other functional traits in bryophytes (Fernández-Martínez, Corbera, Cano-Rocabayera, Sabater, & Preece, 2021), vascular plants (Furey & Tilman, 2023) and phytoplankton (Hofmann et al., 2021). Our results thus support the view that expanding elemental analyses beyond C, N and P to include also other macronutrients, micronutrients and trace elements may greatly improve predictions of plant functioning (Fernández-Martínez, 2022; Kaspari et al., 2021; Peñuelas et al., 2019). The best-performing models for explaining A_{max}, A_{qe}, LCP and R_{dark} used a subset of elements rather than the full suite of 21 elements and two isotopic ratios, showing that a smaller set of elements can effectively capture the necessary information. The dimensionality of the optimal elemental set, that is, the number of elements of the best-performing models, differed among traits and was higher for A_{max}, A_{qe} and R_{dark} than for LCP. This finding suggests that a greater number and/or more complex physiological processes underpin A_{max}, A_{qe} and R_{dark} compared to LCP.

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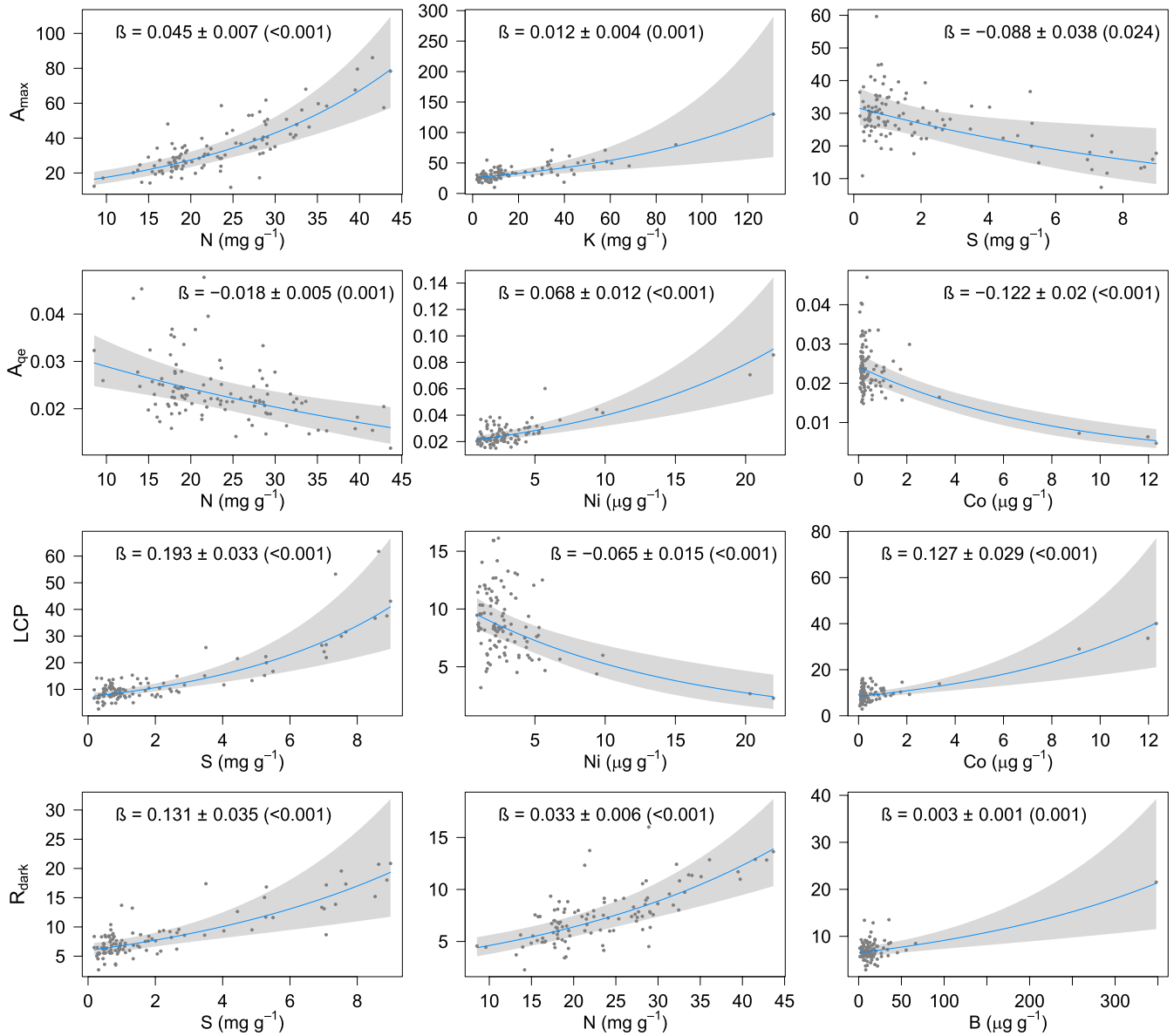

FIGURE 4 Modelled relationships (lines and 95% confidence bands) between photosynthetic parameters and element concentrations for elements that had the largest coefficients in the averaged best models. Modelling was carried out on the best model in each best-model subset (ΔAIC <2). Also shown are the coefficients describing the relationship between the element and the log-transformed response variable ± standard error and the *p*-value (in parenthesis). A_{max}, maximum rate of net photosynthesis (nmol CO_2 g^{-1} s^{-1}); A_{qe}, apparent quantum yield (nmol CO_2 g^{-1} (µmol photons m^{-2})$^{-1}$); LCP, light compensation point (µmol photons m^{-2} s^{-1}); R_{dark}, dark respiration (nmol CO_2 g^{-1} s^{-1}). Points are partial residuals.

4.3 | Potential mechanisms driving element–trait relationships

The optimal elemental set differed among the four photosynthetic light response traits, and included various macronutrients, micronutrients and trace elements, in line with our third hypothesis. This highlights that different traits are influenced by distinct physiological processes and demands for specific nutrients. Here, we propose physiological mechanisms that could underpin the observed element–trait relationships, but note that, given the correlational nature of our study, further experimental work should confirm specific mechanisms. For A_{max}, the most important variables were N, K and $\delta^{13}C$ (positive effects), and S (negative effects). The positive effects of N and K align with their known functions in photosynthesis, where N is a key component of chlorophyll and enzymes (Evans, 1989) and K regulates CO_2 diffusion and enzyme activity (Tränkner et al., 2018). The positive correlation we found between A_{max} and $\delta^{13}C$ is contrary to theory that high CO_2 diffusion, which is generally associated with high A_{max}, reduces Rubisco discrimination against ^{13}C and thus leads to lower $\delta^{13}C$, as observed in bryophytes (Grau-Andrés, Kardol, et al., 2022; Rice et al., 2008) and vascular plants (Farquhar et al., 1989). This discrepancy could be because CO_2 diffusion is not actively regulated in bryophytes due to their lack of stomata and other structures, and may instead be driven by

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canopy-level characteristics (e.g. thickness of the canopy, height to the water surface) unaccounted for in our study, which could indirectly drive the relationship between A_{max} and $\delta^{13}C$. The negative association between S and A_{max} may reflect increased respiratory demands under elevated S, which could limit net photosynthesis. This interpretation is consistent with the observed positive relationship between S and R_{dark} and with known roles of S in supporting mitochondrial respiration via sulphur-containing amino acids and cofactors (Zenda et al., 2021).

For A_{qe}, the most important variables were Ni (positive effect) and Co, N and $\delta^{15}N$ (negative effects). At lower concentrations, Ni can enhance plant growth because it is required for enzymes that catalyse urea, which contribute to nitrogen metabolism and prevent toxicity effects of urea accumulation (Brown, 2007; Lilay et al., 2024; Shahzad et al., 2018). In line with this, the negative association between Co and A_{qe} suggests toxicity effects, possibly through inhibiting the activity of photochemical systems (Palit et al., 1994). The negative relationship between A_{qe} and $\delta^{15}N$ may arise because lower $\delta^{15}N$ could indicate more readily usable nitrogen sources (Högberg, 1997), which could result in higher nitrogen use efficiency and, consequently, higher A_{qe}. Regarding LCP, we found that it increased with S and Co and decreased with K and Ni. As lower LCP indicates that less light is required to compensate for respiratory efflux of CO_2, these results show that net assimilation rates at low light levels are positively related to K and Ni and negatively linked to S and Co, broadly in line with our results for A_{max} and A_{qe}. The strong positive effect of S on LCP may be attributed to increased basal respiration, as noted above. Besides S, we found that R_{dark} was also positively associated with N and B. This positive relationship between N and R_{dark} agrees with its known role in basal metabolic processes (Reich et al., 2008; Wright et al., 2004), while the positive correlation with B could result from its central roles in maintaining membrane integrity, ATP production and metabolic processes (Brown et al., 2002; Lilay et al., 2024), although this was mainly driven by a single sample with very high B concentration. Hence, further research is needed to support our findings regarding the correlation between B and R_{dark}. Overall, our results show that many different elements are associated with photosynthetic light response traits in bryophytes, and that the number and identity of those elements depend on the specific trait.

Concentrations of some essential elements for photosynthesis such as P and Fe (Lilay et al., 2024) were not important in explaining photosynthetic light response traits. This may be because the bryophytes in our study had accumulated enough of those elements to support photosynthesis, meaning that variations in their concentrations were not limiting photosynthetic function. Furthermore, whole-tissue elemental concentrations might not accurately reflect the bioavailability of nutrients within chloroplasts, where they play a direct role in photosynthesis. For example, Fe is essential for chlorophyll synthesis and electron transport but is often stored in vacuoles or bound to chelators, reducing its bioavailability for chloroplasts (Briat et al., 2007). This underscores that the elements driving photosynthesis, and the extent of their effects, may depend on the environmental context and may vary with species-specific element requirements and habitat-specific element availability.

4.4 | Future insights on elementomes research

Our findings demonstrate that the strong relationships observed between plant elementomes and some functional traits (Fernández-Martínez, Corbera, Cano-Rocabayera, Sabater, & Preece, 2021; Sardans et al., 2023) are also evident for photosynthetic traits in bryophytes. By integrating a broad spectrum of elements into our analyses, we show that utilising high-dimensional plant elementomes may improve predictions of photosynthetic light response traits compared to limited elementomes (e.g. only C, N and P). As these traits determine C acquisition, the strong relationships we observed indicate that elementomes capture important aspects of plant physiological performance, which could map to ecosystem-level processes such as CO_2 uptake. Our results suggest that the optimal set of elements for studying photosynthetic traits comprises N, Ni, S, K, Co, Mn, Cu and Zn.

In ecosystems where bryophytes play a central role in ecosystem processes, bryophyte elementome studies could be leveraged to assess their contribution to carbon and nutrient cycling (e.g. mires, northern forests; Lindo & Gonzalez, 2010; Hupperts et al., 2021) or to inform management strategies to preserve their function as refugia for biota (e.g. spring-fed ecosystems; Fernández-Martínez et al., 2024). Furthermore, given the high sensitivity of bryophytes to environmental changes (e.g. in response to nitrate pollution; Martín et al., 2024), elementome-based studies could serve as effective tools for assessing responses to stressors and for monitoring ecosystem health. This could be achieved through longitudinal monitoring of bryophyte elementomes alongside known stressors (e.g. indicators of drought, water quality).

One limitation of our study for assessing overall plant functioning is that elementomes–trait relationships were established only for photosynthetic traits. For example, since bryophyte productivity depends not only on photosynthetic performance but also on water retention capacity (Vitt et al., 2014), elementomes that optimise both traits would signal greater overall productivity. Future studies investigating the relationships between elementomes and multiple functional traits simultaneously (e.g. C uptake potential, water- and nutrient-use efficiency) may improve predictions of plant functioning and their response to environmental change (e.g. altered water or nutrient availability). Moreover, by identifying the optimal number and specific elements that best explain each trait, elementome-based studies can guide further experimental physiological and molecular research to determine the mechanisms underlying those associations.

Finally, our focus on hygrophytic bryophytes from spring-fed ecosystems precludes wide applicability of our findings. Future research should investigate whether the relationships described here are applicable to algae, bryophytes from other habitats, horsetails, ferns or phanerogam leaves. Extending this research to other plant

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groups and ecosystems (Sardans et al., 2023) and considering the elementomes of whole plant communities or ecosystems (Bartrons et al., 2018; Fernández-Martínez et al., 2020) will be crucial for generalising the findings and refining predictive models of elementome–functional trait relationships at broader levels of organisation.

AUTHOR CONTRIBUTIONS

Marcos Fernández-Martínez, Ana M Yáñez-Serrano, Josep Peñuelas, Catherine Preece, Francesc Sabater and Jordi Sardans designed the study, and Marcos Fernández-Martínez, Ana M Yáñez-Serrano, Jordi Corbera and Joan Llusià carried it out. Roger Grau-Andrés and Marcos Fernández-Martínez analysed the data, and Roger Grau-Andrés wrote the manuscript with contributions from all authors. All authors live and work in Catalonia, where the study took place. The authors have engaged with land managers and local stakeholders to disseminate the results.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data and code to perform analyses presented in this study can be found in Figshare: https://doi.org/10.6084/m9.figshare.27061429 (Grau-Andrés et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1:

Table S1. Photosynthetic parameters averaged for each bryophyte species (standard deviation in parenthesis). A_{max} is the maximum rate of net photosynthesis (in nmol CO_2 $g^{-1}s^{-1}$), A_{qe} is the apparent quantum yield (in nmol CO_2 g^{-1} (µmol photons $m^{-2})^{-1}$), LCP is the light compensation point (in µmol photons $m^{-2}s^{-1}$) and R_{dark} is dark respiration (in nmol CO_2 $g^{-1}s^{-1}$).

Table S2. Summary of elemental concentrations and isotopic ratios. CV is the coefficient of variation. Elements are arranged in descending order of their mean concentrations.

Table S3. Standardised coefficients and standard errors (in parenthesis) of averaged best model subsets (i.e. those with $\Delta AIC < 2$) of photosynthetic parameters A_{max}, A_{qe}, LCP and R_{dark}. Statistically significant effects ($p < 0.05$) are indicated in bold.

Figure S1. Location of the 51 sampled springs.

Figure S2. (top) Difference in net assimilation rates between each gas exchange measurement and the preceding one within each PPDF level (measuring time was 4–6 min; measuring frequency was 1–2 samples per minute). (bottom) Vapour pressure deficit of the air cuvette for each PPDF level.

Figure S3. Light response curves (net CO_2 uptake [A] against photosynthetic photon flux density [PPFD] levels) in 26 bryophyte species. Within each panel (species), different symbols indicate different replicates, and blue lines are averaged model fits.

Figure S4. Correlation between photosynthetic parameters of bryophyte samples (A_{max}, maximum rate of net photosynthesis; A_{qe}, apparent quantum yield; LCP, light compensation point; R_{dark}, dark respiration). The upper diagonal shows log-transformed data and the lower diagonal, untransformed data. Pearson's product moment correlation coefficients are shown in the upper right corner of the panels, followed by their statistical significance (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; no stars, $p > 0.05$).

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Figure S5. Pearson product–moment correlation coefficient of elemental variables.

Figure S6. Coefficients in averaged best models (ΔAIC <2) of A_{max}, A_{qe}, LCP and R_{dark}, computed from a modified dataset where element concentrations >3 SD above the mean were set to 3 SD above the mean. Symbols in black indicate that effects are statistically significant ($p < 0.05$), and in grey, that $p > 0.05$. Variables with no symbol were not retained in the best model subsets. Elementome variables are grouped by type: isotopes, macronutrients, micronutrients, trace elements and interactions.

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