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Coordination Between Bioelements Induce More Stable Macroelements Than Microelements in Wetland Plants

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ABSTRACT

Elements are the basic substances that make up living organisms, and the element composition in plants quantitatively reflect the adaptation of plants to environment. However, the drivers that constitute the species-specific plant elementome, as well as the bivariate bioelemental correlations in determining the stability of different bioelements are yet unclear. Based on 1058 leaf observations of 84 plant species from 232 wetlands across large environmental gradients, we found that bioelements with higher concentration were more stable and evolutionary constrained. We proposed a stability of well-coordinated elements hypothesis, suggesting that bioelements that coordinate well in driving certain physiological functions constrain each other, thus maintaining relatively stable ratios in plants. In contrast, those functionally independent bioelements fluctuate greatly with environmental nutrient availability. Cold and saline stresses decreased plant stoichiometric network connectivity, complexity, and stability. Our research filled the gap in study of wetland plant elementome, and provided new evidences of plant–environment interactions in regions sensitive to climate change.

1 | Introduction

All living beings are built with a specific range of the ratio of bioelements (Schimel 2003; Sterner and Elser 2002), namely, the elementome (Peñuelas et al. 2019). For plants, about 30 bioelements have been detected to serve vital but varied functions in participating in individual physiological processes and environmental adaptions (Ågren 2008). Fundamentally, elementomes of organisms are determined by physiological requirements and are assumed to be species-specific and phylogenetically conserved (Atkinson, van Ee, and Pfeiffer 2020; Sardans et al. 2021; Watanabe et al. 2007). However, the realised elemental composition is the consequence of multiple environmental filtering, including climate and habitat conditions (nutrient supply and stress, etc.) (Fernández-Martínez et al. 2021; Joswig et al. 2022; Zuo et al. 2022). In the classic

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framework of Hutchinson's (1957) "*n*-dimensional hypervolume", the elementome is one of the best indicators to quantify the plant fitness to environments in multi-dimensions (Fernández-Martínez et al. 2021; Furey and Tilman 2023; Peñuelas et al. 2019). Plants integrate multiple elements in perhaps optimal ratios to maximise their multifunctionality and to adapt to environmental heterogeneity (He et al. 2020), causing biogeographic patterns of the elementomes (Han et al. 2011; Reich and Oleksyn 2004; Xing et al. 2021). Therefore, the variations in plant elemental composition along environmental gradients may reflect the joint controls of plant evolutionary history and present environments.

In terrestrial ecosystems, macroelements centered on C:N:P stoichiometry has been used to analyse plant–environment relationships (Han et al. 2011), identify species life-history strategies (Reich 2014), probe community assembly mechanisms (Atkinson, van Ee, and Pfeiffer 2020), determine the species biogeochemical niches (Fernández-Martínez et al. 2021; Peñuelas et al. 2019), and predict ecosystem responses to global change (Tang et al. 2018), whereas microelements also play important roles in homeostatic regulation, redox, and energy storage in plants (Kaspari 2021; Lilay et al. 2024; Marschner 2012). However, few studies have focused on the formation mechanisms of plant elementome per se, especially for both macroelements and microelements. In wetlands, mineral elements carried by surface runoff from surrounding soils sink in sediments, producing more concentrated element micro-environments than upland soils (Herbert et al. 2015; Zuo et al. 2022). Since habitat elemental conditions in wetlands differ from those of terrestrial ecosystems, elemental stoichiometry of wetland plants is an ideal indicator reflecting the plant fitness to environments, as well as the generalities and differences in relation to environmental heterogeneity between wetland and non-wetland plants (Pan et al. 2020; Yang et al. 2021). However, no field study has linked plant elementome with plant phylogeny and functional biogeography in wetlands along large environmental gradients, especially under ongoing global change and hydrological regime changes (Pan, García-Girón, and Iversen 2023).

Wetlands are distinguished from upland habitats with unique biogeochemical processes, light, CO_2 and O_2 availability, and hydrological regime (Moor et al. 2017). Wetland plants are characterised by sufficient water availability and nutrient supply in sediments, but suffer from additional stresses of osmotic pressure, gas limitation, and strong hydraulic forces in water (Maberly and Gontero 2018), and thus evolved a suite of morphological and eco-physiological traits to adapt to water saturated environments (e.g., leaf gas film formation and enhanced shoot and root porosity, Pan, García-Girón, and Iversen 2023). In the economic strategy dimension, the leaf economics spectrum (LES), which was built based on coordination amongst six mass-based leaf traits, indicates that plants with high leaf N and P concentrations and specific leaf area show quick-return strategies on investment of nutrients (Reich 2014; Reich, Walters, and Ellsworth 1997; Wright et al. 2004). Amongst the plant growth forms, wetland plants are ones often using quick-return strategies (Pan et al. 2020; Yang et al. 2021). Previous studies have focused on plant photosynthetic physiology (Pedersen, Colmer, and Sand-Jensen 2013), and leaf C:N:P stoichiometry (Hu et al. 2021; Wang et al. 2015) in wetland habitats. However, as the essential participants in plant physiological processes, the stoichiometry of bioelements other than C, N, and P in wetland plants and their controlling factors are yet unclear.

The alpine and arid regions in western China are often considered as amplifiers for climate change with continued warming, spatially heterogeneous changes in precipitation and anthropogenic disturbances (Piao et al. 2010; Song et al. 2021), resulting in the loss or salinisation of wetlands. Wetland plants in these regions are exposed to harsh environments such as low temperature and high salinity (Wang et al. 2015), shaping its realised elementome from the phylogeny-determined fundamental elementome by both climate and habitat filtering (Figure 1a). However, the shaping processes are bioelement-specific, and lead to differences in bioelemental stability. Furthermore, the realised elementome is also the consequence of coordination amongst bioelements, but received less attention. Environmental change not only affect the bioelemental concentrations, but adjust the complex networks amongst bioelements (He et al. 2020; Li et al. 2022), then forming the plant elementome (Figure 1b). Based on 1058 leaf samples collected by uniform protocols in the study regions (Figure S1), we aimed to clarify the stoichiometric patterns and their phylogenetic and environmental controls of plant elementome, and explore the variations of plant element networks in stressful conditions. We hypothesised that environmental changes induce allometric accumulations of different bioelements, alter the connectivity and complexity of the plant element networks, but plant bioelements that coordinate well with each other maintain higher stability in different environments, and *vice versa*.

2 | Methods and Materials

2.1 | Study Region and Field Investigation

This study region ranges from 27.4° N to 48.7° N, 76.2° E to 109.8° E, and 195 to 5127 m a.s.l., and covers almost all the alpine and arid regions in western China (Figure S1). This region is characterised by alpine and arid climate, with mean annual air temperature and mean annual precipitation ranging from −4.7°C to 12.5°C and from 17.2 to 685.4 mm, respectively (Song et al. 2021).

The alpine and arid regions of western China are rich in various wetland habitats (Wang et al. 2015; Zuo et al. 2022), yet also face the impacts of climate change and anthropogenic activities, which can alter the nutrient resources and water resources of wetland ecosystems (Piao et al. 2010). The habitats we investigated included shallow areas (no deeper than 1.5 m) of lakes, rivers, and marshes, as well as streams, ponds, and channels, while ephemeral water bodies were excluded. Moreover, we recorded the information of sampling site as summarised in Table S1.

We conducted a large-scale field investigation across the western China during the growing season in 2018 and 2019. Detailed methods of field sampling and laboratory analysis were provided in Appendix S1. Briefly, sediment, water and plant (including emergent, floating-leaved and submerged plants) samples were collected in 232 wetlands, and 17 elements (C, N, P, S, K, Ca, Mg, Na, Fe, Al, Mn, Si, B, Zn, Cu, Ni, and Co) of the sediment (232

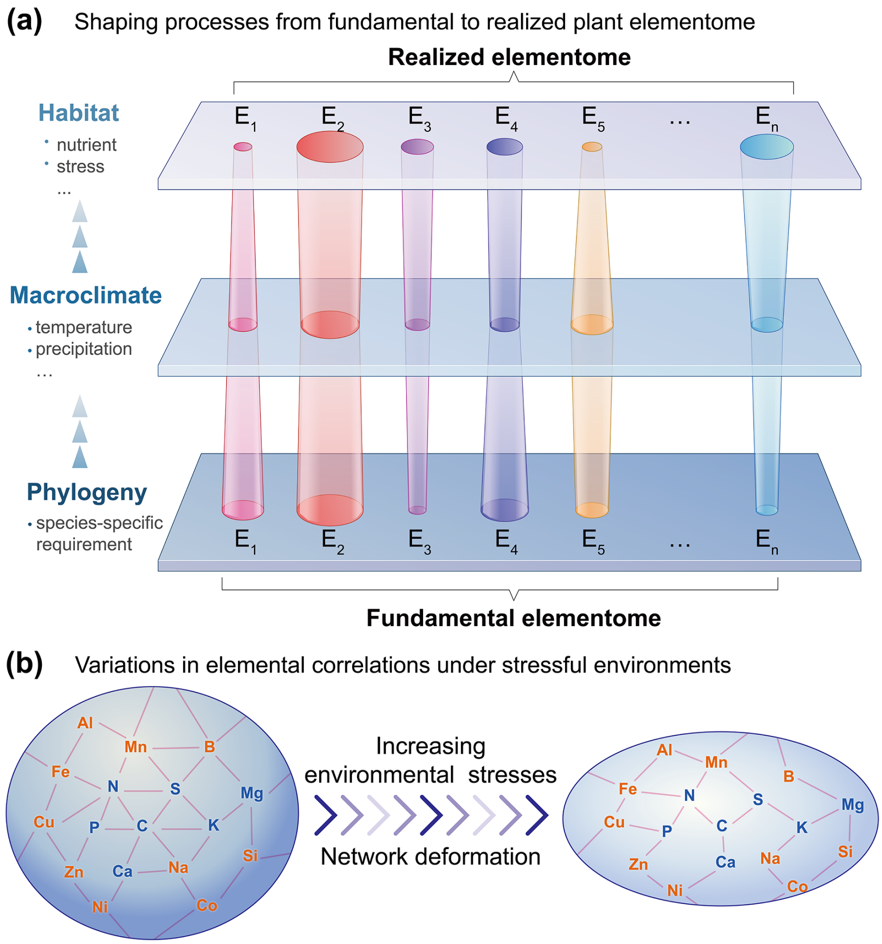

FIGURE 1 | Conceptual frameworks for the shaping processes of plant elementome and the variations of plant element networks under stressful environments. (a), The realised plant elementomes are filtered by macroclimates and habitats from phylogeny-determined fundamental elementome. The bottom layer represents the species-specific physiological requirements for each element (E_1, E_2...) of plants, which determines the plant fundamental elementome. The middle layer indicates the influences of macroclimate (e.g., temperature, precipitation and their combination). Macroclimate can determine the plant bioelemental concentrations by affecting the biochemical processes (e.g., the Temperature-Plant Physiological Hypothesis, Reich and Oleksyn 2004). The up layer is the realised elementome finally shaped by the habitat conditions (e.g., nutrient supply and stresses). The nutrient supply determines the resource availability, while the environmental stresses limit the use of elements by plants. (b), The bivariate correlations amongst bioelements are spatialized into an element network (He et al. 2020). The variations in network topology towards stressful conditions can reflect the alterations in the element-element correlations, indicating the changes in bioelemental synergies to adapt to special habitats.

samples), water (232 samples), and plants (1058 leaf samples) were measured.

2.2 | Data Analysis

2.2.1 | Data Arrangement

For each of the 17 bioelements, arithmetic mean value, standard deviation, maximum and minimum values, and coefficient of variation (CV) for overall species, emergent plants, floating-leaved plants, and submerged plants were sorted out respectively. The CV, which was calculated by dividing standard deviation by mean value, was introduced to represent the variability in bioelemental concentrations (Han et al. 2011; Karimi and Folt 2006). Marschner (2012) provided the average concentrations of 14 mineral elements in plant shoot dry matter that are sufficient for adequate growth, including 12 elements (Ca, K, N, S, Mg, P, Fe, Mn, B, Zn, Cu and Ni) in this study. The concentration that does not limit plant growth are considered the physiological requirement of a certain bioelements in plants.

Before analysis, all data of bioelemental concentrations were checked for normality of residual using Shapiro–Wilk normality tests and homogeneity of variances by Bartlett tests. Then the non-parametric methods (Kruskal-Wallis test and Dunn's Post Hoc Multiple Comparisons) were used to compare the differences in bioelemental concentrations amongst life-forms.

In this study, growing season mean air temperature (GST) is the mean temperature from May to September, while growing season precipitation (GSP) is the total precipitation of the 5 months (Wang et al. 2015). We used eight environmental variables, including two climatic variables (GST and GSP), three sediment variables (elemental concentration, pH and electrical conductivity), and three water variables (elemental concentration, pH and salinity). Each bioelement was fitted against the environmental variables, as well as latitude and altitude, by simple linear regressions to illustrate the bioelement-environment correlations.

2.2.2 | Linear Mixed Effect Model

We constructed a phylogenetic tree of 84 sampled species to test the phylogenetic signals (Blomberg's K) of 17 bioelements of wetland plants (Blomberg, Garland, and Ives 2003). Detailed methods of phylogenetic signal detection are provided in Appendix S2.

The linear mixed effect model (LMM) and variance partitioning analysis were employed to partition the bioelement variations into phylogeny and environments by using residual maximum likelihood estimation (Watanabe et al. 2007). We excluded plant families from which less than one species was sampled (Zhao et al. 2016). The phylogenetic effects were represented by a hierarchically nested structure "order/family/species". This method enabled us to investigate the degree of variation at each phylogenetic level. Variations in bioelemental concentrations effected by environmental variables (including climate, sediment, and water properties) were assigned to the 'site' component of the model (Watanabe et al. 2007; Zhao et al. 2016). The overall random term within LMM was written as 'site + [(order/family/species)]', and no fixed factor was defined. We used the "*lmer*" function of the "*lme4*" package in *R* (Bates et al. 2015).

2.2.3 | Phylogenetically Controlled Linear Mixed Model

We tested the effects of climate, sediment, and water properties on elementome and stoichiometric ratios between macroelements of wetland plants using Bayesian phylogenetic linear mixed models and the R "*brms*" package (Büerkner 2017). In each Bayesian model, we used eight predictor variables (GST, GSP, sediment pH, sediment electrical conductivity, water pH, water salinity, and concentrations of corresponding elements in sediment and water) as fixed effects, with species as a random effect and controlled for phylogenetic effects using phylogenetic tree (Fernández-Martínez et al. 2021; Sardans et al. 2021). 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 (Fernández-Martínez et al. 2021). Based on the null hypothesis of Mean = 0, we further estimated the probability of direction and Bayes factors of all predictors using the R "*bayestestR*" package (Makowski, Ben-Shachar, and Lüdecke 2019), as an estimation of the relevance of predictor variables.

2.2.4 | Partial Least Squares Path Modelling (PLS-PM)

To explore the underlying regulatory mechanisms of environmental patterns of bioelements, partial least squares path modelling was further applied to identified the direct and indirect effects of geography, climate, sediment, and water properties on variations in bioelements. We performed PLS-PM for eight macroelements (C, N, P, S, K, Ca, Mg and Na) and nine microelements (Fe, Al, Mn, Si, B, Zn, Cu, Ni and Co), respectively. All the 11 observation variables were classified into four latent variables—geography (latitude, longitude and altitude), climate (GST and GSP), sediment properties (sediment pH, electrical conductivity and elemental concentrations), and water properties (water pH, salinity, and elemental concentrations). The plant bioelements were controlled by all the observation variables directly or indirectly. The models were constructed by "*innerplot*" function of the "*plspm*" package in *R* (Sanchez 2013). Goodness of fit index (*GoF*), R^2, path coefficients (standardised direct effects), and standardised indirect effects were used to estimate model performance and compare the effects of different latent variables on the patterns of elements.

2.2.5 | Leaf Element Network (LEN) Analysis

With reference to plant trait network (He et al. 2020), we introduced LEN to clarify the complex relationships between bioelements and further assess the variations in the synergies of bioelements across environmental gradients. Detailed methods of LEN analysis are provided in Appendix S3 and Table S2. Briefly, we selected temperature and water salinity as proxies for climate and salt stresses, and constructed LENs at different temperature and salinity levels. We employed six overall parameters (edge density, average path length, diameter, average clustering coefficient, modularity, and vulnerability) to quantify the "connectivity", "complexity" and "stability" of LENs, and five node parameters (degree, weighted degree, closeness, betweenness and clustering coefficient) to assess the "connectedness" and "centrality" of bioelements within LENs (Felipe-Lucia et al. 2020; He et al. 2020). We further tested the stability of the node parameters for 17 bioelements in different conditions, to explore the consistency of the importance of each bioelement across environmental gradients (Li et al. 2022). If a certain bioelement with high node parameter shows high stability, it means that such bioelements always play central roles in different environmental conditions (Rao et al. 2023).

3 | Results

3.1 | Stoichiometric Characteristics of Wetland Plants

For all the 1058 observations, the mean concentrations of the 17 bioelements varied by six orders of magnitude from the most (C: 374.93 mg g^{-1} or 31.25 mol kg^{-1}) to the least abundant one (Co: 0.0024 mg g^{-1} or 0.41×10^{-4} mol kg^{-1}, Figure 2a, Table S3), with mass-based ratio of C_{155305}:Ca_{12747}:K_{10186}:N_{9822}:Na_{3706}:S_{2631}:Mg_{2621}:P_{1191}:Fe_{1152}:Al_{701}:Mn_{518}:Si_{176}:$B_{64.8}$:$Zn_{26.7}$:$Cu_{2.99}$:$Ni_{2.09}$:Co_1 or atom ratio of C_{763580}:Ca_{18802}:K_{15409}:N_{41392}:Na_{9508}:S_{4852}:Mg_{6445}:P_{2267}:Fe_{1214}:Al_{1531}:Mn_{555}:Si_{370}: B_{347}:$Zn_{24.2}$:$Cu_{2.76}$:$Ni_{2.12}$:Co_1. Considering the high concentrations of Na, we defined it as a macroelement in this study. Amongst the three life-forms, there were different bioelemental concentrations except for S (Figure 2a). Submerged plants concentrated more mineral

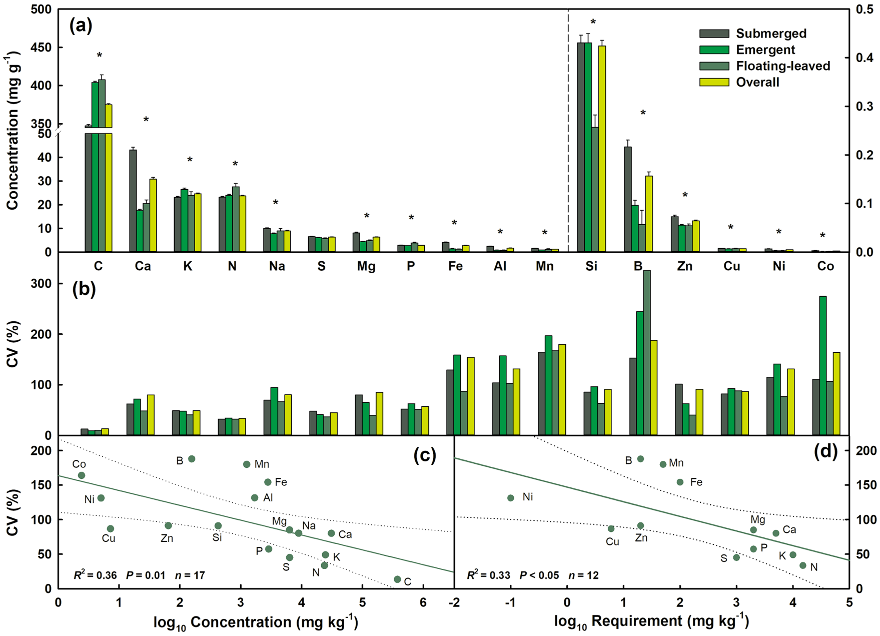

FIGURE 2 | Stoichiometric characteristics of 17 bioelements of wetland plants. (a), Concentrations of 17 bioelements for overall observations (n = 1058) and different life-forms (submerged plants: N = 543; emergent plants: N = 475; floating-leaved plants: N = 40) of wetland plants. The concentrations of the left 11 bioelements refer to the left Y-axis, while the right 6 ones refer to the right Y-axis. Asterisks indicate statistical significance ($p < 0.05$) in leaf elements between different life-forms. (b), Coefficient of variation (CV, %) of 17 bioelements for overall observations and different life-forms of wetland plants (n = 17). (c), Linear regressions between bioelemental concentration and its CV. (d), Linear regressions between bioelemental physiological requirement and its CV (n = 12).

elements, but had less leaf C and K than floating-leaved plants and emergent plants. Both N and P showed the highest concentrations in floating-leaved plants.

The variations of the 17 bioelements differed greatly. The nine microelements varied more (CV = 87%–188%) than the eight macroelements (CV = 13%–85%, Figure 2b). The CV was negatively correlated with both the mean concentrations of bioelements ($R^2 = 0.36$, $p = 0.01$, Figure 2c) and their physiological requirements ($R^2 = 0.33$, $p < 0.05$, Figure 2d), indicating that the bioelements with higher concentrations and higher requirements were more stable in plants.

3.2 | Geographic and Environmental Patterns of Bioelements

For all the 17 bioelements of overall 1058 observations, four (Na, S, Mg and Zn) increased, whereas seven (K, P, Fe, Al, Si, B, and Co) decreased towards high latitude (Figures S3a and S4). Because of the special topographical features in the study areas, the high-altitude Tibetan Plateau lies in the south, altitudinal trends of bioelements were opposite to latitudinal gradients (Figure S5). Sixteen of the 17 bioelements (except Ca) were significantly correlated with GST, of which, Na, S, Mg, Mn, Zn, Cu and Ni increased while C, K, N, P, Fe, Al, Si, B, and Co decreased with increasing GST (Figures S3c and S6). The bioelement–GSP relationships were opposite to the bioelement–GST relationship (Figure S7).

All of the 17 bioelements showed significant positive correlations with their corresponding nutrient levels in sediments (Figures S3e and S8). Fourteen bioelements positively, but K negatively correlated with their water nutrients, while P showed no correlations (Figure S9). Six bioelements (Ca, Na, S, Mg, Si and B) increased, whereas 10 (K, N, P, Fe, Al, Mn, Zn, Cu, Ni and Co) decreased towards high sediment or water pH (Figures S10 and S11). With increasing environmental stress towards high water salinity, concentrations of Na, S, Mg and B increased, but all the other 13 bioelements decreased (Figures S3i, S12 and S13). Furthermore, these biogeographic patterns of the 16 bioelements were basically consistent amongst three life-forms (Table S4).

3.3 | Phylogenetic and Environmental Controls on Bioelements

Blomberg's K statistical identified 15 of 17 bioelements with significant phylogenetic signals (except Mg and B), with K values ranged from 0.089 (S and Cu) to 0.223 (K) (Table S5). LMM revealed that phylogeny and environments co-regulated the variations in bioelemental concentrations (Figure 3a), with a mean degree of explanation 23% (with ranges of 4%–56%) by phylogenetic level (incorporating effects of order, family and species levels) and 36% (7%–56%) by sites (Table S6). However, phylogenetic level accounted for a greater amount of the variation in macroelements (31%) than microelements (15%). On the contrary, sites explained microelements (44%) more than macroelements (27%). Furthermore, the variance explained by phylogeny positively correlated with bioelemental concentrations at all phylogenetic levels ($p < 0.05$; Figure 3b), while those by environments (sites) increased with decreasing bioelemental concentrations ($p < 0.001$; Figure 3c). That is, the higher concentrations of bioelements, the more regulated by phylogeny, and

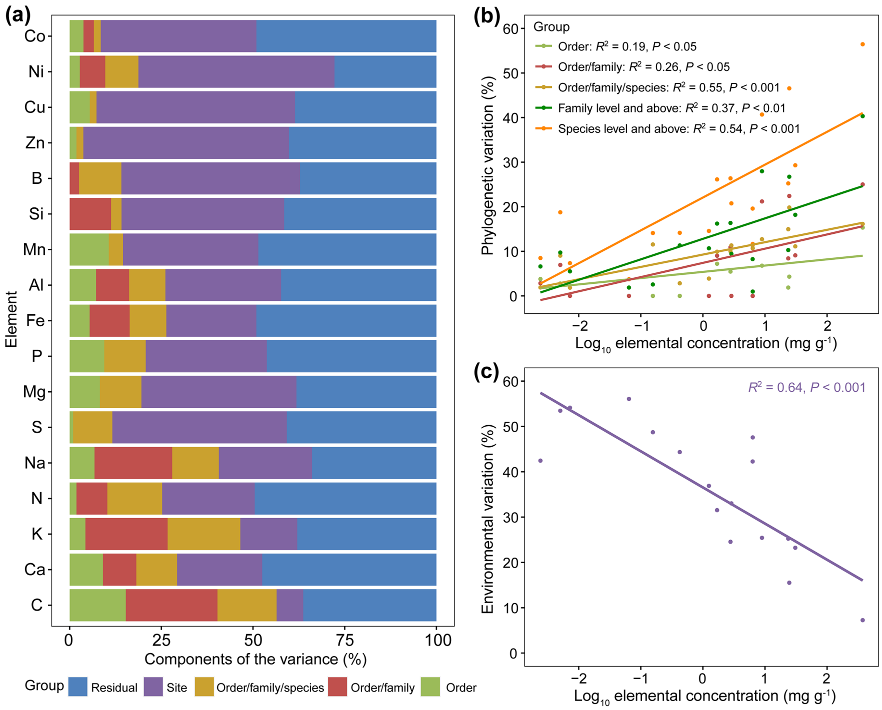

FIGURE 3 | Phylogenetic and environmental controls on 17 bioelements of wetland plants. (a), Variance partitioning for 17 bioelement variations using linear mixed effect model ($n = 1028$). Columns with different colours represent different variance components. (b), Linear regressions between bioelemental concentrations and phylogenetic variation ($n = 17$). Phylogenetic levels including the order level, order/family level, order/family/species level, family level and above, and species level and above. (c), Linear regressions between bioelemental concentrations and environmental variation ($n = 17$). Solid lines represent significant fits ($p < 0.05$).

the lower concentrations of bioelements, the more regulated by environments.

Bayesian phylogenetic linear mixed models explained 28% (N)-64% (Na) of the variations in bioelements (Figure 4a; Table S7). Within environmental variables, nutrient supplies in sediment and water affected the variations in most bioelements, especially for microelements. Climate, especially GST, explained more for macroelements than microelements (Figure 4b). Correspondingly, the models explained 24% (N:P)-61% (C:Ca) of the variations in 28 stoichiometric ratios (Figure S14). Sediment elemental concentration and GST were the main drivers of the variations in most stoichiometric ratios, and water salinity also showed high correlations with Na- and S-relevant stoichiometric ratios.

PLS-PM explained 47% and 43% of the variances of macroelements and microelements, but illustrated different regulatory mechanisms for environmental patterns of the two bioelement groups (Figure 4c–f; Table S8). For macroelements, water properties, climate and sediment properties positively affected the bioelements significantly with the standardised direct effects of 0.37, 0.24 and 0.24 (Figure 4c), but climate presented to be the strongest explanatory variable with considering the total effect of 0.65 (Figure 4d). For microelements, sediment properties (0.34) and water properties (0.30) had significantly positive effects, but climate showed no direct effects ($p > 0.05$, Figure 4e). Sediment properties presented to be the first explanatory variable with the total effect of 0.53 (Figure 4f). Geographic variables indirectly, via influencing climate, sediment, and water properties, affected both the macroelements and microelements.

3.4 | Variations in Leaf Element Networks (LENs) Along GST and Salinity Gradients

Most of the 17 bioelements showed significant correlations between each other (Figure 5a). Leaf C weakly positively correlated with N, Pm and K, and more strongly negatively correlated with all the other bioelements (except Zn with $R = -0.05$ and $p = 0.096$). N, P and six metallic microelements (Fe, Al, Mn, Zn, Cu, and Ni) showed positive correlations with each other (Figure S15). Towards stressful conditions (low temperature and high salinity), the edge density and average path length of LENs decreased, whereas the diameter, average clustering coefficient, and vulnerability increased (Figure 5b). Modularity was higher at low-GST but lower at saline water (Figure 5b). Variations in overall parameters of networks showed that the connectivity, complexity, and stability of LENs were lower in stressful conditions, and thus indicated that the synergies of bioelements became weaker. Euclidean distances between paired LENs showed that, both along temperature and salinity gradients, the greater the environmental differences, the more disparities of LENs (Appendix S4; Figure S16).

For node parameters of LENs, leaf C was the hub trait with high degree at all temperature levels and the lower three salinity levels (Figure S17), while the degree of some stress resistance related bioelements (e.g., S) increased sharply at the highest salinity level (Figure S17b). Environmental stress rearranged the module composition (Figure S18). Additionally, the stability of the five node parameters (degree, weighted degree, closeness, betweenness, and clustering coefficient) for the 17 bioelements positively correlated

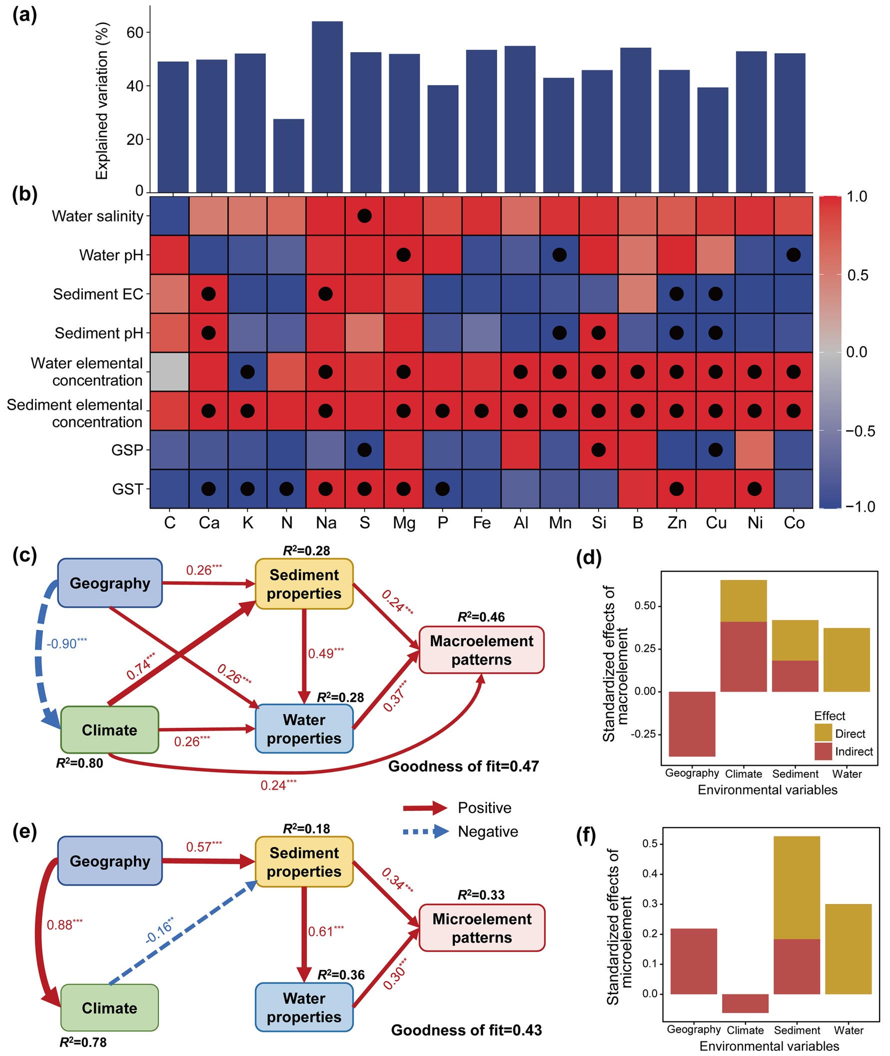

FIGURE 4 | Geographic and environmental drivers of bioelements of wetland plants ($n = 1058$). (a, b), Heat map of the relationships between17 bioelements and environmental variables based on Bayesian phylogenetic linear mixed models. Colours indicate the probability of direction of the posterior distributions of the relationship between pairs of variables, where red and blue indicate positive and negative relationships respectively. Black dots indicate Bayes factors > 1. Partial least squares path modelling (PLS-PM) for macroelements (c) and its standardised effects (d). PLS-PM for microelements (e) and its standardised effects (f). For panels (d) and (f), standardised effects are categorised into standardised direct effects and standardised indirect effects. Only significant pathways ($p < 0.05$) are showed in these models. The values adjacent to arrows are standardised path coefficients and the arrow width is proportional to the intensity of relationship. R^2 indicates the explained variance of dependent variable by the model.

to the corresponding parameter values (Figure S19), indicating that the important bioelements (e.g., hub traits, C) tended to maintain their importance across environmental gradients.

4 | Discussion

4.1 | Differentiation in Elemental Stoichiometry Amongst Life-Forms

Leaf bioelements varied significantly amongst different plant life-forms in wetlands. Submerged plants possessed less C than other life-forms (Hu et al. 2021; Wang et al. 2015). Physiologically, C in plants is mainly invested in carbon skeletons as structural C (C_S), for example in the cell wall, to support plants (Ma et al. 2018). However, the additional support from water buoyancy reduces the needed strength of plant supporting tissues, and thus lowers the requirement for C, which always is a limiting element for plant photosynthesis underwater (Maberly and Gontero 2018; Pedersen, Colmer, and Sand-Jensen 2013). Further calculation about C_S concentrations in this study demonstrated that both the absolute values and relative amount of the C_S in submerged plants were significantly lower than that in the other two life-forms of plants (Appendix S5; Table S3).

For the mineral elements, 13 of the 16 bioelements were detected in the highest concentrations in submerged plants (Figure 2a), reflecting the special elementome of this life-form in adapting to the submerged environment. For example, Ca-containing calcium pectate (Xing et al. 2021) and Si (Schoelynck and

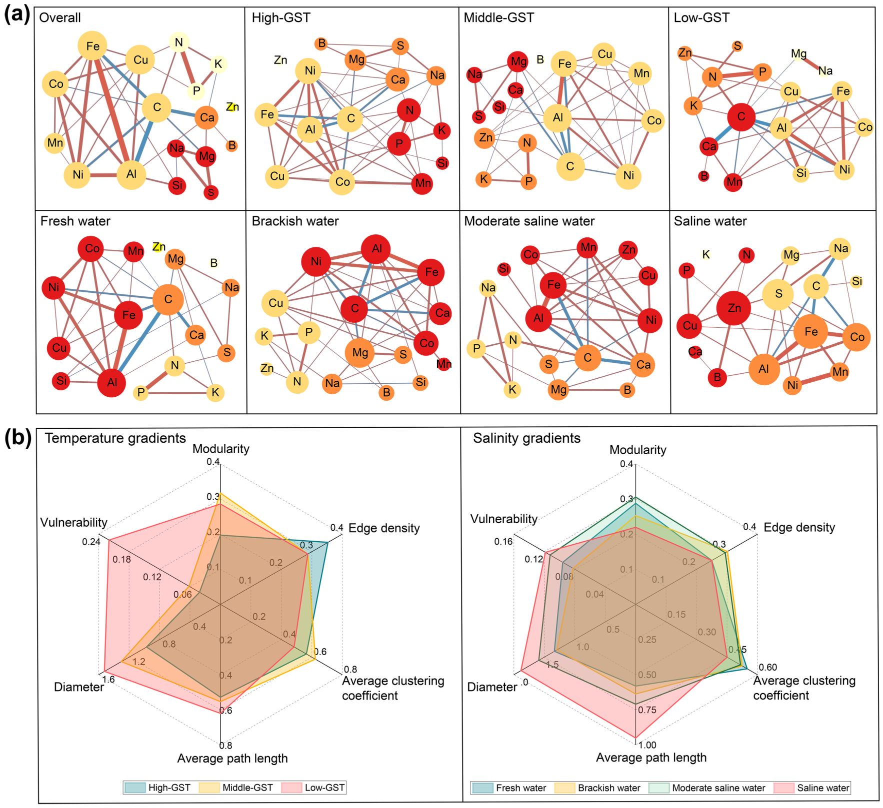

FIGURE 5 | Shifts in leaf element networks (LENs) and network parameters along environmental gradients of wetland plants. (a), The network topologies of LENs for all data ($n = 1058$) and different temperature and salinity gradients. High-GST ($n = 346$), middle-GST ($n = 498$) and low-GST ($n = 214$) represent 20°C–30°C, 10°C–20°C and 0°C–10°C of growing season mean temperature (GST), respectively. Fresh water ($n = 757$), brackish water ($n = 202$), moderate saline water ($n = 69$) and saline water ($n = 30$) represent 0‰–0.5‰, 0.5‰–2‰, 2‰–5‰ and >5‰ of water salinity, respectively. Different colours in each network represent different modules. The size of the node represents its degree, and the width of the edge represents the strength of positive (red lines) and negative (blue lines) correlations. (b), The variations in network overall parameters (modularity, edge density, average clustering coefficient, average path length, diameter and vulnerability) across temperature and salinity gradients, respectively.

Struyf 2016) serve load-bearing functions in cell walls, enhancing the flexibility and resistibility of submerged plants to hydraulic forces. In underwater environments, plants suffer from reduced light penetration and CO_2 diffusion, which constrain the photosynthesis of submerged plants (Pedersen, Colmer, and Sand-Jensen 2013). Considering that the light-driven photosynthesis is enzymatic-dependent process, the enrichment of ionic elements, such as Mg, Mn, Fe and Cu (Ågren 2008; Grusak, Broadley, and White 2016), for the synthesis of chlorophyll, enzymes (e.g., Rubisco), and coenzyme factors in plants help to improve the limited photosynthetic potential underwater. Unlike emergent plants, submerged leaves are surrounded by water and thus directly face the osmotic stress from the solute in water. Submerged plants reserve more inorganic (e.g., Na^+, SO_4^{2-}) or low molecular weight organic compounds (e.g., S-containing compounds) as osmoprotectants in leaves to maintain osmotic balance (Deinlein et al. 2014; Zuo et al. 2022). In this study, the higher the element contents in water, the more enriched the bioelements in submerged plant leaves (Figure S9). Furthermore, the alkaline microenvironment around leaves produced by photosynthesis may promote the enrichment of metal cations in leaves (Pedersen, Colmer, and Sand-Jensen 2013). In addition, lower C concentrations is also a reason inducing higher mass-based fractions of the mineral elements in submerged plants.

4.2 | Variability of Bioelements and the Relative Effects of Phylogeny and Environments

In this study, we extracted three highlights illustrating the regulatory mechanisms of variations in wetland plant bioelements in alpine and arid regions (H1-H3 in Figure 6a,b).

Firstly, wetland plants were more stable in macroelements than microelements, that is, the higher the concentrations, or the higher the physiologically requirement, the more stable (smaller CV) the bioelements are in plants (Figure 2c,d), coinciding with the stability of limiting elements hypothesis (Han et al. 2011). The differences in stability between macroelements and microelements involves the degree to which each bioelement once acquired will cause a shift in the concentrations of other bioelements, which for example are required in certain ratios to build certain tissues or to drive specific processes and functions. Macroelements with high demands (N, P, K, etc.) are always the key elements limiting productivity (i.e., accumulation of C at the whole plant scale). In this study, N, P, and K functionally coordinated to each other tightly (Figure 5a). A change in one macroelement will constrain or influence the shift in others. For example, more N accumulation might lead to more P and K absorption, and promote C fixation by enhancing photosynthesis. More C accumulation

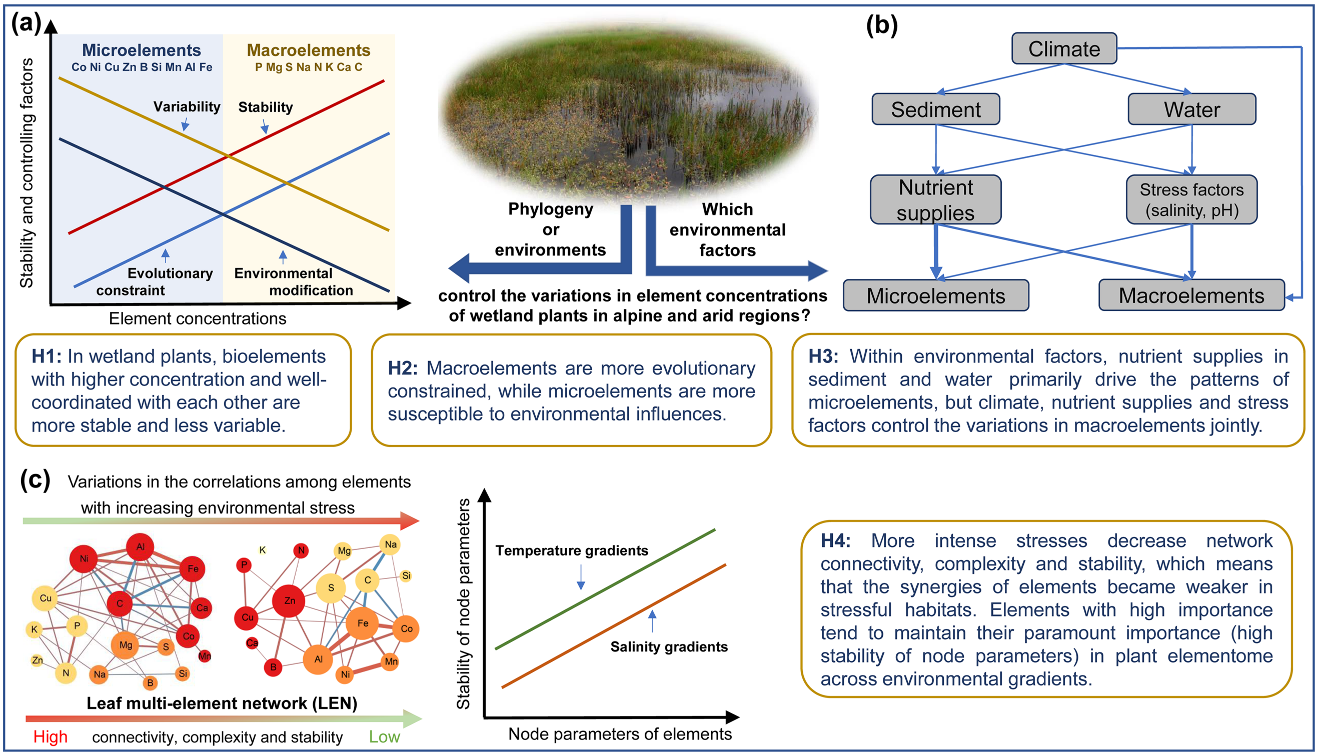

FIGURE 6 | Highlights for explaining the shaping mechanisms of wetland plant elementome. (a), With increasing bioelemental concentrations from microelements to macroelements, the elements show more stable (red line) and less variable (brown line), and the driving factors for the variations of bioelements shift from environmental modification (black line) to evolutionary constraint (blue line). (b), The underlying environmental controls of macroelements and microelements are divergent. Nutrient supplies in sediment and water are the primary controlling factors in determining the patterns of microelements, but climate play more important roles in the variations in macroelements than microelements. (c), The topologies of leaf element network vary along environmental gradients. More intense stresses decrease network connectivity, complexity and stability, which means that the synergies amongst bioelements become weaker in stressful habitats. Elements with high importance consistently maintain their paramount importance in plant elementome across environmental gradients.

create the "nutrient dilution effect" (Kaspari 2021), which in turn reduces the mass-based N concentration and keeps it relative stable. In contrast, microelements had weak relationships to macroelements, even negatively correlated to C (Figure S15), showing relatively independent function in driving specific processes. In addition, the microelements are almost always found at levels much beyond where they influence function (Kaspari 2021). Thus, if there is more available in environment, the microelements passively end up with more (e.g., what is sometimes called luxury absorption) but it doesn't change N or C concentrations. Similarly, if the microelements are passively acquired, it doesn't matter what the N and C concentrations are. Hence, the microelements vary more in lockstep with availability. In summary, we proposed a stability of well-coordinated elements hypothesis, suggesting that bioelements which coordinate together well in driving certain physiological functions (e.g., biomass production) constrain each other and thus are kept relatively stable in plants, while those functionally independent bioelements fluctuated greatly with the nutrient availability in environment.

Secondly, macroelements are more evolutionary constrained, while microelements are more susceptible to environmental influences. Both the physiological requirements and environmental nutrient limitations can influence the regulation strength of phylogeny and environments on bioelement variations (Ågren 2008; Peñuelas et al. 2019). Macroelements are components of biological macromolecules, often in fixed ratios and coordinated relations, and thus their strong stabilities perhaps also contribute to the evolutionary conservatism of the macro-elementome to maintain in different taxa (Wang et al. 2015; Zhao et al. 2016). In contrast, most microelements are the main components of coenzymes (Grusak, Broadley, and White 2016), which are functionally independent to macroelements and more sensitive to environmental nutrients (Han et al. 2011). Fundamental biochemical processes have distinct rates across species, which induce different requirements for various bioelements, resulting in different regulations of macroelements and microelements (Sardans et al. 2021). To date, there have been few studies focusing on the phylogenetic signals of plant elementome, especially microelements (but see Fernández-Martínez et al. 2021). Evolutionary history (Ackerly 2009), genetic variation (Crisp and Cook 2012), and stable selection (Donoghue 2008) could control the variations in species-specific plant functional traits. In this study, the relative effects of phylogeny on bioelements increased while that of environments decreased with increasing bioelemental concentrations (Figure 3).

Thirdly, environmental variation had greater effects on microelements than macroelements, which may be because microelements are environment sensitive, physiologically required in low amounts, and have weak functional coordination with other bioelements (Han et al. 2011; Karimi and Folt 2006; Zhao et al. 2016). Within environmental factors, nutrient supplies are the primary ones in determining the patterns of microelements, but nutrient supplies, stress factors, and climate control the variations in macroelements jointly. Variations in macroelements are influenced by climate (Han et al. 2011; Reich and Oleksyn 2004), soil factors (Joswig et al. 2022), water chemistry (Fernández-Martínez et al. 2021), and environmental stresses (e.g., salinity, Zuo et al. 2022). In this study, climate had significant direct and indirect effects on macroelements, while only a weak indirect effect on microelements (Figure 4c–f). Temperature and precipitation are critical factors determining plant growth and survival in alpine and arid regions (Shen et al. 2022). Directly, climatic factors regulate the physiological metabolic process and growth rate of plants, and thus affect the absorption and accumulation of elements (the Temperature-Plant Physiological Hypothesis, Reich and Oleksyn 2004). Indirectly, climatic factors regulate microbial mineralisation and biogeochemical cycles of elements (Delgado-Baquerizo et al. 2013), resulting in heterogenetic resource availability and environmental stresses in different environments, further causing nutrient limitation of macroelements (e.g., N and P in the Temperature-Biogeochemical Hypothesis, Reich and Oleksyn 2004). However, microelements are mainly determined by the nutrient status of soil parent material rather than climatic factors, and thus are not the limiting elements in environments, which are consistent with our results (Figure 4). The specific biological function, weak mobility and high environmental plasticity of microelements together lead to their high dependence on nutrient supply.

This study further emphasised the significant effects of environmental nutrients on bioelements beyond C, N, and P, especially microelements, which had rarely been mentioned in previous studies. Our findings highlighted that intrinsic species identities, theoretical physiological requirements and practical environmental constraints jointly optimise the elementome of plants (Peñuelas et al. 2019). However, further studies on the homeostasis/plasticity of bioelements would be much helpful for understanding the linkages between plant elementome and species adaptation and ecosystem functioning (Fernández-Martínez 2022).

4.3 | Linking Element Network With Plant Response to Environment

Beyond concentrations, correlations amongst bioelements and their variations also reflect the plant response to environments (He et al. 2020). In this study, the correlations amongst bioelements showed lower connectivity, complexity, and stability in cold and saline habitats (Figure 5b), indicating that stressful environments restricted inter-element synergism in plants (Li et al. 2022; Rao et al. 2023). Maintaining stable and complex bioelemental correlations requires high construction cost, and may be disadvantageous for plants in stressful habitats (Alon 2003; Flores-Moreno et al. 2019). In contrast, networks with high connectivity, complexity and stability in non-stressed environments may signify a tight integration amongst bioelements which allows plants to access resources more efficiently (Rao et al. 2023), namely, “complexity begets stability” (Yuan et al. 2021).

Plants responded to cold and saline environments by adjusting the correlations amongst the bioelements, which could be detected from the variations in modular composition and node parameters of LENs. Firstly, changes in network connectivity have been considered as the trade-off between connection efficiency and connection cost (Flores-Moreno et al. 2019). LENs exhibited lower connection (e.g., lower edge density) amongst elements to reduce the cost of bioelemental collaboration under stressful environments. In addition, we found a higher network modularity at low-GST level (Figure 5b), which allowed plants to perform their specific functions more independently, and prevented one module failure from spreading to other modules (Gilarranz et al. 2017; Rao et al. 2023). Secondly, maintaining the robust correlations amongst certain bioelements is an important basis for plants to accomplish physio–biochemical processes. N and P always constituted a module across temperature and salinity gradients (Figure 5a), which was consistent with the results of woody plants across climatic regions (Flores-Moreno et al. 2019). N and P are central to the leaf economic spectrum and their robust correlation is critical to the resource trade-off strategies of plants in diverse environments (Reich 2014; Reich et al. 2010; Reich and Oleksyn 2004; Wright et al. 2004). Similarly, Al, Fe, Ni and Co always constituted a module to maintain necessary biochemical reactions (Grusak, Broadley, and White 2016). Thirdly, LENs could shift the connectedness and centrality of bioelements to respond to stresses. For example, the hub traits, C, consistently maintained their high importance at all levels of environments (Figure S19), and exhibited the highest stability across environmental gradients in this study, indicating the important role of C on plant phenotype and biomass production (Ma et al. 2018). On the contrary, the degree of S increased with increasing salinity, confirming the crucial role of S on salt resistance (Zuo et al. 2022). Therefore, we inferred that connections related to hub traits are more robust, while correlations amongst non-hub traits are more likely to change or even break (e.g., the decoupling of plant N-S correlation in high-salt environment, Zuo et al. 2022), resulting in deformations of LENs with environmental changes (Figure 6c).

5 | Conclusions

Using multidimensional approaches, we evaluated the variations in wetland plant elementome and their correlations beyond C, N, and P across life-forms, phylogeny, climate, and environments in alpine and arid regions. The variation patterns of bioelements suggest general rules about how phylogeny and environments co-regulate the elementome. Bioelements with higher concentrations were more stable, and the drivers of the variations in bioelements shifted from environmental modification to evolutionary constraint. Tighter correlations amongst bioelements might mean better coordination in driving physiological functions, which are regulated by species-specific requirements, and constrained by functional requirements for certain ratios, resulting in less variable concentrations. In contrast, functionally independent bioelements with weak coordination are more influenced by nutrient availability in habitats. The variations of microelements were primarily controlled by nutrient supplies, while macroelements were mainly affected by climate, followed by environmental nutrients and stresses. Stressful (cold or saline) habitats lead to looser leaf element correlations and lower inter-element coordination and stabilities. The highlights extracted in this study advance our understanding of the causes and consequences of wetland plant elementome in harsh environments.

Author Contributions

Z. Wang designed research; Z. Zuo, H. Zhao, L. Zhang, L. Yang, T. Lv, and Z. Wang performed research and collected field data. Z. Zuo, H. Zhao, X. Qiao, and Z. Wang analysed data. Z. Zuo and Z. Wang wrote the paper. P.B. Reich, X. Qiao, Z. Tang, and D. Yu helped interpret the data and revise the paper.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw data and R code that supporting the findings of this study are available on Figshare at: https://doi.org/10.6084/m9.figshare.25952017.v4.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.