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RESEARCH ARTICLE

Beyond salinity: Plants show divergent responses to soil ion composition

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Abstract

Aim: In salt-affected environments, salinity shapes ecosystem functions and species composition. Apart from salinity, however, we know little about how soil chemical factors affect plant species. We hypothesized that specific ions, most of which contribute to salinity, co-determine plant niche differentiation. We asked if the importance of ions differs for species with (halophytes) and without (associated species) physiological adaptations to saline soils.

Location: Carpatho-Pannonian region (Central and Eastern Europe).

Time period: 2005–2021.

Major taxa studied: Vascular plants.

Methods: We recorded species occurrences and collected soil samples in 433 plots in saline habitats. We measured pH, salinity (electrical conductivity), and concentrations of Ca^{2+}, K^+, Mg^{2+}, Na^+, SO_4^{2-} Cl^-, CO_3^{2-} and mineral nitrogen (mN) and calculated the sodium adsorption ratio (SAR). For 88 species, we fitted response curves with Huisman–Olff–Fresco (HOF) models. To study ions' effects on species composition and ions' variance, we compared unconstrained and constrained ordinations and performed a principal component analysis. We used random forests to analyse the importance of ions for individual species and created two-dimensional species niche plots for key ions.

Results: Ion concentration niches varied among species and did not necessarily correspond to soil salinity or alkalinity. We frequently observed monotonic, sigmoidal model responses, while skewed unimodal responses were rare. Ions explained a considerable proportion of species compositional variation. Particularly, Na^+, SO_4^{2-}, Cl^-, and CO_3^{2-} contributed to the ions' variance. Na^+, followed by SO_4^{2-}, Cl^-, CO_3^{2-}, Ca^{2+}, Mg^{2+}, and mN, was most important for the occurrence of individual species. Compared to associated species, Na^+, SO_4^{2-}, and mN were significantly less important for halophytes, whereas Cl^- and CO_3^{2-} played a significant role.

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Main conclusions: We show that ion composition co-determines niche differentiation in saline soils, suggesting evolved physiological adaptations in halophytes. Our study calls for incorporating high-resolution data on soil ion composition in ecological research.

KEYWORDS
alkalinity, high-resolution soil data, indicator plants, inland saline soils, plant–soil relationship, realized niche, salt-affected environments, sodicity, soil ion composition

1 | INTRODUCTION

Halophytic vegetation occurs on all continents except Antarctica. It encompasses more than 5.5 Mha of coastal marshes and grasslands worldwide (Mcowen et al., 2017) and vast areas of inland saline steppes and salt pans, for example, in Africa and Central Asia. Understanding ecological processes in salt-affected environments is becoming increasingly important. On the one hand, the functioning of (semi-)natural saline habitats is threatened by land-use change and global warming, for example, sea-level rise, enhanced evapotranspiration, limited salt leaching, or road salt application. On the other hand, the effects of global warming increase the extent of saline soils on our planet (Dugan et al., 2017; Qadir & Schubert, 2002; Talat, 2020).

Coastal marshes are influenced by tides and occur on sodium chloride-rich soils (Bonis et al., 2005; Leuschner & Ellenberg, 2017). In contrast, inland halophytic vegetation occurs in semi-humid to arid regions, where intrazonal high sodium solonchak and solonetz soils develop. Next to sodium, solonchak and solonetz soils contain a wide variety of ions, for example, bicarbonate, calcium, carbonate, chloride, magnesium, potassium, and sulphate. Their varying concentrations co-determine the characteristic soil features such as high sodicity or alkalinity (e.g. Albert et al., 2020; Blume et al., 2010; Mezősi, 2017; Tóth, 2011; Ungar, 1973). Although edaphic and climatic differences between coastal and inland halophytic vegetation are well known, ecological processes and plant community structure are less understood in the latter.

Knowledge of realized niches of plants is an integral part of ecological research and species distribution modelling. While coarse-scale (e.g. macroclimatic) data are widely applied in niche assessments (Soberón & Townsend, 2005), fine-scale edaphic factors are largely ignored (but see, for example, Chenchouni, 2017; Wagner et al., 2017). However, edaphic properties are essential for species occurrence and plant community assembly (Hulshof & Spasojevic, 2020) in saline environments (e.g. Bernáldez & Rey Benayas, 1992; Szabolcs, 1994; Tóth & Rajkai, 1994; Ungar, 1973; Volkmar et al., 1998).

Theory predicts that physiological adaptations control plant tolerance to environmental factors. In saline environments, halophytes tolerate abiotic soil properties owing to their physiological adaptations, such as succulence or salt excretion strategies. By contrast, species not adapted to these conditions have a limited capacity to grow and compete in these environments (Austin, 1980; Breckle, 2004; Chaudhary, 2019; Del Vecchio et al., 2020; Hayward & Wadleigh, 1949). Abiotic stress, such as extreme soil conditions, defines a species' fundamental niche. Meanwhile, a realized niche is modified by interspecific interactions, including competition (Bonis et al., 2005; Pennings & Callaway, 1992; Reimann & Breckle, 1995) and facilitation (e.g. Bertness & Shumway, 1993; Pennings et al., 2003). In response to competition, the width of ecological niches can shrink, and non-Gaussian response curves occur that shift along environmental gradients. In extreme environments, left-skewed responses (Austin & Smith, 1989; Oksanen & Minchin, 2002a) are common, in which the species' niche shifts to higher stress factor values.

As early as 1936, Iversen pointed out that in plants growing in a saline environment, soil ion composition causes differences in realized niche position relative to salinity (Iversen, 1936). Within (semi-)natural salt-affected vegetation, some studies have explored certain species' occurrences or niches in relation to edaphic factors, including ion composition on a local scale (Álvarez Rogel et al., 2001; Chenchouni, 2017; Zlatković et al., 2019). However, no study has assessed edaphic niches across a large region and multiple species in saline environments. To better understand plant community composition and predict species occurrences in saline environments, it is crucial to understand the species' response to individual ions rather than just salinity.

We studied one of the major saline areas in Europe, the Pannonian Basin and adjacent areas to the east. Its plains and endorheic basins host mosaics of saline grasslands, herb-dominated vegetation, and open vegetation dominated by highly specialized annual salt-adapted species that occur in extensive steppes with diverse microtopographical levels or on salt pans (Danihelka et al., 2022; Dítě et al., 2017; Eliáš et al., 2020; Molnár et al., 2008; Wendelberger, 1943). Given the dependence on stable, seasonally fluctuating groundwater and extensive grazing, halophytic vegetation in the region is vulnerable to land-use change (Dítě, Šuvada, & Dítě, 2021; Janssen et al., 2016) and of conservation concern (EU Habitats Directive; European Commission, 2013; Šefferová Stanová et al., 2008).

By using plants of halophytic vegetation as study species, we investigated how ecological niches vary along gradients of salinity, pH, sodicity, and ion composition. We hypothesize that ions, most of which contribute to salinity, are important determinants of plant species distribution and niche differentiation in salt-affected habitats.

As a result, species should have varying niche positions in the multidimensional environmental space. We further hypothesize that the realized niches of many species show right- or left-skewed responses due to extreme edaphic conditions and interspecific competition. We used two-dimensional niche plots to depict the width and optimum of species niches along gradients of salt ion concentration. We further asked if the importance of ions for species occurrences differs across all species and between species with physiological adaptations to saline soils (halophytes) and species without such adaptations (associated species). Insights of our study could improve the understanding of plant–soil relationships, including the importance of plant physiological adaptations, and advance our understanding of community assembly in environments affected by different types of salinity.

2 | METHODS

2.1 | Study area

The study area is situated in eastern-Central and Eastern Europe and comprises the Pannonian Basin, the Transylvanian Plateau, and Romanian Moldavia (hereafter, the Carpatho-Pannonian region). It covers approximately 250,000 km^2, stretching across a latitudinal range of 45.2° N to 49.1° N and a longitudinal span of 16.2° E to 28.0° E (Figure 1).

Large salt lakes covered the Pannonian Basin in the Middle Miocene to Pliocene, which were later filled with alluvial and aeolian sediments (Geary et al., 2000; Horváth et al., 2015; Mezősi, 2017). The regional continental climate has favoured the formation of saline, sodic, and alkaline soils in different landforms, such as plains, pans, or ditches. The soils encompass intrazonal solonchak and solonetz soils on sedimentary deposits and are affected by saline groundwater or surface water. These soils are moist or waterlogged in winter and spring when large amounts of salts dissolve in the soil water. The hot and dry summers result in high evapotranspiration and limited leaching of salts in the soils. This favours an increase in dissolved salts in capillary soil water, an accumulation of salt ions in near-surface soil horizons, and a decrease in soil water potential (Appendix S1; Dítě, Šuvada, Tóth, et al., 2021; Karger et al., 2017).

2.2 | Data collection

In 2021, we conducted a plot-based survey of halophytic vegetation in the Carpatho-Pannonian region. We sampled 228 vegetation

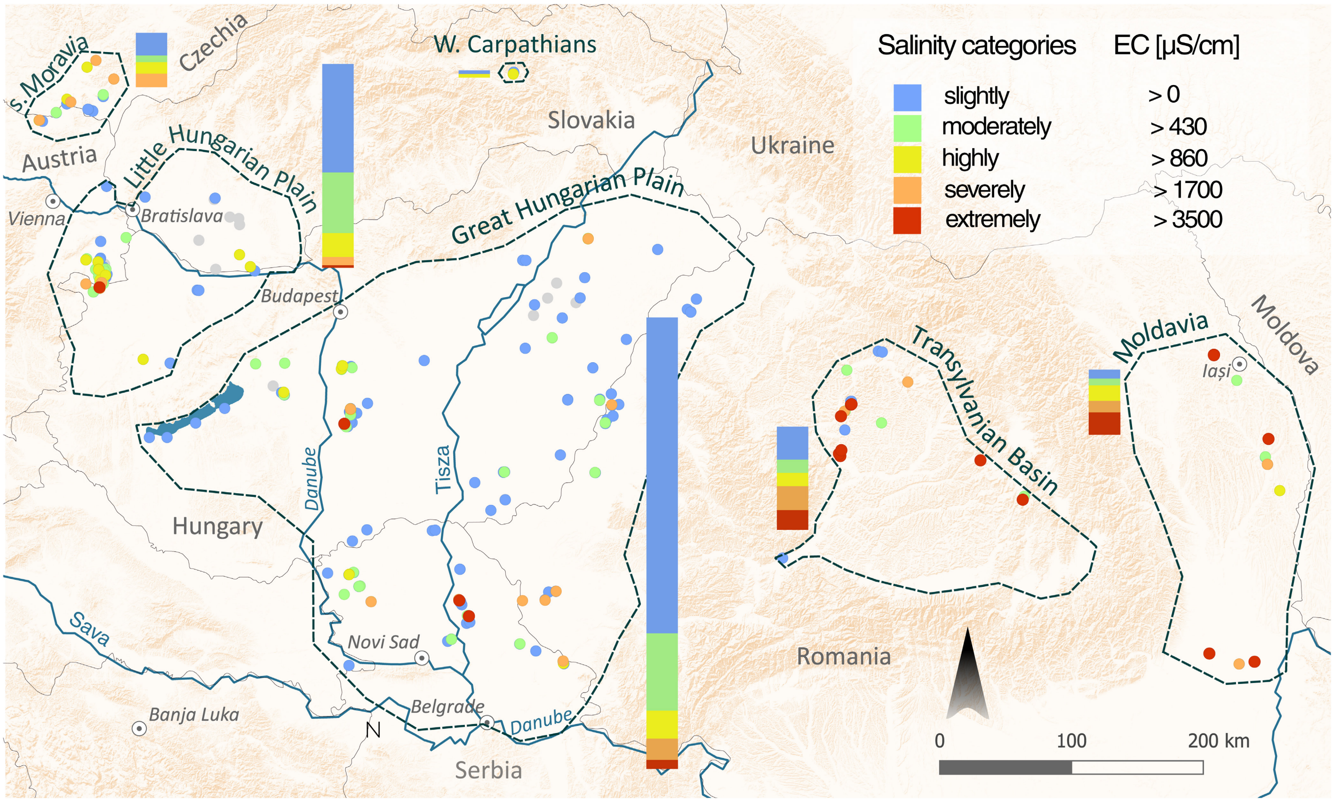


FIGURE 1 Geographic distribution of sampled plots in the Carpatho-Pannonian region categorized by topsoil salinity, assessed by electrical conductivity (EC). No EC values were available for the plots indicated in grey. Dashed lines delineate the six subregions (southern Moravia, Little Hungarian Plain, Great Hungarian Plain, Western Carpathians, Transylvanian Basin, and Moldavia), and bars indicate regional numbers of plots belonging to specific salinity categories. The map was created using QGIS94 (v. 3.18.3-Zürich; https://www.qgis.org; basemap: ESRI Terrain). Maps of sampled plots categorized by alkalinity (pH) and sodium adsorption ratio (SAR) can be found in Appendix S2.

plots randomly placed in a broad range of slightly to extremely saline plant communities. The plot area encompassed 16 m^2, which was consistent with recommendations for grassland vegetation surveys (Dierschke, 1994). Saline vegetation occurs in patches of various shapes, which made it necessary to adjust the plot area and shape in some places. Hence, we modified the size of 30% of our plots to 0.6–15 m^2. We recorded the abundance of all vascular plants in each plot using a nine-grade abundance scale (Dierschke, 1994).

We took topsoil samples from the plant root zone (0–15 cm; henceforth: soil), assuming that this is where the main establishment and root growth occurs, but did not sample deeper soil layers. We pooled three randomly placed samples into one soil sample per plot for laboratory analyses. We supplemented our field data with 76 plots of 10 m^2 sampled between 2010 and 2020 (Danihelka et al., 2022; Prokešová, 2013) and 177 plots of 12 to 16 m^2 sampled between 2005 and 2020 (Dítě & Dítě, unpublished).

To reduce spatial clustering of plots with similar vegetation, we classified the vegetation data into eight main vegetation types using the modified Twinspan algorithm (cut levels of percentage cover: 0, 5, 25; Roleček et al., 2009) in the program JUICE (Tichý, 2002) and assigned each plot to a grid cell of 1.25 longitudinal × 0.75 latitudinal minutes, that is, approximately 1.5 × 1.4 km. We applied stratified-random resampling by selecting a maximum of two plots of the same vegetation type per grid cell. Taxonomy follows Euro+Med (2022). Species in taxonomically difficult groups were aggregated. For example, because *Juncus compressus* and *Juncus gerardi* are frequently misidentified and difficult to recognize without flowers or fruits, we combined the two species as *Juncus compressus* agg.

Our final dataset consisted of 433 plots with 398 taxa recorded between May and October 2005 to 2021 (Appendix S2). The plots were distributed proportionally across all subregions of the Carpatho-Pannonian region. While slightly saline plots were associated with salt steppe grasslands, many severely to extremely saline or (very) strongly alkaline plots were from salt pans (Figure 1; Appendix S2).

2.3 | Soil analyses

We analysed 236 topsoil samples from our fieldwork in 2021 and from Danihelka et al. (2022) in the Laboratory of Water, Sediment and Soil Chemistry in the Department of Botany and Zoology, Masaryk University. Soil samples were homogenized by sieving through a 2 mm mesh. We measured electrical conductivity (EC, a standard measure to estimate salinity) and pH using a Hach HQ40D multi-meter (Hach, Loveland, CO, US) in a 1:5 soil–water suspension.

We measured the concentrations of soluble ions, most of which contribute to salinity. We analysed the concentrations of calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^+), and sodium (Na^+) in both a 1:10 soil-Mehlich 3 solution (to best approximate plant-available concentrations; Mehlich, 1984) and a 1:5 soil–water extract (for calculation of the sodium adsorption ratio = SAR). We analysed the samples using flame atomic absorption spectrometry (AAS novAA 350, Analytik Jena, DE) following the standards ISO 7980 (Water quality—Determination of calcium and magnesium—Atomic absorption spectrometric method) and ISO 9964 (Water quality—Determination of sodium and potassium).

We determined the concentrations of soluble chloride (Cl^-), inorganic carbon (C_{inorg}, to approximate HCO_3^- and CO_3^{2-}), and mineral nitrogen (mN, to approximate nitrates [NO_3^-] and ammonium [NH_4^+]) in a 1:5 soil–water extract. For Cl^-, we applied the titration method according to the standard ISO 9297 (Water quality—Determination of chloride—Silver nitrate titration with chromate indicator [Mohr's method]). $C_{inorg.}$ and mN were determined based on oxidation to nitrogen or carbon oxides (Shimadzu laboratory analyser, TOC-VCPH with TNM-1 module) according to the standards EN 12260 (Water quality—Determination of nitrogen—Determination of bound nitrogen [TNb]) and ISO 8245 (Water analysis—Guidelines for the determination of total organic carbon (TOC) and dissolved organic carbon [DOC]). Sulphates (SO_4^{2-}) were measured in a 1:5 soil–water extract using a turbidimetric method with solid barium chloride.

We supplemented our laboratory measurements with soil data from Prokešová (2013; EC, pH, and Ca^{2+}, Na^+, K^+, measured in water) and Dítě and Dítě (unpublished data; EC, pH, mN, Mg^{2+}, measured in water and Mehlich 3, and Ca^{2+}, Na^+, K^+, measured in Mehlich 3). These soil samples were also collected from the topsoil layer using comparable methods and had value ranges and median values matching our laboratory results (confirmed visually using boxplots). To achieve compatibility, we recalculated EC_e from Dítě and Dítě to $EC_{1:5}$ (henceforth EC) based on Klaustermeier et al. (2016):

$$EC_{1:5} = \frac{10^{log\left(\frac{EC_e}{10^{0.7659}}\right)}}{1.2562}$$

We calculated the sodium adsorption ratio (SAR) from Na^+, Ca^{2+}, and Mg^{2+} concentrations measured in water using this formula:

$$SAR = \frac{Na\ \frac{meq}{L}}{\sqrt{(Ca\frac{meq}{L} + Mg\ \frac{meq}{L})\ /\ 2}}$$

The data from Prokešová (2013) and Dítě and Dítě (unpublished) did not contain all the 11 soil characteristics we evaluated. Consequently, the final dataset of 433 plots contains subsets for each soil variable with sizes ranging from 229 to 406 (Appendix S2). For further analyses, we log_{10}-transformed all variables except pH.

2.4 | Species response models

Because our dataset included records from plots of different sizes (0.6 to 16 m^2), we tested the relationship between species numbers and plot size by calculating a generalized linear model ($p = 0.696$, McFadden's $r^2 < 0.1$; R Core Team, 2022). The absence of a significant relationship indicated that smaller plots did not have lower species numbers (Appendix S2); consequently, we kept all plots for further analysis. The species included in our study were geographically representative, with most species recorded in all subregions where they occur; the absence of species relates to local rarity, local extinction, or the small size of the subregion (Western Carpathians).

We determined the central tendency (optimum) and the width of one-dimensional realized niches of species in relation to 11 soil variables by linking species' presence–absence data to soil variables measured in each plot. We calculated the likelihood of species occurrence using Huisman–Olff–Fresco (HOF) models based on hierarchical logistic regression (package: *eHOF*, version 1.12; Jansen & Oksanen, 2013; R Core Team, 2022, version 4.1.3). HOF models fit seven curve types of increasing complexity to species occurrence data (I: linear, flat, II and III: monotonic sigmoidal, IV: unimodal symmetric, V: unimodal skewed, VI and VII: bimodal). Given that extreme edaphic factors or interspecific competition shape realized niche responses in complex ways, integrating multiple responses while emphasizing model simplicity and stability (bootstrapping) is an essential feature of HOF models (Austin & Smith, 1989; Huisman et al., 1993; Jansen & Oksanen, 2013; Oksanen & Minchin, 2002a, 2002b; Santika & Hutchinson, 2009). We limited the calculations to model types I to V and excluded bimodal model types that assume two optima since they resulted in model overfitting. On the one hand, bimodal models often showed exaggeratedly steep increases in species occurrence probability at the ends of the variable ranges. On the other hand, some bimodal models showed either extremely narrow niches located directly adjacent within a small fraction of the variable's range or extremely broad niches that covered significant parts of the variable's range. The latter display niche differentiations that do not allow for ecologically meaningful interpretation. Instead, we used linear or monotonic sigmoidal responses, which yielded more interpretable results.

We calculated HOF models with adjusted model variation (bootstrap = 1000) for each species that occurred more than ten times (model default) in the variable's specific subset. We chose the best models based on the corrected Akaike Information Criterion (AICc). If AICc and bootstrap results differed, we chose the best model according to the weight of the highest average AICc over 1000 runs. To determine the central ecological position of species, we derived information on optima (highest likelihood of species occurrence) and central niche width for model types II to V following Heegaard (2002). In some cases, niche borders and optima were modelled outside the measured variable ranges, which we corrected to the lowest and highest measured values. Niche borders for model type I were set to the lowest and highest measured values of each variable.

In total, we quantified niches for EC (87 species), pH (83), SAR (60), and ions (80: mN; 77: Na^+, Mg^{2+}, K^+; 78: Ca^{2+}; 61: CO_3^{2-}, SO_4^{2-}, 62: Cl^-,77). For an easy-to-grasp interpretation, we added commonly used thresholds or categories to the model graphs of EC (slightly, moderately, highly, severely or extremely saline; thresholds were calculated for loamy to clayey soils), pH (<7 = slightly acid, 7–8 = slightly alkaline, 8–9 = moderately alkaline, 9–10 = strongly alkaline, >10 = very strongly alkaline), and SAR (Blume et al., 2010; Department of Primary Industries and Regional Development, 2022).

2.5 | Overall variance and importance of soil ions

To better compare the effect of ion concentrations, the latter were recalculated to mg of substance per 1 kg of soil, while $C_{inorg.}$ was recalculated to its CO_3^{2-} weight equivalent (henceforth treated as a proxy for CO_3^{2-} and HCO_3^- because the proportions of these ions vary to an unknown extent in each soil sample). We excluded EC, pH, and SAR from further analyses because of their high correlation ($r \geq 0.7$) with other variables (Appendix S3).

We explored the main gradients of ion concentrations in salt-affected soils by conducting a Principal Component Analysis (PCA) on the ion correlation matrix (plots = 228; variables = 8), removing the greater influence of larger values on the results (package: *stats*; R Core Team, 2022, version 4.1.3). The contributions and contribution shares of ions for the first four principal components (pc1-pc4) were derived using the package: *factoextra* (Kassambara & Mundt, 2020).

We studied the relation of ion concentrations to the overall species composition by conducting unconstrained (Correspondence Analysis, CA) and constrained (Canonical Correspondence Analysis, CCA) ordination on the presence–absence species composition matrix (plots = 228; species = 119). We down-weighted rare species and, in the CCA, accounted for spatial dependency in the data by including latitude and longitude as conditional terms. The eight studied soil ions constrained the full CCA model. We identified the best CCA model by stepwise model selection using adjusted R^2 and tested for model, variable, and axes significance in the CCA using an ANOVA-like permutation test. The CA and the CCA configurations were compared using a symmetrical Procrustes analysis.

2.6 | Importance of soil ions for individual species and species groups

We aimed to visualize two-dimensional niche plots for the most crucial ions in saline environments and explore whether ion importance differs across all species and between halophytes and associated species.

We assessed the importance of soil variables for the occurrence of each of the 60 species for which we had values for all soil variables by applying random forests (RF; R package *randomForest*; Breiman, 2001; Liaw & Wiener, 2002) to the species presence–absence data. We calculated classification trees based on 1000 bootstrap samples ('bagging') and chose the best tree using majority voting. At each node, we calculated splits using a random sample of three out of eight variables (applying up to six variables led to minor changes). We measured the importance of variables for the occurrence of each species (henceforth RF ranks) as the mean decrease in model accuracy (MDA). MDA quantifies the predictive power of a given variable based on the normalized average error of the variables in the out-of-bag (OOB) dataset using permutation. We chose MDA because it is less biased than the Gini impurity index (Grömping, 2009). To compare variable importance across models, we sum-normalized MDA values (henceforth: adjusted MDA) for each variable in each model.

We designated each species as either a halophyte or an associated species following Dítě et al. (2023). The halophyte group included all species physiologically adapted to saline environments that either occur exclusively (obligate halophytes) or predominantly (facultative halophytes) in saline environments. Associated species lack such adaptations and frequently occur in habitats not affected by salinity. To assess significant differences for each variable, we calculated sums of the adjusted MDA values for (i) all species and (ii) each species group. We performed Friedman tests to assess the differences across the calculated sums, which account for dependencies across groups (here: variables). We compared all species, halophytes, and associated species across all variables, followed by post hoc pairwise Wilcoxon tests. To compare each variable across species groups, we applied Wilcoxon tests.

3 | RESULTS

3.1 | Niche differentiation

Realized niches of halophytes and associated species in the studied saline habitats differed along soil salinity (EC), alkalinity (pH), and sodicity (SAR) gradients. More specifically, 5% of species were confined to severely and extremely saline soils (high EC) or soils with a SAR > 15, while those bound to strongly and very strongly alkaline soils accounted for 11% of all species niches calculated along the pH gradient (Figure 2; Appendices S4–S6).

Species showed distinct realized niches with respect to soil ions, generally not similar to those observed for EC or pH. In other words, species with overlapping niches at specific EC or pH gradient positions differed on other niche axes defined by specific ions. For example, halophytes adapted to severely to extremely saline soils (e.g. *Puccinellia distans* agg., *Camphorosma annua*, *Crypsis aculeata*, and *Suaeda pannonica*) differed along the niche axes defined by SO_4^{2-}, Cl^-, CO_3^{2-}, or Ca^{2+}. In contrast, some halophytes (e.g. *Plantago tenuiflora* and *Pholiurus pannonicus*, or *Salicornia perennans* and *Suaeda prostrata*) shared similar positions and niche widths along all measured variables, indicating their common ecological position. Only a few species were indifferent (model type I) to most (seven or eight) variables (e.g. *Atriplex prostrata*, *Bromus commutatus*, and *Lepidium ruderale*) (Figures 2 and 3; Appendices S4–S7).

Across all variables, niche differentiation reflected by narrow niches (≤1/3 of the value range) was found for 44% of the species, with the highest shares of narrow niches related to SO_4^{2-} (59%) and SAR (52%). Narrow niches dominated at high values of the variable ranges except for Cl^-. However, few species were bound to these high positions (on average 17%), while 45% of the species had their niche entirely in the lowest third of the variable's ranges (Appendices S4–S6; a graphical summary of niche overlaps along all variables can be found in Appendix S8).

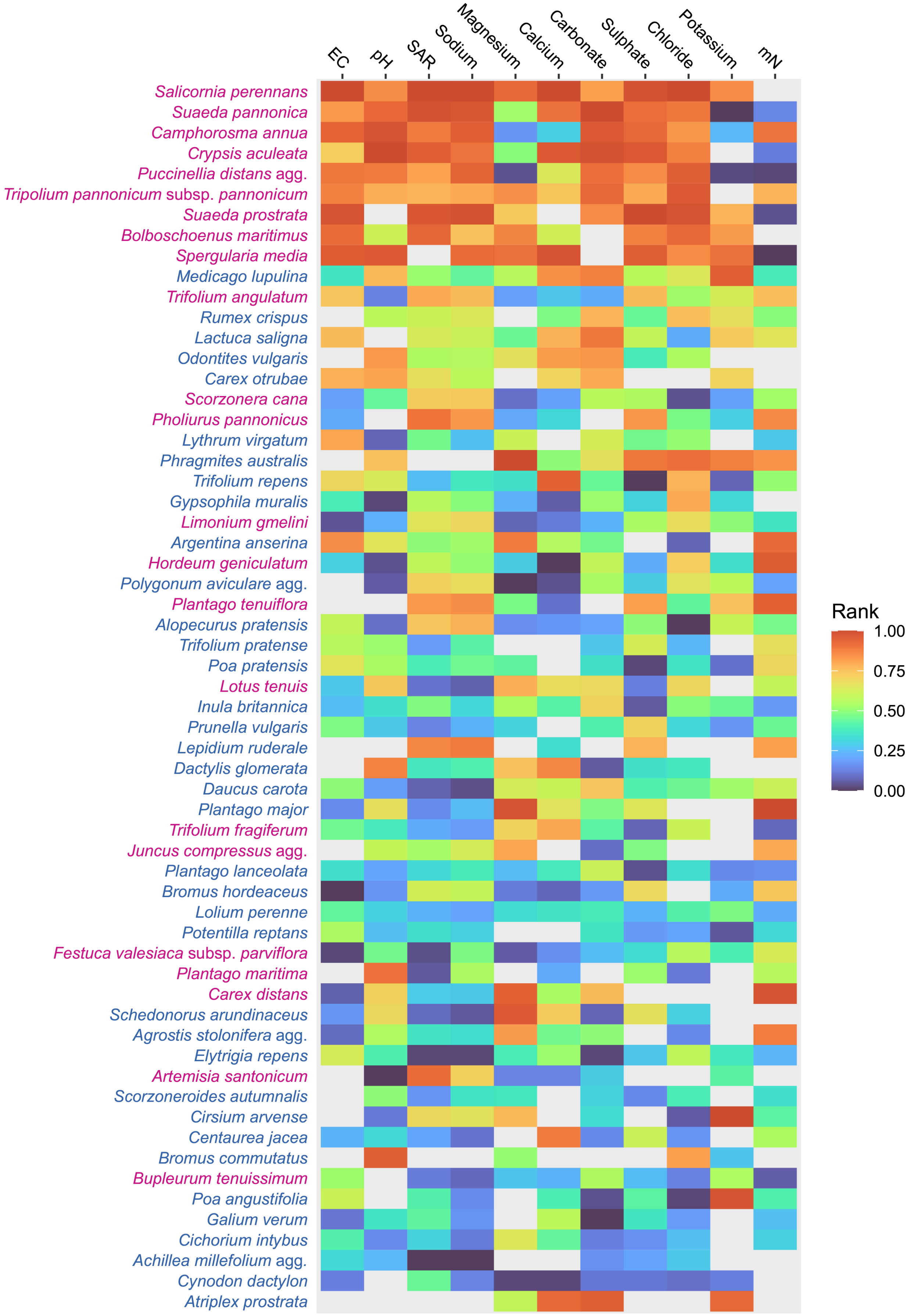
Across all variables, only 15% of the species showed skewed unimodal responses, most frequently to Mg^{2+} (25%) and least frequently to Cl^- (5%; Appendices S4 and S5). Instead, most of the observed responses were monotonic sigmoidal with optima (model type II, 31%) or with a plateau (model type III, broad optimum, 22%) at either end of the variable range. Across all variables, 17% of the species showed no response to any variable (model type I), mostly related to K^+ (40%), followed by EC (22%) and Ca^{2+} (22%; Appendices S4 and S5).

3.2 | Overall variance and importance of soil ions

Na^+ (26%), SO_4^{2-} (24%), Cl^- (22%), and CO_3^{2-} (14%) significantly contributed to the cumulative proportion of the variance explained by the first PCA axis (34%) and Mg^{2+} (37%), mN (24%), and Ca^{2+} (24%) contributed significantly to the second (20%) PCA axis. The third axis still explained 16% of the total variance, with the most significant contributions deriving from CO_3^{2-} (32%) and Ca^{2+} (21%), while the fourth axis explained 12%, with K^+ (67%) as the only variable providing a significant contribution (Appendix S3).

The best CCA model included all studied ions ($p < 0.001$), explaining 11% of the variance in the species composition matrix, which is 32% of what they could have explained according to the first eight CA axes. Ca^{2+}, Mg^{2+}, Na^+, Cl^-, CO_3^{2-} SO_4^{2-}, and mN were significantly correlated with the floristic gradient on the first and second CA and CCA axes, respectively. Additionally, Mg^{2+} and mN were significantly correlated with the third CCA axis. K^+ was significantly correlated with the second CA and third CCA axes but only with marginal significance ($p < 0.1$) with the third CA axis (function: *envfit*; correlation > |0.8|; $p < 0.01$; Figure 4; Appendix S3). We further validated the ions' importance as co-determinants of the studied salt-affected vegetation by finding a significant similarity between the ordination configurations of the CCA and the CA (Procrustes sum of squares: 0.32; correlation in Procrustes rotation: 0.825; Appendix S3).

FIGURE 2 Species niche rankings of 60 species, sorted by decreasing rank sums of Na^+ and CO_3^{2-} and the soil variables EC and pH, which correlate strongly with these ions. In each column, the colour scale refers to the species' position of the realized central niche and the optimum along each variable's range, spanning from dark blue (low niche position) to red (high niche position; Appendix S6). Species name colours indicate halophytes (pink) and associated species (blue). Species-variable combinations for which we had no information on niche position (HOF model type I with linear, flat response) are shown in light grey. EC, electrical conductivity; mN, mineral nitrogen; SAR, sodium adsorption ratio.


EC
pH
SAR
Sodium
Magnesium
Calcium
Carbonate
Sulphate
Chloride
Potassium
mN
Salicornia perennans
Suaeda pannonica
Camphorosma annua
Crypsis aculeata
Puccinellia distans agg.
Tripolium pannonicum subsp. pannonicum
Suaeda prostrata
Bolboschoenus maritimus
Spergularia media
Medicago lupulina
Trifolium angulatum
Rumex crispus
Lactuca saligna
Odontites vulgaris
Carex otrubae
Scorzonera cana
Pholiurus pannonicus
Lythrum virgatum
Phragmites australis
Trifolium repens
Gypsophila muralis
Limonium gmelini
Argentina anserina
Hordeum geniculatum
Polygonum aviculare agg.
Plantago tenuiflora
Alopecurus pratensis
Trifolium pratense
Poa pratensis
Lotus tenuis
Inula britannica
Prunella vulgaris
Lepidium ruderale
Dactylis glomerata
Daucus carota
Plantago major
Trifolium fragiferum
Juncus compressus agg.
Plantago lanceolata
Bromus hordeaceus
Lolium perenne
Potentilla reptans
Festuca valesiaca subsp. parviflora
Plantago maritima
Carex distans
Schedonorus arundinaceus
Agrostis stolonifera agg.
Elytrigia repens
Artemisia santonicum
Scorzoneroides autumnalis
Cirsium arvense
Centaurea jacea
Bromus commutatus
Bupleurum tenuissimum
Poa angustifolia
Galium verum
Cichorium intybus
Achillea millefolium agg.
Cynodon dactylon
Atriplex prostrata
Rank
1.00
0.75
0.50
0.25
0.00

3.3 | Importance of soil ions for individual species and species groups

Overall, PCA, CA, and RF analyses gave similar results, considering the first four RF ranks crucial for species occurrences. More specifically, across all 60 species of the studied saline habitats, Na^+ was significantly more important than all other variables for species occurrences, followed by SO_4^{2-}. In decreasing order but without significant differences, Cl^-, CO_3^{2-}, Ca^{2+}, Mg^{2+}, and mN were of medium importance, while K^+ was significantly less important than all other variables (Appendices S9 and S11).

Halophytes and associated species differed in their response to different ions. While the importance of ions for associated species remained consistent with the overall trend described above, it varied considerably for halophytes. Specifically, for halophytes, we found no significant difference in the importance of Na^+, SO_4^{2-}, Cl^-, CO_3^{2-}, Ca^{2+}, and Mg^{2+}, except for the significant difference between Na^+ (more important) and Mg^{2+} (less important). Remarkably, the importance of Na^+, SO_4^{2-}, and mN was significantly higher for associated species than for halophytes. By contrast, the importance of Cl^- and CO_3^{2-} was significantly higher for halophytes than for associated species (Figure 5; Appendix S11).

4 | DISCUSSION

Soil salinity is a well-known driver of plant species occurrence in saline environments (e.g. Dítě et al., 2017; Szabolcs, 1994; Tóth & Rajkai, 1994; Ungar, 1973; Volkmar et al., 1998). However, little is known about the effects of ion composition in saline soils (Álvarez Rogel et al., 2001; Iversen, 1936; Stevanović et al., 2010; Talat, 2020; Zlatković et al., 2019). Using a large dataset of fine-scale vegetation and topsoil data, our research provides new insights into the realized niches of 88 European plant species in relation to topsoil ions in the context of saline soils.

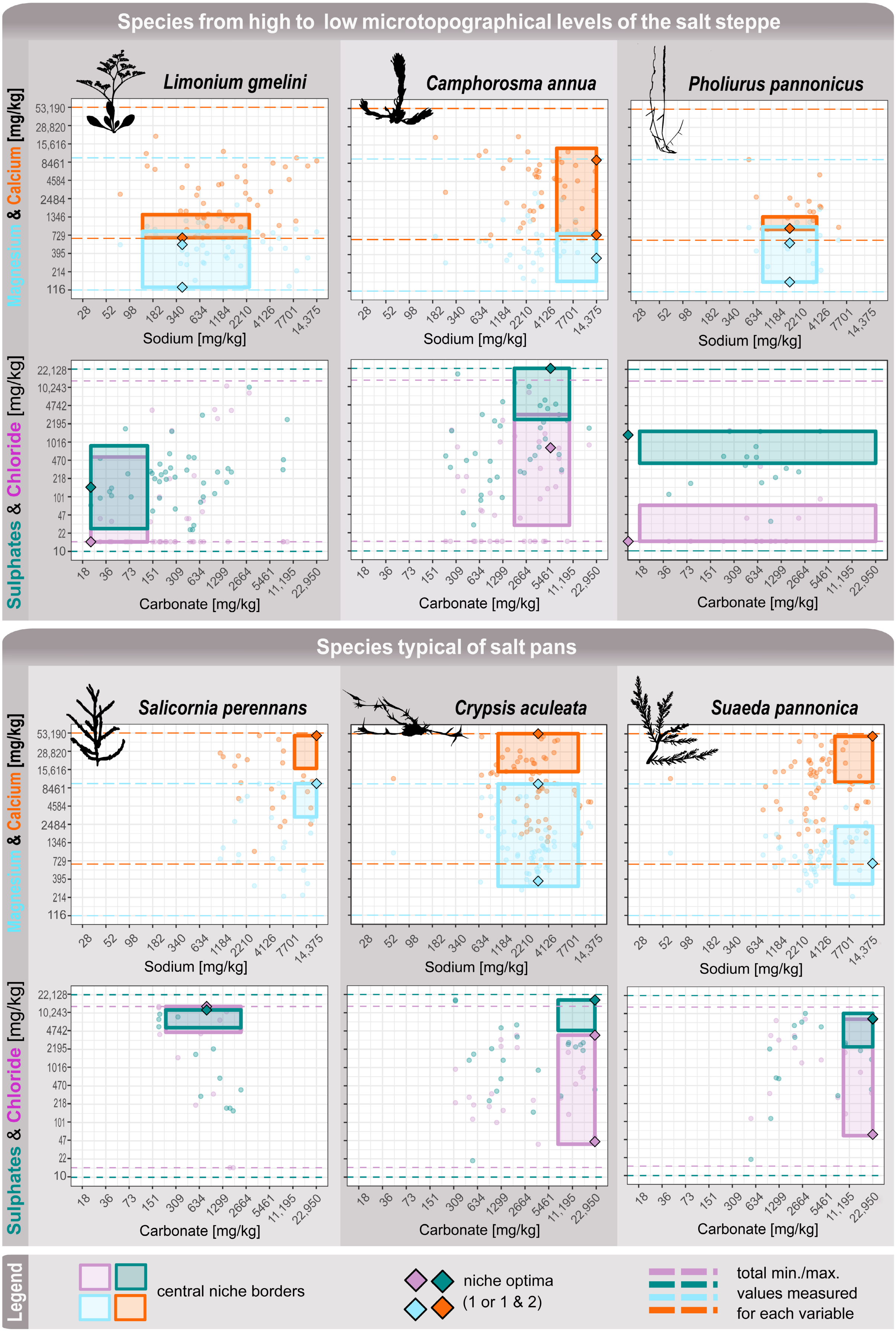
4.1 | Niche differentiation

Consistent with the literature (e.g. Chenchouni, 2017; Eliáš et al., 2020; Tóth & Rajkai, 1994; Zlatković et al., 2019), we found distinct differentiation of realized niches in halophytes and associated species along the soil salinity (EC) gradient. However, in line with our hypothesis, halophytes and associated species also differed in their realized niches in relation to concentration gradients of different soil ions. In addition to soil salinity, we showed that salt composition is important in structuring plant species occurrences in saline environments and shaping the realized niches of the plant species (Iversen, 1936). Our findings support previous research that found relations of divergent soil ions to vegetation types of salt-affected soils and their diagnostic species (Zlatković et al., 2019) and ion composition explaining plant zonation and distribution patterns in saline soils (Álvarez Rogel et al., 2000, 2001; Chenchouni, 2017).

For example, obligate halophytes occurring in severely to extremely saline soils displayed divergent niches with respect to individual ions (Figure 2; Appendices S4–S7 and S10). While *Salicornia perennans* and *Suaeda prostrata* occupy narrow niches at high Cl^- and low CO_3^{2-} values, *Suaeda pannonica* and *Crypsis aculeata* are indifferent to Cl^- and occur in CO_3^{2-}-rich soils. Other obligate halophytes, such as *Tripolium pannonicum* subsp. *pannonicum* and *Puccinellia distans* agg., occur in soils with a high content of both Cl^- and CO_3^{2-}. These results suggest different physiological adaptations to otherwise toxic ion levels that evolved in different lineages of halophytes growing in comparable saline conditions (Albert et al., 2020; Flowers & Colmer, 2015). Adaptations to high Cl^- concentrations often encompass Cl^- accumulation and succulence since excessive Cl^- could adversely affect a plant's metabolism (Breckle, 2004; Chaudhary, 2019; Leuschner & Ellenberg, 2017). Halophytes adapted to both high Cl^- and high CO_3^{2-} content tolerate more than one stress factor, that is, salinity and alkalinity (correlated with Cl^- and CO_3^{2-} contents, respectively; Appendix S3; Flowers & Colmer, 2015; Szabolcs, 1994).

Some obligate and most facultative halophytes and associated species of slightly to moderately saline habitats display broad niches in low-to-medium concentrations of ions contributing to salinity. However, their niches are set up differently in the multidimensional space. Additionally, many species display narrow niches for ions not contributing to salinity. They are generally less tolerant to increased Na^+ uptake into the plant tissue than obligate halophytes of extreme saline habitats (Hayward & Wadleigh, 1949). However, some tolerate high SARs (e.g. *Limonium gmelini* and *Trifolium angulatum*), causing physiological stress for the plant (Lesch & Suarez, 2009; Naidu & Rengasamy, 1993; Qadir & Schubert, 2002). High SAR values adversely affect plant growth directly due to Na^+-induced toxicity in the plant tissue. Indirect effects on plants occur through high SAR-induced soil structure degradation, like increased mechanical impedance, leading to decreased water infiltration and seasonal anaerobic conditions (Naidu & Rengasamy, 1993; Qadir & Schubert, 2002; Stevanović et al., 2010). However, some species with niches at higher SARs,

FIGURE 3 Two-dimensional niche plots of six selected species for cations (Na^+, Mg^{2+}, Ca^{2+}) and anions (CO_3^{2-}, SO_4^{2-}, Cl^-) that were correlated with the species composition matrix, contributed most to the variance in the soil data (PCA) and were most important for the occurrence of species (RF). *Limonium gmelini* grows at high microtopographical levels of the salt steppe, whereas *Camphorosma annua* and *Pholiurus pannonicus* grow at low levels. Two rhombs indicate a broad optimum (plateau, model type III). If no optimum is indicated, the species did not respond to the specific ions (HOF model type I with linear, flat response). Niche plots for all species studied can be found in Appendix S7.


Species from high to low microtopographical levels of the salt steppe
Limonium gmelini
Camphorosma annua
Pholiurus pannonicus
Magnesium & Calcium [mg/kg]
53,190
28,820
15,616
8461
4584
2484
1346
729
395
214
116
28
52
98
182
340
634
1184
2210
4126
7701
14,375
Sodium [mg/kg]
Sulphates & Chloride [mg/kg]
22,128
10,243
4742
2195
1016
470
218
101
47
22
10
18
36
73
151
309
634
1299
2664
5461
11,195
22,950
Carbonate [mg/kg]
Species typical of salt pans
Salicornia perennans
Crypsis aculeata
Suaeda pannonica
Legend
central niche borders
niche optima
(1 or 1 & 2)
total min./max.
values measured
for each variable

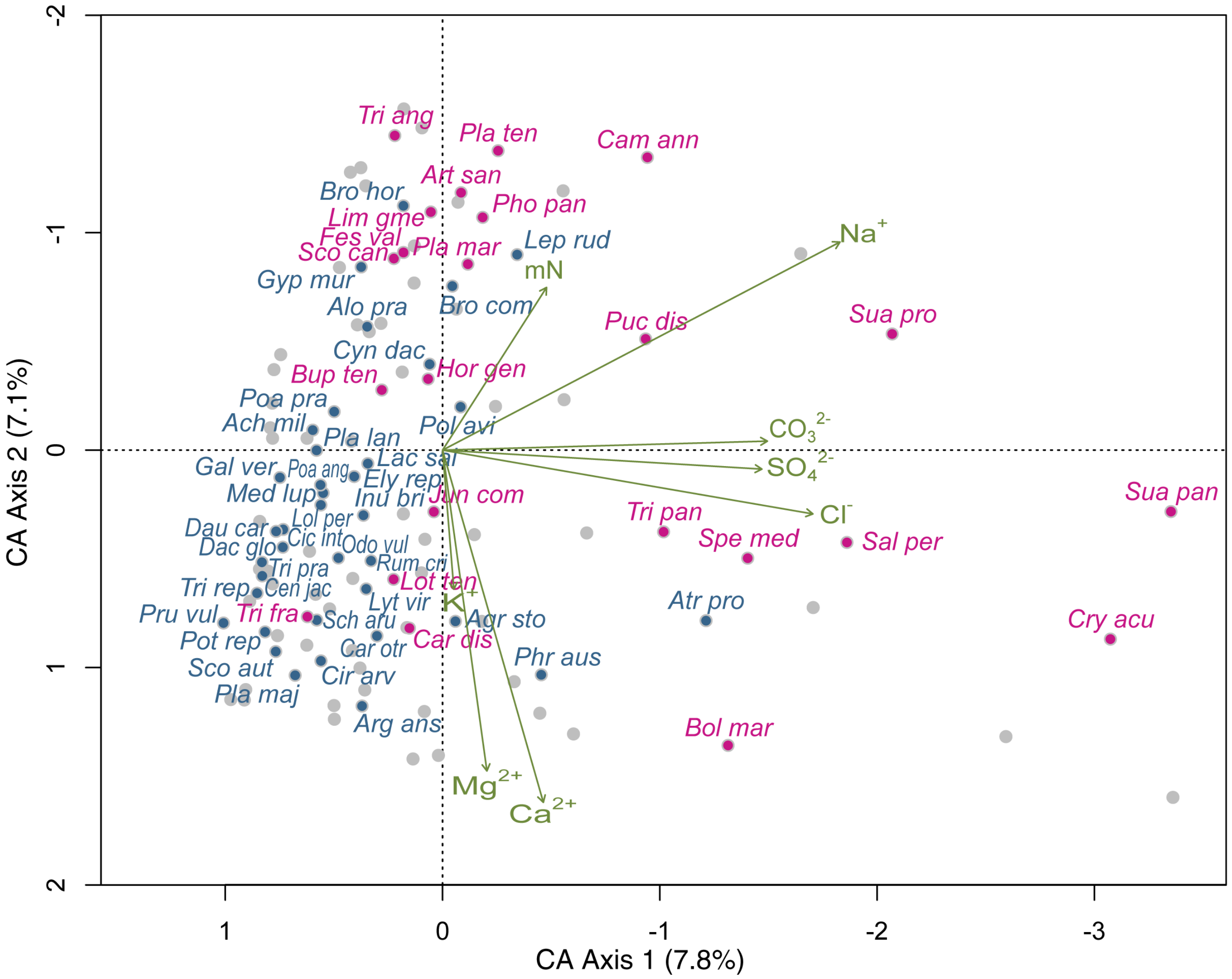


FIGURE 4 First and second CA axes based on all vegetation plots for which we had information on the studied ions (Ca^{2+}, K^+, Mg^{2+}, Na^+, Cl^-, CO_3^{2-}, SO_4^{2-}, and mN). Grey points indicate the species' positions in the ordination space. The labelled pink and blue points indicate the 60 species listed in Figure 2. The colours of species names indicate halophytes (pink) and associated species (blue). Variables were added post hoc. Eigenvalues: axis 1: 0.556, axis 2: 0.505. Labels: *Ach mil*, *Achillea millefolium* agg.; *Agr sto*, *Agrostis stolonifera*; *Alo pra*, *Alopecurus pratensis*; *Arg ans*, *Argentina anserina*; *Art san*, *Artemisia santonicum*; *Atr pro*, *Atriplex prostrata*; *Bol mar*, *Bolboschoenus maritimus*; *Bro com*, *Bromus commutatus*; *Bro hor*, *Bromus hordeaceus*; *Bup ten*, *Bupleurum tenuissimum*; *Cam ann*, *Camphorosma annua*; *Car dis*, *Carex distans*; *Car otr*, *Carex otrubae*; *Cen jac*, *Centaurea jacea*; *Cic int*, *Cichorium intybus*; *Cir arv*, *Cirsium arvense*; *Cry acu*, *Crypsis aculeata*; *Cyn dac*, *Cynodon dactylon*; *Dac glo*, *Dactylis glomerata*; *Dau car*, *Daucus carota*; *Ely rep*, *Elytrigia repens*; *Fes val*, *Festuca valesiaca* subsp. *parviflora*; *Gal ver*, *Galium verum*; *Gyp mur*, *Gypsophila muralis*; *Hor gen*, *Hordeum geniculatum*; *Inu bri*, *Inula britannica*; *Jun com*, *Juncus compressus* agg.; *Lac sal*, *Lactuca saligna*; *Lep rud*, *Lepidium ruderale*; *Lim gme*, *Limonium gmelini*; *Lol per*, *Lolium perenne*; *Lot ten*, *Lotus tenuis*; *Lyt vir*, *Lythrum virgatum*; *Med lup*, *Medicago lupulina*; *Odo vul*, *Odontites vulgaris*; *Pho pan*, *Pholiurus pannonicus*; *Phr aus*, *Phragmites australis*; *Pla lan*, *Plantago lanceolata*; *Pla maj*, *Plantago major*; *Pla mar*, *Plantago maritima*; *Pla ten*, *Plantago tenuiflora*; *Poa ang*, *Poa angustifolia*; *Poa pra*, *Poa pratensis*; *Pol avi*, *Polygonum aviculare* agg.; *Pot rep*, *Potentilla reptans*; *Pru vul*, *Prunella vulgaris*; *Puc dis*, *Puccinellia distans* agg.; *Rum cri*, *Rumex crispus*; *Sal per*, *Salicornia perennans*; *Sch aru*, *Schedonorus arundinaceus*; *Sco can*, *Scorzonera cana*; *Sco aut*, *Scorzoneroides autumnalis*; *Spe med*, *Spergularia media*; *Sua pan*, *Suaeda pannonica*; *Sua pro*, *Suaeda prostrata*; *Tri ang*, *Trifolium angulatum*; *Tri fra*, *Trifolium fragiferum*; *Tri pra*, *Trifolium pratense*; *Tri rep*, *Trifolium repens*; *Tri pan*, *Tripolium pannonicum* subsp. *pannonicum*.

for example, *Trifolium angulatum*, finish their life cycle in early summer, so they may be less affected during the wet spring season than indicated by our model results.

Surprisingly, some obligate halophytes display indifferent or broad (>2/3 of the variables' range) niches along the gradients of salinity and pH. For example, *Plantago tenuiflora* and *Pholiurus pannonicus* are indifferent or have broad niches along these gradients but occur where Na^+ and SO_4^{2-} values are intermediate. Therefore, their occurrences in saline vegetation are linked to their tolerance to a single or few ions whose concentration in the soil does not lead to extremely saline or highly alkaline conditions. Other obligate halophytes that are indifferent to salinity and occur outside saline sites indicate alkaline soils (Figure 2). Our results corroborate findings from earlier studies that found halophytes, such as *Plantago maritima*,

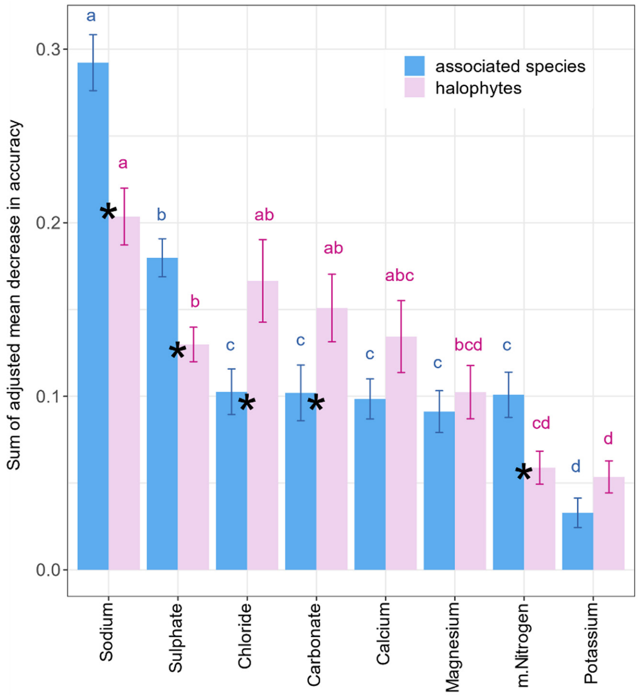


FIGURE 5 Importance of soil variables across halophytes (pink bars) and associated species (blue bars), given as the sum-normalized mean decrease in RF model accuracy. Error bars show the standard deviation. Blue and pink letters indicate significant differences across associated species and halophytes. Asterisks indicate significant differences between associated species and halophytes for each soil variable. Significant differences are based on a Friedman test with post hoc pairwise Wilcoxon tests (between variables) or Wilcoxon tests (between species groups separately for each variable).

to be widespread within salt-affected habitats from slightly to highly saline soils (Bernáldez & Rey Benayas, 1992) or in fens on high-pH soils rich in the cations Ca^{2+}, Na^{+}, Mg^{2+} and anions CO_3^{2-} and SO_4^{2-} (Hájek et al., 2006; Hájek, personal communication, 2023).

4.2 | Model responses

In line with Zlatković et al. (2019), our results do not indicate that shifts from symmetric to skewed species responses to environmental gradients are likely in environments shaped by extreme abiotic factors such as saline soils (Oksanen & Minchin, 2002a; Suchrow & Jensen, 2010). Skewed responses are mainly associated with variables uncorrelated to salinity (Mg^{2+} and mN), showing shifts of their mean towards low or high values. However, the skewed niche responses might be partially explained by stress. For example, the niche shifts towards low Mg^{2+} values might refer to physical stress in the plant tissue caused by high Mg^{2+} values that adversely affect the plant life cycle. However, high levels of Mg^{2+} might also be limited by the presence of Ca^{2+} or could alleviate salt stress caused by other ions (Chaudhary, 2019; Hayward & Wadleigh, 1949). Although skewed responses to EC or salinity-correlated variables are rare (5%–16%), those we observed are most common in associated species (70%) or halophytes of slightly saline sites (23%). Their right-skewed responses reflect a strong effect of stress in highly saline habitats.

Interspecific competition may also play a role in shaping realized niches (Pennings & Callaway, 1992), although it is considered minor in salt-affected habitats (Bonis et al., 2005; Cantero et al., 1998), where a few adapted halophytes gain an advantage over many associated species (Austin, 1980; Flowers & Colmer, 2015; Reimann & Breckle, 1995). For example, shifts to low mN values might be explained by the low competitive strength of some species (e.g. *Crypsis aculeata* and *Galium verum*), which are suppressed by strong competitors in N-rich soils. Other examples relate to obligate halophytes. They showed left-skewed responses towards (low values of) salinity-correlated variables (e.g. *Suaeda pannonica* to SO_4^{2-}), probably caused by increased interspecific competition with low stress (Oksanen & Minchin, 2002a; Santika & Hutchinson, 2009).

4.3 | Overall variance and importance of soil ions

The overall importance of soil ion concentration, notably of Na^{+}, SO_4^{2-}, Cl^{-}, CO_3^{2-}, Mg^{2+}, and Ca^{2+}, suggests that ions might be essential drivers of species distribution in salt-affected soils. The significant similarity between the ordination configurations of the CCA and the CA also supports this conclusion. However, we acknowledge that we examined correlations, which cannot prove causality but offered valuable information on potential drivers of species composition.

Other factors not accounted for in our study likely co-determine further variation in the species distribution. For example, judging from the species composition, soil water content, and duration of inundation, which are related to topography, may increase somewhat along the second axis of the CA-biplot shown in Figure 4. In addition, the variation in species composition might be co-determined by land-use or climatic-related variables (Danihelka et al., 2022; Eliáš et al., 2020).

Although ion concentration varies locally, the studied ions make up the most significant proportions of soluble ions in inland salt-affected soils. The ions' specific composition leads to low to extreme saline or alkaline soils. Some of the ions studied may alter soil conditions indirectly, for example, by limiting permeability for water or nutrient availability, which affects plant growth rather than the direct effect of ions on plant physiological processes (Appendix S3; e.g. Álvarez Rogel et al., 2001; Dítě et al., 2017; Naidu & Rengasamy, 1993).

Salinity and alkalinity both influence the occurrence of halophytes (Chenchouni, 2017). However, in agreement with Zlatković et al. (2019), we found that alkalinity (CO_3^{2-}) co-determines realized species niches somewhat independently of salinity. Like high Na^{+} concentrations, high soil pH can lead to nutrient deficiency and ion toxicity in plant tissues (Naidu & Rengasamy, 1993) and exclude species that cannot cope with stress and meet metabolic requirements (Albert et al., 2020). In addition, many plant species have broad fundamental pH niches. Therefore, the divergent pH niches of studied plants are probably related to the pH-induced alteration of soil nutrient availability.

4.4 | Importance of soil ions for individual species and species groups

Of the four ions best related to the floristic gradient and with the highest variance, we found Na^+ and SO_4^{2-} to be significantly more important than all other ions for all species and the associated species group alone. Associated species did not occur at high soil Na^+ and SO_4^{2-} concentrations (Appendix S10). Na^+ and SO_4^{2-} significantly impede water and nutrient uptake by accelerating the negative soil–water potential in the plant root zone, leading to increased osmotic stress (Albert et al., 2020; Leuschner & Ellenberg, 2017). In addition, the aforementioned adverse effect of Na^+ on the soil structure could further complicate the establishment and growth of associated species (Breckle, 2004; Naidu & Rengasamy, 1993; Qadir & Schubert, 2002). The limited tolerance of associated species to Na^+ can relate to the limited K^+, Mg^{2+}, or Ca^{2+} uptake, dysfunctions of cell processes, or adversely altered membrane or ion-channel structures caused by increased Na^+ uptake (Hayward & Wadleigh, 1949). Thus, increased Na^+ soil content relates to the transitions from non-halophytic to halophytic vegetation (Tóth & Rajkai, 1994). Many associated species are bound to low Na^+ and SO_4^{2-} soil content and slightly to moderately saline conditions. However, others, like the widely distributed graminoids *Schoenoplectus lacustris* subsp. *glaucus* and *Agrostis stolonifera*, occur where these ions reach relatively high levels (Iversen, 1936). The occurrence of associated species in more extreme edaphic conditions could be due to interspecific facilitation, which, in saline environments, may be more important for species not physiologically adapted to salinity than for halophytes (Pennings et al., 2003; Tanner et al., 2022).

The picture was different when considering only halophytes, for which many ions are a crucial predictor of occurrence. Although their physiological adaptations may somewhat mitigate nutrient deficiencies, halophytes are exposed to potential salt-induced physical damage and water and nutrient deficiencies, most notably in terms of Ca^{2+} and Mg^{2+} (Albert et al., 2020; Naidu & Rengasamy, 1993). mN shortage might also decrease the physiological capacity of halophytes to regulate the tolerance to salinity (Leuschner & Ellenberg, 2017). This link might explain why Ca^{2+}, Mg^{2+}, and mN co-determine the realized niches of halophytes to a similar degree as salinity-correlated ions (Figure 5). Additionally, our results can partly explain the niches of some halophytes in nutrient-rich soils with high amounts of Ca^{2+} and Mg^{2+} (Dítě et al., 2017).

5 | CONCLUSIONS

Our study revealed that, in addition to salinity, specific soil ions are highly correlated with species occurrences and composition in inland saline environments. Halophytes that grow under extremely to severely saline conditions may have evolved physiological adaptations that explain their distinct realized niches with respect to individual soil ions. Most associated species growing in slightly to moderately saline sites show divergent niches with respect to ions that do not contribute to salinity.

The evidence from our study suggests that information on the realized niches of plants along concentration gradients of essential ions is crucial for ecological research in inland salt-affected environments. In addition, visualization of realized niches in two-dimensional plots can inform regional botanists and conservationists and support decisions on conservation measures for (semi-)natural saline vegetation. However, our assessment of species niches is limited to salt-affected soils, which is essential to bear in mind for species not restricted to saline habitats.

Our study emphasizes that ecological research in salt-affected habitats should incorporate high-resolution soil data on ion composition. We argue that such data should be used, for example, when inspecting plant–soil interactions, evaluating species as indicators of soil quality, modelling species distribution in saline environments, or comparing niches across regions.

AUTHOR CONTRIBUTIONS

Ricarda Pätsch and Milan Chytrý conceived the idea and developed the study. Ricarda Pätsch, Zuzana Dítě, Daniel Dítě, Gabriele Midolo, Mirjana Ćuk, Jiří Danihelka, Zdenka Preislerová, Helena Chytrá, Hans Georg Stroh, and Milan Chytrý collected field data. Michal Pavonič and Ricarda Pätsch conducted the lab work. Ricarda Pätsch, Gabriele Midolo, Milan Chytrý, and Viktoria Wagner developed the graphs. Ricarda Pätsch led the writing of the manuscript with input from Milan Chytrý, Viktoria Wagner, Zuzana Dítě, Daniel Dítě, and Tibor Tóth, while all authors gave substantial feedback.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and R code accompanying this publication can be retrieved from the Zenodo repository https://doi.org/10.5281/zenodo.10650235.

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BIOSKETCH

Ricarda Pätsch is a vegetation ecologist interested in open landscapes, particularly lowland to mountain meadows and coastal and inland salt-affected vegetation in Europe and western to central North America. Her research focuses on plant community assembly, functional diversity patterns, and species niches in grasslands and meadows subjected to extreme and changing conditions. She frequently conducts field surveys and supplements her data with information from data repositories (https://ricardapaetsch.weebly.com/). The author team includes local botanists, experts in salt-affected flora and vegetation and soil analyses, soil scientists, and macro-ecologists.

SUPPORTING INFORMATION

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