UNIWERSYTET MIKOŁAJA KOPERNIKA W TORUNIU
WYDZIAŁ NAUK BIOLOGICZNYCH I WETERYNARYJNYCH

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Cechy funkcjonalne gatunków jako cecha zespołów roślinnych europejskich solnisk śródlądowych

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Spis treści

Streszczenie

Roślinność solnisk śródlądowych została uznana za cenną i unikalną w skali Europy, dlatego zgodnie z Dyrektywą Rady Europy 92/43/EWG z 1992 r. jest prawnie chroniona w ramach sieci Natura 2000. Jednak liczba stanowisk tego siedliska wciąż maleje, w konsekwencji umieszczono je na Europejskiej Czerwonej Liście Siedlisk. Istniejące programy ochrony odnoszą się do jednostek syntaksonomicznych roślinności. Dlatego skuteczna ochrona powinna bazować na jednolitym systemie syntaksonomicznym, opartym na danych z różnych lokalizacji europejskich. Taki system do tej pory nie powstał. Ponadto dotychczasowe strategie ochrony nie uwzględniają związku pomiędzy syntaksonomiczną i funkcjonalną koncepcją roślinności. W związku z tym, celem niniejszej rozprawy doktorskiej było w pierwszym kroku stworzenie ujednoliconego systemu klasyfikacji syntaksonomicznej roślinności europejskich solnisk śródlądowych klimatu umiarkowanego do poziomu zespołów oraz identyfikacja parametrów środowiskowych najważniejszych w różnicowaniu poszczególnych grup. W następnym kroku, celem było zidentyfikowanie cech funkcjonalnych charakterystycznych dla poszczególnych jednostek roślinnych i powiązanie tych cech z czynnikami środowiskowymi. W ostatnim kroku, celem była weryfikacja roli gatunków diagnostycznych w kształtowaniu cech funkcjonalnych jednostek syntaksonomicznych i uwzględnienie cech biochemicznych pomijanych dotychczas w ekologii roślinności. Hipoteza badawcza zakładała, że czynniki środowiskowe determinujące występowanie gatunków roślin w poszczególnych zbiorowiskach skutkują zróżnicowaniem cech funkcjonalnych, które mogą decydować o odrębności funkcjonowania poszczególnych jednostek syntaksonomicznych. W oparciu o dane literaturowe stworzono bazę zawierającą blisko 1000 zdjęć fitosocjologicznych, obejmującą główne obszary występowania solnisk śródlądowych na terenie Europy o klimacie umiarkowanym. Wykonano analizę klasyfikacji z wykorzystaniem metody Cocktail i systemu eksperckiego w celu wyróżnienia jednostek sytaksonomicznych roślinności, a następnie przeanalizowano zróżnicowanie występowania poszczególnych jednostek w gradiencie zmiennych środowiskowych. Dane dotyczące cech funkcjonalnych poszczególnych gatunków roślin uzyskano z istniejących baz danych CLO-PLA oraz LEDA Traitbase. Obliczono średnie cech funkcjonalnych dla poszczególnych płatów roślinnych ważone przez pokrycie gatunków. Następnie porównano średnie dla wyróżnionych wcześniej jednostek syntaksonomicznych. Do stworzenia modeli łączących cechy funkcjonalne z konkretnymi

klasami i zespołami roślinnymi oraz parametrami środowiskowymi posłużono się analizami numerycznymi. Rolę gatunków diagnostycznych w funkcjonowaniu zespołów roślinnych analizowano w oparciu o dane z baz oraz badań terenowych i labolatoryjnych gatunków uznanych za diagnostyczne dla typowych zespołów roślinności solniskowej. Wykonano pomiary morfometryczne zebranych roślin i analizy parametrów biochemicznych. W wyniku przeprowadzonych badań roślinność występującą na solniskach śródlądowych zaklasyfikowano do dziewięciu klas: *Ruppietea maritimae, Polygono-Poetea annuae, Artemisietea vulgaris, Potamogetonetea, Bidentetea, Phragmito-Magnocaricetea* i *Molinio-Arrhenatheretea*, w tym dwóch typowych dla solnisk – *Therosalicornietea* i *Festuco-Puccinellietea*. W obrębie tych dwóch klas wyróżniono dwa związki i łącznie pięć zespołów, tj.: *Salicornietum ramosissimae, Puccinellio-Spergularietum salinae, Triglochino maritimae-Glaucetum maritimae, Scorzonero parviflorae-Juncetum gerardii* i *Agrostio stoloniferae-Juncetum ranarii*. Klasy roślinności różniły się najbardziej pod względem preferencji gatunków co do zasolenia, wilgotności gleby, dostępności światła oraz zawartości azotu w podłożu, a zespoły solniskowe ponadto preferencjami co do odczynu oraz zawartości materii organicznej w glebie. Najważniejszymi cechami funkcjonalnymi odróżniającymi poszczególne klasy i zespoły roślinne były cechy związane z trwałością gatunków. Wartości tych cech były w większości negatywnie skorelowane z zasoleniem gleby, a pozytywnie z wilgotnością oraz zaprzestaniem użytkowania pastwiskowo-łąkarskiego. Klasy roślinności typowej dla solnisk wykazały najniższą zdolność do regeneracji, co wskazuje, że są najbardziej wrażliwe na zmiany środowiskowe. Za najbardziej wrażliwy zespół można uznać *Salicornietum ramosissimae*. Zespoły *Puccinellio-Spergularietum salinae* i *Agrostio stoloniferae-Juncetum ranarii* charakteryzowały się istotnie niższą stabilnością, ale większą zdolnością regeneracyjną. Zespoły *Triglochino maritimae-Glaucetum maritimae* i *Scorzonero parviflorae-Juncetum gerardii* cechowała niska zdolność regeneracyjna, ale drugi z nich odróżniał się istotnie większą stabilnością. Analizy cech biochemicznych pokazały, że zespoły typowe dla stanowisk o najwyższym zasoleniu podłoża charakteryzuje najlepsze przystosowanie do warunków abiotycznego stresu osmotycznego oraz oksydacyjnego. Uzyskane wyniki wskazują, że syntaksonomiczne jednostki roślinności solnisk mają znaczenie funkcjonalne. Gatunki diagnostyczne odgrywają kluczową rolę nie tylko w wyróżnianiu jednostek fitosocjologicznych, ale także w ich funkcjonowaniu. Dlatego należy zwrócić na nie uwagę przy planowaniu ochrony, w tym ochrony gatunkowej. Badania zrealizowane w ramach niniejszej pracy doktorskiej

wykazały ścisły związek pomiędzy syntaksonomiczną i funkcjonalną koncepcją roślinności, a ponadto wskazały cechy funkcjonalne zespołów roślinności solniskowej, które mogą być pomocne w planowaniu zrównoważonego zarządzania solniskami i odegrać istotną rolę w tworzeniu nowych strategii ich rekultywacji i ochrony.

Słowa kluczowe

biochemiczne cechy funkcjonalne roślin, cechy funkcjonalne, gatunki diagnostyczne, halofity, klasyfikacja syntaksonomiczna, metoda Cocktail, morfologiczne cechy funkcjonalne roślin, podejście Braun-Blanqueta, regeneracja, rozprzestrzenianie, trwałość, zasolenie

Abstract

The vegetation of inland salt marshes has been considered valuable and unique in Europe. Therefore, under the Council of Europe Directive 92/43/EEC of 1992, it is legally protected as part of the Natura 2000 network. However, the number of sites in this habitat is constantly decreasing, so they were placed on the European Red List of Habitats. Existing conservation programs refer to syntaxonomical units of vegetation. Therefore, effective protection should be based on a unified syntaxonomical system based on data from various European locations. Such a system has not been created yet. Moreover, existing conservation strategies do not consider the relationship between the syntaxonomical and functional concepts of vegetation. Therefore, in the first step, this doctoral dissertation aimed to create a unified syntaxonomical classification system of the European temperate inland salt marsh vegetation to the associations level and identify the environmental parameters most important in differentiating individual groups. The next step aimed to identify functional traits characteristic of individual plant units and link these traits with environmental factors. In the last step, the aim was to verify the role of diagnostic species in shaping the functional traits of syntaxonomical units and to consider biochemical traits previously omitted in vegetation ecology. The research hypothesis assumed that environmental factors determining the occurrence of plant species in individual communities result in differences in functional traits that may determine the distinctive functioning of individual syntaxonomical units. Based on literature data, a database containing nearly 1,000 phytosociological plots was created, covering the main areas of inland salt marshes in temperate Europe. Classification analysis was performed using the Cocktail method and an expert system to distinguish plant syntaxonomical units. Then, the occurrence of individual units in the gradient of environmental variables was analyzed. Data on the functional traits of individual plant species were obtained from the existing CLO-PLA and LEDA databases. Means of functional traits were calculated for individual plots, weighted by species cover. Then, the means for the previously distinguished syntaxonomical units were compared. Numerical analyzes were used to create models combining functional traits with particular plant classes and associations as well as environmental parameters. The role of diagnostic species in the functioning of plant associations was analyzed based on data from databases and field and laboratory research of species considered diagnostic for typical salt marsh associations. Morphometric measurements of the collected plants and analyzes of biochemical parameters were performed. As a result of the conducted research, the vegetation occurring on inland salt marshes was classified into nine classes: *Ruppietea maritimae*, *Polygono-Poetea annuae*, *Artemisietea vulgaris*, *Potamogetonetea*, *Bidentetea*, *Phragmito-Magnocaricetea*, and *Molinio-Arrhenatheretea*, including two classes typical of salt marshes – *Therosalicornietea* and *Festuco-Puccinellietea*. Within these two classes, two alliances and a total of five associations were distinguished, i.e., *Salicornietum ramosissimae*, *Puccinellio-Spergularietum salinae*, *Triglochino maritimae-Glaucetum maritimae*, *Scorzonero parviflorae-Juncetum gerardii* and *Agrostio stoloniferae-Juncetum ranarii*. Vegetation classes differed most in terms of species' preferences regarding salinity, soil moisture, light availability, and nitrogen content in the substrate, and the salt marsh associations also differed in preferences regarding pH and organic matter content in the soil. The most important functional traits distinguishing particular classes and associations were those related to the species’ persistence. The values of these traits were mostly negatively correlated with soil salinity and positively correlated with moisture and the cessation of mowing and grazing. Vegetation classes typical of salt marshes showed the lowest ability to regenerate, indicating that they are the most sensitive to environmental changes. *Salicornietum ramosissimae* can be considered the most sensitive association. The *Puccinellio-Spergularietum salinae* and *Agrostio stoloniferae-Juncetum ranarii* associations were characterized by significantly lower stability but higher regenerative capacity. The *Triglochino maritimae-Glaucetum maritimae* and *Scorzonero parviflorae-Juncetum gerardii* associations were characterized by low regenerative capacity, but the second was significantly more stable. Analyzes of biochemical traits showed that the best adaptation to abiotic osmotic and oxidative stress conditions characterizes the associations typical of sites with the highest soil salinity. The results indicate that syntaxonomical units of salt marsh vegetation are also functional. Diagnostic species play a key role in their functioning. Therefore, attention should be paid to them when planning protection, including the protection of species. The research demonstrated a close relationship between the syntaxonomical and functional concepts of vegetation. Also, it indicated the functional traits of salt marsh plant associations, which may be helpful in planning the sustainable management of salt marshes and play an important role in creating new strategies for their regeneration and protection.

Keywords

plants’ biochemical functional traits, functional traits, diagnostic species, halophytes, syntaxonomical classification, Cocktail method, plants’ morphological functional traits, Braun-Blanquet approach, regeneration, dispersability, persistence, salinity

1. Wstęp

Solniska śródlądowe na terenach Europy o klimacie umiarkowanym występują w sąsiedztwie wypiętrzonych przy powierzchni Ziemi złóż soli kamiennej oraz związanych z nimi słonych źródeł (Bank i Spitzenberg, 2001; Wilkoń-Michalska, 1963). Występują także na zasolonych obszarach przemysłowych związanych z działalnością przemysłu solnego, sodowego i potasowego (Garve i Garve, 2000; Karasińska i in., 2021). Zasiedlane są głównie przez gatunki roślin przystosowane do zasolenia podłoża, zwane halofitami (Flowers i Colmer, 2008; Piernik, 2021) oraz gatunki halotolerancyjne. Halofity są roślinami specyficznymi, ponieważ mogą przetrwać i wytworzyć nasiona w miejscach, gdzie stężenie soli sięga ok. 200 mM NaCl, a nawet więcej (Flowers i Colmer, 2008). Umiejętność tę posiada niespełna 0,2% roślin na całym świecie (Flowers i Colmer, 2015). Badania oraz dokumentacja roślinności solnisk w Europie prowadzone były od lat (np. Hayon, 1968; Lee, 1977; Wilkoń-Michalska, 1963) i proces ten trwa do dzisiaj (np. Lubińska-Mielińska i in., 2022; Piernik, 2012), gdyż stanowi ona niezaprzeczalnie ważny element lokalnej różnorodności biologicznej. Roślinność europejskich solnisk śródlądowych objęto ochroną prawną w ramach sieci Natura 2000 na mocy Dyrektywy Rady Europy 92/43/EWG (1992), ponieważ została uznana za cenną i unikatową w skali całego kontynentu. Poza ochroną międzynarodową w poszczególnych państwach funkcjonują również inne formy ochrony tego siedliska takie jak polskie rezerwaty przyrody, np. rezerwat halofitów w Ciechocinku lub rezerwat halofitów w Owczarach koło Buska Zdroju (Lubińska-Mielińska i in., 2022; Wilkoń-Michalska, 1970). Obecnie ochrona naturalnej różnorodności biologicznej roślinności słonolubnej nabiera coraz większego znaczenia. Ze względu na ocieplenie klimatu narasta problem suszy na świecie, a co za tym idzie wzmaga się również globalny problem zwiększania powierzchni gleb zasolonych w rolnictwie (FAO, 2021). Dodatkowo, szybko rosnąca populacja ludzka wpływa na wzrost zapotrzebowania na żywność (Tripathi i in., 2019). W tym kontekście solniska mogą służyć przyszłemu rolnictwu zarówno jako źródło gatunków uprawnych i pastewnych naturalnie tolerujących wysokie stężenia soli, a także do modyfikacji konwencjonalnych upraw jako źródło genów odporności na zasolenie (Cárdenas-Pérez i in., 2021; Cuevas i in., 2019). Pomimo długoterminowej prawnej ochrony liczba stanowisk tego typu roślinności wciąż maleje. Z tego powodu śródlądowe solniska umieszczono na aktualnej Europejskiej Czerwonej Liście Siedlisk jako zagrożone (Janssen i in., 2016).

Koncepcja ochrony solnik śródlądowych w Europie zarówno w ramach ochrony rezerwatowej, jak i ochrony siedlisk w ramach sieci Natura 2000 odnosi się do roślinności jako jednostek syntaksonomicznych (Komisja Europejska, 2013; Nienartowicz i Piernik, 2004a, 2004b). Niestety, istnieje luka w obecnym systemie klasyfikacji roślinności solnisk śródlądowych (Mucina i in., 2016). W praktyce mimo, że często są to te same lub podobne zbiorowiska, to każdy kraj, a nawet poszczególni autorzy posługują się własną nomenklaturą, sposobem ich rozróżniania czy podziału. W najnowszej syntezie na temat roślinności Europy Mucina i in. (2016) zintegrowali jednostki proponowane od lat przez badaczy europejskiej roślinności i zaprezentowali kompleksowy system klasyfikacji syntaksonomicznej oparty na podejściu Braun-Blanqueta (Braun-Blanquet, 1964). Jednak synteza Muciny i in. (2016) porządkuje roślinność jedynie do poziomu związków. W tym systemie roślinność solnisk śródlądowych została zaklasyfikowana do dwóch klas: *Therosalicornietea* Tx. in Tx. et Oberd. 1958 (THE) i *Festuco-Puccinellietea* Soó ex Vicherek 1973 (FEP). Klasa THE, w rzędzie *Therosalicornietalia* Pignatti 1952 i związku *Salicornion ramosissimae* Tx. 1974 obejmuje pionierską roślinność jednorocznych halofitów o charakterze sukulentów. Natomiast klasa FEP w rzędzie *Scorzonero-Juncetalia gerardi* Vicherek 1973 i związku *Juncion gerardi* Wendelberger 1943 obejmuje zasolone tereny regularnie zalewanych łąk i pastwisk południowo-wschodniej Europy Środkowej. Zatem, aby dokonać analizy roślinności europejskich solnisk śródlądowych na poziomie zespołów, należy odwoływać się do starszych propozycji klasyfikacji roślinności, które często mają zasięg lokalny lub krajowy jak np. szczegółowo porównane przez Piernik (2021) klasyfikacje Matuszkiewicza (2017) dla Polski i Potta (1992) dla Niemiec. Badania ostatnich lat pokazują, że obecnie konieczne jest ujednolicanie oraz rozpowszechnianie zaktualizowanych systemów klasyfikacji roślinności (np. Bergmeier, 2020; Danihelka i in., 2022). Nadal brakuje jednak usystematyzowanej klasyfikacji roślinności solnisk śródlądowych w skali całej Europy o klimacie umiarkowanym. Tylko niewielka część z nich została ostatnio przeanalizowana na podstawie danych z Niziny Północnoniemieckiej przez Dítě i in. (2022).

Dodatkowo ciągle brak uogólnień dotyczących wymagań środowiskowych poszczególnych jednostek syntaksonomicznych. Warto podkreślić, że charakterystyczne dla solnisk gatunki halofilne uznano za czułe wskaźniki nie tylko zasolenia, ale także związanej z nim wilgotności gleby (Piernik, 2003a, 2012). Ponadto badania wykazały, że halofity są organizmami niezwykle światłożądnymi, dlatego najlepiej radzą sobie na otwartych, nasłonecznionych przestrzeniach (Wilkoń-Michalska, 1962, 1970). Jedynie nieliczni badacze analizowali właściwości gleby w całych płatach roślinnych solnisk, a następnie badali relacje pomiędzy występowaniem gatunków a parametrami środowiska (np. Piernik, 2005, 2012; Piernik i in., 1996; Wilkoń-Michalska, 1963, 1970). Ich badania często grupowały płaty roślinności ze względu na dominację gatunkową (np. Piernik, 2003a, 2003b; Piernik i in., 2015), a tylko niektóre z nich odnosiły się do zespołów roślinnych w sensie podejścia Braun-Blanqueta (np. Wilkoń-Michalska, 1963, 1970; Zlatković i in., 2019).

Dotychczasowe strategie ochrony roślinności solnisk śródlądowych, odnoszące się do wybranych jednostek syntaksonomicznych, nie uwzględniają związku pomiędzy syntaksonomiczną i funkcjonalną koncepcją roślinności (np. Nienartowicz i Piernik, 2004a, 2004b). Tymczasem podejście oparte na cechach funkcjonalnych ma kluczowe znaczenie dla zrozumienia funkcjonowania syntaksonów i w konsekwencji może umożliwić ocenę ich kondycji oraz zapewnić trwałość poprzez skuteczniejszą ochronę. Podejście funkcjonalne może pomóc w zrozumieniu procesów ekologicznych, takich jak tworzenie i stabilność zespołów oraz sukcesja, a także ułatwić wykrywanie i przewidywanie reakcji na zmiany środowiskowe w różnej skali (Duckworth i in., 2000). Trwa ciągły postęp w ekologii, która stara się odpowiedzieć na problemy globalne poprzez uwzględnianie cech funkcjonalnych poszczególnych gatunków w badaniach makroekologicznych, aby lepiej zrozumieć funkcjonowanie całych ekosystemów (He i in., 2019). W tym kontekście można połączyć podejście syntaksonomiczne i funkcjonalne. Funkcjonalne podejście do roślinności opiera się na koncepcji istnienia cech funkcjonalnych poszczególnych roślin. Według Violle i in. (2007) cechy funkcjonalne to np. cechy morfologiczne, biochemiczne, fizjologiczne, strukturalne czy fenologiczne, które można zmierzyć na poziomie osobniczym od komórki po cały organizm bez powiązania ich ze środowiskiem lub jakimkolwiek innym poziomem organizacji. Cechami funkcjonalnymi są wszystkie cechy, które mogą wpływać na kondycję roślin, w tym na ich wzrost, rozmnażanie lub przeżycie. Cechy funkcjonalne odzwierciedlają strategie życiowe, a tym samym określają, w jaki sposób rośliny reagują na warunki środowiskowe, w tym determinują ich zdolność pozyskiwania zasobów oraz reagowania na konkurencję i stres siedliskowy, czyli niekorzystne warunki środowiskowe ograniczające wzrost biomasy. Przykładowo wysokość rośliny ma kluczowe znaczenie dla jej zdolności do konkurowania o światło, parametry nasion dla ich zdolności do kolonizacji różnych siedlisk, a stosunek powierzchni liścia do jego masy w optymalizacji efektywności fotosyntezy (Goldstein, 2018). Istnieje pogląd, że rośliny wykazują określone strategie życiowe, aby jak najskuteczniej radzić sobie w warunkach, w jakich żyją. Niektóre cechy morfologiczne pozwalają na ocenę specyficznych warunków siedliskowych, na które wystawione były konkretne rośliny (Adler i in., 2014; Cárdenas-Pérez i in., 2022b). W ostatnich latach często zainteresowanie budzi wpływ stresu na cechy roślin (Cárdenas-Pérez i in., 2022a, 2022b; Ludwiczak i in., 2023; Schöb i in., 2013). Zbiorowiska solnisk narażone są głównie na abiotyczny stres generowany przez wysoki poziom zasolenia gleby. Jak wspomniano powyżej, w ich skład wchodzą m.in. halofity, które wytworzyły liczne adaptacje do funkcjonowania w takich warunkach (Duarte i in., 2014; Grigore i in., 2012; Grigore i Toma, 2017; Hamed i in., 2013; Yuan i in., 2019). Wykształcone przystosowania wpływają na specyfikę cech funkcjonalnych tych gatunków. Można sądzić, że skoro każdy gatunek ma zespół cech, które go charakteryzują, to także każde zbiorowisko roślinne składające się z określonych gatunków ma swój charakterystyczny zestaw cech funkcjonalnych. Nadal jednak niewiele jest informacji na temat zmienności cech funkcjonalnych zbiorowisk roślinnych pod wpływem czynników środowiskowych (Albert, 2010; Kambach i in. 2023; Ulrich i in., 2018). Jedynie w pojedynczych pracach wykorzystuje się cechy funkcjonale gatunków do porównywania jednostek syntaksonomicznych całej roślinności (Lengyel i in., 2020) lub porównuje się jednostki na podstawie cech gatunków charakterystycznych (Ladouceur i in., 2019). Roślinność solnisk śródlądowych w Europie nie została dotychczas szczegółowo opisana w kontekście funkcjonalnym. W niewielu pracach analizowano adaptacje cech funkcjonalnych roślin na obszarach zasolonych (np. Guo i in., 2015; Matinzadeh i in., 2022; Minden i in., 2012; Minden i Kleyer, 2015; Ulrich i in. 2019). Ponadto w żadnej z nich nie uwzględniono cech biochemicznych związanych z reakcjami roślinności na stres solny.

Gatunki roślin, które najskuteczniej wyrażają określone zależności ekologiczne w obrębie danego zbiorowiska, wykorzystywane są jako wskaźniki i nazywane są gatunkami diagnostycznymi (Dg; Braun-Blanquet, 1964). Charakterystyczna kombinacja gatunków Dg służy do tworzenia hierarchicznego systemu klasyfikacji syntaksonomicznej. System ten jest konsekwentnie rozwijany i rozszerzany w oparciu o zasadę maksymalnego podobieństwa florystycznego i ekologicznego, którego podstawową jednostką jest zespół (Westhoff i van der Maarel, 1978). W rzeczywistości identyfikacja poszczególnych zbiorowisk jest uzależniona od obecności lub braku gatunków roślin uznanych za Dg (Barkman i in., 1995). Postęp technologiczny wprowadził specjalistyczne oprogramowanie, takie jak JUICE (Tichý, 2002), służące do porządkowania zbiorów zdjęć fitosocjologicznych, co pomogło w analizie dużych baz danych i przyspieszyło tworzenie ujednoliconych klasyfikacji roślinności dużych obszarów, jak np. wspomniana już klasyfikacja roślinności Europy do poziomu związków stworzona przez Mucinę i in. (2016). Wykorzystanie specjalistycznego oprogramowania gwarantuje, że decyzje dotyczące kryteriów tworzonych klasyfikacji opierają się na rygorze statystycznym, zwiększając ogólną wiarygodność tego procesu (Tichý, 2002). Tego typu badania roślinności opierają się na danych pochodzących z dużych baz, obejmują wszystkie odnotowane gatunki i skupiają się na syntaksonomicznym ujęciu roślinności, nadając tym samym gatunkom Dg funkcję wskaźników fitosocjologicznych. Do dziś nie zbadano jednak czy gatunki Dg mają też istotne znaczenie funkcjonalne dla jednostek, które charakteryzują pod względem syntaksonomicznym. Być może gatunki Dg jako istotne dla zespołów roślinnych, które reprezentują ze względu na swoją wysoką wierność, procent pokrycia oraz frekwencję wpływają decydująco na ich funkcjonowanie poprzez swoje charakterystyczne kombinacje cech. Skoncentrowanie się na tych najważniejszych gatunkach może przynieść istotne informacje o funkcjonowaniu analizowanej roślinności, a przez to wpłynąć na skuteczniejszą ochronę całych siedlisk, które reprezentują.

Niniejsza rozprawa doktorska odpowiada na luki istniejące w dotychczasowym stanie wiedzy odnośnie jednostek syntaksonomicznych roślinności występującej na solniskach śródlądowych, wymagań środowiskowych tych jednostek, cech funkcjonalnych charakterystycznych dla poszczególnych syntaksonów oraz roli gatunków Dg w ich funkcjonowaniu. Wyniki badań przedstawiono w trzech artykułach naukowych, w tym dwóch manuskryptach złożonych w redakcjach indeksowanych czasopism naukowych.

2. Hipoteza badawcza i cele pracy

Hipoteza badawcza przyjęta w niniejszej pracy doktorskiej zakłada, że czynniki środowiskowe determinujące występowanie gatunków roślin w poszczególnych zbiorowiskach roślinnych europejskich solnisk śródlądowych klimatu umiarkowanego skutkują zróżnicowaniem cech funkcjonalnych, które mogą decydować o odrębności funkcjonowania poszczególnych jednostek syntaksonomicznych. Założono zatem, że każdy syntakson posiada pakiet specyficznych cech o podobnych parametrach, które go charakteryzują.

Celem pracy było w pierwszej kolejności stworzenie ujednoliconego systemu klasyfikacji syntaksonomicznej roślinności europejskich solnisk śródlądowych klimatu umiarkowanego oraz ustalenie wymagań środowiskowych poszczególnych jednostek. Polegało to na: (1) identyfikacji klas roślinności występujących na terenie europejskich solnisk śródlądowych klimatu umiarkowanego, (2) klasyfikacji roślinności klas typowych dla solnisk do poziomu zespołów, (3) ustaleniu listy gatunków Dg poszczególnych zespołów, (4) znalezieniu głównych zmiennych środowiskowych wpływających na zróżnicowanie analizowanej roślinności na poziomie klas i zespołów. Realizację wymienionych powyżej zamierzeń zaplanowano w ramach pierwszego artykułu, w którym przetestowano pierwszą część hipotezy o zależności jednostek syntaksonomicznych od wymagań środowiskowych.

Kolejnym celem było zidentyfikowanie cech funkcjonalnych charakterystycznych dla poszczególnych jednostek roślinnych i powiązanie tych cech z czynnikami środowiskowymi. Wymagało to zastosowania nowego podejścia w badaniach syntaksonomicznych, opartego na cechach funkcjonalnych gatunków roślin. Wykorzystano średnie cech funkcjonalnych ważonych przez pokrycie gatunków w płacie. Prace polegały na: (1) identyfikacji cech funkcjonalnych różnicujących poszczególne klasy i zespoły roślinne oraz (2) znalezieniu zależności tych cech od czynników środowiskowych. Realizację tych zadań zaplanowano w ramach drugiego artykułu, w którym przetestowano drugą część hipotezy o odrębności poszczególnych jednostek roślinności ze względu na charakterystyczne zbiory ich cech funkcjonalnych.

Ostatnim celem była weryfikacja roli gatunków Dg w kształtowaniu cech funkcjonalnych jednostek syntaksonomicznych i uwzględnienie cech biochemicznych pomijanych dotychczas w ekologii roślinności. Prace polegały na: (1) określeniu zróżnicowania cech morfologiczych i biochemicznych (niedostępnych w bazach cech funkcjonalnych) gatunków Dg typowych zespołów solniskowych oraz (2) ustaleniu roli gatunków Dg dla funkcjonowania tych jednostek. Do analiz wybrano trzy najliczniejsze w Polsce zespoły typowe dla solnisk i w oparciu o ustaloną listę gatunków Dg zmierzono ich cechy funkcjonalne. Realizację wymienionych celów podjęto w ramach przygotowania trzeciego artykułu. W tej części badań przetestowano drugą część hipotezy badawczej, o determinacji funkcjonowania poszczególnych jednostek syntaksonomicznych przez zestawy ich cech funkcjonalnych, ale w oparciu jedynie o gatunki Dg i typowe zespoły solniskowe.

3. Materiały i metody

3.1. Dane

3.1.1. Baza zdjęć fitosocjologicznych

Na podstawie źródeł literaturowych stworzono bazę i ostatecznie, po weryfikacji pod kątem źródła zasolenia, analizie poddano 968 zdjęć fitosocjologicznych wykonanych metodą Braun-Blanqueta (Braun-Blanquet, 1964), które pochodzą z terenu sześciu krajów Europy Środkowej i Północno-Zachodniej: Polski, Niemiec, Czech, Francji, Wielkiej Brytanii i Luksemburga. Dane reprezentują całe spektrum występowania solnisk śródlądowych w Europie w strefie klimatu umiarkowanego. Łącznie w bazie odnotowano 426 roślin naczyniowych (w tym oznaczone jedynie nazwą rodzajową), których nazewnictwo ujednolicono za pomocą World Flora Online (World Flora Online, 2020) i EuroMedPlant (Euro+Med, 2006+). Wykorzystano portal Google Earth (google.com/intl/pl/earth/), aby do poszczególnych zdjęć przypisać przybliżone współrzędne geograficzne na podstawie danych o miejscu ich wykonania, jeśli nie były podane w źródłach. Do analiz roślinności konieczna była transformacja danych dotyczących pokrycia gatunków ze skali Braun-Blanqueta (Braun-Blanquet, 1964) na skalę porządkową van der Maarela (van der Maarel, 2007) w następujący sposób: r → 1, + → 2, 1 → 3, 2 → 5, 3 → 7, 4 → 8, 5 → 9.

3.1.2. Parametry środowiskowe

Dane dotyczące parametrów glebowych oraz sposobu użytkowania gruntów w miejscu wykonywania zdjęć fitosocjologicznych, jeżeli były dostępne, pochodziły z publikacji źródłowych w oparciu, o które powstała baza (np. Piernik, 2012). W pracy wykorzystano informacje odnoszące się do: zasolenia wyrażonego jako przewodność elektrolityczna ekstraktu nasyconego (EC_e), wilgotności, pH, zawartości materii organicznej oraz azotu ogólnego (N_{tot}), a także informacje o kategoriach użytkowania gruntów: 1) tereny nieużytkowane (zaprzestanie koszenia i wypasu), 2) pola uprawne, 3) tereny przemysłowe, 4) łąki kośne lub pastwiska.

Ze względu na brak danych literaturowych dla większości zdjęć, jako oszacowane parametry środowiskowe wykorzystano średnie ważone obliczone na podstawie liczb wskaźnikowych Ellenberga (EIV – Ellenberg Indicator Values; Ellenberg i in., 1992).

W tym celu użyto sześciu wskaźników: dostępność światła (L), temperatura (T), wilgotność (M), odczyn/kwasowość gleby (R), zawartość azotu/trofia (N) i zasolenie (S).

3.1.3. Cechy funkcjonalne

Dane dotyczące cech funkcjonalnych gatunków uzyskano z baz internetowych, w tym informacje o klonalności (C) i indeksie klonalności (CI) z bazy CLO-PLA (Klimešová i in., 2017), a informacje o pozostałych 10 cechach z bazy LEDA Traitbase (Kleyer i in., 2008). Wybrano te właśnie bazy, ponieważ zgromadzone w nich dane pochodzą z pomiarów roślin zebranych z obszaru pokrywającego się z terenem badań. W sumie wykorzystano dane dotyczące 12 cech odpowiedzialnych za trzy różne funkcje u roślin według koncepcji Kleyer'a i in. (2008), tj. trwałość – powierzchnia liścia (LA), masa liścia (LM), wysokość rośliny (CH), powierzchnia właściwa liścia (SLA), zawartość suchej masy w liściu (LDMC), a także wspomniane CI i C; regeneracja – masa nasion (SM), liczba nasion (SN), liczba nasion na pęd (SNPS) i zdolność do rozprzestrzeniania – wysokość uwalniania (RH), prędkość końcowa (TV). W oparciu o dane dotyczące tych cech dla poszczególnych gatunków, obliczono średnie ważone przez pokrycie gatunków w płacie dla każdego zdjęcia fitosocjologicznego. Jak wspomniano powyżej, w badaniach przyjęto koncepcję zaproponowaną przez Kleyer'a i in. (2008), którzy skupili się na trzech głównych kategoriach funkcji poszczególnych cech u roślin. Jednak ramy przynależności cech funkcjonalnych do tych kategorii nie są sztywne, ponieważ pewne cechy mogą odpowiadać za różne bardziej szczegółowo ujęte funkcje u roślin. Zdecydowano się przeanalizować cechy związane z liśćmi, wysokością roślin i nasionami, ponieważ według Westoby'ego (1998) strategia LHS (z angl. leaf-height-seed) reprezentuje główny wymiar zmienności roślin wzdłuż najbardziej typowych gradientów ekologicznych. Pod uwagę wzięto także cechy związane z klonalnością roślin, ponieważ są one odpowiedzialne za adaptację roślin do zaburzeń środowiskowych (Klimešová i in., 2016).

Na podstawie własnych pomiarów laboratoryjnych z użyciem okazów zebranych w terenie zgromadzono również dane dotyczące morfologicznych i biochemicznych cech funkcjonalnych łącznie dziewięciu gatunków uznanych w wyniku pierwszej części badań za Dg dla trzech zespołów roślinnych typowych na solniskach śródlądowych, tj. *Salicornietum ramosissimae* (*Sr*), *Puccinellio-Spergularietum salinae* (*P-Ss*), *Triglochino maritimae-Glaucetum maritimae* (*Tm-Gm*). Gatunkami tymi były: *Salicornia europaea* L., *Triglochin maritima* L., *Glaux maritima* L. (= *Lysimachia maritima* (L.) Galasso, Banfi & Soldano), *Phragmites australis* (Cav.) Steud., *Juncus compressus*

Jacq., *Potentilla anserina* L., *Spergularia marina* (L.) Besser, *Puccinellia distans* (Jacq.) Parl. i *Atriplex prostrata* Boucher ex DC. Próbki roślin zebrano na solnisku położonym w Inowrocławiu, gdzie występują wszystkie trzy analizowane zespoły. Ponadto na jego terenie od lat utrzymuje się stabilny, bardzo wysoki poziom zasolenia gleby powyżej 16 $dS \cdot m^{-1}$ (Kalwasińska i in, 2023; Piernik i in., 1996, 2015), który w okresie pobierania próbek wynosił ok. 36 $dS \cdot m^{-1}$. Pod uwagę wzięto następujące parametry morfologiczne: długość pędu i korzenia (SL i RL), liczba liści (NoL), świeża i sucha masa pędów (SFW i SDW), świeża i sucha masa korzeni (RFW i RDW), świeża i sucha masa liści (LFW i LDW), masa pojedynczego liścia (LM), powierzchnia liści (LA) i powierzchnia asymilacyjna (AA). Pomiary wykonano na 10 okazach z każdego gatunku. Na podstawie zmierzonych parametrów obliczono pięć wskaźników wzrostu: wskaźnik masy pędów (SWR), wskaźnik masy korzeni (RWR), wskaźnik masy liści (LWR), zawartość suchej masy w liściu (LDMC) oraz powierzchnię właściwą liścia (SLA). Wykonano również analizę parametrów biochemicznych, w tym: zawartości barwników fotosyntetycznych – chlorofilu a (chla), b (chlb) i całkowitego (chlt) oraz karotenoidów (car); zawartości substancji o działaniu osmoregulacyjnym – proliny i węglowodanów; zawartości substancji stanowiących wskaźniki stresu – nadtlenku wodoru (H_2O_2) i dialdehydu malonowego (MDA); aktywności enzymów antyoksydacyjnych – katalazy (CAT) i peroksydazy askorbinianowej (APX). Materiał roślinny poddany analizom biochemicznym stanowiły próbki liści poszczególnych gatunków. Dokładne procedury pobrania próbek materiału roślinnego, mierzenia cech morfologicznych oraz analiz biochemicznych zostały opisane w załączonej publikacji drugiej (manuskrypt). Dla trzech gatunków objętych w Polsce ochroną, tj. *S. europaea*, *T. maritima* i *G. maritima* (*L. maritima*) badania przeprowadzono za zgodą Regionalnego Dyrektora Ochrony Środowiska w Bygoszczy (WOP.6400.9.2023.MWK).

3.2. Analizy statystyczne i numeryczne

3.2.1. Klasyfikacja roślinności

W pracy skupiono się na roślinności solnisk śródlądowych klimatu umiarkowanego, aby ograniczyć ewentualne nieporozumienia związane z zasięgiem geograficznym gatunków, podążając za podziałem przyjętym przez Janssen'a i in. (2016), którzy wyróżnili trzy kategorie siedlisk solnisk śródlądowych w Europie, tj. solniska klimatu umiarkowanego, kontynentalnego oraz solniska śródziemnomorskie. W pierwszym etapie badań na podstawie stworzonej bazy zdjęć fitosocjologicznych przeprowadzono klasyfikację roślinności, do której wykorzystano metodę Cocktail (Bruelheide, 1997, 2000) oraz komputerowy system ekspercki (Tichý i in., 2011). Użyto programu JUICE 7.0 (Tichý, 2002). Pomimo standardowego stosowania stratyfikacji geograficznej w analizie baz fitosocjologicznych (np. Chytrý i in., 2007; Knollová i in., 2005) postanowioną ją pominąć, ponieważ w przypadku zbiorowisk solnisk śródlądowych, które są stosunkowo rzadkie i występują jedynie lokalnie, spowodowałoby to utratę dużej ilości danych. Nazwy klas, rzędów i związków podano zgodnie z europejskim systemem klasyfikacji syntaksonomicznej autorstwa Muciny i in. (2016). Nomenklaturę zespołów oparto na opracowaniu Matuszkiewicza (2017), internetowej bazie danych Pladias (Chytrý i in., 2021; Pladias, 2022) oraz na nazwach przyjętych niedawno przez Dítě i in. (2022).

3.2.2. Zależności pomiędzy jednostkami syntaksonomicznymi a zmiennymi środowiskowymi

Aby znaleźć główne czynniki środowiskowe wpływające na zróżnicowanie pogrupowanej na drodze klasyfikacji roślinności, wykorzystano zarówno dane glebowe, jak i parametry środowiskowe oszacowane na podstawie liczb wskaźnikowych Ellenberga (Ellenberg i in., 1992). Zastosowano analizę zmiennych kanonicznych (Canonical Variate Analysis – CVA) jako analizę dyskryminacyjną. Użyto metody postępującej selekcji zmiennych środowiskowych oraz testu permutacyjnego Monte Carlo w celu oszacowania statystycznej istotności zmiennych. Skoncentrowano się na efektach warunkowych, które wykluczają wpływ najbardziej skorelowanych zmiennych objaśniających i w ten sposób wyselekcjonowano zmienne środowiskowe objaśniające w największym stopniu zróżnicowanie pomiędzy jednostkami roślinności (ter Braak i Šmilauer, 2012). Wykorzystano pakiet CANOCO 5.0 (ter Braak i Šmilauer, 2012). Różnice w wartościach średnich zmiennych środowiskowych dla poszczególnych jednostek porównano za pomocą nieparametrycznych testów Kruskala-Wallisa (test Shapiro-Wilka, $p \leq 0.05$) z porównaniami post-hoc Dunna w pakiecie STATISTICA 13.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

3.2.3. Identyfikacja cech funkcjonalnych różnicujących jednostki syntaksonomiczne

Do identyfikacji cech funkcjonalnych różnicujących rozpatrywane jednostki syntaksonomiczne ponownie użyto analizy zmiennych kanonicznych (CVA) jako analizy dyskryminacyjnej, koncentrując się na efektach warunkowych (Šmilauer i Lepš, 2014). Wykorzystano pakiet CANOCO 5.0 (ter Braak i Šmilauer, 2012). Średnie wartości cech funkcjonalnych poszczególnych jednostek porównano za pomocą nieparametrycznych testów Kruskala-Wallisa (test Shapiro-Wilka, p≤0.05) z porównaniami post-hoc Dunna. W analizach pominięto klasę *Ruppietea maritimae* ze względu na brak danych dotyczących cech funkcjonalnych charakterystycznych dla niej gatunków. Użyto oprogramowania PAST 4.11 (Hammer i in., 2001).

Aby odnaleźć podobieństwa pod względem cech funkcjonalnych pomiędzy jednostkami syntaksonomicznymi przeprowadzono dwukierunkowe grupowanie wykorzystując odległość euklidesową do porównania grup oraz metodę nieważonych par grup ze średnią arytmetyczną (UPGMA – unweighted pair group method with arithmetic mean) do skonstruowania dendrogramów. Przed analizą dane dotyczące cech funkcjonalnych wymagały standaryzacji w celu wyeliminowania różnic wynikających z różnych jednostek pomiarowych, co wykonano przy użyciu programu MVSP 3.1 (Kovach, 2007). Analizę klasyfikacji przeprowadzono w programie PAST 4.11 (Hammer i in., 2001).

3.2.4. Zależności pomiędzy wielkością cech funkcjonalnych a parametrami środowiskowymi

W celu zbadania związku pomiędzy cechami funkcjonalnymi a czynnikami środowiskowymi przeprowadzono analizę redundancji (RDA – Redundancy Analysis). Aby wyselekcjonować zmienne w największym stopniu odpowiedzialne za zróżnicowanie cech funkcjonalnych zastosowano metodę postępującej selekcji zmiennych środowiskowych z testem permutacyjnym Monte Carlo do oceny ich statystycznej istotności. Analizę RDA zastosowano dwukrotnie z różnymi zestawami danych. W pierwszej analizie jako zmienne środowiskowe użyto średnie ważone EIV, w drugiej – parametry glebowe i sposób użytkowania. Do przeprowadzenia analizy ordynacji RDA wykorzystano pakiet CANOCO 5.0 (ter Braak i Šmilauer, 2012).

Dokonano również oceny niezależnych efektów poszczególnych parametrów środowiskowych, w tym danych glebowych, w oparciu o korelacje Spearmana z tym samym zestawem cech funkcjonalnych. Natomiast wpływ różnych sposobów użytkowania oceniono na podstawie nieparametrycznych testów Kruskala-Wallisa (test Shapiro-Wilka, p≤0.05) ze szczegółowymi porównaniami testami post-hoc Dunna. Użyto oprogramowania PAST 4.11 (Hammer i in., 2001).

3.2.5. Funkcjonalne zróżnicowanie zespołów roślinnych w oparciu o gatunki diagnostyczne

Do analiz wykorzystano zdjęcia fitosocjologiczne z bazy przypisane w wyniku przeprowadzonej wcześniej klasyfikacji do trzech zespołów roślinnych – *Sr*, *P-Ss*, *Tm-Gm* (łącznie 323) oraz zidentyfikowane dla tych zespołów dziewięć gatunków Dg. Użyto również dane o morfologicznych i biochemicznych cechach funkcjonalnych zmierzonych u gatunków Dg zebranych w terenie. Na ich podstawie policzono średnie cech funkcjonalnych ważone przez pokrycie gatunków w poszczególnych płatach roślinnych z bazy.

Średnie ważone morfologicznych cech funkcjonalnych analizowanych zespołów porównano za pomocą nieparametrycznych testów Kruskala-Wallisa z porównaniami post-hoc Dunna, gdyż test Shapiro-Wilka wykazał brak normalności rozkładu danych ($p \leq 0.05$). Dla cech biochemicznych porównania dokonano za pomocą parametrycznych testów ANOVA (test Shapiro-Wilka, $p > 0.05$) z porównaniami post-hoc Tukeya. W celu analizy powiązań pomiędzy poszczególnymi zespołami w oparciu o cechy funkcjonalne wykorzystano metodę ordynacji pośredniej – analizę głównych składowych (PCA) oddzielnie dla cech morfologicznych i biochemicznych. Cechy skorelowano również z dwiema pierwszymi osiami ordynacyjnymi korzystając ze współczynnika korelacji Spearmana, aby znaleźć wzorzec głównego zróżnicowania zespołów. Wszystkie analizy wykonano przy pomocy oprogramowania PAST 4.12 (Hammer i in., 2001).

3.2.6. Funkcjonalne znaczenie gatunków diagnostycznych

Aby sprawdzić rolę gatunków Dg w funkcjonowaniu trzech analizowanych szczegółowo zespołów typowych dla solnisk, porównano wyniki średnich ważonych cech funkcjonalnych z bazy LEDA Traitbase (Kleyer i in. 2008) obliczone na podstawie samych gatunków Dg oraz wszystkich gatunków odnotowanych w zdjęciach fitosocjologicznych ze stworzonej bazy. Do porównania średnich wartości cech funkcjonalnych zespołów wykorzystano testy Kruskala-Wallisa (test Shapiro-Wilka, $p \leq 0.05$) z testami post-hoc Dunna.

Dodatkowo, wykonano walidację wyników uzyskanych na podstawie danych z bazy cech funkcjonalnych LEDA Traitbase (Kleyer i in., 2008). W tym celu porównano rezultaty uzyskane w oparciu o dane z bazy z wynikami otrzymanymi podczas pomiarów roślin zebranych w terenie przy użyciu testów Kruskala-Wallisa (test Shapiro-Wilka,

$p \leq 0.05$) porównaniami post-hoc Dunna. Ponownie bazowano na danych o dziewięciu gatunkach Dg. Do wszystkich analiz wykorzystano program PAST 4.12 (Hammer i in. 2001).

4. Wyniki

4.1. *Vegetation of temperate inland salt-marshes reflects local environmental conditions*

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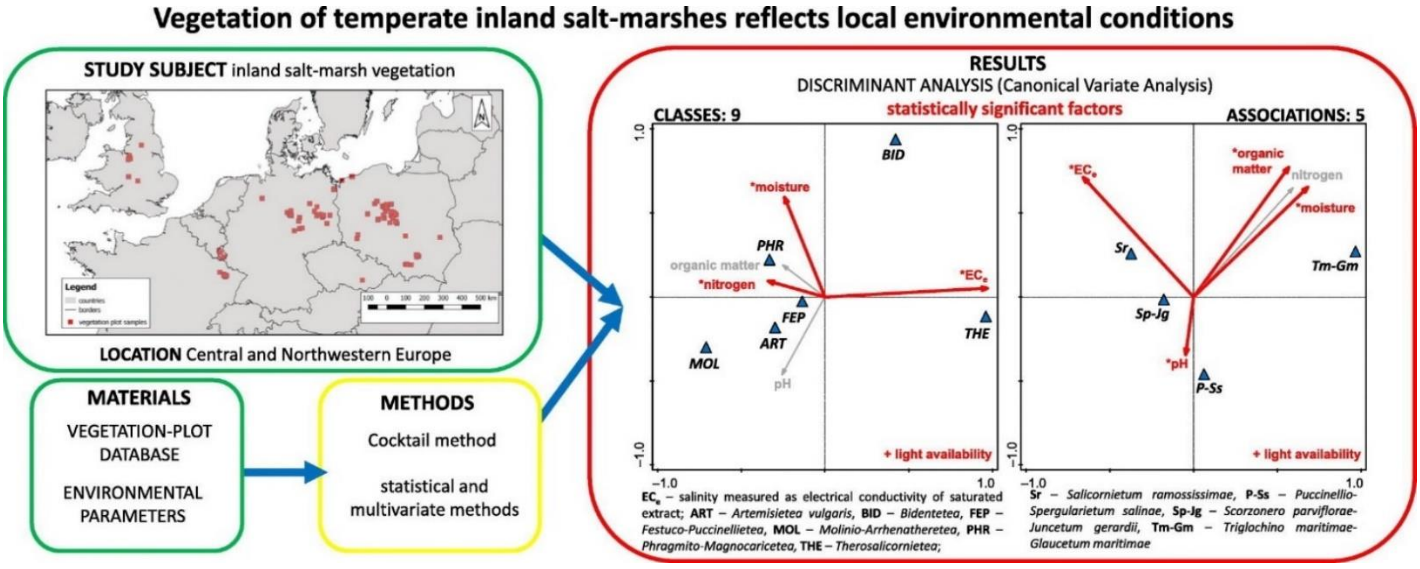

EC$_e$ – salinity measured as electrical conductivity of saturated extract; **ART** – *Artemisietea vulgaris*, **BID** – *Bidentetea*, **FEP** – *Festuco-Puccinellietea*, **MOL** – *Molinio-Arrhenatheretea*, **PHR** – *Phragmito-Magnocaricetea*, **THE** – *Therosalicornietea*;

Sr – *Salicornietum ramosissimae*, **P-Ss** – *Puccinellio-Spergularietum salinae*, **Sp-Jg** – *Scorzonero parviflorae-Juncetum gerardii*, **Tm-Gm** – *Triglochino maritimae-Glaucetum maritimae*

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Vegetation of temperate inland salt-marshes reflects local environmental conditions☆

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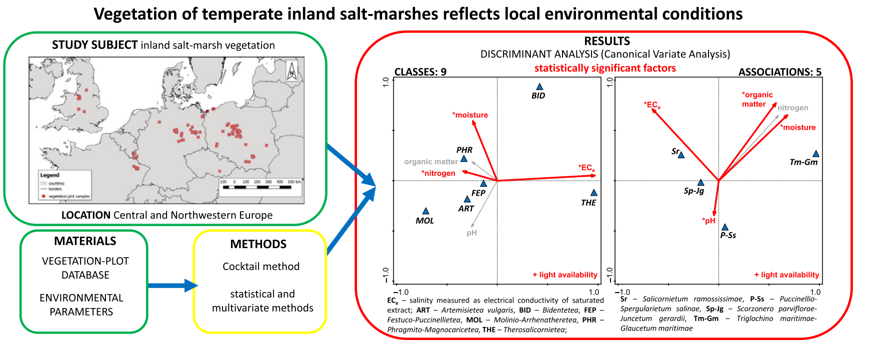
HIGHLIGHTS

- Inland temperate salt marsh vegetation is diversified into different units.
- Vegetation syntaxonomical units depend on environmental properties.
- Salinity, moisture, light availability and nitrogen content drive the class level.
- Associations are determined by salinity, organic matter, soil pH and moisture.
- Environmental requirements provide direct implications for salt marsh management.

GRAPHICAL ABSTRACT



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ABSTRACT

Inland salt marshes are recognized as habitats of unique and valuable vegetation at the European scale. There is still a lack of generalization regarding its vegetation syntaxonomy and environmental requirements, which is needed for its effective protection. To falsify our hypothesis about vegetation dependence on environmental requirements we aimed at description of the syntaxonomical units present in temperate European inland salt marshes and identification of their main environmental drivers. In our work we focused on the vegetation from the northern part of temperate salt marshes to limit confusion related to the geographical ranges of species. We collected the database of 968 vegetation plots from different European countries and applied the Cocktail method to analyze the data. Based on results, expert knowledge, existing syntaxonomical classifications and information from the literature, we identified diagnostic, constant and dominant species for individual syntaxonomical units. Then, we compiled maps of the vegetation unit distribution, and identified the most important environmental factors for the analyzed vegetation using statistical and multivariate methods, including canonical variate analysis. We classified the analyzed vegetation into nine classes, including two typical for salt-marsh vegetation – the *Therosalicornietea* and *Festuco-Puccinellietea*. Within these two classes, we distinguished two alliances and a total of five associations. The classes differ the most in terms of species preferences to salinity, soil moisture, light availability and soil nitrogen content. In addition salt marsh associations differ also by soil reaction and soil organic matter content. This provides direct implications for salt marsh sustainable management.

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1. Introduction

Saline areas are inhabited by organisms that are adapted to high soil salinity (Flowers and Colmer, 2008; Pétillon et al., 2011). Plant species typical for saline habitats called halophytes can perform their whole life cycle at high salinity over 200 mM NaCl (Flowers and Colmer, 2008). However, many other species with wide ecological responses are also present there. Species salt tolerance is reflected in the numerous classifications that divide them into different categories, e.g., obligatory and facultative halophytes, indifferential and accidental species (Parida and Das, 2005; Wilkoń-Michalska, 1963). Grigore and Cojocariu (2021) compared several of such classifications. Currently, some of the species are used as bioindicators of soil salinity (Arora and Dagar, 2019; Piernik, 2003a). It is worth emphasizing that halophytes are species recognized as a sensitive indicator not only of salinity but also of soil moisture and they are extremely light-sensitive (Wilkoń-Michalska, 1970). Therefore, the environmental factors have a significant impact on the salt marsh species composition (Erfanzadeh et al., 2010; Piernik, 2012). This vegetation frequently is characterized by species zonation defined by dominance of some species and determined mostly by salinity and tides on coastal marshes and by salinity level on inland salt marshes (Lee et al., 2016; Piernik et al., 1996; Piernik et al., 2015). The saline habitats in Europe has been studied and documented for years (e.g., Lee, 1977; Wilkoń-Michalska, 1963; Zulka et al., 1997), and this process continues to this day, because they are undeniably an important elements in our local biodiversity (Dajić-Stevanović et al., 2019; Dítě et al., 2021, 2022; Fantinato and Buffa, 2019; Lubińska-Mielińska et al., 2022; Piernik, 2012).

The present research concerns vegetation-environment relations of the temperate European part of inland salt-marshes. Inland saline areas of temperate Europe are related to the presence of salt stratums uplifted near the surface, salt springs and salt, soda and potassium industry (Brandes, 1999; Lee, 1977; Piernik et al., 2015). They have to be supported continuously by saline water because of excess precipitation over evapotranspiration which washes salts out of the upper part of the soil profile (Waisel, 1972). Moreover, as many semi natural habitats they should be managed by extensive mowing and grazing (Nienartowicz and Piernik, 2004a) because of potential expansion of *Phragmites australis* or *Elymus repens* and habitat degradation (Piernik, 2006). As rare and valuable habitats they have been designated to be under protection by *Council of Europe Directive 92/43/EEC* (Council of Europe, 1992) and they have been included into the Natura 2000 network. Apart of protection within Natura 2000, in individual countries they are legally protected as parts of nature reserves, e.g., Valea Ilenei (Iaşi) in Romania (Grigore and Toma, 2014), Artern, Jerxheim, Barstorf in Germany (Brandes, 1999), or Owczary and Ciechocinek in Poland (Kostuch and Misztal, 2006; Lubińska-Mielińska et al., 2022). Although natural inland temperate salt marshes have been designated as priorities for the European Union and have been protected for years (Bank and Spitzenberg, 2001; Pusch, 2007), recently they have been listed as endangered in the *European Red List of Habitats* (Janssen et al., 2016).

The syntaxonomical classification of this vegetation, which is helpful in its management planning, is still under question. In the latest synthesis on vegetation of Europe, Mucina et al. (2016) integrated the units proposed for years by European vegetation researchers and presented a comprehensive syntaxonomical classification system based on the Braun-Blanquet approach (Braun-Blanquet, 1964). Unfortunately, the synthesis of Mucina et al. (2016) arranges vegetation only to the level of alliances. In order to analyze the vegetation of European inland salt marshes at the association level, it is necessary to refer to the older proposals of vegetation classification systems, which are often local or national in scope, e.g., systems by Matuszkiewicz (2017) and Pott (1992), which have already been thoroughly compared by Piernik (2020). As the research of recent years shows, unification of vegetation classification systems and their dissemination are more and more frequent and necessary. A comparative overview of the syntaxonomical units based on the *EuroVegChecklist* (Mucina et al., 2016) was made for vegetation in Germany by Bergmeier (2020). Recently, Landucci et al. (2020) carried out classification to the association level of European marsh vegetation. Pätsch et al. (2019) classified vegetation of saline and brackish grasslands of the Baltic Sea coast. Classification of the south European coastal part of salt marsh communities also already exists, based on Croatian data (Dítě et al., 2019). Danihelka et al. (2022) presented halophytic vegetation of southern Moravia and northern Lower Austria. However, there is still a gap in the current classification system for inland salt-marsh vegetation across whole temperate Europe, although some of it was analyzed on the basis of data from the North German Plain (Dítě et al., 2022). The effective protection of inland salt-marsh vegetation that will allow for broad-scale comparisons require the syntaxonomical classification system based on data from various European locations.

Another lack of information is related to the environmental requirements of vegetation syntaxonomical units. Few researchers investigated soil properties in vegetation patches and then vegetation-environment relations (e.g., Piernik et al., 1996; Piernik, 2005, 2012; Wilkoń-Michalska, 1963, 1970). Quite frequently they related vegetation patches according to the species dominance (e.g., Piernik, 2003a, 2003b; Piernik et al., 2015) only some of them referred vegetation units to vegetation associations in the sense of Braun-Blanquet system (Wilkoń-Michalska, 1963, 1970; Zlatković et al., 2019).

Therefore, we used the data collected and published by various researchers from Central and Northwestern Europe to classify vegetation according to the currently used nomenclature and to find environmental drivers for their differentiation. To falsify the hypothesis about vegetation syntaxonomical units dependence on environmental requirements we aimed at (1) identification of the vegetation classes present in temperate European inland salt marshes, (2) checking if they species composition is affected by saline environment, (3) classification of the typical salt-marsh vegetation classes to the associations level, and (4) identification of the main environmental variables influencing the differentiation of analyzed vegetation. Following Janssen et al. (2016), who distinguished three categories of inland salt marsh habitats in Europe, i.e. temperate inland salt marsh, Mediterranean inland salt steppe and continental inland salt steppe, in our work we focused on the vegetation from the northern part of temperate salt marshes to limit confusion related to the geographical ranges of species.

2. Methods

2.1. Vegetation-plot database

We have created a vegetation-plot database containing data from six countries in Central and Northwestern Europe: Czech Republic (CZ), France (FR), Germany (DE), Luxemburg (LU), Poland (PL) and the United Kingdom (UK). Into account were taken all vegetation plots (hereafter also called ‘plots’) collected in saline areas, in which the salt marsh species occurred. The data was obtained partly from collected bibliographic sources and partly from the *Polish Vegetation Database* (Kącki and Śliwiński, 2012). Several vegetation plots were derived from our own unpublished field observations. The list of 32 bibliographic sources and two items with unpublished data on vegetation plots are provided in Table A.1.

Initially, the database consisted of 1231 vegetation plots. We carried out a thorough selection of plots and excluded duplicate data and plots collected at typically coastal sites. We have only left data on vegetation plots along the Polish coastline, sites within Kołobrzeg and Chrząszczewska Island, where the salinity is related to the underground supply, not to the influence of the seawater (Ćwikliński, 1977; Piotrowska, 1974). Finally, we analyzed 968 vegetation plots with the size range of 0,5–400 m^2, including 426 vascular plants (including plants marked only by genus name), from the period of 63 years collected in 1952–2015. Geographical distribution of all vegetation-plot samples in the database is shown in Fig. A.1.

Nomenclature of species in vegetation-plot database followed the authors of the bibliographic sources. In the file used for analyzes, the names of species were unified using the World Flora Online (World Flora Online, 2020; http://www.worldfloraonline.org/) and EuroMedPlant (Euro + Med, 2006 + [continuously updated]; http://www.europlusmed.org). The coordinates for all vegetation plots were used to present the results of classification on the map of Europe. The maps were prepared using the QGIS 2.14.2 "Essen" software (QGIS Development Team - Version 2.14.2, 2016).

2.2. Data classification

We used the Cocktail method (Bruelheide, 1997, 2000) and computer expert system (Tichý et al., 2011). Cocktail method (Bruelheide, 1997, 2000; Kočí et al., 2003) ensures stable, repeatable, and consistent classification outcome, e.g., Kącki et al. (2020) or Landucci et al. (2020). We decided to use this method because it applies unambiguous definitions of individual plant units. Based on expert knowledge, existing syntaxonomical classifications and information from the literature, we identified diagnostic species for classes *Therosalicornietea* and *Festuco-Puccinellietea* and alliances *Salicornion ramosissimae* and *Juncion gerardi* and we created #TC functional groups (Mucina et al., 2016; Tichý, 2002). Using these groups we prepared formal definitions (Kočí et al., 2003). As a base we used a nested expert system created by Kącki et al. (2020). However, we applied a new formal definition for all classes of no-forest vegetation found in Poland including *Crypsietea aculeatae* Vicherek 1973 class which is not reported in Poland. Performing classification we defined diagnostic species (Dg) as those with fidelity equal to or higher than 25. The fidelity measure used here was the phi coefficient (Bruelheide, 2000; Chytrý et al., 2002). For constant species (Cs) we set the frequency threshold at 50 %. The coverage value threshold of the dominant species (Dm) was 25 % with a minimum frequency of 20 %. At the association level we applied the same criteria except Dg species, which were defined as those with fidelity equal to or higher than 25 and percentage frequency equal to/higher than 50 %. We used a hierarchically nested classification system in which a vegetation plot classified to a specific unit must also meet the formulas of higher syntaxonomical units (Kącki et al., 2020; Landucci et al., 2020). JUICE software (Tichý, 2002) was used for the analyzes.

The preliminary classification showed that 26 vegetation plots were classified simultaneously into two syntaxa, and no syntaxon was identified for 58 plots. Therefore, 84 vegetation plots were not included in the final classification. Groups representing classes with less than six plots were also omitted as outliers. Therefore, the next 10 plots cumulatively were not considered. In this way, the final groups were based on 874 plots.

Although the standard use of geographic stratification in the analysis of phytosociological databases (Chytrý et al., 2007; Knollová et al., 2005), we did not apply it. This would result in a loss of large amounts of data, because inland halophytic communities are relatively rare and local. Such solutions have been already practiced (e.g., Jarolímek and Šibík, 2008; Stupar et al., 2015).

Names of classes, orders and alliances follow the European syntaxonomical classification system by Mucina et al. (2016). The nomenclature of associations follow Matuszkiewicz (2017), Pladias online database (Chytrý et al., 2021; Pladias, 2022), and names recently adopted by Dítě et al. (2022). Lichens, bryophytes and algae, which some authors noted in the vegetation plots, were not taken into account, because of their marginal role in these habitat types and uneven distribution in the dataset. This is a common practice, although it may change soon (Berg et al., 2020). In addition, the European system of floristic classification (Mucina et al., 2016) includes all these groups separately.

2.3. Environmental data

Due to the lack of data obtained from the environment for all plots in our database, we used weighted averages for individual vegetation plots calculated on the basis of Ellenberg indicator values (Ellenberg et al., 1992) as estimated environmental parameters (Schaffers and Sýkora, 2000). For this purpose we used: light availability (L), temperature (T), moisture (M), reaction/soil acidity (R), nitrogen content/trophy (N) and salinity (S). To perform the calculations, it was necessary to transform the data from the Braun-Blanquet cover/abundance scale (Braun-Blanquet, 1964) to the van der Maarel (2007) ordinal scale as follows: r → 1, + → 2, 1 → 3, 2 → 5, 3 → 7, 4 → 8, 5 → 9.

As the second set of environmental data, we analyzed soil parameters from bibliographic sources: salinity expressed as electrical conductivity of saturated extract (EC_e), moisture, pH, total nitrogen and organic matter content. It was possible only for some vegetation plots ($n = 285$) from our database, where the authors provided such data with the same methodology.

2.4. Ordination and statistical analyzes

To find main drivers for vegetation differentiation we applied Canonical Variate Analysis (CVA) as discriminant analysis and the Canoco 5.0 package (ter Braak and Šmilauer, 2012). We used forward selection procedure and Monte Carlo permutation tests, and focused on conditional effects, which exclude the effect of the most correlated predictors (ter Braak and Šmilauer, 2012). The predictors are chosen in the order of their decreasing explained variation. We skipped simple effects, that summarize the independent effects of all explanatory variables, because we decided to compare this effect by non-parametric Kruskal-Wallis test with Dunn post-hoc comparisons using Statistica 13.0 software (StatSoft Inc., Tulsa, Oklahoma, USA).

3. Results

3.1. Vegetation units

Results of classification demonstrate presence of nine classes of vegetation in the inland saline areas (Table 1): *Ruppietea maritimae* (RUP), *Therosalicornietea* (THE), *Festuco-Puccinellietea* (FEP), *Polygono-Poetea annuae* (POL), *Artemisietea vulgaris* (ART), *Potamogetonetea* (POT), *Bidentetea* (BID), *Phragmito-Magnocaricetea* (PHR) and *Molinio-Arrhenatheretea* (MOL). Classes of typical salt-marsh vegetation, i.e. *Festuco-Puccinellietea* and *Therosalicornietea* were represented by the highest number of plots – respectively ca. 50 % and 14 % out of the analyzed 874 vegetation plots. Most of the vegetation plots assigned to the *Therosalicornietea* class represented one association: *Salicornietum ramosissimae* (Se). Plots in the *Festuco-Puccinellietea* class were assigned to four different associations: *Scorzonero parviflorae-Juncetum gerardii* (Sp-

Table 1
Classification results: syntaxonomical synopsis and the number of vegetation plots assigned to each syntaxonomical unit; for high-rank units the number of plots assigned is given followed by the number of plots assigned to lower units. Abbreviations: Cl. – class, O. – order, All. – alliance, Ass. – association. Main vegetation units are given in bold.

Code Mucina et al. (2016)	Syntaxon name	Number of plots
RUP	**Cl.: *Ruppietea maritimae* J. Tx. ex Den Hartog et Segal 1964**	**6**
THE	**Cl.: *Therosalicornietea* Tx. in Tx. et Oberd. 1958**	**137**
THE-01	O.: *Therosalicornietalia* Pignatti 1952	137
THE-01C	All.: *Salicornion ramosissimae* Tx. 1974	137
–	Ass.: *Salicornietum ramosissimae* Christiansen 1955	133
FEP	**Cl.: *Festuco-Puccinellietea* Soó ex Vicherek 1973**	**485**
FEP-05	O.: *Scorzonero-Juncetalia gerardi* Vicherek 1973	469
FEP-05A	All.: *Juncion gerardi* Wendelberger 1943	469
–	Ass.: *Scorzonero parviflorae-Juncetum gerardii* (Wenzl 1934) Wendelberger 1943	121
–	Ass.: *Agrostio stoloniferae-Juncetum ranarii* Vicherek 1962	6
–	Ass.: *Triglochino maritimae-Glaucetum maritimae* Wilkoń--Michalska, 1963 ex Dítě et al. ass. nov. 2022	56
–	Ass.: *Puccinellio-Spergularietum salinae* (Feekes 1936) R.Tx. at Volk 1937	134
POL	**Cl.: *Polygono-Poetea annuae* Rivas-Mart. 1975**	**10**
ART	**Cl.: *Artemisietea vulgaris* Lohmeyer et al. in Tx. Ex von Rochow 1951**	**14**
POT	**Cl.: *Potamogetonetea* Klika in Klika et Novák 1941**	**12**
BID	**Cl.: *Bidentetea* Tx. et al. ex von Rochow 1951**	**22**
PHR	**Cl.: *Phragmito-Magnocaricetea* Klika in Klika et Novák 1941**	**112**
MOL	**Cl.: *Molinio-Arrhenatheretea* Tx. 1937**	**76**

Jg), *Agrostio stoloniferae-Juncetum ranarii* (As-Jr), *Triglochino maritimae-Glaucetum maritimae* (Tm-Gm) and *Puccinellio-Spergularietum salinae* (P-Ss). The number of plots in individual associations is presented in Table 1.

From the set of diagnostic species (Dg) we identified these specific for temperate inland salt marsh vegetation. The diagnostic species for classes *Therosalicornietea* and *Festuco-Puccinellietea* identified on investigated inland salt-marshes are demonstrated in Table A.2. For the *Therosalicornietea* class Dg species included *Salicornia europaea*, *Puccinellia distans*, *Spergularia marina* and *Spergularia media*. *S. europaea* was identified also as only one dominant (Dm) species. Constant species (Cs) included *S. europaea*, *P. distans* and *Tripolium pannonicum* (see also Table A.3). Vegetation representing this class was recorded in Poland, Germany and France. For the *Festuco-Puccinellietea* class the group of Dg species consisted only of *Juncus gerardii*. Additionally, *P. distans* was a Dm and Cs species. Vegetation representing this class is much more widespread than that of the *Therosalicornietea*, because it was recorded in all analyzed countries. Geographic distribution of *Therosalicornietea* and *Festuco-Puccinellietea* classes are presented in Fig. 1.

In the next step we focused on halophytic associations. Diagnostic species for all of them are presented in Table 2. For the *Salicornietum ramosissimae* only one Dg species was *S. europaea*. This species was also identified as dominant and additionaly as constant together with *P. distans* and *S. marina* (see also Table A.4). For *Puccinellio-Spergularietum salinae* association three species passed Dg rule including *S. marina*, *P. distans* and

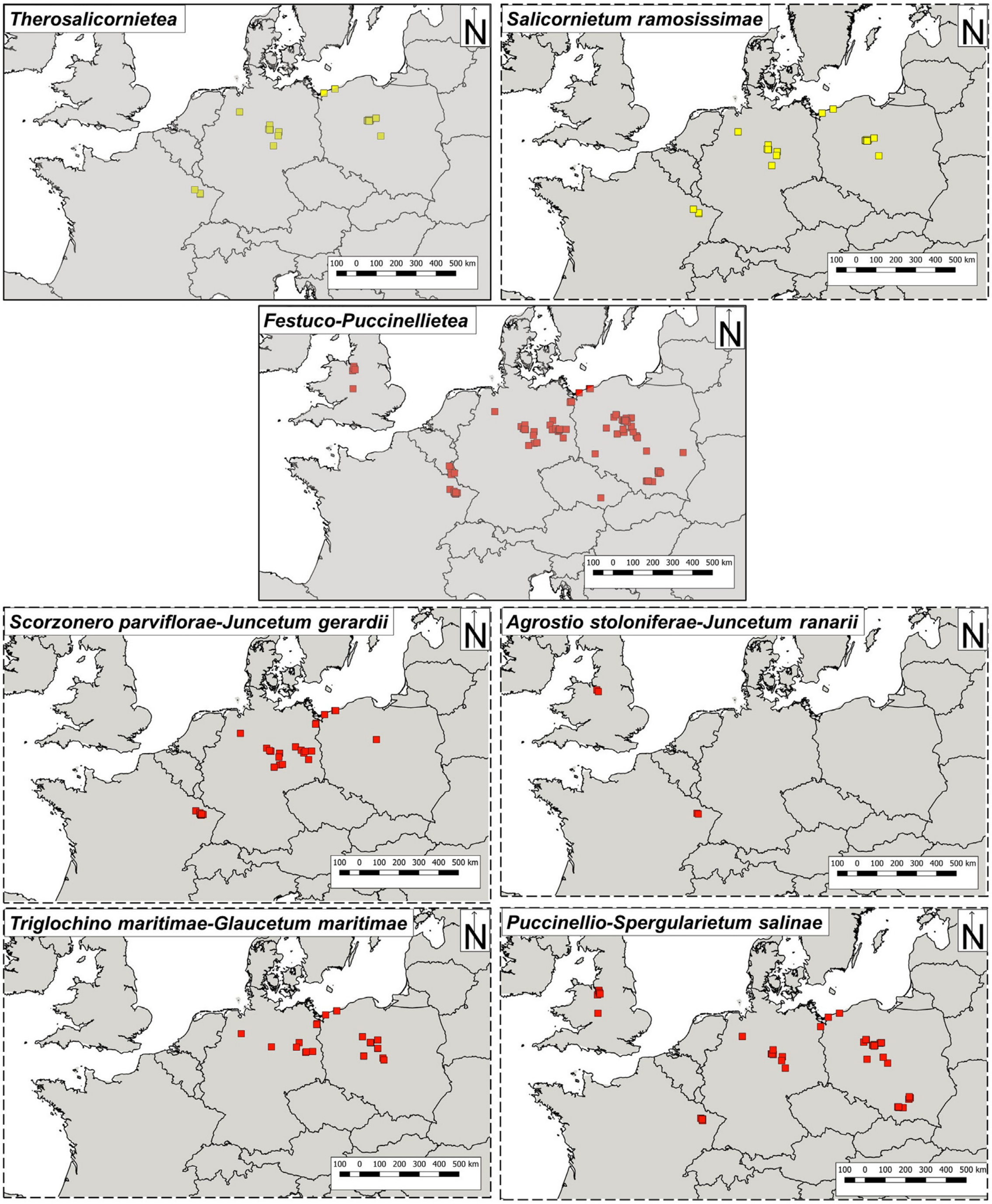

Fig. 1. Geographic distribution of *Therosalicornietea*, *Festuco-Puccinellietea* classes and associations identified on salt marshes based on the coordinates of individual vegetation sample plots.

Table 2

Shortened synoptic table with percentage frequency and fidelity index added in superscript for associations identified on salt marshes. The values for diagnostic species (with fidelity index ≥ 25 and percentage frequency ≥ 50 %) within associations are marked in gray, for constant species (with percentage frequency ≥ 50 %) have bold font, and for dominant species (with plant cover ≥ 25 % and percentage frequency ≥ 20 %) are marked with asterisk in superscript. Zero fidelity is assigned to species with insignificant fidelity to the cluster (Fisher's exact test at $p > 0.01$). Abbreviations: Se – *Salicornietum ramosissimae*, P-Ss – *Puccinellio-Spergularietum salinae*, Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii*, Tm-Gm – *Triglochino maritimae-Glaucetum maritimae*, As-Jr – *Agrostio stoloniferae-Juncetum ranarii*.

↓ Species Associations →	Se	P-Ss	Sp-Jg	Tm-Gm	As-Jr
THEROSALICORNIETEA					
Salicornietum ramosissimae					
Salicornia europaea	**$100^{83.7*}$**	18^{---}	10^{---}	4^{---}	$.^{---}$
FESTUCO-PUCCINELLIETEA					
Scorzonero parviflorae-Juncetum gerardii					
Juncus gerardii	13^{---}	10^{---}	**$100^{62.5*}$**	39^{---}	33^{---}
Agrostio stoloniferae-Juncetum ranarii					
Juncus ranarius	$.^{---}$	9^{---}	4^{---}	5^{---}	**$100^{89.7*}$**
Tripolium pannonicum	49^{---}	29^{---}	**$55^{1.6}$**	36^{---}	**$100^{46.3}$**
Oxybasis rubra	1^{---}	4^{---}	1^{---}	$.^{---}$	**$50^{62.1}$**
Agrostis stolonifera	5^{---}	15^{---}	40^{5}	$48^{13.9}$	**67^{---}**
Triglochino maritimae-Glaucetum maritimae					
Triglochin maritima	23^{---}	10^{---}	$48^{12.2}$	**$100^{66.4*}$**	$.^{---}$
Glaux maritima	7^{---}	7^{---}	32^{---}	**$93^{72.8*}$**	$.^{---}$
Phragmites australis	16^{---}	15^{---}	$36^{7.4}$	**64^{38}**	17^{---}
Juncus compressus	2^{---}	15^{---}	7^{---}	**$63^{59.8}$**	$.^{---}$
Potentilla anserina	$.^{---}$	12^{---}	$26^{8.3}$	**$61^{51.3}$**	$.^{---}$
Puccinellio-Spergularietum salinae					
Spergularia marina	**50^{---}**	**100^{47*}**	13^{---}	2^{---}	**100^{---}**
Puccinellia distans	**$80^{7.8}$**	**100^{30*}**	36^{---}	**52^{---}**	**100^{---*}**
Atriplex prostrata s. l.	38^{---}	**$72^{32.6}$**	39^{---}	34^{---}	17^{---}

Atriplex prostrata. All of them were constant in this association, while *S. marina* and *P. distans* were also dominant. This association is the most widespread among associations in the *Festuco-Puccinielietea* class. It was recorded in Germany, the United Kingdom, Poland and France. For the *Scorzonero parviflorae-Juncetum gerardii* association only *J. gerardii* passed the criteria for Dg species. This species was also identified as Dm, and Cs

Table 3

Shortened synoptic table with percentage frequency and fidelity index added in superscript for vegetation classes identified on salt marshes with a complete list of diagnostic (Dg), constant (Cs) and dominant (Dm) species for *Therosalicornietea* and *Festuco-Puccinellietea* classes and identified salt marsh associations. Obligatory halophytes are marked in bold font and in gray, facultative halophytes in bold font (according to Wilkoń-Michalska, 1963). Abbreviations: PHR – *Phragmito-Magnocaricetea*, MOL – *Molinio-Arrhenatheretea*, ART – *Artemisietea vulgaris*, BID – *Bidentetea*, POL – *Polygono-Poetea annuae*, POT – *Potamogetonetea*, RUP – *Ruppietea maritimae*.

↓ Species Classes →	PHR	MOL	ART	BID	POL	POT	RUP
Puccinellia distans	**31^{---}**	**18^{---}**	**21^{---}**	**55^{---}**	**$100^{41.7}$**	**$.^{---}$**	**$.^{---}$**
Atriplex prostrata s. l.	**47^{---}**	**16^{---}**	**50^{---}**	**$100^{49.4}$**	**10^{---}**	**$.^{---}$**	**$.^{---}$**
Phragmites australis	$74^{43.7}$	34^{---}	14^{---}	36^{---}	$.^{---}$	$.^{---}$	$.^{---}$
Agrostis stolonifera	$43^{19.4}$	$51^{26.8}$	29^{---}	27^{---}	$.^{---}$	$.^{---}$	$.^{---}$
Tripolium pannonicum	**17^{---}**	**4^{---}**	**14^{---}**	**14^{---}**	**$.^{---}$**	**100^{59}**	**$.^{---}$**
Potentilla anserina	$37^{20.7}$	$67^{50.5}$	7^{---}	$.^{---}$	$.^{---}$	$.^{---}$	$.^{---}$
Juncus compressus	28^{---}	$46^{37.4}$	7^{---}	5^{---}	$.^{---}$	$.^{---}$	$.^{---}$
Triglochin maritima	**33^{---}**	**29^{---}**	**7^{---}**	**$.^{---}$**	**$.^{---}$**	**8^{---}**	**$.^{---}$**
Juncus gerardii	**21^{---}**	**4^{---}**	**21^{---}**	**5^{---}**	**$.^{---}$**	**$.^{---}$**	**$.^{---}$**
Glaux maritima	**15^{---}**	**17^{---}**	**14^{---}**	**$.^{---}$**	**$.^{---}$**	**$.^{---}$**	**$.^{---}$**
Spergularia marina	**10^{---}**	**1^{---}**	**7^{---}**	**27^{---}**	**$.^{---}$**	**$.^{---}$**	**$.^{---}$**
Oxybasis rubra	3^{---}	$.^{---}$	$.^{---}$	9^{---}	10^{---}	$.^{---}$	$.^{---}$
Juncus ranarius	6^{---}	5^{---}	$.^{---}$	$.^{---}$	$.^{---}$	$.^{---}$	$.^{---}$
Salicornia europaea	**1^{---}**	**1^{---}**	**7^{---}**	**$.^{---}$**	**$.^{---}$**	**$.^{---}$**	**$.^{---}$**
Spergularia media	1^{---}	$.^{---}$	$.^{---}$	$.^{---}$	$.^{---}$	$.^{---}$	$.^{---}$

together with *T. pannonicum*. Association was reported from Poland, Germany and France. For the *Triglochino maritimae-Glaucetum maritimae* association the set of five Dg species were identified: *Triglochin maritima*, *Glaux maritima*, *Phragmites australis*, *Juncus compressus* and *Potentilla anserina*, among which Dm species were *G. maritima* and *T. maritima*. All five were also constant in this association together with *P. distans*. The association was noted in the same countries as *Scorzonero parviflorae-Juncetum gerardii*, but except in France. The *Agrostio stoloniferae-Juncetum ranarii* association had three Dg species: *Juncus ranarius*, *T. pannonicum* and *Oxybasis rubra*. Dominant species in this association covered *J. ranarius* and *P. distans*, while constant species also included *S. marina* and *Agrostis stolonifera*. This association was recorded in the United Kingdom and France.

Results revealed that all analyzed vegetation units were affected by salinity. The variation of vegetation representing not typical halophytic classes has been presented in Table A.3. The occurrence of species with the highest diagnostic value for *Therosalicornietea* and *Festuco-Puccinellietea* classes in other syntaxonomical units is shown in Table 3. A total of 15 Dg, Cs and Dm species were distinguished for typical salt marsh classes and associations together and most of them were also present in other vegetation units. However, it is worth to focus on obligatory and facultative halophytes in this group (Wilkoń-Michalska, 1963). Among them obligatory halophytes *A. prostrata* and *T. pannonicum*, and facultative *P. distans* have the widest distribution within non-halophytic vegetation units. They were noted in plots belonging to five different classes. Even the most salt tolerant halophyte *S. europaea* passed to vegetation of *Artemisietea vulgaris*, *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea* classes. The highest number of halophytes passed to *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea*, followed by *Artemisietea vulgaris* and *Bidentetea* classes (Fig. A.2).

3.2. Vegetation-environment relations

In the first step we focused on the class level of vegetation. Canonical Variate Analysis (CVA) demonstrated that vegetation classes present on temperate inland salt marshes differ significantly in terms of species preferences to soil salinity, moisture, light availability and nitrogen content as presented in Fig. 2. The species preferences to soil salinity, and moisture explained over 14 % of variance between vegetation classes (Table A.5). Taking into account available soil data, analyzed syntaxonomical units differ the most in terms of salinity expressed as electrical conductivity of saturated soil extract, total nitrogen and soil moisture, which together explained over 10 % of soil parameters variation between vegetation classes (Table A.6).

The detailed statistical comparison of single environmental effects on vegetation units based on EIV (Fig. 3) showed that species belonging to the *Therosalicornietea* and *Ruppietea maritimae* classes are characterized by high salt tolerance, and together with *Potamogetonetea* by high reaction values. In addition, species belonging to these classes together with *Phragmito-Magnocaricetea* class are the most preferential to high soil moisture while belonging to the *Polygono-Poetea annuae* and *Artemisietea vulgaris* classes the least preferential. Considering light indicator value, the vegetation of *Therosalicornietea* class is the most preferential to high insolation. However, it is the least preferential to high nitrogen content in the soil. The preference for temperature value is the factor that differentiates the analyzed groups the least.

The results of statistical analyzes based on available soil data demonstrated that the highest salinity, measured as electrical conductivity of saturated extract, was characteristic for vegetation of *Therosalicornietea* and *Bidentetea* classes (*Ruppietea maritimi* class missing the soil data) (Fig. 4). The highest soil moisture, as expected, was recorded in the soils occupied by vegetation of *Phragmito-Magnocaricetea* class, whereas the highest soil nitrogen in patches of *Molinio-Arrhenatheretea* class. The analyzed classes of vegetation do not differ significantly in terms of pH and the content of organic matter in the soil. Detailed soil results are presented in Table A.7.

3.3. Environmental pattern of salt-marsh plant associations

Regarding plant associations we focused on vegetation typical for salt marshes from *Therosalicornietea* and *Festuco-Puccinellietea* classes. Results of discriminant analysis (Fig. 5) revealed that based on EIV the most important for vegetation differentiation were preferences of species to light availability and soil reaction correlated with salinity, followed by moisture and nitrogen and temperature. All together explained ca. 33 % of variability between associations (Table A.5). Taking into account available soil measurements the most important for association differentiation were salinity expressed as EC_e and organic matter content, followed by pH and soil moisture, explaining over 30 % of variance in soil parameters between associations (Table A.6).

The comparison of single environmental effects between associations based on EIV (Fig. 6) demonstrated that species, which build the associations *Salicornietum ramosissimae* and *Agrostio stoloniferae-Juncetum ranarii* are the

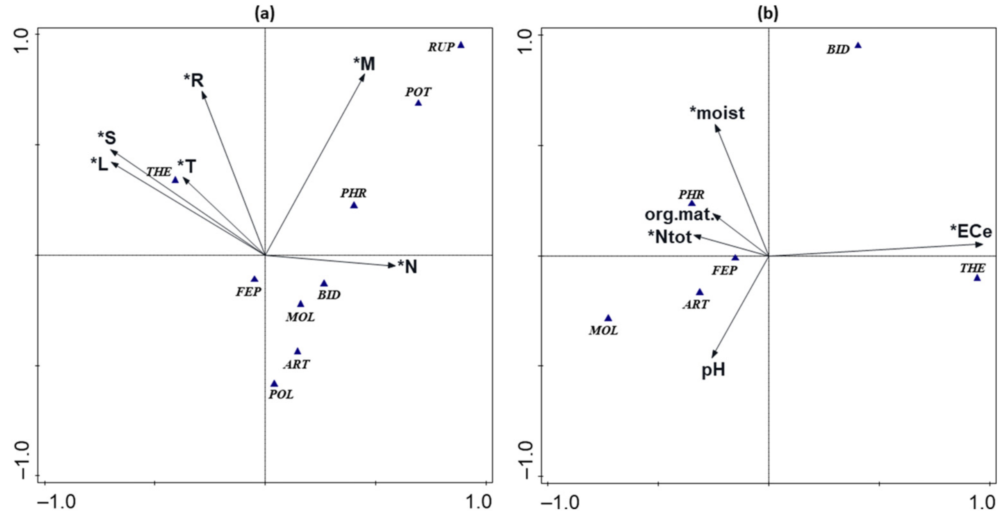

Fig. 2. Results of discriminant Canonical Variate Analysis (CVA): (a) relation between analyzed vegetation classes and environmental variables based on Ellenberg indicator values (EIV); (b) relation between analyzed vegetation classes and soil parameters. Distance between points is expressed as Mahalanobis distance. Statistically significant factors are marked by asterisk ($p < 0.05$). Abbreviations of vegetation classes: ART – *Artemisietea vulgaris*, BID – *Bidentetea*, FEP – *Festuco-Puccinellietea*, MOL – *Molinio-Arrhenatheretea*, PHR – *Phragmito-Magnocaricetea*, POL – *Polygono-Poetea annuae*, POT – *Potamogetonetea*, RUP – *Ruppietea maritimae*, THE – *Therosalicornietea*. Abbreviations of environmental variables: L – light availability, M – moisture, N – nitrogen content/trophy, R – reaction/soil acidity, S – salinity, T – temperature. Abbreviations of environmental parameters: ECe – salinity measured as electrical conductivity, moist – moisture, Ntot – total nitrogen, org.mat. – organic matter content.

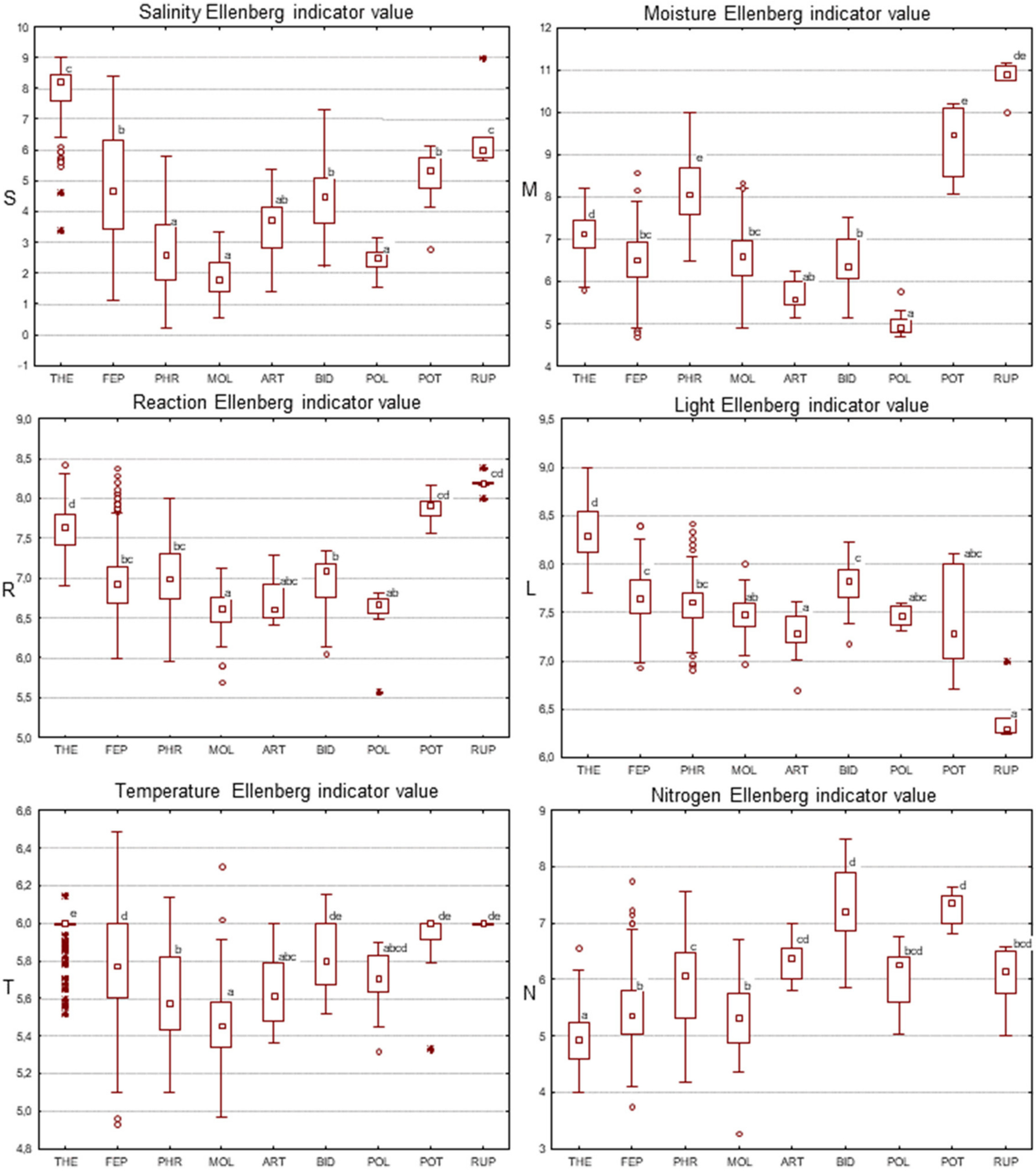

Fig. 3. Comparison of Ellenberg indicator values (EIV) for vegetation classes. Significantly different groups according to Kruskal-Wallis test with Dunn post hoc comparisons are denoted by different letters at $p < 0.05$. Abbreviations of vegetation classes: THE – *Therosalicornietea* ($n = 137$), FEP – *Festuco-Puccinellietea* ($n = 485$), PHR – *Phragmito-Magnocaricetea* ($n = 112$), MOL – *Molinio-Arrhenatheretea* ($n = 76$), ART – *Artemisietea vulgaris* ($n = 14$), BID – *Bidentetea* ($n = 22$), POL – *Polygono-Poetea annuae* ($n = 10$), POT – *Potamogetonetea* ($n = 12$), RUP – *Ruppietea maritimae* ($n = 6$). Abbreviations of environmental variables: S – salinity, M – moisture, R – reaction/soil acidity, L – light availability, T – temperature, N – nitrogen content/trophy.

most preferential to high soil salinity and light availability. *Salicornietum ramosissimae* association is also characterized by the greatest tolerance to high soil reaction. In the salinity gradient it is followed by *Puccinellio-Spergularietum salinae* association, but the set of species there turned out to be the least preferential to high values of soil moisture, but the most to high nitrogen content. Less salt tolerant *Scorzonero parviflorae-Juncetum gerardii* and *Triglochino maritimae-Glaucetum maritimae* associations differed in terms of light and temperature preferences, significantly lower in the second association, and of significantly higher there nitrogen indication.

Results obtained on the basis of available soil parameters confirmed that the highest soil salinity is typical for the *Salicornietum ramosissimae* association (Fig. 7 and Table A.8). However, on the second position has been placed *Scorzonero parviflorae-Juncetum gerardii* with significantly higher soil salinity and pH than in patches of *Triglochino maritimae-Glaucetum maritimae* association but significantly lower soil moisture and total nitrogen contents. *Puccinellio-Spergularietum salinae* association is noted in areas with the lowest content of organic matter and total nitrogen compared to other groups. Soil parameters were missing for *Agrostio stoloniferae-Juncetum ranarii*.

4. Discussion

4.1. Vegetation classification approach

The effective protection of inland salt-marsh vegetation that will allow for broad-scale comparisons require, as it was already mentioned, the

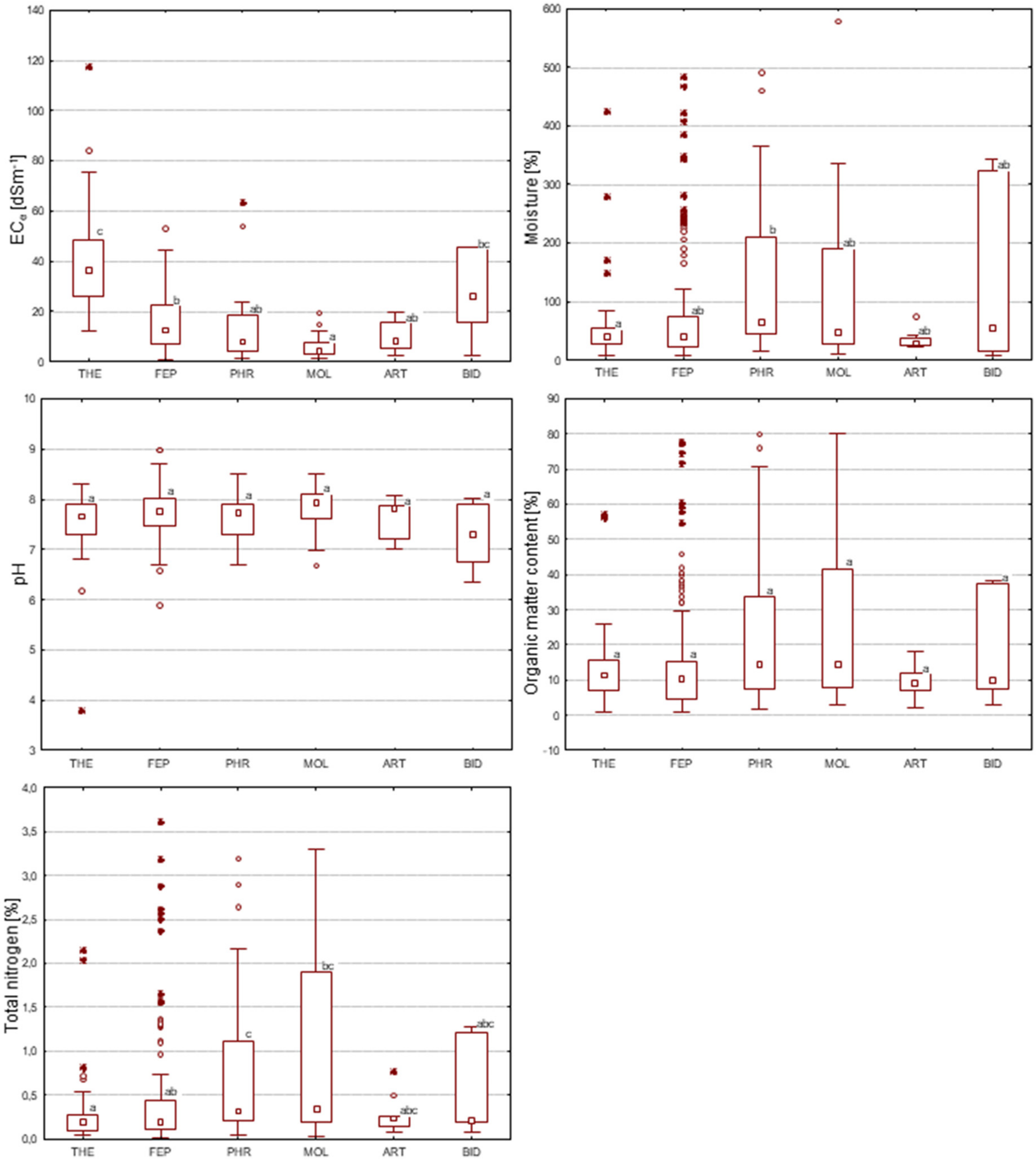

Fig. 4. Comparison of environmental parameters for vegetation classes. Significantly different groups according to Kruskal-Wallis test with Dunn post hoc comparisons are denoted by different letters at $p < 0.05$. Abbreviations of vegetation classes: THE – *Therosalicornietea* ($n = 54$), FEP – *Festuco-Puccinellietea* ($n = 134$), PHR – *Phragmito-Magnocaricetea* ($n = 38$), MOL – *Molinio-Arrhenatheretea* ($n = 24$), ART – *Artemisietea vulgaris* ($n = 9$), BID – *Bidentetea* ($n = 7$). Abbreviation of environmental parameter: EC_e – salinity expressed as electrical conductivity.

unified syntaxonomical classification system based on data from various European locations. In our research, following the concept of Braun-Blanquet (Braun-Blanquet, 1964; Mucina et al., 2016), we made an effort first to classify vegetation to syntaxonomical units, then to assess their environmental dependence. At the first stage, apart from already known from saline areas vegetation representing *Therosalicornietea* and *Festuco-Puccinellietea* classes we identified as integral parts of inland salt marshes classes representing other vegetation types. However, this vegetation has its own specificity. We noticed that species thought as limited to narrow environmental conditions can present relatively wide ecological responses. They can play an important role in classification difficulties on one hand and on the second can shape vegetation variety. All 15 species, including eight halophytes, being Dg, Cs and Dm for halophytic classes and associations of *Therosalicornietea* and *Festuco-Puccinellietea*, entered other vegetation units. Among them obligatory halophyte *T. pannonicum* together with *A. prostrata* and facultative *P. distans* had the widest distribution within non-halophytic vegetation units and were noted in plots belonging to five different classes. Even the most salt tolerant halophyte *S. europaea* passed to vegetation of *Artemisietea vulgaris*, *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea* classes. This wide response curve of species is consistent with findings of Piernik (2003a, 2012), who demonstrated that even obligatory halophytes can be recorded on non- or slightly saline soils. Recent studies on *S. europaea* also showed that although the lack of salinity and the salinity of over 800 mM NaCl (≈ 80 dS $\times$ m^{-1}) conditions are extreme for this plant and limit its functional traits, they still do not completely stop its development (Cárdenas-Pérez et al., 2022). Moreover,

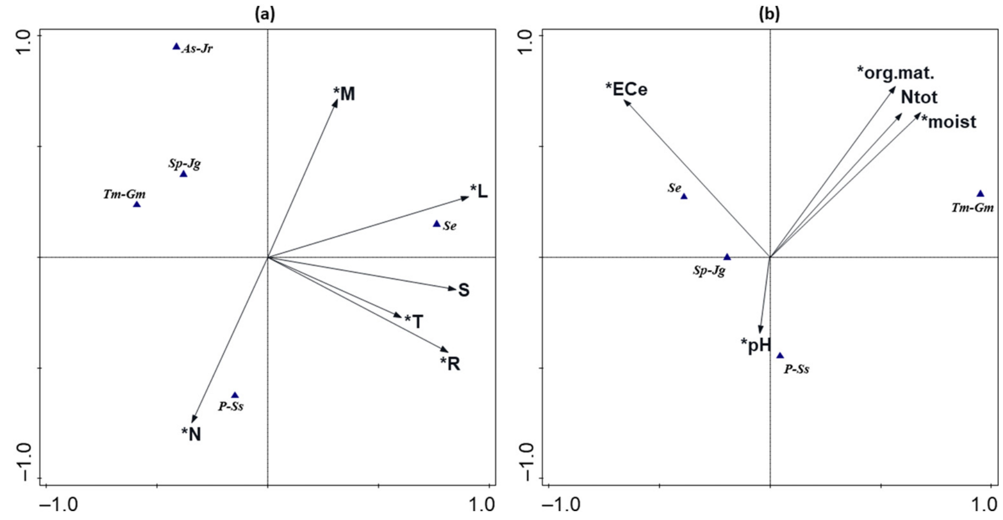

Fig. 5. Results of discriminant Canonical Variate Analysis (CVA): (a) relation between analyzed associations and environmental variables based on Ellenberg indicator values (EIV); (b) relation between analyzed associations and soil parameters. Distance between points is expressed as Mahalanobis distance. Statistically significant factors are marked by asterisk ($p < 0.05$). Abbreviations of vegetation associations: As-Jr – *Agrostio stoloniferae-Juncetum ranarii*, Se – *Salicornietum ramosissimae*, P-Ss – *Puccinellio-Spergularietum salinae*, Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii*, Tm-Gm – *Triglochino maritimae-Glaucetum maritimae*. Abbreviations of environmental variables: L – light availability, M – moisture, N – nitrogen content/trophy, R – reaction/soil acidity, S – salinity, T – temperature. Abbreviations of environmental parameters: EC_e – salinity measured as electrical conductivity, moist – moisture, Ntot – total nitrogen, org.mat. – organic matter content.

data from America shows high competitive ability, speed spread and high seed production of *P. distans* (Cusick, 1982; Tarasoff et al., 2007). Research from the United Kingdom shows that *P. distans* and *S. marina* permanently occupy roadsides due to salinity caused by the use of salt to defrost roads, although other species such as *Plantago maritima* are disappearing with time (Scott and Davison, 1985). The highest number of halophytes passed to *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea*, followed by *Artemisietea vulgaris* and *Bidentetea* classes. This is due to the high tolerance of these species to fluctuations in the soil salinity level and this decides about specificity of investigated vegetation. On the other hand the presence of vegetation from not typical salt marsh vegetation classes is due to relatively high salt resistance of many glicophytic species including diagnostic, constant and dominant. As demonstrated by Piernik (2012) the group of the most frequent species on inland salt marshes includes *Festuca rubra* which is according to Kącki et al. (2013) Dg and Cs species for *Molinio-Arrhenatheretea* class. Ecotype of this species was noted on inland salt marshes even at very high salinity (EC_e up to 25 dS × m^{-1}). In the most frequent group of species is present also *P. australis*, Dg and Dm species for *Phragmito-Magnocaricetea* class, noted in saline sites between EC_e 2.5 and 118 dS × m^{-1} (Kącki et al., 2013; Piernik, 2012). Three more species from the most frequent group are typical for *Artemisietea vulgaris* class, i.e. *E. repens* (Dg, Cs, Dm), *Cirsium arvense* (Dg, Cs) and *Achillea millefolium* (Cs). Also three species for *Bidentetea* class, i.e. *Plantago intermedia* (Dg), *Chenopodium glaucum* (Dg, Dm) and *A. prostrata* (Cs). All of them were recorded on even extremely saline soils (Piernik, 2012). That is why, not only vegetation classes typical for saline sites can be present on saline soils. However, all this creates difficulties with vegetation classification. The latest revision of the *Phragmito-Magnocaricetea* class classification even uses species of saline habitats as a functional species group to refine the definitions of some marsh vegetation associations (Landucci et al., 2020). Often, associations reacting to local environmental conditions form transitional patches with slightly different species compositions and complicate systematic classification. Despite the current simplicity of using numerical classifications, the final decisions about vegetation units are still subjective, but all these decisions are statistically sound (Tichý, 2002). As our research has shown, this problem largely concerns inland salt marshes. More than 28 % of the finally analyzed plots have been classified into seven atypical for saline areas classes. However, they should also be taken into consideration as an integral part while management and protection is planning.

4.2. Environmental drivers for vegetation

Our results positively verified the main research hypothesis on vegetation syntaxonomical units dependence on environmental requirements. Vegetation of inland salt marshes is very diverse, which reflects the syntaxonomic division at the class level as it was already discussed. We proved that its arrangement is determined by gradients of environmental factors, the most important of which are salinity, soil moisture and the availability of light. All statistically significant environmental factors, both applied as soil measurements or EIV, are able to explain respectively from 10 to 24 % of variation between groups (Tables A.5 and A.6). This is satisfactory taking into account high vegetation variability, different biogeographical locations and other factors that may affect vegetation formation as different species interactions or strategies and finally not taken into consideration environmental factors, as management type (Piernik, 2012; Piernik et al., 2015; Ulrich et al., 2018, 2019). Our results not only prove already reported field observations, e.g., that *Therosalicornietea* class is the most related to the highest soil salinity, then *Festuco-Puccinellietea* class but also demonstrate that *Phragmito-Magnocaricetea* class can cover vegetation not only resistant to high soil moisture but also to relatively high salinity and preferring relatively high nitrogen soil content. This is important, because high nitrogen availability can enhance species salt tolerance (e.g., Sikder et al., 2020). Definitely the last salt tolerant is vegetation from *Molinio-Arrhenatheretea* class, but on inland salt marshes its environmental requirements seems to overlap with *Phragmito-Magnocaricetea* class. It can mean that in our data the group of *Phragmito-Magnocaricetea* could include former meadows overgrown by *P. australis* as a result of its abandonment (Bosiacka et al., 2011). It is worth noting that vegetation from different classes usually coexist within particular locations. The coexistence of such diverse groups in the salinity gradient is known as zonation of salt marsh vegetation and it is formed not only by vegetation form *Therosalicornietea* and *Festuco-Puccinellietea* classes (Piernik et al., 1996; Piernik, 2006). It has been demonstrated also for continental halophytic grassland vegetation of Southeastern Europe (Dajić Stevanović et al., 2016). Moreover, zonation is also known for other organisms in saline areas, e.g., arthropods (Finch et al., 2007). This shapes the salt marsh biodiversity depending among others on the environmental gradients length (Ulrich et al., 2018).

Taking into consideration analyzed plant associations, the most important role in their pattern is played by the salinity, availability of light,

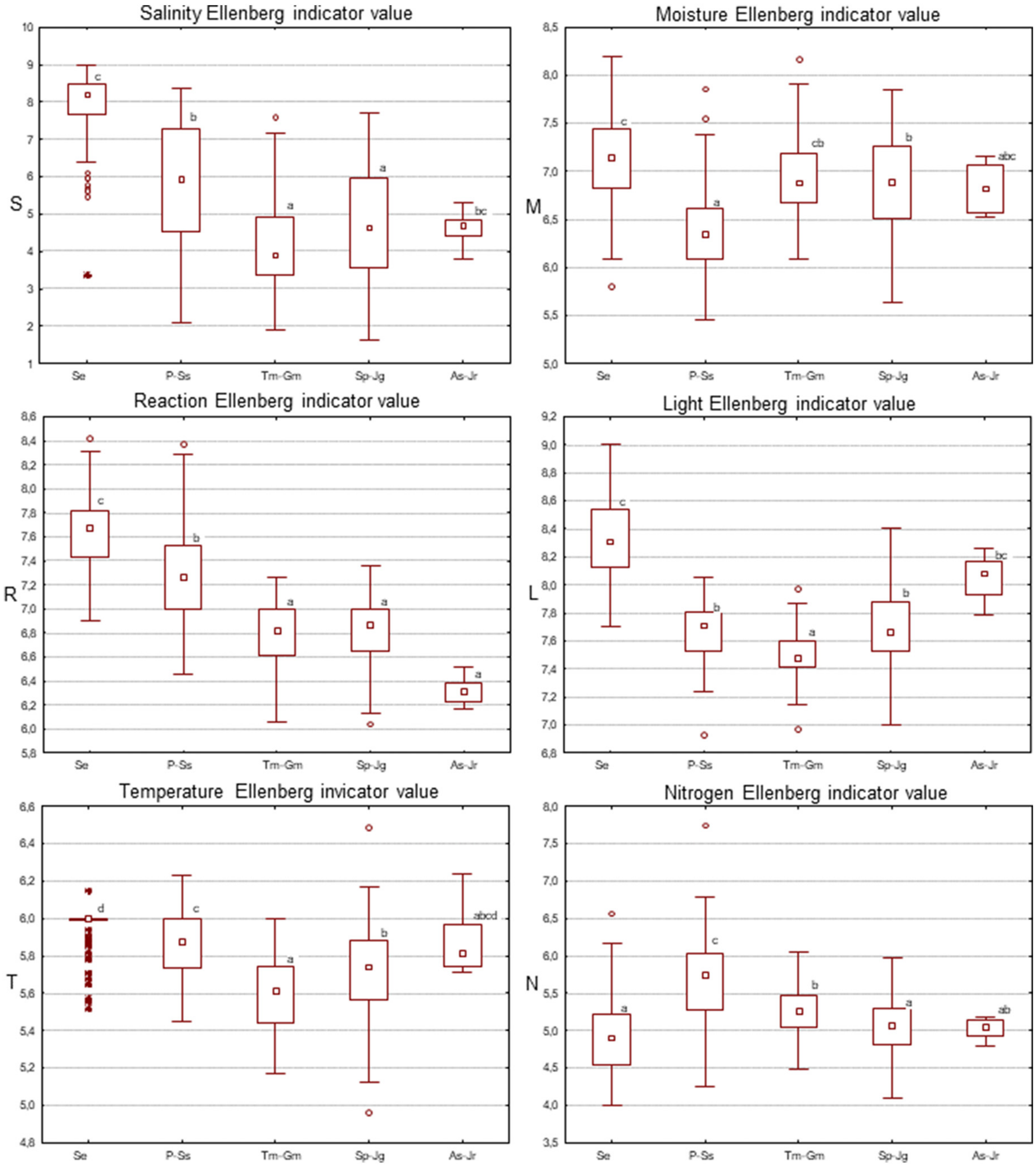

Fig. 6. Comparison of Ellenberg indicator values (EIV) for vegetation associations. Significantly different groups according to Kruskal-Wallis test with Dunn post hoc comparisons are denoted by different letters at $p < 0.05$. Abbreviations of vegetation associations: Se – *Salicornietum ramosissimae* ($n = 133$), P-Ss – *Puccinellio-Spergularietum salinae* ($n = 134$), Tm-Gm – *Triglochino maritimae-Glaucetum maritimae* ($n = 56$), Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii* ($n = 121$), As-Jr – *Agrostio stoloniferae-Juncetum ranarii* ($n = 6$). Abbreviations of environmental variables: S – salinity, M – moisture, R – reaction/soil acidity, L – light availability, T – temperature, N – nitrogen content/trophy.

moisture, reaction and the content of organic matter in the soil. It is worth emphasizing that discriminant analysis based on EIV representing long term environmental conditions and on soil measurements representing temporal measurements overlap in this case. The results demonstrate that environmental parameters explain respectively 33 and 30 % of the total variance between associations. The results obtained for individual associations based on EIV are confirmed in the literature from other inland sites in Europe (Dítě et al., 2021, 2022). *Salicornietum ramosissimae* is characterized by the highest EIV of salinity, moisture and soil reaction in comparison to other associations. This high soil salinity typical for this association has been also confirmed by analysis based on soil measurements. The next in the salinity gradient is placed *Puccinellio-Spergularietum salinae*, characterized also by relatively low moisture requirements and relatively high nitrogen preferences. It frequently follows *Salicornietum ramosissimae* as the next vegetation zone in the salinity gradient (Piernik et al., 1996; Piernik, 2006). However, based on soil parameters it is not so visible, probably due to possible high fluctuations in soil salinity e.g., after rains and presence of this association in the industrial, not stable habitats (Piernik, 2003b; Piernik and Hulisz, 2011). There is relatively little known about *Triglochino maritimae-Glaucetum maritimae* association which has been described firstly by Wilkoń-Michalska (1963) by the name *Triglochin maritimum-Glaux maritima* as occurring in inland salt meadows in Poland.

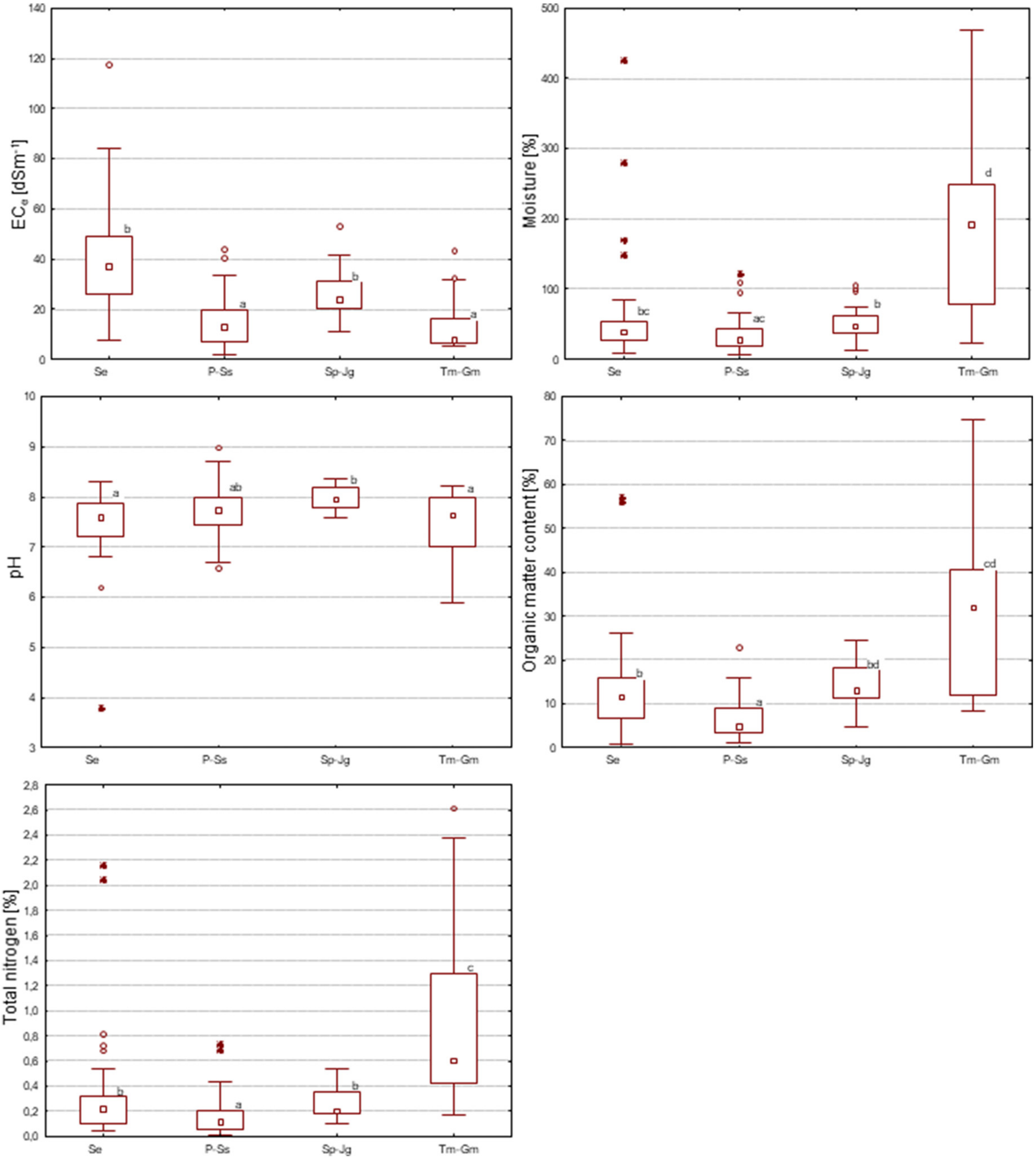

Fig. 7. Comparison of environmental parameters for vegetation associations. Significantly different groups according to Kruskal-Wallis test with Dunn post hoc comparisons are denoted by different letters at $p < 0.05$. Abbreviations of vegetation associations: Se – *Salicornietum ramosissimae* ($n = 50$), P-Ss – *Puccinellio-Spergularietum salinae* ($n = 45$), Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii* ($n = 23$), Tm-Gm – *Triglochino maritimae-Glaucetum maritimae* ($n = 23$). Abbreviation of environmental parameter: EC_e – salinity expressed as electrical conductivity.

Then it has been proved with the current name by Dítě et al. (2022) on inland salt marshes on the North German Plain. Our results confirm this finding. Unfortunately, these authors did not find any statistical differences in EIV properties between this association and known already from Germany *Scorzonero parviflorae-Juncetum gerardii*. From our data for *Triglochino maritimae-Glaucetum maritimae* has been classified 56 plots, located both in Poland and Germany, while for *Scorzonero parviflorae-Juncetum gerardii* 121 plots located mostly in Germany. Based on EIV we found differences in nitrogen preferences higher for the first association and light and temperature higher for second confirming *Scorzonero parviflorae-Juncetum gerardii* preferences to the warmer climate of western Europe. For direct soil comparisons we had only 23 plots in each group. However, we confirmed that patches of *Triglochino maritimae-Glaucetum maritimae* are typical for organic soils with high organic matter and high total nitrogen content, while *Scorzonero parviflorae-Juncetum gerardii* prefer mineral soils. Moreover, we found significantly higher soil salinity and pH for *Scorzonero parviflorae-Juncetum gerardii*. This is in line with our results on species composition because we found distinct differences between these units, i.e. higher number of diagnostic species for preferring lower salinity *Triglochino maritimae-Glaucetum maritimae*. Unfortunately, we had only six plots classified as *Agrostio stoloniferae-Juncetum ranarii* association and none with soil data. That is why the environmental interpretation for this vegetation unit should be postponed for the future more extended research.

4.3. Biogeographic distribution of typical halophytic vegetation

The *Therosalicornietea* class is widespread in Europe. Apart from the sites considered in our study, which partially correspond to the areas analyzed by Dítě et al. (2022), research was carried out also, e.g., in Romania (Dítě et al., 2021), Croatia (Dítě et al., 2019), Italy (Tomaselli et al., 2020) and generally in Southeastern Europe (Dajić Stevanović et al., 2016). The class is also listed outside our continent, e.g., in Central Asia, near the salty lakes and at the dry bottoms of intermountain depressions of eastern Siberia (Korolyuk et al., 2017). All of these confirm this class as azonal vegetation. Locally quite common is *Salicornietum ramosissimae* association from this class, which occurs not only throughout almost the entire area of our research, but also, e.g., in coastal areas in southern Europe, Croatia (Dítě et al., 2019).

The *Festuco-Puccinellietea* class is definitely more widespread than the *Therosalicornietea*. It shows a greater variety of species, more complex dependence on the local environment and thus a more complex syntaxonomic system. Generally it represents halophytic-steppe communities on the solonetz soils of the inner regions of Eurasia (Yuritsyna, 2021). It occupies, e.g., slightly saline, moist and wet substrates along the depressions and inter-ridge lowlands in the floodplains of rivers and along the highways (Bulokhov, 2018). In the past, this class was not described in the inland salt marshes of Europe with a temperate climate. However, Mucina et al. (2016) provoked a new syntaxonomical approach of temperate inland salt marsh vegetation classified to the *Juncetea maritimi* class before. In the new vegetation classification system they distinguished three classes containing the vegetation of natural salt marshes: *Therosalicornietea*, *Juncetea maritimi* and *Festuco-Puccinellietea*. The *Therosalicornietea* class as pioneer vegetation of annual succulent halophytes is not under question. The *Juncetea maritimi* class is declared to contain perennial grasslands, herb-rich vegetation of coastal and inland-salt marshes but any order or alliance is dedicated to cover inland part of salt-marsh vegetation. The *Festuco-Puccinellietea* class in this system comprises two groups of orders from which one covers vegetation typical of flooded, moist/wet (mainly solonchak) soils in order *Scorzonero-Juncetalia gerardi* Vicherek 1973 and alliance *Juncion gerardi* Wendelberger 1943, which could include inland temperate salt marsh vegetation. Consequently, a similar approach is presented by other researchers in the temperate salt marshes of Europe (e.g., Dítě et al., 2021, 2022). Moreover, Dítě et al. (2022) based on data from the southern Baltic Sea coast and inland German salt marshes, proved the difference between inland salt marsh vegetation denoted as *Festuco-Puccinellietea* class and coastal vegetation representing *Juncetea maritimi* class. They are based on limited data sets not including environmental parameters and therefore, this syntaxonomical doubt can be thought as still open for future research and discussion. Regardless, the most common in this class is *Puccinellio-Spergularietum salinae* association. This name has been around for years and the authors of the plots in our database used it most frequently, see Table A.9. Interestingly, it was not noted in the latest study of salt marshes in North German Plain by Dítě et al. (2022), who classified this vegetation, rather to the *Puccinellietum limosae* Soó 1933 and *Atriplex prostrata* community, despite the large share of *S. marina*. The *Scorzonero parviflorae-Juncetum gerardii* association is also widespread in European inland salt marshes as shows research from the Balkans (Dítě et al., 2015) or individual countries – Romania (Dítě et al., 2021). In our dataset *Triglochino maritimae-Glaucetum maritimae* association has been documented only in Poland and Germany, as confirmed by the results of Dítě et al. (2022). Currently association is rather not listed in southern or western Europe, incl. in Romania (Dítě et al., 2021). This may be related to the local extinction of *T. maritima* and *G. maritima* (Danihelka et al., 2022), which was earlier noted also in inland positions of western Europe. The *Agrostio stoloniferae-Juncetum ranarii* association was recorded in our data set only on inland salt marshes in the United Kingdom and France. This association is typical of slightly moist, saline soils with frequently disturbed surfaces. It is reported also from dry areas of northern Bohemia (Ohře river basin) and southern Moravia (Eliáš et al., 2012; Novák and Šumberová, 2007).

4.4. Conservation and protection implications

As it was already mentioned inland salt marsh vegetation is protected under the Natura 2000 network. Two habitats, 1310 - *Salicornia* and other annuals colonizing mud and sand and *1340 - Inland salt meadows (*Glauco-Puccinellietalia*), were created. The vegetation included by us in the *Salicornietum ramosissimae* association is classified as representing habitat 1310 (Nienartowicz and Piernik, 2004b). The remaining analyzed associations from the *Festuco-Puccinellietea* class represent habitat *1340 (e.g., Nienartowicz and Piernik, 2004a). As it was proved by us, the most important environmental factors shaping inland salt marsh vegetation is salinity and moisture, frequently related to each other, because salty ground water can serve as the source of soil salinity both in natural and industry habitats (Piernik and Hulisz, 2011). Therefore, this vegetation is sensitive to any water regulations that can also change soil pH and organic matter decomposition. Moreover, the research by Čížková et al. (2020) showed that the water level has an impact on the abundance of individual species of halophytes in salt marshes. Some species grow both on moist and dry soils, such as *T. pannonicum* or *S. marina*, some on rather dry soils like *Melilotus dentatus*. Another significant factor is light availability, which proves necessity of management by regular mowing, as well as grazing livestock, which results in gnawing and trampling on plants and creation free spaces for annual species as *S. europaea* or *S. marina* (Bakker and De Vries, 1992). Grazing is most important for short species of halophytes such as *S. europaea*, *Suaeda maritima* and *G. maritima* (Jensen, 1985). Research shows that moderate grazing generally increases plant richness and diversity, while lack of grazing and overgrazing reduces the plant diversity and richness of salt marshes (Bouchard et al., 2003; Kiehl et al., 1996). That is why, it is also important to consider the appropriate density and species of herbivores, e.g., cattle, horses or sheep (Milotić et al., 2010; Nolte et al., 2014). Moreover, some species can be sensitive to mowing or grazing. As research on *Bolboschoenus martimus*-dominated vegetation in Europe show it covers inland wetlands in a broad range of both freshwater and saline habitats (Hroudová et al., 2009; Ljevnaić-Mašić et al., 2020). Therefore, it copes well with the salinity and high humidity of the soil, but is very threatened by mowing and grazing (Ljevnaić-Mašić et al., 2020). It should be taken into consideration if it is a target species for some areas.

The cessation of mowing or grazing usually results in a gradual overgrowing of the light-requiring halophyte associations (Wilkoń-Michalska, 1970) and formation of communities with higher species. In the case of high soil moisture, these are often reed communities of the *Phragmito-Magnocaricetea* class. As our results show, this may be a common and easy effect, because we classified over 12 % of samples into this class. The spreading of *P. australis* is a common and important problem (Burdick et al., 2001). Tall shoots of this species cover halophilous vegetation, which initially remain in the form of patches scattered in vast reeds, but then disappear (Bosiacka et al., 2011). Finally, it is worth emphasizing that the most important thing in effective protection is the appropriate involvement of people responsible for the protected areas, who will ensure the systematic conduct of active treatments (e.g., Lubińska-Mielińska et al., 2022). After all, there are known for years effective actions that imitate the traditional way of land use, which guarantee not only the maintenance, but also the improvement of the condition of the salt marsh vegetation (Brandes, 1999).

5. Conclusions

Our results demonstrates that in addition to *Therosalicornietea* and *Festuco-Puccinellietea* other vegetation classes, such as *Ruppietea maritimae*, *Polygono-Poetea annuae*, *Artemisietea vulgaris*, *Potamogetonetea*, *Bidentetea*, *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea*, are an integral part of temperate inland saline habitats and include halophytic species. These classes differ the most in terms of species preferences to salinity, soil moisture, light availability and soil nitrogen content. In addition, identified typical salt marsh associations differ also by soil reaction and soil organic matter content. This indicates a large diversity of the analyzed vegetation type, but also its sensitivity to changes in environmental conditions. Targeting biodiversity conservation and restoration these requirements should be taken into account.

CRediT authorship contribution statement

SLM – prepared first draft of publication, prepared and managed database, performed classification analyses, ZK – design the definitions of syntaxonomical units and performed classification, DK – supported classification designing and interpretation, JP – collected part of the data from France, CE – collected the part of the data from Germany, AP – supervised the project, prepared the rules for syntaxonomical units, collected part of the data from Poland and performed statistical vegetation-environment analysis. All authors substantially contributed to the final version of the manuscript.

Data availability statement

After acceptance of publication data will be available from the authors under request.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.159015.

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Vegetation of temperate inland salt-marshes reflects local environmental conditions

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Appendix A – supporting information to the paper:
Lubińska-Mielińska, S. et al. Vegetation of temperate inland salt-marshes reflects local environmental conditions

Table A.1 Bibliographic sources used to create the vegetation-plot database

No.	Biblioreference	*Polish Vegetation Database
1	Wilkoń-Michalska J. 1963. Halofity Kujaw. Stud. Soc. Scient. Tor. Sec. D (Botanica), 7.1: 1-121	-
2	Jackowiak B. 1983. Halofity okolic kopalni soli w Wapnie (woj. pilskie). Badania Fizjograficzne nad Polską Zachodnią. T. XXXIV. Ser. B (Botanika): 131-147	-
3	Trzcińska-Tacik H. 1988. Halofity nad dolną Nidą. Zes. Nauk. UJ. Prace Botan. 17:133-154	-
4	Brzeg A. 1998. Geobotaniczna charakterystyka planowanego rezerwatu częściowego "Łąki Pyzdrskie" w Nadwarciańskim Parku Krajobrazowym. Roczn. Nauk. PTOP "Salamandra" 2: 5-37	-
5	Jackowiak B. 1982. Występowanie Puccinelia distans (Jacq) Parl. na terenie miasta Poznania. Bad. Fizjogr. Pol. Zach. 33, ser. B, Botanika: 129-142	-
6	Kucharski L. 1996. Szata roślinna gleb hydrogenicznych Kujaw Południowych. III Zespoły i zbiorowiska roślinne łąk, torfowisk i zarośli. Acta Univ. Lodz., Folia bot. 11:33-63	-
7	Brandes D., Heimhold W., Ullrich H. 1973. Bericht uber die Excursionen der Floristisch-soziologischen Arbeitgemeinschaft wahrend der Tagung in Braunschweig. W: R.Tuxen, H. Dierschke (Herrausgegeben) Mitteilungen der Floristisch-soziologischen Arbeitsgemeinschaft. N.F. Heft 15/16 Todenmann-Gottingen	-
8	Janssen von Ch. 1986. Ökologische Untersuchungen an Binnensalzstellen in Südostniedersachsen. Phytocoenologia 14 (1): 109-142	-
9	Kucharski L. 1993. Szata roślinna gleb hydrogenicznych Kujaw Południowych. I Zespoły i zbiorowiska roślinne pochodzenia antropogenicznego. Acta Univ. Lodz., Folia bot. 10:69-92	-
10	Piernik A. 2012. Ecological pattern of inland salt marsh vegetation in Central Europe. Nicolaus Copernicus University Press. Toruń.	-
11	Kucharski L. 1996. Szata roślinna gleb hydrogenicznych Kujaw Południowych. II Zespoły i zbiorowiska szuwarowe. Acta Univ. Lodz., Folia bot. 11:3-32	-
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13	Gawenda-Kempczyńska D., Kamiński D. 2008. Gopło-Potrzymiech (unpublished)	-
14	Wilkoń-Michalska J. 1970. Zmiany sukcesyjne w rezerwacie halofitów Ciechocinek w latach 1954-1965. Zakład Ochrony Przyrody PAN. Ochr. Przyr. R. 35: 25-51	-
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Appendix A – supporting information to the paper:
Lubińska-Mielińska, S. et al. Vegetation of temperate inland salt-marshes reflects local environmental conditions

Fig. A.1 Geographical distribution of all vegetation-plot samples in the database

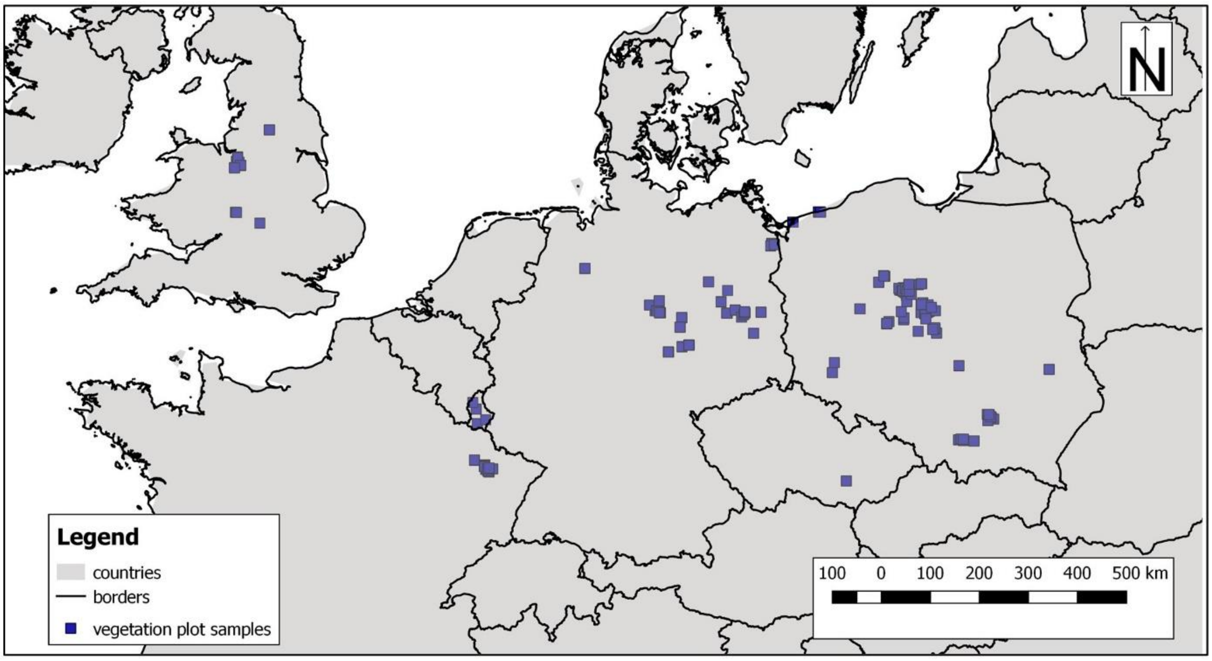

Table A.2 Shortened synoptic table with percentage frequency and fidelity index added in superscript for *Therosalicornietea* and *Festuco-Puccinellietea* classes. The values for diagnostic species (with fidelity index ≥25) within classes are marked in gray, for constant species (with percentage frequency ≥50%) have bold font, and for dominant species (with plant cover ≥25% and percentage frequency ≥20%) are marked with asterisk in superscript. Zero fidelity is assigned to species with insignificant fidelity to the cluster (Fisher's exact test at p>0.01). Abbreviations: THE – *Therosalicornietea*, FEP – *Festuco-Puccinellietea*.

↓ Species Classes →	**THE**	**FEP**
THEROSALICORNIETEA		
Salicornia europaea	**99**$^{\mathbf{88.9*}}$	12^{---}
Puccinellia distans	**81**$^{\mathbf{28.1}}$	**70**$^{\mathbf{20.1*}}$
Tripolium pannonicum	**50**$^{\mathbf{18.6}}$	39$^{10.4}$
Spergularia marina	49$^{34.6}$	36$^{21.5}$
Spergularia media	13$^{27.3}$	5^{---}
FESTUCO-PUCCINELIETEA		
Juncus gerardii	14^{---}	39$^{30.5}$

Appendix A – supporting information to the paper:
Lubińska-Mielińska, S. et al. Vegetation of temperate inland salt-marshes reflects local environmental conditions

Table A.3 Synoptic table (394 species) with fidelity index (phi coefficient) and percentage frequency for classes identified on salt marshes. The values for diagnostic species (with fidelity index ≥25) within classes are marked in gray, for constant species (with percentage frequency ≥50%) have bold font, and for dominant species (with plant cover ≥25% and percentage frequency ≥20%) are marked with asterisk in superscript. Zero fidelity is assigned to species with insignificant fidelity to the cluster (Fisher's exact test at p>0.01). Species meeting these criteria in the other classes are marked in the same manner. Species defined as Dg, Cs and Dm for *Therosalicornietea* and *Festuco-Puccinellietea* classes and associations identified on salt marshes, which passing to the other transitional classes noted on salt marshes are marked in yellow. Obligatory and facultative halophytes are marked in bold font according to Wilkoń-Michalska (1963). Abbreviations of vegetation classes: RUP – *Ruppietea maritimae*, THE – *Therosalicornietea*, FEP – *Festuco-Puccinellietea*, POL – *Polygono-Poetea annuae*, ART – *Artemisietea vulgaris*, POT – *Potamogetonetea*, BID – *Bidentetea*, PHR – *Phragmito-Magnocaricetea*, MOL – *Molinio-Arrhenatheretea*.

↓ Species	**Classes→**	**RUP**		**THE**		**FEP**		**POL**		**ART**		**POT**		**BID**		**PHR**		**MOL**	
Number of plots		**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
		fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
THEROSALICORNIETEA																			
Salicornia europaea		---	0	**88.9**	**99***	---	12	---	0	**---**	**7**	---	0	---	0	**---**	**1**	**---**	**1**
Spergularia marina		---	0	**34.6**	49	21.5	36	---	0	**---**	**7**	---	0	**---**	**27**	**---**	**10**	**---**	**1**
Puccinellia distans		---	0	**28.1**	**81**	20.1	**70***	41.7	100*	**---**	**21**	---	0	**---**	55	**---**	**31**	**---**	**18**
Spergularia media		---	0	**27.3**	13	---	5	---	0	---	0	---	0	---	0	---	1	---	0
FESTUCO-PUCCINELLIETEA																			
Juncus gerardii		---	0	---	14	**30.5**	39	---	0	**---**	**21**	---	0	**---**	**5**	**---**	**21**	**---**	**4**
RUPPIETEA MARITIMAE																			
Ruppia maritima		**100**	**100***	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0
Myriophyllum spicatum		**90.4**	**83**	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0
Zannichellia palustris		**50.8**	**67***	---	0	---	1	---	0	---	0	**50.8**	**67***	---	0	---	3	---	0
POLYGONO-POETEA ANNUAE																			
Chenopodium album agg.		---	0	---	0	---	3	**70**	**60**	---	0	---	0	---	5	---	1	---	0
Polygonum aviculare s. l.		---	0	---	0	---	14	**67.7**	**90***	---	14	---	0	---	18	---	7	---	13
Matricaria discoidea		---	0	---	0	---	2	**63.8**	**50**	---	0	---	0	---	5	---	0	---	0
Ochlopoa annua		---	0	---	0	---	6	**59.9**	**60**	---	0	---	0	---	5	---	0	8.8	17
Lolium perenne		---	0	---	0	---	10	**57.4**	**70**	---	0	---	0	---	18	---	0	12.7	26
Atriplex patula		---	0	---	1	---	1	**50.8**	40	---	7	---	0	---	0	---	4	---	0
Artemisia vulgaris		---	0	---	1	---	4	**47.9**	40	---	0	---	0	---	9	---	3	---	3
Achillea millefolium agg.		---	0	---	2	---	8	**43.9**	**50**	---	0	---	0	---	9	---	3	18.7	28
ARTEMISIETEA VULGARIS																			
Elytrigia repens		---	0	---	5	---	23	---	40	**58.5**	**100***	---	0	---	27	---	17	---	29

↓ Species **Classes→**	**RUP**		**THE**		**FEP**		**POL**		**ART**		**POT**		**BID**		**PHR**		**MOL**	
Number of plots	**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
	fidelity	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**
Galium aparine	---	0	---	0	---	1	---	0	**41.1**	21	---	0	---	0	---	1	---	1
Festuca rubra s. l.	---	0	---	0	---	11	---	0	**35.7**	43	---	0	---	0	---	11	**27.5**	36
Cirsium arvense	---	0	---	1	---	7	---	0	**34.5**	36	---	0	---	0	---	13	15.9	21
POTAMOGETONETEA																		
Ranunculus baudotii	---	0	---	0	---	1	---	0	---	0	**84.6**	**75***	---	0	---	1	---	0
Tripolium pannonicum	---	0	18.6	**50**	10.4	39	---	0	**---**	**14**	**59**	**100***	**---**	**14**	**---**	**17**	**---**	**4**
Bolboschoenus maritimus agg.	---	0	---	2	---	11	---	0	---	0	**58.8**	**92**	---	27	**29.5**	**57***	---	12
Ranunculus trichophyllus	---	0	---	0	---	0	---	0	---	0	**47.8**	25	---	0	---	0	---	0
Alopecurus geniculatus	---	0	---	0	---	5	---	0	---	0	**41.1**	42	---	14	---	11	---	8
BIDENTETEA																		
Atriplex prostrata s. l.	---	0	---	37	---	45	**---**	**10**	**---**	**50**	---	0	**49.4**	**100***	**---**	**47**	**---**	**16**
Holcus lanatus	---	0	---	0	---	4	---	0	---	0	---	0	**27.5**	18	---	1	---	9
Epilobium hirsutum	---	0	---	0	---	1	---	0	---	0	---	0	**27**	14	---	4	---	3
PHRAGMITO-MAGNOCARICETEA																		
Phragmites australis	---	0	---	15	---	28	---	0	---	14	---	0	---	36	**43.7**	74*	---	34
Schoenoplectus lacustris subsp. glaucus	---	0	---	0	---	11	---	0	---	7	---	0	---	5	**37.5**	38	---	17
Eleocharis palustris agg.	---	0	---	0	---	9	---	0	---	0	---	0	---	0	**31.3**	32	**30.5**	32
Carex disticha	---	0	---	0	---	1	---	0	---	0	---	0	---	0	**25.3**	10	---	3
MOLINIO-ARRHENATHERETEA																		
Potentilla anserina	---	0	---	0	---	28	---	0	---	7	---	0	---	0	20.7	37	**50.5**	67
Carex hirta	---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	1	**43.4**	24
Trifolium repens	---	0	---	0	---	8	---	20	---	0	---	0	---	0	---	1	**42.3**	39
Schedonorus arundinaceus	---	0	---	1	12.1	18	---	0	---	0	---	0	---	5	---	11	**41.7**	41
Ranunculus repens	---	0	---	0	---	7	---	0	---	0	---	0	---	9	---	14	**40.5**	38
Juncus articulatus	---	0	---	0	---	5	---	0	---	0	---	0	---	0	---	10	**39.6**	29
Trifolium fragiferum	---	0	---	0	16.9	21	---	0	---	0	---	0	---	5	---	10	**37.5**	37
Blysmus compressus	---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	5	**37.5**	22
Juncus compressus	---	0	---	1	---	20	---	0	---	7	---	0	---	5	---	28	**37.4**	46
Ranunculus acris	---	0	---	0	---	3	---	0	---	0	---	0	---	0	---	5	**36.7**	22
Cerastium fontanum subsp. vulgare	---	0	---	0	---	1	---	0	---	0	---	0	---	5	---	0	**35.8**	20

↓ Species	Classes→	RUP		THE		FEP		POL		ART		POT		BID		PHR		MOL	
Number of plots		**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
		fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Trifolium pratense s. l.		---	0	---	0	---	4	---	0	---	0	---	0	---	5	---	3	**34.7**	22
Equisetum palustre		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	6	**34.7**	20
Odontites vernus		---	0	---	1	---	7	---	0	---	0	---	0	---	5	---	1	**33.4**	22
Poa pratensis s. l.		---	0	---	1	---	10	---	0	---	29	---	0	---	0	---	6	**31.4**	34
Carex secalina		---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	0	**31.4**	13
Deschampsia cespitosa		---	0	---	1	---	6	---	0	---	7	---	0	---	5	---	7	**31**	26
Prunella vulgaris		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	**30.7**	12
Schedonorus pratensis		---	0	---	0	---	5	---	0	---	0	---	0	---	0	---	7	**29.4**	18
Agrostis gigantea		---	0	---	0	---	8	---	0	---	0	---	0	---	0	---	13	**29.2**	22
Scorzoneroides autumnalis		---	0	---	0	18.9	19	---	0	---	0	---	0	---	5	---	5	**28.5**	25
Potentilla reptans		---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	4	**28.1**	14
Carex vulpina s. l.		---	0	---	0	---	11	---	0	---	0	---	0	---	0	19.7	20	**27.6**	25
Equisetum arvense		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	**27.1**	9
Taraxacum sect. Ruderalia		---	0	---	0	4.4	17	---	30	---	14	---	0	---	9	---	6	**26.9**	38
Agrostis stolonifera		---	0	---	5	---	31	---	0	---	29	---	0	---	27	19.4	43	**26.8**	51
Bellis perennis		---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	2	**26.8**	12
Plantago major s. l.		---	0	---	0	---	14	---	40	---	14	---	0	---	5	---	11	**26.6**	39
Plantago media		---	0	---	0	---	3	---	0	---	0	---	0	---	0	---	2	**26.6**	12
Inula britannica		---	0	---	0	---	4	---	0	---	0	---	0	---	0	---	3	**26.3**	13
Carex nigra		---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	4	**25.6**	12
Carex distans		---	0	---	0	---	9	---	0	---	0	---	0	---	0	---	10	**25.4**	18
OTHER SPECIES																			
Achillea ptarmica		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Acorus calamus		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	15.3	3
Agrostis canina		---	0	---	1	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Agrostis capillaris		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Alchemilla vulgaris agg.		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Alisma plantago-aquatica		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Allium scorodoprasum		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Allium vineale		---	0	---	0	---	1	---	0	---	7	---	0	---	0	---	1	---	0

↓ Species Classes→	RUP		THE		FEP		POL		ART		POT		BID		PHR		MOL	
Number of plots	**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Alnus glutinosa	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Alopecurus aequalis	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Alopecurus bulbosus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	0
Alopecurus myosuroides	---	0	---	0	---	0	---	0	---	0	---	0	---	5	---	0	---	0
Alopecurus pratensis	---	0	---	0	---	1	---	0	---	0	---	0	---	5	---	3	---	1
Althaea officinalis	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	3	---	3
Amaranthus retroflexus	---	0	---	0	---	1	---	10	---	0	---	0	---	0	---	0	---	0
Anacamptis palustris	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	19	7
Anagallis arvensis	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	0
Angelica sylvestris	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Anthemis arvensis	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Anthoxanthum odoratum s. l.	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	1
Apera spica-venti	---	0	---	0	---	1	---	10	---	7	---	0	---	0	---	2	---	0
Apium graveolens	---	0	---	3	---	2	---	0	---	7	---	0	---	14	---	2	---	3
Arabidopsis arenosa	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Arctium tomentosum	---	0	---	0	---	0	---	10	---	0	---	0	---	0	---	0	---	3
Arrhenatherum elatius	---	0	---	0	---	0	---	0	---	7	---	0	---	0	---	1	---	3
Artemisia absinthium	---	0	---	0	---	1	---	0	---	0	---	0	---	5	---	0	---	0
Artemisia campestris s. l.	---	0	---	0	---	0	---	10	---	0	---	0	---	0	---	0	---	0
Artemisia maritima	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Atriplex sagittata	---	0	---	1	---	2	---	0	---	0	---	0	---	5	---	0	---	1
Atriplex tatarica	---	0	---	1	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Avena sativa	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Berteroa incana	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Berula erecta	---	0	---	0	---	1	---	0	---	0	---	0	---	0	20.2	6	---	1
Bidens cernuus	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Bidens frondosus	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Bidens melanocarpus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Bidens tripartitus	---	0	---	0	---	1	---	0	---	7	---	0	22.4	14	---	2	---	3
Blysmopsis rufa	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0

↓ Species	Classes→	RUP		THE		FEP		POL		ART		POT		BID		PHR		MOL	
Number of plots		**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
		fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Brachypodium sylvaticum		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Brassica napus		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Brassica nigra		---	0	---	0	---	0	---	0	---	0	---	0	---	5	---	0	---	0
Briza media		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Bromopsis inermis		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Bromus arvensis		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Bromus commutatus		---	0	---	0	---	1	---	0	---	0	---	0	---	5	---	1	---	0
Bromus hordeaceus		---	0	---	0	---	5	---	0	---	0	---	0	---	5	---	2	---	8
Bromus racemosus		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Buglossoides arvensis		---	0	---	0	---	0	---	0	---	0	---	0	---	5	---	0	---	0
Bupleurum tenuissimum		---	0	---	1	13.2	3	---	0	---	0	---	0	---	0	---	0	---	0
Calamagrostis canescens		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Calamagrostis epigejos		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	4	---	1
Calamagrostis neglecta		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Caltha palustris		---	0	---	0	---	1	---	0	---	0	---	0	---	0	18.5	7	---	4
Calystegia sepium		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	3	---	3
Capsella bursa-pastoris		---	0	---	0	---	1	---	10	---	0	---	0	---	5	---	0	---	1
Cardamine pratensis		---	0	---	0	---	1	---	0	---	0	---	0	---	0	16.2	4	---	1
Carduus sp.		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Carex acuta		---	0	---	0	---	1	---	0	---	0	---	0	---	0	21.5	8	---	3
Carex acutiformis		---	0	---	0	---	0	---	0	---	0	---	0	---	0	14.7	4	---	3
Carex caryophyllea		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Carex diandra		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Carex elata		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Carex flacca		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	3
Carex flava agg.		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	3
Carex hordeistichos		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Carex lasiocarpa		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Carex leporina		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Carex panicea		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	4

↓ Species	Classes→	RUP		THE		FEP		POL		ART		POT		BID		PHR		MOL	
Number of plots		**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
		fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Carex pseudocyperus		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Carex rostrata		---	0	---	0	---	0	---	0	---	0	---	0	---	0	17.9	4	---	0
Carex sp.		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Carex vesicaria		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	1
Carum carvi		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	3
Centaurea jacea agg.		---	0	---	0	---	2	---	0	---	0	---	0	---	5	---	1	14.5	7
Centaurea stoebe		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	20.2	5
Centaurium erythraea		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	15.3	3
Centaurium littorale		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Centaurium pulchellum		---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	2	---	5
Cerastium dubium		---	0	---	0	---	2	---	0	---	0	---	0	---	9	---	0	---	0
Cerastium glomeratum		---	0	---	0	---	1	---	0	---	0	---	0	---	5	---	0	---	1
Cerastium semidecandrum		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Chenopodium botryoides		---	0	---	0	---	1	---	0	---	0	---	0	---	9	---	4	---	1
Cichorium intybus		---	0	---	0	---	1	---	10	---	0	---	0	---	0	---	0	---	1
Cicuta virosa		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Cirsium canum		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Cirsium oleraceum		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Cirsium palustre		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	3
Cirsium vulgare		---	0	---	0	---	2	---	0	---	14	---	0	---	0	---	3	---	5
Cladium mariscus		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Colchicum autumnale		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Comarum palustre		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Convolvulus arvensis		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Corispermum hyssopifolium		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Crepis biennis		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	3
Crepis capillaris		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Crepis sp.		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Cuscuta sp.		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Cynosurus cristatus		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	3

↓ **Species**	**Classes→**	**RUP**		**THE**		**FEP**		**POL**		**ART**		**POT**		**BID**		**PHR**		**MOL**	
Number of plots		**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
		fidelity	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**
Dactylis glomerata		---	0	---	0	---	2	---	0	---	14	---	0	---	0	---	1	---	7
Dactylorhiza incarnata		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	1
Dactylorhiza majalis s. l.		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	1
Danthonia decumbens		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Daucus carota		---	0	---	1	10.4	8	---	0	---	0	---	0	---	9	---	3	---	7
Descurainia sophia		---	0	---	0	---	0	---	10	---	0	---	0	---	0	---	0	---	0
Dianthus superbus		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Dipsacus fullonum		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Draba verna		---	0	---	0	---	1	---	0	---	0	---	0	---	5	---	0	---	0
Echinochloa crus-galli		---	0	---	0	---	2	---	10	---	0	---	0	---	0	---	2	---	1
Echinocystis lobata		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Eleocharis quinqueflora		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Elytrigia intermedia		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Epilobium palustre		---	0	---	0	---	1	---	0	---	7	---	0	---	0	---	4	---	0
Epilobium parviflorum		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	0
Epilobium sp.		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Epilobium tetragonum		---	0	---	0	---	4	---	0	---	14	---	0	---	0	---	3	---	0
Epipactis palustris		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Equisetum fluviatile		---	0	---	0	---	0	---	0	---	0	---	0	---	0	15.5	3	---	0
Erigeron canadensis		---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	0	---	5
Eriophorum angustifolium		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Eriophorum latifolium		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Eryngium planum		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Eupatorium cannabinum		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	2	---	3
Euphorbia helioscopia		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Euphorbia lucida		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Euphrasia stricta		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Fallopia convolvulus		---	0	---	0	---	0	---	10	---	0	---	0	---	0	---	0	---	0
Festuca ovina agg.		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Filipendula ulmaria		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0

↓ Species Classes→	RUP		THE		FEP		POL		ART		POT		BID		PHR		MOL	
Number of plots	**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Frangula alnus	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Fumaria officinalis	---	0	---	0	---	0	---	0	---	0	---	0	---	5	---	0	---	0
Galinsoga parviflora	---	0	---	0	---	0	---	10	---	0	---	0	---	0	---	0	---	0
Galinsoga quadriradiata	---	0	---	0	---	0	---	10	---	0	---	0	---	0	---	0	---	0
Galium mollugo agg.	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Galium palustre agg.	---	0	---	0	---	2	---	0	---	0	---	0	---	0	24.4	14	---	9
Galium uliginosum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	3
Galium verum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	23.4	7
Geranium pratense	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	19.6	5
Glaux maritima	---	0	---	7	22.7	27	---	0	**---**	**14**	---	0	---	0	**---**	**15**	**---**	**17**
Glechoma hederacea	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	18.8	4
Glyceria fluitans	---	0	---	0	---	1	---	0	---	0	---	0	---	0	20.6	6	---	1
Glyceria maxima	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Glyceria notata	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Gnaphalium uliginosum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Gypsophila perfoliata	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0	---	0
Gypsophila sp.	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Halimione pedunculata	---	0	18.9	5	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Helosciadium nodiflorum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Heracleum sphondylium s. l.	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	3
Hieracium umbellatum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Holcus mollis	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Hordeum jubatum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Hordeum secalinum	---	0	---	0	---	3	---	0	---	14	---	0	---	0	---	3	---	0
Hordeum vulgare	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Humulus lupulus	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Hutchinsia sp.	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0	---	0
Hydrocotyle vulgaris	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	3	---	3
Hypericum maculatum	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Hypericum perforatum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0

↓ Species Classes→	RUP		THE		FEP		POL		ART		POT		BID		PHR		MOL	
Number of plots	6		137		485		10		14		12		22		112		76	
	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Hypochaeris radicata	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Iris pseudacorus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	4	17.7	7
Jacobaea aquatica	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Jacobaea erratica	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Jacobaea vulgaris	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Juncus alpinoarticulatus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Juncus bufonius	---	0	---	0	---	3	---	10	---	0	---	0	---	0	---	3	---	3
Juncus conglomeratus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Juncus effusus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Juncus inflexus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	3	18.6	7
Juncus ranarius	---	0	---	0	11.9	7	---	0	---	0	---	0	---	0	---	6	---	5
Juncus sp.	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Juncus subnodulosus	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Juncus tenuis	---	0	---	0	---	1	---	10	---	0	---	0	---	0	---	0	---	0
Lactuca serriola	---	0	---	1	---	2	---	10	---	0	---	0	---	5	---	0	---	0
Lamium album	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Lathyrus palustris	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	1
Lathyrus pratensis	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	1
Lathyrus tuberosus	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Lemna minor	---	0	---	0	---	1	---	0	---	0	---	0	---	0	19.4	4	---	0
Leontodon hastilis	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Leontodon hispidus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	3
Leontodon saxatilis	---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	0	---	4
Lepidium ruderale	---	0	---	4	---	5	---	20	---	0	---	0	---	5	---	0	---	1
Leucanthemum vulgare s. l.	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Linum catharticum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	18.2	4
Linum usitatissimum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Lolium multiflorum	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	15.3	3
Lotus corniculatus	---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	2	20.5	8
Lotus maritimus	---	0	---	0	---	2	---	0	---	0	---	0	---	5	---	2	---	7

↓ Species	Classes→	RUP		THE		FEP		POL		ART		POT		BID		PHR		MOL	
Number of plots		**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
		fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Lotus pedunculatus		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	18.8	5
Lotus tenuis		---	0	---	0	23.7	16	---	0	---	0	---	0	---	5	---	4	---	9
Lycopus europaeus		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	4	23	9
Lysimachia nummularia		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	1
Lysimachia vulgaris		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	16	4
Lythrum salicaria		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	4	---	5
Malva neglecta		---	0	---	0	---	1	---	10	---	0	---	0	---	0	---	0	---	0
Matricaria chamomilla		---	0	---	0	---	2	---	0	---	0	---	0	---	9	---	0	---	0
Medicago falcata		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Medicago lupulina		---	0	---	0	---	4	---	10	---	0	---	0	---	9	---	2	23.9	20
Medicago polymorpha		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Medicago sativa		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Medicago sp.		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Melilotus albus		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	1
Melilotus altissima		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Melilotus dentatus		---	0	---	0	---	6	---	0	---	7	---	0	---	5	---	9	---	7
Melilotus officinalis		---	0	---	0	---	2	---	0	---	7	---	0	---	5	---	0	---	1
Mentha aquatica		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	4	---	4
Mentha arvensis		---	0	---	0	---	4	---	0	---	0	---	0	---	0	---	4	---	8
Mentha longifolia		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Mentha x verticillata		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	15.3	3
Mercurialis annua		---	0	---	0	---	1	---	0	---	7	---	0	---	0	---	0	---	0
Molinia caerulea s. l.		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	3
Myosotis scorpioides s. l.		---	0	---	0	---	1	---	0	---	0	---	0	---	0	16.5	4	---	1
Myosoton aquaticum		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	3
Myosurus minimus		---	0	---	0	---	1	---	0	---	0	---	0	---	9	---	0	---	0
Odontites litoralis		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Oenanthe aquatica		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Oenanthe fistulosa		---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Ononis spinosa		---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1

↓ **Species** **Classes**→	**RUP**		**THE**		**FEP**		**POL**		**ART**		**POT**		**BID**		**PHR**		**MOL**	
Number of plots	**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
	fidelity	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**
Ononis spinosa subsp. hircina	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Ophioglossum vulgatum	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Oxybasis glauca	---	0	---	1	---	5	---	10	---	0	---	0	---	9	---	4	---	0
Oxybasis rubra	---	0	---	1	---	3	---	10	---	0	---	0	---	9	---	3	---	0
Oxybasis urbica	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Parnassia palustris	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Pastinaca sativa	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	21.2	5
Pedicularis palustris	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Persicaria amphibia	---	0	---	0	---	1	---	0	---	0	---	0	---	0	20.6	6	---	1
Persicaria hydropiper	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Persicaria lapathifolia s. l.	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	1
Persicaria maculosa	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	0
Petasites albus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Peucedanum palustre	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Phalaroides arundinacea	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	3	---	3
Phleum pratense	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	4
Picris hieracioides	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Pilosella officinarum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Pimpinella major	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Pimpinella saxifraga	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	18.2	4
Pinguicula vulgaris	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Plantago lanceolata	---	0	---	0	---	5	---	20	---	0	---	0	---	0	---	1	23.8	20
Plantago major subsp. intermedia	---	0	---	1	16.1	14	---	0	---	0	---	0	---	0	---	12	---	14
Plantago major subsp. winteri	---	0	---	2	12	5	---	0	---	0	---	0	---	0	---	4	---	1
Plantago maritima	---	0	---	4	14.9	6	---	0	---	0	---	0	---	0	---	1	---	0
Plantago sp.	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Poa compressa	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Poa palustris	---	0	---	0	---	0	---	0	---	0	---	0	---	0	14.7	4	---	3
Poa trivialis	---	0	---	0	---	6	---	0	---	14	---	0	---	9	---	5	15.8	16
Portulaca oleracea subsp. sativa	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0

↓ Species Classes→	RUP		THE		FEP		POL		ART		POT		BID		PHR		MOL	
Number of plots	**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Prunus spinosa	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Pulicaria dysenterica	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	0
Ranunculus bulbosus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	3
Ranunculus flammula	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	1
Ranunculus lingua	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Ranunculus sardous	---	0	---	0	5.6	4	---	0	---	0	---	0	---	9	---	0	---	1
Ranunculus sceleratus	---	0	---	0	---	2	---	0	---	7	---	0	---	9	---	5	---	3
Reseda luteola	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0	---	0
Rhinanthus angustifolius	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	20.7	5
Rorippa amphibia	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	1
Rorippa palustris	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Rorippa sylvestris	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Rubus caesius	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	15.3	3
Rumex acetosa	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	4
Rumex conglomeratus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	16.1	4	---	0
Rumex crispus	---	0	---	0	---	6	---	0	---	21	---	0	---	18	---	7	---	13
Rumex hydrolapathum	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	2	---	1
Rumex maritimus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	17.2	4	---	0
Rumex obtusifolius	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Rumex thyrsiflorus	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Sagina nodosa	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Sagina procumbens	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Salix cinerea	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Salvia pratensis	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Samolus valerandi	---	0	---	0	---	1	---	0	---	0	---	0	---	0	18.9	6	---	1
Sanguisorba officinalis	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Scirpus sylvaticus	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	15.3	3
Scorzonera laciniata	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Scrophularia nodosa	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Scutellaria galericulata	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1

↓ Species Classes→	RUP		THE		FEP		POL		ART		POT		BID		PHR		MOL	
Number of plots	**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Secale cereale	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Selinum carvifolia	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	15.3	3
Selinum dubium	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Senecio leucanthemifolius	---	0	---	0	---	1	---	0	---	7	---	0	---	0	---	0	---	0
Senecio vulgaris	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Serratula tinctoria	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	15.3	3
Setaria pumila	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Silaum silaus	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	2	---	0
Silene flos-cuculi	---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	4	---	4
Silene latifolia	---	0	---	1	---	0	---	0	---	0	---	0	---	5	---	0	---	0
Silybum marianum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Sisymbrium loeselii	---	0	---	0	---	1	---	10	---	0	---	0	---	0	---	0	---	0
Sium latifolium	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	2	---	0
Solanum dulcamara	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Sonchus arvensis	---	0	---	0	10.6	14	---	0	---	14	---	0	---	5	---	13	---	12
Sonchus asper	---	0	---	0	---	1	---	0	---	0	---	0	---	5	---	0	---	3
Sonchus oleraceus	---	0	---	4	---	5	---	10	---	14	---	0	---	14	---	4	---	4
Sonchus sp.	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Sparganium erectum agg.	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Stellaria media s. l.	---	0	---	0	---	0	---	0	---	0	---	0	---	5	---	1	---	0
Stellaria palustris	---	0	---	0	---	1	---	0	---	0	---	0	---	0	17.2	4	---	0
Suaeda maritima	---	0	20.4	9	---	1	---	0	---	0	---	0	---	5	---	0	---	0
Succisa pratensis	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Symphytum officinale	---	0	---	0	---	1	---	0	---	0	---	0	---	0	14.4	4	---	3
Tanacetum vulgare	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Taraxacum sect. Palustria	---	0	---	0	11.2	6	---	0	---	0	---	0	---	0	---	4	---	7
Taraxacum sp.	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	2	---	1
Tephroseris palustris	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Teucrium scordium	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Thalictrum flavum	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	19.6	5

↓ Species **Classes→**	**RUP**		**THE**		**FEP**		**POL**		**ART**		**POT**		**BID**		**PHR**		**MOL**	
Number of plots	**6**		**137**		**485**		**10**		**14**		**12**		**22**		**112**		**76**	
	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Thlaspi arvense	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Torilis japonica	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Trifolium dubium	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	19	5
Trifolium hybridum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	3
Trifolium patens	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Triglochin maritima	---	0	---	23	21.8	38	---	0	**---**	**7**	**---**	**8**	---	0	**---**	**33**	**---**	**29**
Triglochin palustris	---	0	---	1	---	5	---	0	---	0	---	0	---	0	---	5	24.1	14
Tripleurospermum inodorum agg.	---	0	---	1	---	7	---	0	---	7	---	0	---	14	---	4	---	4
Triticum aestivum	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Tussilago farfara	---	0	---	1	---	2	---	0	---	0	---	0	---	0	---	1	18.6	7
Typha latifolia	---	0	---	0	---	0	---	0	---	0	---	0	---	5	10	4	---	0
Urtica dioica	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	3
Utricularia vulgaris s. l.	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1	---	0
Valeriana dioica	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	0	---	1
Veronica arvensis	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Veronica scutellata	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	1	---	0
Vicia cracca	---	0	---	0	---	2	---	0	---	0	---	0	---	0	---	4	---	7
Vicia grandiflora	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Vicia hirsuta	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	1
Vicia sepium	---	0	---	0	---	1	---	0	---	0	---	0	---	0	---	0	---	0
Vicia tetrasperma	---	0	---	0	---	1	---	0	---	7	---	0	---	0	---	0	---	1
Viola arvensis	---	0	---	0	---	0	---	10	---	0	---	0	---	0	---	0	---	0

Table A.4 Synoptic table (219 species) with fidelity index (phi coefficient) and percentage frequency for associations identified on salt marshes. The values for diagnostic species (with fidelity index ≥25 and percentage frequency ≥50%) within associations are marked in gray, for constant species (with percentage frequency ≥50%) have bold font, and for dominant species (with plant cover ≥25% and percentage frequency ≥20%) are marked with asterisk in superscript. Zero fidelity is assigned to species with insignificant fidelity to the cluster (Fisher's exact test at p>0.01). Abbreviations of vegetation associations: Se – *Salicornietum ramosissimae*, P-Ss – *Puccinellio-Spergularietum salinae*, Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii*, Tm-Gm – *Triglochino maritimae-Glaucetum maritimae*, As-Jr – *Agrostio stoloniferae-Juncetum ranarii*.

↓ Species **Associations →**	**Se**		**P-Ss**		**Sp-Jg**		**Tm-Gm**		**As-Jr**	
Number of plots	**133**		**134**		**121**		**56**		**6**	
	fidelity	**% frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**
THEROSALICORNIETEA										
Salicornietum ramosissimae										
Salicornia europaea	**83.7**	**100***	---	18	---	10	---	4	---	0
FESTUCO-PUCCINELLIETEA										
Scorzonero parviflorae-Juncetum gerardii										
Juncus gerardii	---	13	---	10	**62.5**	**100***	---	39	---	33
Agrostio stoloniferae-Juncetum ranarii										
Juncus ranarius	---	0	---	9	---	4	---	5	**89.7**	**100***
Oxybasis rubra	---	1	---	4	---	1	---	0	**62.1**	**50**
Tripolium pannonicum	---	49	---	29	1.6	**55**	---	36	**46.3**	**100**
Agrostis stolonifera	---	5	---	15	5	40	13.9	48	---	**67**
Triglochino maritimae-Glaucetum maritimae										
Glaux maritima	---	7	---	7	---	32	**72.8**	**93***	---	0
Triglochin maritima	---	23	---	10	12.2	48	**66.4**	**100***	---	0
Juncus compressus	---	2	---	15	---	7	**59.8**	**63**	---	0
Potentilla anserina	---	0	---	12	8.3	26	**51.3**	**61**	---	0
Phragmites australis	---	16	---	15	7.4	36	**38**	**64**	---	17
Puccinellio-Spergularietum salinae										
Spergularia marina	---	**50**	**47**	**100***	---	13	---	2	---	**100**
Puccinellia distans	7.8	**80**	**30**	**100***	---	36	---	**52**	---	**100***
Atriplex prostrata s. l.	---	38	**32.6**	**72**	---	39	---	34	---	17
Other species										
Achillea millefolium agg.	---	2	16	10	---	2	---	5	---	0

↓ Species	**Associations →**	**Se**		**P-Ss**		**Sp-Jg**		**Tm-Gm**		**As-Jr**	
Number of plots		**133**		**134**		**121**		**56**		**6**	
		fidelity	**% frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**
Achillea ptarmica		---	0	---	0	---	1	---	2	---	0
Agrostis canina		---	2	---	1	---	0	---	0	---	0
Agrostis capillaris		---	0	---	0	---	0	---	2	---	0
Agrostis gigantea		---	0	---	6	---	5	32.5	23	---	0
Allium vineale		---	0	---	0	---	2	---	0	---	0
Alnus glutinosa		---	0	---	1	---	0	---	0	---	0
Alopecurus bulbosus		---	0	---	0	16.3	3	---	0	---	0
Alopecurus geniculatus		---	0	---	5	18.7	9	---	0	---	0
Althaea officinalis		---	0	---	1	16.1	4	---	0	---	0
Anacamptis palustris		---	0	---	0	---	0	27	9	---	0
Anagallis arvensis		---	0	---	1	---	0	---	0	---	0
Apera spica-venti		---	0	15.5	3	---	0	---	0	---	0
Apium graveolens		---	3	---	1	---	2	---	4	---	0
Artemisia absinthium		---	0	---	1	---	0	---	0	---	0
Artemisia maritima		---	0	---	0	21.6	6	---	0	---	0
Artemisia vulgaris		---	1	---	3	---	0	---	0	---	0
Atriplex patula		---	2	---	0	---	0	---	0	---	0
Atriplex sagittata		---	2	18.4	6	---	0	---	0	---	0
Atriplex tatarica		---	1	---	0	---	0	---	0	---	0
Avena sativa		---	0	---	1	---	0	---	0	---	0
Bellis perennis		---	0	---	1	---	2	---	2	---	0
Berula erecta		---	0	---	0	---	2	---	0	---	0
Bidens tripartitus		---	0	19	4	---	0	---	0	---	0
Blysmopsis rufa		---	0	---	0	---	1	---	4	---	0
Blysmus compressus		---	0	---	0	---	2	19	7	---	0
Bolboschoenus maritimus agg.		---	2	---	6	9	16	---	11	---	17
Bromus arvensis		---	0	---	1	---	0	---	0	---	0
Bromus commutatus		---	0	---	1	---	2	---	0	---	0
Bromus hordeaceus		---	0	---	1	---	6	---	9	---	17
Bupleurum tenuissimum		---	0	---	4	---	3	---	0	---	0

↓ Species Associations →	Se		P-Ss		Sp-Jg		Tm-Gm		As-Jr	
Number of plots	133		134		121		56		6	
	fidelity	% frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Calamagrostis epigejos	---	0	15.5	3	---	0	---	0	---	0
Calystegia sepium	---	0	---	0	---	1	---	0	---	0
Capsella bursa-pastoris	---	0	---	2	---	0	---	0	---	0
Cardamine pratensis	---	0	---	0	---	2	---	0	---	0
Carduus sp.	---	0	---	1	---	0	---	0	---	0
Carex acuta	---	0	---	0	---	0	---	4	---	0
Carex distans	---	0	---	1	---	10	37.9	29	---	0
Carex flava agg.	---	0	---	0	---	1	---	4	---	0
Carex hirta	---	0	---	0	---	2	---	0	---	0
Carex hordeistichos	---	0	---	0	---	2	---	0	---	0
Carex leporina	---	0	---	0	---	2	---	0	---	0
Carex nigra	---	0	---	0	---	2	---	4	---	0
Carex panicea	---	0	---	0	---	2	---	2	---	0
Carex vulpina s. l.	---	0	---	1	16.6	18	28.6	25	---	0
Centaurea jacea agg.	---	0	---	0	---	1	18.6	5	---	0
Centaurea stoebe	---	0	---	0	---	0	---	2	---	0
Centaurium littorale	---	0	---	0	20	5	---	0	---	0
Centaurium pulchellum	---	0	---	1	---	3	---	2	---	0
Cerastium dubium	---	0	---	0	28.5	10	---	0	---	0
Cerastium fontanum subsp. vulgare	---	0	---	1	---	1	---	0	---	0
Cerastium glomeratum	---	0	---	0	---	1	---	0	---	0
Cerastium semidecandrum	---	0	---	1	---	1	---	0	---	0
Chenopodium botryoides	---	0	---	1	---	0	---	0	---	0
Cichorium intybus	---	0	---	1	---	1	---	0	---	0
Cirsium arvense	---	1	---	2	---	2	---	2	---	17
Cirsium canum	---	0	---	0	---	1	---	0	---	0
Cirsium palustre	---	0	---	0	---	1	---	4	---	0
Cirsium vulgare	---	0	---	1	---	0	---	0	---	0
Crepis sp.	---	0	---	1	---	0	---	0	---	0
Cynosurus cristatus	---	0	---	0	---	1	---	0	---	0

↓ Species Associations →	Se		P-Ss		Sp-Jg		Tm-Gm		As-Jr	
Number of plots	133		134		121		56		6	
	fidelity	% frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Dactylis glomerata	---	0	---	2	---	0	---	0	---	0
Daucus carota	---	1	14.9	9	---	4	---	4	---	0
Deschampsia cespitosa	---	1	---	2	---	4	---	9	---	0
Draba verna	---	0	---	0	---	1	---	0	---	0
Echinochloa crus-galli	---	0	15.5	3	---	0	---	0	---	0
Eleocharis palustris agg.	---	0	---	0	6.9	12	39	30	---	0
Elytrigia intermedia	---	0	---	0	---	1	---	2	---	0
Elytrigia repens	---	4	---	23	20.4	26	---	11	---	0
Epilobium hirsutum	---	0	---	0	---	1	---	0	---	17
Epilobium palustre	---	0	---	1	---	1	---	4	---	0
Epilobium parviflorum	---	0	---	0	---	0	---	2	---	0
Epilobium tetragonum	---	0	---	1	12.4	12	---	0	---	17
Equisetum palustre	---	0	---	0	---	1	---	2	---	0
Erigeron canadensis	---	0	---	2	---	0	---	0	---	0
Euphorbia lucida	---	0	---	0	---	0	---	2	---	0
Festuca ovina agg.	---	0	---	1	---	0	---	0	---	0
Festuca rubra s. l.	---	0	---	4	---	12	26.5	21	---	0
Galium palustre agg.	---	0	---	0	---	3	---	5	---	0
Galium uliginosum	---	0	---	0	---	2	---	0	---	0
Glyceria fluitans	---	0	---	0	---	1	---	0	---	0
Glyceria notata	---	0	---	0	---	0	---	0	---	17
Gnaphalium uliginosum	---	0	---	1	---	0	---	0	---	0
Gypsophila perfoliata	---	1	---	0	---	0	---	0	---	0
Halimione pedunculata	16.8	5	---	0	---	1	---	0	---	0
Helosciadium nodiflorum	---	0	---	0	---	1	---	0	---	0
Hieracium umbellatum	---	0	---	0	---	0	---	2	---	0
Holcus lanatus	---	0	---	2	18.4	7	---	0	---	0
Holcus mollis	---	0	---	0	---	2	---	2	---	0
Hordeum jubatum	---	0	---	3	---	2	---	0	---	0
Hordeum secalinum	---	0	---	1	8	9	---	0	---	17

↓ Species	**Associations →**	**Se**		**P-Ss**		**Sp-Jg**		**Tm-Gm**		**As-Jr**	
Number of plots		**133**		**134**		**121**		**56**		**6**	
		fidelity	**% frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**
Hordeum vulgare		---	0	---	1	---	0	---	0	---	0
Hutchinsia sp.		---	1	---	0	---	0	---	0	---	0
Inula britannica		---	0	---	3	---	1	---	5	---	0
Iris pseudacorus		---	0	---	0	---	1	---	0	---	0
Jacobaea aquatica		---	0	---	0	---	1	---	0	---	0
Jacobaea vulgaris		---	0	---	0	16.3	3	---	0	---	0
Juncus alpinoarticulatus		---	0	---	0	---	0	---	4	---	0
Juncus articulatus		---	0	---	0	14.7	9	---	9	---	0
Juncus bufonius		---	0	19.4	7	---	0	---	2	---	0
Juncus conglomeratus		---	0	---	0	---	1	---	0	---	0
Juncus effusus		---	0	---	0	---	2	---	4	---	0
Juncus inflexus		---	0	---	1	---	2	---	0	---	0
Juncus sp.		---	0	---	1	---	0	---	0	---	0
Juncus tenuis		---	0	---	1	---	0	---	0	---	0
Lactuca serriola		---	2	---	2	---	0	---	0	---	0
Lathyrus pratensis		---	0	---	0	---	1	---	0	---	0
Lemna minor		---	0	---	1	---	0	---	0	---	0
Leontodon hastilis		---	0	---	1	---	0	---	0	---	0
Leontodon hispidus		---	0	---	0	---	1	---	0	---	0
Leontodon saxatilis		---	0	---	3	---	2	---	0	---	0
Lepidium ruderale		---	3	20.1	8	---	0	---	0	---	0
Leucanthemum vulgare s. l.		---	0	---	1	---	0	---	0	---	0
Lolium perenne		---	0	---	7	---	4	---	7	---	17
Lotus corniculatus		---	0	---	1	---	0	18.8	5	---	0
Lotus maritimus		---	0	---	2	---	0	---	2	---	0
Lotus pedunculatus		---	0	---	0	---	0	---	2	---	0
Lotus tenuis		---	0	---	7	13.9	26	19.2	30	---	17
Lycopus europaeus		---	0	---	0	---	0	---	2	---	0
Lysimachia nummularia		---	0	---	0	---	2	---	0	---	0
Lythrum salicaria		---	0	---	0	---	1	18.6	5	---	0

↓ Species Associations →	Se		P-Ss		Sp-Jg		Tm-Gm		As-Jr	
Number of plots	133		134		121		56		6	
	fidelity	% frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Matricaria chamomilla	---	0	---	3	---	0	---	0	---	17
Medicago lupulina	---	0	19.9	6	---	1	---	0	---	0
Medicago polymorpha	---	0	---	1	---	0	---	0	---	0
Melilotus albus	---	0	---	1	---	0	---	0	---	0
Melilotus altissima	---	0	---	0	---	0	---	0	---	17
Melilotus dentatus	---	0	---	4	---	3	---	9	---	0
Melilotus officinalis	---	0	---	2	---	0	---	2	---	0
Mentha aquatica	---	0	---	0	---	1	---	0	---	0
Mentha arvensis	---	0	---	1	---	2	24.1	11	---	0
Myosotis scorpioides s. l.	---	0	---	0	---	0	---	2	---	0
Myosoton aquaticum	---	0	---	1	---	0	---	0	---	0
Myosurus minimus	---	0	---	3	---	1	---	0	---	0
Ochlopoa annua	---	0	---	4	---	1	---	2	---	0
Odontites litoralis	---	0	---	0	---	2	---	4	---	0
Odontites vernus	---	1	---	4	---	8	---	13	---	0
Oxybasis glauca	---	2	19.9	7	---	0	---	0	---	0
Oxybasis urbica	---	0	---	0	---	0	---	2	---	0
Parnassia palustris	---	0	---	0	---	0	---	2	---	0
Persicaria lapathifolia s. l.	---	0	---	1	---	0	---	0	---	0
Persicaria maculosa	---	0	---	1	---	0	---	0	---	0
Plantago lanceolata	---	0	---	5	---	2	---	2	---	0
Plantago major s. l.	---	0	---	8	---	7	---	13	---	33
Plantago major subsp. intermedia	---	2	---	13	---	4	37.9	34	---	0
Plantago major subsp. winteri	---	2	---	0	---	10	24.9	18	---	0
Plantago maritima	---	4	---	2	20.4	14	---	5	---	0
Plantago media	---	0	---	0	---	1	---	4	---	0
Plantago sp.	---	0	---	1	---	0	---	2	---	0
Poa compressa	---	0	---	1	---	0	---	0	---	0
Poa pratensis s. l.	---	2	---	2	26	19	---	9	---	0
Poa trivialis	---	0	---	1	10.3	13	---	7	---	17

↓ Species Associations →	Se		P-Ss		Sp-Jg		Tm-Gm		As-Jr	
Number of plots	133		134		121		56		6	
	fidelity	% frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency	fidelity	%frequency
Polygonum aviculare s. l.	---	0	7.4	16	---	2	---	4	---	33
Potentilla reptans	---	0	---	2	---	3	---	2	---	0
Prunella vulgaris	---	0	---	0	---	1	---	2	---	0
Pulicaria dysenterica	---	0	---	0	16.3	3	---	0	---	0
Ranunculus acris	---	0	---	0	---	2	---	5	---	0
Ranunculus flammula	---	0	---	1	---	0	---	0	---	0
Ranunculus repens	---	0	---	2	20.1	12	---	5	---	0
Ranunculus sardous	---	0	---	1	25.2	11	---	2	---	0
Ranunculus sceleratus	---	0	---	4	---	0	---	2	---	17
Reseda luteola	---	1	---	0	---	0	---	0	---	0
Rorippa amphibia	---	0	---	0	---	1	---	0	---	0
Rumex conglomeratus	---	0	---	1	---	1	---	0	---	0
Rumex crispus	---	0	---	2	21.5	8	---	0	---	0
Rumex obtusifolius	---	0	---	1	---	0	---	0	---	0
Rumex thyrsiflorus	---	0	---	0	---	0	---	2	---	0
Sagina nodosa	---	0	---	1	---	0	---	0	---	0
Sagina procumbens	---	0	---	0	---	1	---	0	---	0
Samolus valerandi	---	0	---	1	---	2	---	4	---	0
Schedonorus arundinaceus	---	1	---	7	12.2	26	24.4	36	---	17
Schedonorus pratensis	---	0	---	1	---	7	18.3	11	---	0
Schoenoplectus lacustris subsp. glaucus	---	0	---	1	---	15	21.6	32	---	33
Scorzonera laciniata	---	0	---	0	---	1	---	0	---	0
Scorzoneroides autumnalis	---	0	---	9	---	15	41.8	41	---	0
Scutellaria galericulata	---	0	---	0	---	0	---	2	---	0
Senecio vulgaris	---	0	---	1	---	0	---	0	---	0
Silene flos-cuculi	---	0	---	0	17.5	6	---	2	---	0
Silene latifolia	---	1	---	0	---	0	---	0	---	0
Sonchus arvensis	---	0	---	7	---	9	26.6	38	---	33
Sonchus asper	---	0	---	1	---	0	---	0	---	0
Sonchus oleraceus	---	5	---	7	---	0	---	5	---	0

↓ **Species**	**Associations →**	**Se**		**P-Ss**		**Sp-Jg**		**Tm-Gm**		**As-Jr**	
Number of plots		**133**		**134**		**121**		**56**		**6**	
		fidelity	**% frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**	**fidelity**	**%frequency**
Sonchus sp.		---	0	---	0	---	1	---	0	---	0
Spergularia media		---	11	---	2	---	10	---	2	---	0
Stellaria palustris		---	0	---	0	---	1	---	0	---	0
Suaeda maritima		18.5	7	---	1	---	1	---	0	---	0
Succisa pratensis		---	0	---	0	---	1	---	2	---	0
Tanacetum vulgare		---	0	---	2	---	0	---	0	---	0
Taraxacum sect. Palustria		---	0	---	1	9.1	10	26.2	18	---	0
Taraxacum sect. Ruderalia		---	0	---	12	---	4	34.4	29	---	0
Taraxacum sp.		---	0	---	0	---	2	---	0	---	0
Teucrium scordium		---	0	---	0	---	1	---	0	---	0
Trifolium dubium		---	0	---	0	---	2	---	0	---	0
Trifolium fragiferum		---	0	---	10	13.5	22	30.6	34	---	0
Trifolium hybridum		---	0	---	2	---	0	---	0	---	0
Trifolium pratense s. l.		---	0	---	0	---	5	---	5	---	0
Trifolium repens		---	0	---	4	---	7	---	7	---	0
Triglochin palustris		---	2	---	3	---	6	---	11	---	17
Tripleurospermum inodorum agg.		---	2	23.7	10	---	2	---	0	---	0
Tussilago farfara		---	1	---	2	---	0	---	0	---	0
Veronica arvensis		---	0	---	0	---	1	---	0	---	0
Veronica scutellata		---	0	---	0	---	1	---	0	---	0
Vicia cracca		---	0	---	1	---	2	---	4	---	0
Vicia grandiflora		---	0	---	1	---	0	---	0	---	0
Vicia hirsuta		---	0	---	0	---	1	---	0	---	0
Vicia sepium		---	0	---	0	---	1	---	0	---	0

Fig. A.2 Number of halophytes within diagnostic (Dg), constant (Cs) and dominant (Dm) species for classes *Therosalicornietea*, *Festuco-Puccinellietea* and associations of THE i FEP in other vegetation classes identified in salt marshes. Abbreviations: THE – *Therosalicornietea*, FEP – *Festuco-Puccinellietea*, RUP – *Ruppietea maritimae*, POL – *Polygono-Poetea annuae*, ART – *Artemisietea vulgaris*, POT – *Potamogetonetea*, BID – *Bidentetea*, PHR – *Phragmito-Magnocaricetea*, MOL – *Molinio-Arrhenatheretea*.

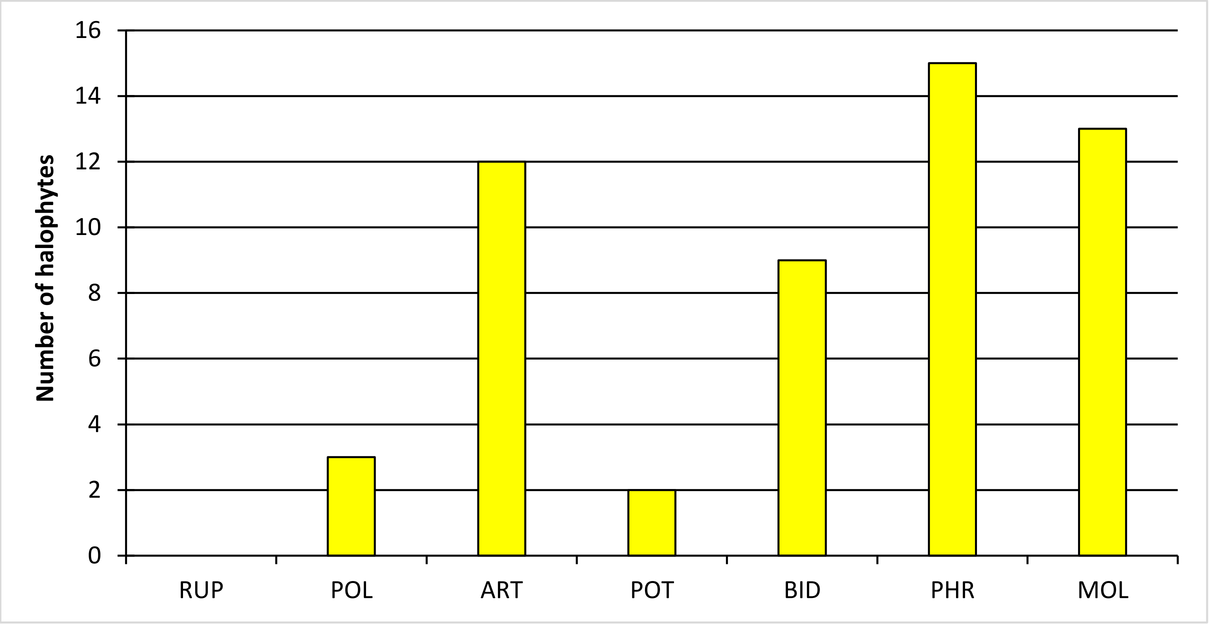

Table A.5 Results of forward selection and Monte Carlo permutation test associated to discriminant CVA analysis of mean Ellenberg indicator values for vegetation classes and associations. Conditional term effect is given. Statistically significant factors are marked in gray (p<0.05). Abbreviations of environmental variables: L – light availability, M – moisture, N – nitrogen content/trophy, R – reaction/soil acidity, S – salinity, T – temperature. Other abbreviations: pseudo-F – Fisher parameter, p – significance level.

Classes				**Associations**			
Variable	% variation explained	pseudo-F	*p*	Variable	% variation explained	pseudo-F	*p*
S	7.1	66.6	0.002	L	15.5	82	0.002
M	7.1	71.6	0.002	R	8.6	50.5	0.002
L	4.5	48.3	0.002	M	5.5	34.5	0.002
N	3.9	44.2	0.002	N	1.7	10.9	0.002
R	1.1	12.3	0.002	T	1.5	10.2	0.002
T	0.4	4.4	0.002	S	<0.1	0.2	0.922

Table A.6 Results of forward selection and Monte Carlo permutation test associated to discriminant CVA analysis of soil properties, vegetation classes and associations. Conditional term effect is given. Statistically significant factors are marked in gray (p<0.05). Abbreviations of environmental parameters: ECe – salinity measured as electrical conductivity, moist – moisture, Ntot – total nitrogen, org.mat. – organic matter content. Other abbreviations: pseudo-F – Fisher parameter, *p* – significance level.

Classes				**Associations**			
Name	% variation explained	pseudo-F	*p*	Name	% variation explained	pseudo-F	*p*
EC_e	7.9	22.8	0.002	EC_e	12.7	20.3	0.002
N_{tot}	1.4	4.1	0.004	org.mat.	12.4	22.9	0.002
moist	1	3.1	0.014	pH	3.1	6	0.004
pH	0.4	1.2	0.314	moist	2.4	4.7	0.008
org.mat.	0.2	0.4	0.826	N_{tot}	0.7	1.4	0.214

Table A.7 Comparison of soil properties for vegetation classes. The ranges and means ± standard deviation are given. Significantly different groups/means are denoted by different letters at $p<0.05$ according to Kruskal-Wallis test with Dunn post hoc comparisons. Abbreviations of vegetation classes: THE – *Therosalicornietea*, FEP – *Festuco-Puccinellietea*, PHR – *Phragmito-Magnocaricetea*, MOL – *Molinio-Arrhenatheretea*, ART – *Artemisietea vulgaris*, BID – *Bidentetea*. Abbreviation of environmental parameter: EC_e – salinity expressed as electrical conductivity.

Classes	**THE**	**FEP**	**PHR**	**MOL**	**ART**	**BID**	***p***
Number of plots	**54**	**134**	**38**	**24**	**9**	**7**	
EC_e [dSm^{-1}]	12.2-117.6	0.73-53.3	1.42-63.7	1.53-19.6	2.3-19.9	2.55-45.6	
	38.5^{c}±19.0	15.4^{b}±11.0	13.1^{ab}±13.0	6.05^{a}±4.43	10.6^{ab}±6.55	29.0^{bc}±16.7	$p<0.0001$
Moisture [%]	8.6-425.9	7.29-484.4	15.6-490.3	9.72-579.0	23.2-74.9	6.75-342.2	
	56.7^{a}±66.8	79.8^{ab}±100.1	134.4^{b}±132.5	121.6^{ab}±134.2	35.3^{ab}±16.1	154.2^{ab}±161.7	$p<0.01$
pH	3.8-8.3	5.9-9.0	6.7-8.5	6.7-8.5	7.0-8.07	6.35-8.01	
	7.53^{a}±0.68	7.72^{a}±0.48	7.65^{a}±0.47	7.84^{a}±0.41	7.59^{a}±0.40	7.23^{a}±0.62	$p>0.05$
Organic matter content [%]	0.87-57.1	0.87-77.8	1.89-80.1	2.97-80.0	2.25-18.2	2.78-38.2	
	12.8^{a}±10.5	15.2^{a}±16.6	23.1^{a}±21.4	25.8^{a}±23.1	9.59^{a}±4.97	19.1^{a}±15.3	$p>0.05$
Total nitrogen [%]	0.04-2.16	0.01-3.61	0.04-3.2	0.03-3.31	0.08-0.77	0.08-1.28	
	0.30^{a}±0.39	0.45^{ab}±0.66	0.77^{c}±0.83	1.02^{bc}±1.05	0.29^{abc}±0.22	0.58^{abc}±0.53	$p<0.01$

Table A.8 Comparison of soil properties for vegetation associations. The ranges and means ± standard deviation are given. Significantly different groups/means are denoted by different letters according to Kruskal-Wallis test with Dunn post hoc comparisons. Abbreviations of associations: Se – *Salicornietum ramosissimae*, P-Ss – *Puccinellio-Spergularietum salinae*, Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii*, Tm-Gm – *Triglochino maritimae-Glaucetum maritimae.* Abbreviation of environmental parameter: EC_e – salinity expressed as electrical conductivity of saturated extrac.

Associations	**Se**	**Pd-Ss**	**Sp-Jg**	**T-Gm**	***p***
Number of plots	**50**	**45**	**23**	**23**	
EC_e [dSm^{-1}]	7.49-117.6	1.91-44.2	10.9-53.3	5.25-43.3	
	$38.9^{b}\pm19.9$	$15.4^{a}\pm9.98$	$25.8^{b}\pm9.88$	$12.6^{a}\pm10.2$	p<0.0001
Moisture [%]	8.6-425.9	7.29-122.2	13.4-105.1	23.0-468.1	
	$58.5^{bc}\pm69.1$	$34.9^{ac}\pm24.7$	$51.7^{b}\pm24.3$	$184.4^{d}\pm126.7$	p<0.0001
pH	3.8-8.3	6.6-9.0	7.58-8.36	5.9-8.23	
	$7.48^{a}\pm0.69$	$7.71^{ab}\pm0.49$	$7.97^{b}\pm0.23$	$7.50^{a}\pm0.58$	p<0.001
Organic matter content [%]	0.87-57.1	1.02-22.9	4.83-24.4	8.31-74.7	
	$12.8^{b}\pm10.9$	$6.56^{a}\pm4.67$	$14.0^{bd}\pm5.09$	$29.4^{cd}\pm18.8$	p<0.0001
Total nitrogen [%]	0.04-2.16	0.01-0.74	0.1-0.53	0.16-2.62	
	$0.31^{b}\pm0.41$	$0.16^{a}\pm0.16$	$0.26^{b}\pm0.13$	$0.89^{c}\pm0.67$	p<0.0001

Table A.9 Original nomenclature of associations used by the authors of the vegetation plots in our database from the inland salt marshes of Europe with a temperate climate

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***Salicornietum ramosissimae* Christiansen 1955 – 137 vegetation plots from 10 sources**

The authors of the plots classified them, e.g., as belonging to *Salicornietum patulae* W. Christiansen 1955 (Wilkoń-Michalska, 1963) and *Salicornietum ramosissimae* (*patulae*) (Brandes, Heimhold & Ullrich, 1973) or *Puccinelio distantis-Salicornietum ramosissimae* (Janssen, 1986) and *Puccinellio-Spergularietum salinae* (Piotrowska, 1974). In other sources, the plots were included in *Salicornietum europeae germanicum* Altehage 1939 (Wilkoń-Michalska, 1957) and *Salicornietum ramosissimae lotharingiense* (Duvigneaud, 1967) or just as association with *Salicornia europaea* or *Salicornia ramosissima* (Bosiacka & Stachowiak, 2007; Hayon, 1968).

***Scorzonero parviflorae-Juncetum gerardii* (Wenzl 1934) Wendelberger 1943 – 121 vegetation plots, 11 sources**

The vegetation-plots representing *Scorzonero parviflorae-Juncetum gerardi* association were classified as *Juncetum gerardii* (Bosiacka & Stępień, 2001; Brandes, Heimhold & Ullrich, 1973; Janssen, 1986), *Juncetum Gerardi asteretosum* (Piotrowska, 1974) and *Agropyreto-Juncetum gerardii*, patch with *Hordeum secalinum* (Duvigneaud, 1967) or association with *Juncus gerardi* (Hayon, 1968; Mony & Muller, 2005). Ćwikliński (1977) distinguished various subtypes of *Juncetum gerardii atlantico-balticum* (Nordh. 1923) Fukarek 1961, such as: asteretosum tripolii, typicum or lototetosum tenuis. As in most cases, there were also discrepancies in our classification with the original one, e.g., *Triglochin maritimum-Glaux maritima* (Wilkoń-Michalska, 1963). And describing the association using the species that contributed the most in the vegetation-plots, e.g., association with *Juncus gerardii*, variant with *Phragmites australis* (Duvigneaud, 1967), association of *Agropyron repens* or association of *Puccinellia distans* and *Aster tripolium* (Hayon, 1968).

***Agrostio stoloniferae-Juncetum ranarii* Vicherek 1962 – 6 vegetation plots, 2 sources**

Authors of plots representing *Agrostio stoloniferae-Juncetum ranarii* association classified the vegetation to the *Junceto-Puccinellietum distantis* (Duvigneaud, 1967) and *Puccinellietum distantis* Feekes (1934) 1943 *juncetosum* (Lee, 1977).

***Triglochino maritimae-Glaucetum maritimae* Wilkoń-Michalska 1963 ex Dítě et al. ass. nov. 2022 – 56 plots, 8 sources**

Originally, these vegetation-plots were most often classified by the author of the syntaxonomical name as the previously functioning form of *Triglochin maritimum-Glaux maritima* (Wilkoń-Michalska, 1963), and even its various facies, e.g., with *Aster tripolium* or with *Triglochin maritimum* (Wilkoń-Michalska, 1970). In the publication by Brzeg (1998) there was already used the name *Triglochino-Glaucetum maritimae* Wilk.-Mich. 1963. Earlier, the author herself classified the plots as *Triglochin maritimum-Scorzonera parviflora* Altehage 1939 (Wilkoń-Michalska, 1957) or in cases inconsistent with our classification, as *Arrhenatheretum elatioris* Tx 1937, subassociation *Lotetosum tenuifolii* (Altehage 1940) (Wilkoń-Michalska, 1963).

***Puccinellio-Spergularietum salinae* (Feekes 1936) R.Tx. at Volk 1937 – 134 vegetation plots, 14 sources**

Some authors classified the vegetation just as the *Puccinelio-Spergularietum salinae*, i.e., Brzeg (1998), Ćwikliński (1977), Dąbrowska & Świeboda (1977) and Jackowiak (1983). The earlier name of the association *Puccinelia distans-Spergularia salina* Feekes (1936) was also common (Trzcińska-Tacik, 1966; Wilkoń-Michalska, 1963). Nomenclature related to *Puccinellia distans* as well functioned, e.g., *Puccinellietum distantis* (Brandes, Heimhold & Ullrich, 1973; Duvigneaud, 1967; Janssen, 1986), *Puccinelia distans-Obione pedunculata* Altehate 1939 subassociation *Spergularia salina* Altehage 1939 (Wilkoń-Michalska, 1957) or *Junceto-Puccinellietum distantis* (Duvigneaud, 1967). It has been common to describe vegetation as representing an association with specific species, e.g., association of *Puccinellia distans* and *Aster tripolium* (Hayon, 1968) or association with *Atriplex hastata* var. *salina* (Duvigneaud, 1967). Lee (1977) classified various developmental stages of the vegetation patches, e.g., *Puccinellietum distantis* Feekes (1934) 1943 'initial' or asteretosum. There were also discrepancies with our classification, e.g., *Festuca arundinacea-Potentilla anserina* syn. *Lolium perenne-Matricaria suaveolens* (Wilkoń-Michalska, 1963) or *Atriplicetum salinae lotharingiense* Duvigneaud 1967 (Lee, 1977).

References

→ See Table A.1

4.2. *Plant functional traits drive syntaxonomical units in temperate European inland salt-marsh vegetation*

Lubińska-Mielińska, S., Kamiński, D., Pétillon, J., Evers, C., Piernik, A. – Plant functional traits drive syntaxonomical units in temperate European inland salt-marsh vegetation

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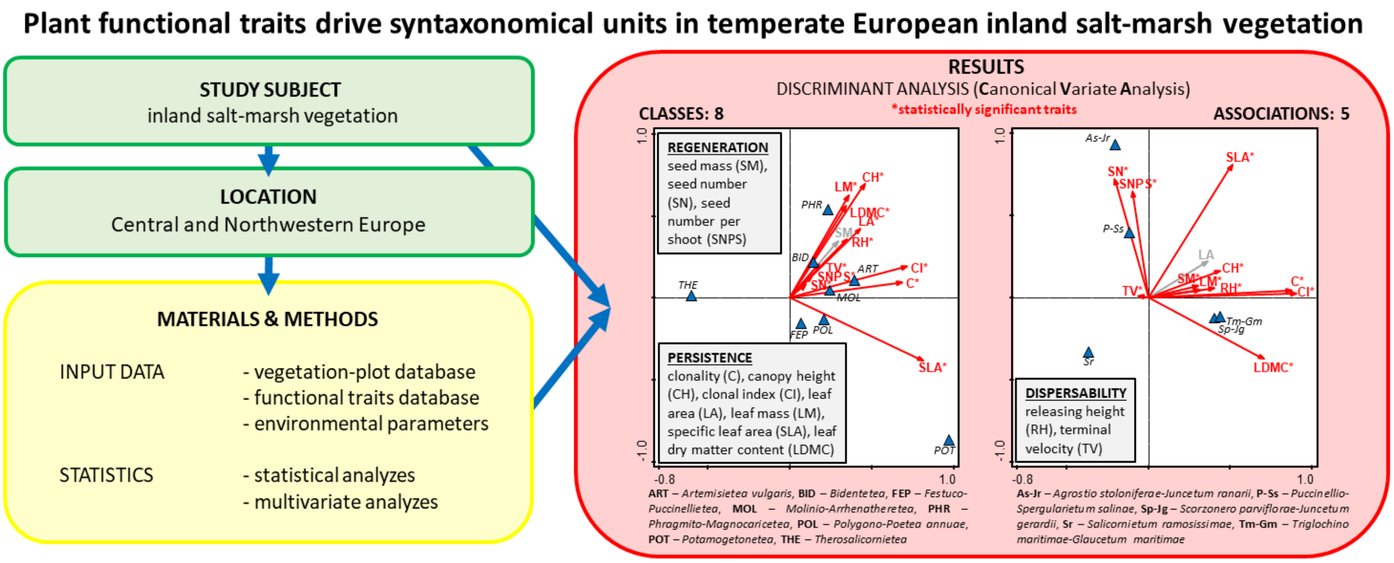

Plant functional traits drive syntaxonomical units in temperate European inland salt marsh vegetation

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Abstract

A functional trait-based approach is crucial for understanding ecosystem function, persistence, and protection. Vegetation in inland salt marsh habitats has been recognized as unique on a European scale and is legally protected under the Natura 2000 network. Despite long-term international protection, this continues to decline. The concept of inland salt marsh protection refers to vegetation in the sense of syntaxonomical units. However, no link has been found between syntaxonomical and functional concepts of vegetation. We aimed to identify functional traits that are distinctive to individual vegetation units and to link these traits to environmental factors. We hypothesized that a) syntaxonomical vegetation units are also functional units in terms of their functional traits, and b) environmental factors determine the functional traits of vegetation patches. We considered a set of traits from the CLO-PLA and LEDA databases responsible for the persistence, regeneration, and dispersability of approximately 400 species recorded in 874 plots classified into nine vegetation classes and five associations typical of salt marshes. We found that the syntaxonomical vegetation units were also functional. The most important factors separating vegetation classes and salt marsh plant associations are the functional traits responsible for plant persistence. The values of these traits were generally negatively correlated with soil salinity and positively correlated with soil moisture and abandonment of mowing or grazing. Traits related to regeneration, such as seed number and seed number per shoot, also play essential roles in grouping species into individual associations. The classes specific to salt marshes, *Therosalicornietea* and *Festuco-Puccinelietea,* had the lowest persistence potential and were thus the most sensitive to environmental changes. The most sensitive association seemed to be *Salicornietum ramossissimae.* Therefore, significant attention should be paid to protecting this vegetation type. *Puccinellio distantis-Spergularietum salinae* and *Agrostio stoloniferae-Juncetum ranarii* had significantly lower stability and higher regenerative ability. Therefore, their regeneration must be easier and more effective. *Triglochino maritimae-Glaucetum maritimae* and *Scorzonero parviflorae-Juncetum gerardi* associations had low regeneration ability, but the latter association denoted significantly higher stability. The functional pattern of the analyzed vegetation may play a crucial role in the effective protection and restoration of endangered natural saline habitats.

KEYWORDS vegetation functional pattern, halophytes, plant dispersability, plant persistence, plant regeneration, soil salinity

1. Introduction

Inland salt marshes in temperate Europe are associated with rock salt deposits uplifted next to their surfaces and salty springs related to them (Bank & Spitzenberg, 2001; Wilkoń-Michalska, 1963). They are also present in industrial saline areas owing to the salt, soda, and potash industries (Garve & Garve, 2000; Karasińska et al., 2021). They are inhabited by salt-adapted plant species known as halophytes (Flowers & Colmer, 2008; Piernik, 2021). However, inland salt marshes are relatively diverse because halophytes are accompanied by halotolerant ecotypes of glycophytic species that are typical of non-saline areas (Piernik, 2012; Wilkoń-Michalska, 1963). The vegetation of inland salt marsh habitats has been recognized as unique on a European scale, and since 1992, it has been legally protected under the Natura 2000 network, according to *Council of Europe Directive 92/43/EEC* (Council of Europe, 1992). However, this vegetation continues to decline despite long-term international and local protection (Lubińska-Mielińska et al., 2022) and is considered endangered. Therefore, inland temperate salt marshes are included in the *European Red List of Habitats* (Janssen et al., 2016). This suggests that adequate protection of inland salt marsh vegetation still requires a better understanding of its function. Currently, these habitats are of increasing importance due to climate warming, the global problem of salinity in agriculture (FAO, 2021), and the rapidly growing human population, which has increased the demand for food (Tripathi et al., 2019). In this context, they can serve as a source of salt-tolerant species for future saline agriculture or salt-tolerant genes for the future modification of conventional crops (Cárdenas-Pérez et al., 2021; Cuevas et al., 2019; Flowers & Colmer, 2015).

The concept of inland salt marsh protection concerns, besides single-species protection, local protection within nature reserves, and more general protection within Natura 2000 habitats. These two concepts refer to vegetation as syntaxonomical units (European Commission, 2013; Nienartowicz & Piernik, 2004a, 2004b). Notably, a unified classification system for European vegetation has been proposed at the alliance level by Mucina et al. (2016). This is based on the Braun-Blanquet approach (Braun-Blanquet, 1964). In this system, the vegetation of the inland salt marshes was divided into two classes: *Therosalicornietea* Tx. in Tx. et Oberd. 1958 and *Festuco-Puccinellietea* Soó ex Vicherek 1973. The class *Therosalicornietea*, order *Therosalicornietalia* Pignatti 1952, alliance *Salicornion ramosissimae* Tx. The pioneering vegetation of annual succulent halophytes was covered in 1974. The *Festuco-Puccinellietea* class, order *Scorzonero-Juncetalia gerardi* Vicherek 1973 and alliance *Juncion gerardi* Wendelberger 1943, includes inland salt meadows of temperate salt marshes. We recently recognized and defined the association levels of these vegetation types on a wide European scale (Lubińska-Mielińska et al., 2023). Within the *Therosalicornietea* class, we identified *Salicornietum ramosissimae* Christiansen 1955 association, and within *Festuco-Puccinellietea* following four associations: *Scorzonero parviflorae-Juncetum gerardii* (Wenzl 1934) Wendelberger 1943, *Agrostio stoloniferae-Juncetum ranarii* Vicherek 1962, *Triglochino maritimae-Glaucetum maritimae* Wilkoń-Michalska 1963 ex Dítě et al. ass. nov. 2022 and *Puccinellio-Spergularietum salinae* (Feekes 1936) R. Tx. in Volk 1937 (Figure S1 in the syntaxonomical hierarchy diagram). However, in addition to the vegetation typical of inland salt marshes, we found vegetation from other classes that are not specific to saline sites as an integral part of these habitats. Although, as was already mentioned, the protection of inland saline habitats refers to vegetation syntaxonomical units, no link has been found between syntaxonomical and functional concepts that could help understand vegetation functioning. Therefore, we decided to analyze salt marsh vegetation syntaxonomy from a functional ecological perspective.

The functional approach to vegetation is based on functional plant traits. According to Violle et al. (2007), plant functional traits are all traits related to morphology, physiology, or phenology, which can be measured in a single individual from the cell to the whole organism level without relating them to the environment or any other level of organization. Functional traits such as growth, reproduction, and survival may affect plant fitness. They reflect plant life strategies and determine how plants respond to environmental conditions. For example, the height of a plant is essential for its ability to compete for light, the parameters of seeds for their ability to colonize various habitats, and the ratio of the leaf surface area to its mass for optimizing the efficiency of photosynthesis (Goldstein, 2018). Ecologists use functional trait data in many ways, such as determining the relationship between the functional traits of species and their life history, survival, and growth indicators (Kleyer et al., 2008). There is also interest in the effects of stress on plant traits (Cárdenas-Pérez, Niedojadło et al., 2022; Cárdenas-Pérez, Rajabi Dehnavi, et al., 2022; Ludwiczak et al., 2023; Schöb et al., 2013). Some morphological plant traits allow the assessment of specific habitat conditions (Adler et al., 2014; Cárdenas-Pérez, Rajabi Dehnavi, et al., 2022). Specific protocols have been developed for tracking traits worldwide (Cornelissen et al., 2003; Pérez-Harguindegirl et al., 2013). As a result of extensive research, numerous databases of the functional traits of species from different parts of the world have been created. The main European plant trait databases include LEDA (Kleyer et al., 2008), Bioflor (Klotz et al., 2002), and CLO-PLA (Klimešová & de Bello, 2009). These databases typically contain data on more than 20 functional traits of various plant species. Additionally, a much larger TRY - Plant Trait Database (Kattge et al., 2011) with worldwide reach is available. These data provide a general overview of the functional traits of a single species. However, little information is available on the variability of functional traits in plants associated with environmental factors (e.g., Albert, 2010; Ulrich et al., 2018). Recently, Kambach et al. (2023) used the functional traits of vegetation from different habitat types to relate them to climatic factors. Few studies have examined plant functional trait adaptations in saline areas (e.g., Guo et al., 2015; Minden et al., 2012; Matinzadeh et al., 2022; Minden & Kleyer, 2015; Ulrich et al. 2019). However, to the best of our knowledge, the inland salt marsh vegetation in Europe has not yet been described in a functional context. Moreover, only single studies use species traits to compare whole vegetation syntaxonomical units (e.g., Lengyel et al., 2020) or compare them based on traits of a few characteristic species (e.g., Ladouceur et al., 2019). Therefore, we used the current knowledge about the functional traits of the species recorded on inland salt marshes in temperate Europe within the described vegetation syntaxonomical units (Lubińska-Mielińska et al., 2023). We believe that such an approach will provide a more complete picture of the functioning of the analyzed vegetation, and thus, may contribute to its more effective protection. Such a functional approach can aid in understanding ecological processes, such as the assembly and stability of associations and succession, and facilitate the detection and prediction of responses to environmental change at various scales (Duckworth et al., 2000). There has been continuous progress in ecology attempting to respond to global problems by including the functional traits of individual species in macroecological research to better understand the functioning of entire ecosystems (He et al., 2019). We want to merge the syntaxonomical and functional approaches in this context.

We aimed to identify the functional traits distinctive to individual vegetation units of temperate inland salt marshes in Europe, and to link these traits with environmental factors. We hypothesized that a) syntaxonomical vegetation units are also functional units in terms of their functional traits, and b) environmental factors determine the functional traits of vegetation patches. We considered a set of traits responsible for plant persistence, regeneration, and dispersability according to the concept of Kleyer et al. (2008) because it reflects strategies under saline conditions.

2. Materials and Methods

2.1. Data

Vegetation and environmental data, except land use type information, were obtained from the database created based on the literature and used in our previous paper (Lubińska-Mielińska et al., 2023). This database contains 874 vegetation plot samples collected by different authors from European temperate inland salt marshes in six countries: the Czech Republic, France, Germany, Luxemburg, Poland, and the United Kingdom. The database contains a list of more than 400 vascular plant species. We classified plots into nine vegetation classes (Lubińska-Mielińska et al., 2023), including two typical salt marshes: *Therosalicornietea* (THE – 137 plots) and *Festuco-Puccinellietea* (FEP – 485 plots), as well as *Ruppietea maritimae* (RUP – 6 plots), *Polygono-Poetea annuae* (POL – 10 plots) and *Artemisietea vulgaris* (ART – 14 plots), *Potamogetonetea* (POT – 12 plots), *Bidentetea* (BID – 22 plots), *Phragmito-Magnocaricetea* (PHR – 112 plots), and *Molinio-Arrhenatheretea* (MOL – 76 plots), see Figure 1a. Within two classes that represent the vegetation typical of salt marshes, we identified five associations: in class *Therosalicornietea*: *Salicornietum ramosissimae* association (Sr – 133 plots), and in class *Festuco-Puccinellietea*: *Scorzonero parviflorae-Juncetum gerardii* (Sp-Jg – 121 plots), *Agrostio stoloniferae-Juncetum ranarii* (As-Jr – 6 plots), *Triglochino maritimae-Glaucetum maritimae* (Tm-Gm – 56 plots), and *Puccinellio-Spergularietum salinae* association (P-Ss – 134 plots), (Figures 1b and Figure S1). We retained the presented syntaxonomical division to test the relationships between the syntaxonomical units and their functional trait specificity. To perform the calculations of weighted averages of functional traits and environmental parameters, it was necessary to transform the data from the database in the

Braun-Blanquet (1964) scale into the van der Maarel (2007) ordinal scale, as follows: r → 1, + → 2, 1 → 3, 2 → 5, 3 → 7, 4 → 8, 5 → 9. The maps (Figure 1a and 1b) were made using the QGIS 2.14.2 "Essen" software (QGIS Development Team, 2016).

Data on the functional traits of plant species were obtained from online databases, including information about the clonal index (CI) and clonality (C) from the CLO-PLA database (Klimešová et al., 2017), and information about the remaining ten traits from the LEDA Traitbase (Kleyer et al., 2008). Both sources represented the species in the investigated area. We used data on twelve traits that are responsible for three different functions in plant species according to Kleyer et al. (2008), i.e., persistence – leaf area (LA), leaf mass (LM), canopy height (CH), specific leaf area (SLA), leaf dry matter content (LDMC), clonal index (CI), clonality (C), regeneration – seed mass (SM), seed number (SN), seed number per shoot (SNPS), and dispersability – releasing height (RH), terminal velocity (TV). We decided to analyze traits related to plant height, leaves, and seeds because, according to Westoby (1998), the leaf-height-seed plant strategy represents the main dimension of plant variability along the most typical ecological gradients. Among the traits identified as being responsible for persistence, CH is responsible for competitive ability, as are LM, LA, SLA, and LDMC, which additionally reflect salt stress tolerance and growth rates (Westoby et al., 2002). We also analyzed traits related to plant clonality because they were found to be responsible for plant adaptation to environmental disturbances (Klimešová et al., 2016). We adopted the three categories proposed by Kleyer et al. (2008), who focused on the main functions of individual traits. However, these are not rigid limits because some traits may be responsible for different categories of functions in plants. For example, traits related to SN and mass, which are included in the regeneration category, influence establishment, response to disturbances, and additionally are important for dispersal (Leishman, 2001; Westoby et al., 2002). The dispersability traits RH and TV are mainly influenced by wind (Tackenberg et al., 2003; van der Pijl, 1982). We calculated weighted averages for each vegetation plot based on these traits. Owing to the lack of data on the species traits of *Ruppietea maritimae* (n=6), we did not consider this class. The final dataset comprised 868 vegetation plots (approximately 400 plant species).

The environmental parameters for each plot were calculated as weighted averages based on six Ellenberg indicator values (EIV; n=868; Ellenberg et al., 1992): salinity (S), moisture (M), reaction (R), light availability (L), temperature (T), and nitrogen content (N). Data on soil parameters (n=266): Salinity expressed as the electrical conductivity of the saturated extract (EC_e), moisture (moist), pH, and organic matter (org.mat.), and total nitrogen (N_{tot}) content, as well as land use/management type information: not used (abandoned mowing and grazing), arable field, industry, and hay/pasture, come from the source literature based on which the vegetation plot database was created (i.e. Piernik, 2012).

2.2. Statistical and multivariate analyzes

To identify the most important distinctive functional traits for the analyzed vegetation units, we used Canonical Variate Analysis (CVA) as discriminant analysis (Šmilauer & Lepš, 2014). We focused on the conditional effects, which excluded the effects of the most correlated traits. Conditional effects summarize the partial effect of each predictor, representing the variation (and its significance) explained by a predictor after accounting for the effect of the predictors already selected (ter Braak & Šmilauer, 2012). The predictors were chosen in the order of decreasing explained variation. The differences in all traits between vegetations syntaxonomical units were compared using the non-parametric Kruskal-Wallis test with Dunn post hoc comparisons because of the not normal distribution of the majority of the trait values (Shapiro–Wilk test, $p \leq 0.05$). To identify apparent functional similarities between syntaxonomical units, we performed two-way clustering based on mean trait values using an unweighted pair group (UPGMA) algorithm and Euclidean distance for similarity comparison. Trait data were standardized to avoid the effects of different units. The relationships between functional traits and environmental factors were investigated using Redundancy Analysis (RDA) with forward selection and the Monte Carlo permutation test to select the most critical factors in trait differentiation. The functional trait data of the single plots were standardized before analysis. We also considered only the conditional effects of the explanatory variables, excluding the effects of the most correlated environmental parameters (ter Braak & Šmilauer, 2012). We applied RDA twice with different sets of environmental parameters: (1) weighted averages of EIV ($n=868$), and (2) soil parameters and land use types ($n=266$). Detailed relationships between the plot-weighted mean trait values were assessed based on Spearman's correlations with the same set of variables. Because the use of EIV to estimate environmental conditions may result in overestimation, we decided to use the permutation p value instead of the classical p value, which allows to eliminate such errors to some extent (Zelený & Schaffers, 2012). We also correlated the related plot EIV and soil parameters ($n=266$; Table S1) to determine the degree of correlation. The impact of the four different management types was evaluated using the Kruskal-Wallis comparison between groups with Dunn's post hoc test. For the CVA and RDA ordination analyses, we used the Canoco 5.0 package (ter Braak and Šmilauer, 2012). Functional trait data analysis was standardized using MVSP 3.1 software (Kovach, 2007). Other analyses were performed using the PAST 4.11 software (Hammer et al., 2001).

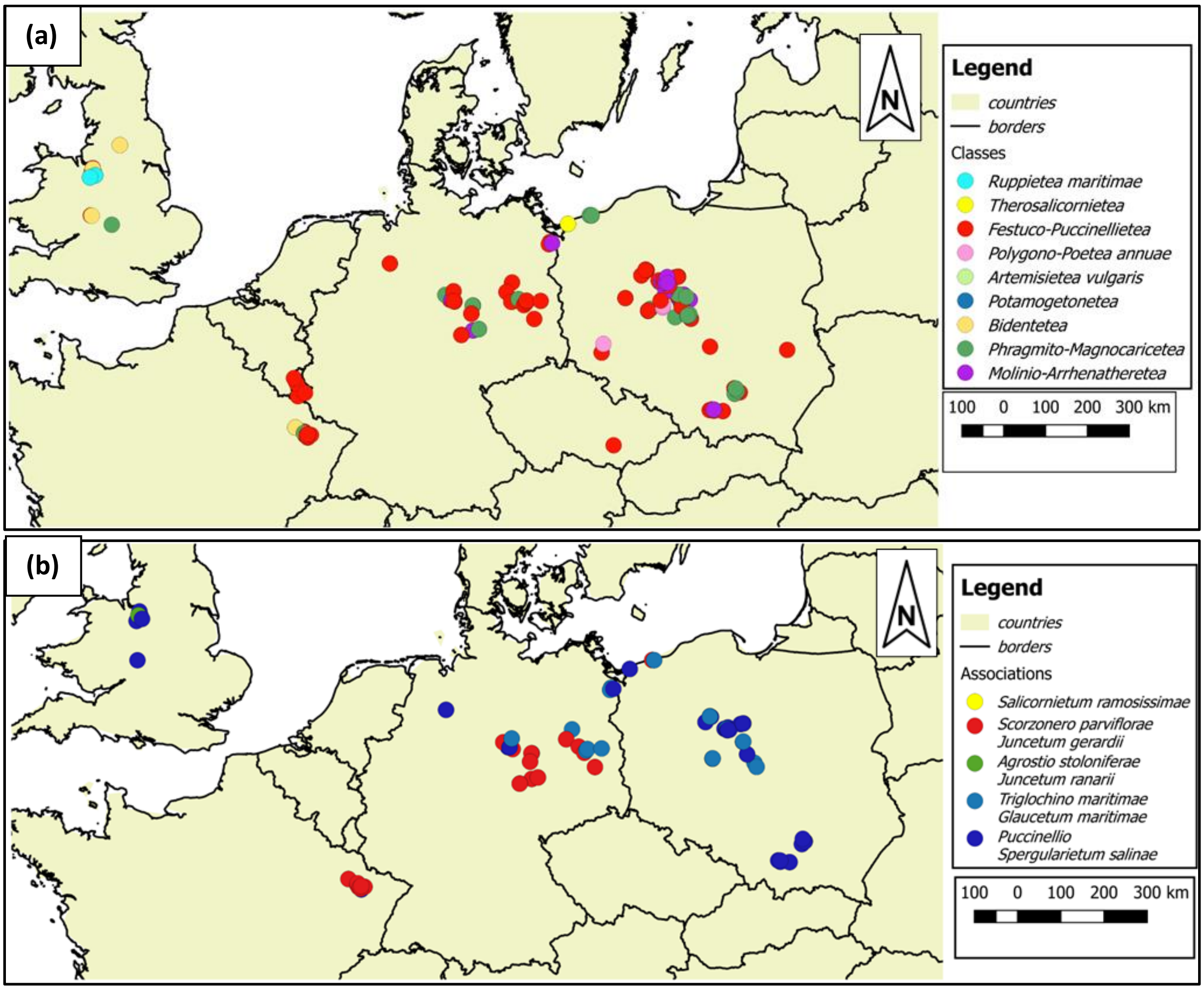

Figure 1. Geographic distribution of: (a) nine classes identified in European temperate inland salt marshes; (b) five associations distinguished among the two classes typical of European temperate inland salt marshes – *Therosalicornietea* and *Festuco-Puccinellietea*. Some points overlap due to the same research area. Created based on classification by Lubińska-Mielińska et al. (2023).

3. Results

3.1. Syntaxonomical classification and functional pattern relations

We compared the relationships between functional traits and vegetation units at the class and association levels (Figures 2–5). First, we focused on vegetation classes. The results of discriminant analysis, i.e., CVA, showed that the classes of temperate inland salt marshes in Europe differed in terms of almost all analyzed functional traits, except for SM, as presented in Figure 2a. The highest variability between them was explained by SLA and CH, explaining 13.9% of the variation, followed by parameters related to clonality (Cl, C) – 5.6%, and leaf parameters such as LDMC and LM – another 3.7% (Table S2). These traits represent the persistence of the plant species.

Detailed comparisons of plot-weighted means for each vegetation class (Figure 3) indicated that, in general, the pioneer typical of salt marshes, the *Therosalicornietea* class, is characterized by low or the lowest values of the analyzed traits. Vegetations from this class had the lowest values for persistence traits (LA, LM, CH, SLA, CI, and C), regeneration traits (SM), and dispersibility (RH and TV). However, a low trait value does not always indicate the same potential as the analyzed function category; thus, we discuss this in detail in the discussion section. The detailed functional trait results are presented in Table S3. The *Festuco-Puccinellietea* class, which is typical of temperate inland salt marshes, was also characterized by low values of the analyzed traits, but higher than those of *Therosalicornietea* class (Figure 3). However, among the eight classes studied, only dispersability (TV) reached its lowest value. Owing to the relatively low values of persistence, regeneration, and dispersability traits, these two classes were most similar and clustered together (Figure 5a). The next vegetation class, *Potamogetonetea,* demonstrated similarly low values for LA, LM, CH (persistence), RH, and TV (dispersability) and even significantly lower LDMC (persistence), SN, and SNPS (regeneration) (Figure 3). Accordingly, *Potamogetonetea* was classified as most similar to the first two classes (Figure 5a). However, in contrast to *Therosalicornietea* and *Festuco-Puccinellietea*, this vegetation type had the highest SLA, CI, C, and SM values. Of the remaining five classes, the *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea* are the most similar and present similar values of some traits related to persistence (LA, LDMC, CI, and C), regeneration (SM), and dispersability (TV), see Figures 3 and 5a. However, *Phragmito-Magnocaricetea* has lower SLA, SN, and SNPS, and *Molinio-Arrhenatheretea* has lower LM, CH, and RH. The *Artemisietea vulgaris* class is most similar to them and is characterized by similar values of all persistence traits (LA, LM, CH, SLA, LDMC, CI, C) and dispersability traits (RH and TV), but higher SM and lower SN and SNPS. The other two classes, *Polygono-Poetea annuae* and *Bidentetea*, were classified together because of the similar values of almost all persistence traits (LA, LM, CH, LDMC, CI, and C), all regeneration traits (SM, SN, SNPS), and dispersability (TV) (Figures 3 and 5a). They differed in two analyzed traits: *Polygono-Poetea annuae* had a higher SLA and *Bidentetea* had a higher RH.

Considering vegetation associations, the results of discriminant analysis (CVA) revealed that they were diverse in terms of all functional traits, except LA (Figure 2b). The highest variability between associations was explained by the persistence traits of SLA, CI, and LDMC (33.3%; Table S2). The SN and SNPS, which are related to plant regeneration, accounted for 8.4% of the variation. The smallest variability (1.9 %) was explained by the dispersibility traits, TV and RH.

The comparison of the single functional effects between the associations showed that *Salicornietum ramosissimae*, the association representing the *Therosalicornietea* class, was characterized by the lowest values of almost all traits except LDMC and TV (Figure 4 and Table S4). *Salicornietum ramosissimae* is the most similar functional term to *Puccinellio-Spergularietum salinae* classified together (see Figure 5b), which has a similar TV but differs by higher values of almost all persistence traits – LA, LM, CH, SLA, CI, and C, but lower LDMC, higher regeneration traits (SM, SN, and SNPS), and dispersability (RH). The second group of the most similar associations was *Triglochino maritimae-Glaucetum maritimae* and *Scorzonero parviflorae-Juncetum gerardii*, which were characterized by the same values of persistence traits (SLA, CI, and C) and regeneration traits (SM, SN, and SNPS) (Figures 4 and

5b). *Agrostio stoloniferae-Juncetum ranarii* was classified as the most similar owing to similar values of traits related to dispersibility (RH, TV) and persistence (LA, LM, and CH). However, it had a higher SLA and lower CI, C, SN, and a higher regeneration trait SNPS but lower SM.

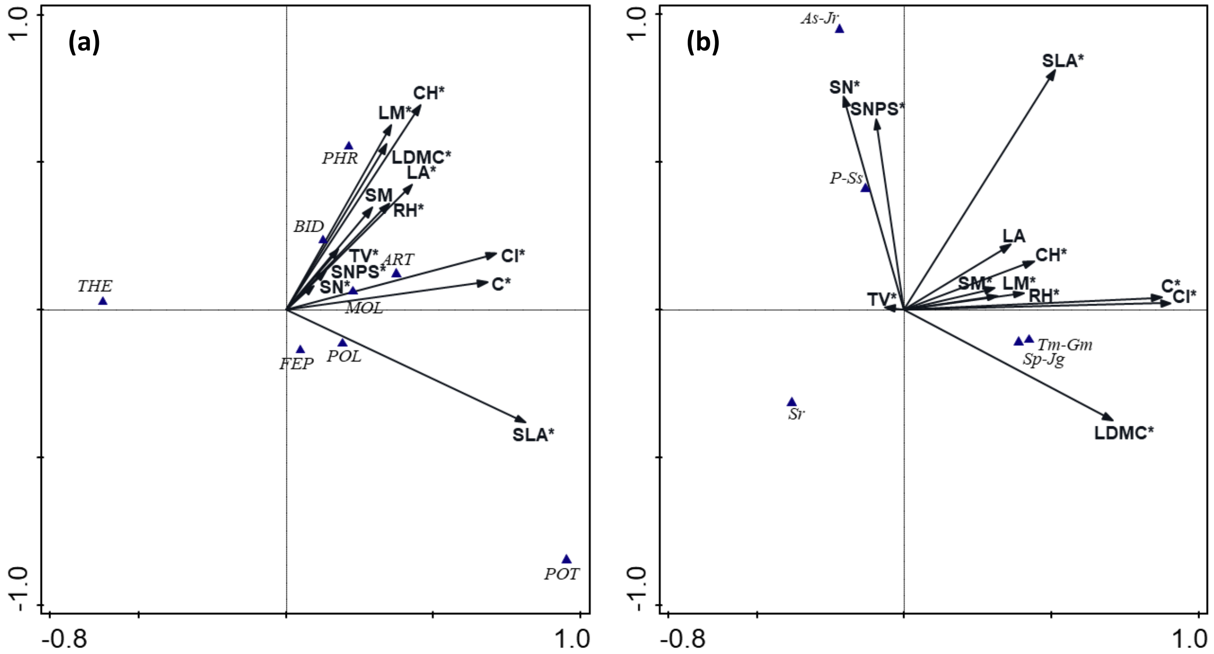

Figure 2. Results of discriminant analysis – Canonical Variate Analysis, presenting relations between analyzed functional traits and: (a) vegetation classes; (b) vegetation associations. Statistically significant factors are marked by an asterisk (*p*≤0.05). Abbreviations of functional traits: C – clonality, CH – canopy height, CI – clonal index, LA – leaf area, LDMC – leaf dry matter content, LM – leaf mass, RH – releasing height, SM – seed mass, SN – seed number, SNPS – seed number per shoot, SLA – specific leaf area, TV – terminal velocity. Abbreviations of vegetation classes (n=868): ART – *Artemisietea vulgaris* (n=14), BID – *Bidentetea* (n=22), FEP – *Festuco-Puccinellietea* (n=485), MOL – *Molinio-Arrhenatheretea* (n=76), PHR – *Phragmito-Magnocaricetea* (n=112), POL – *Polygono-Poetea annuae* (n=10), POT – *Potamogetonetea* (n=12), THE – *Therosalicornietea* (n=137). Abbreviations of vegetation associations (n=450): As-Jr – *Agrostio stoloniferae-Juncetum ranarii* (n=6), P-Ss – *Puccinellio-Spergularietum salinae* (n=134), Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii* (n=121), Sr – *Salicornietum ramosissimae* (n=133), Tm-Gm – *Triglochino maritimae-Glaucetum maritimae* (n=56).

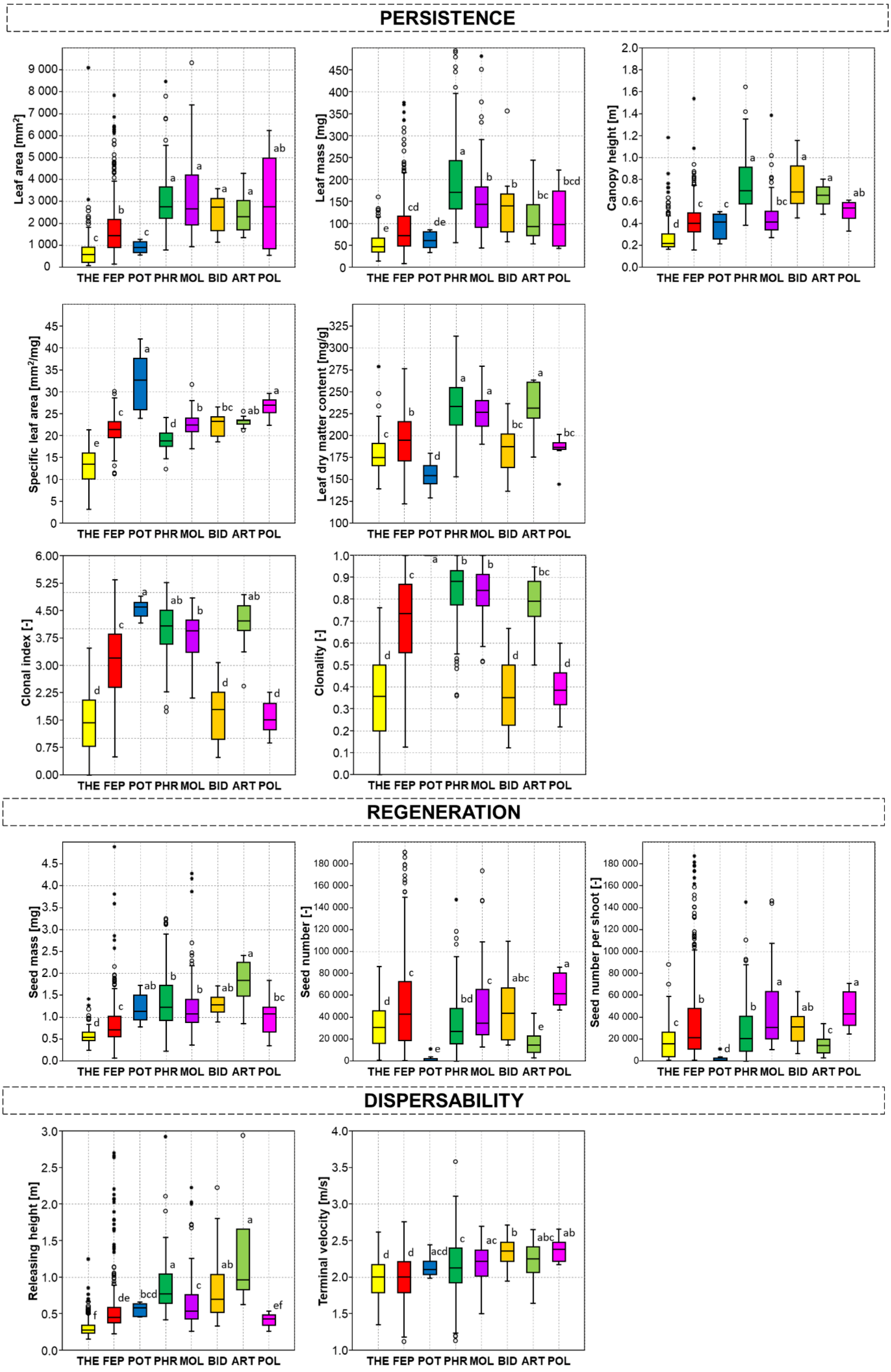
PERSISTENCE
Leaf area [mm²]
Leaf mass [mg]
Canopy height [m]
Specific leaf area [mm²/mg]
Leaf dry matter content [mg/g]
Clonal index [-]
Clonality [-]
REGENERATION
Seed mass [mg]
Seed number [-]
Seed number per shoot [-]
DISPERSABILITY
Releasing height [m]
Terminal velocity [m/s]
THE FEP POT PHR MOL BID ART POL

Figure 3. Comparison of functional traits for vegetation classes. Significantly different groups, according to the Kruskal-Wallis test with Dunn post hoc comparisons, are denoted by different letters at $p \leq 0.05$. Abbreviations of vegetation classes (n=868): THE – *Therosalicornietea* (n=137), FEP – *Festuco-Puccinellietea* (n=485), POT – *Potamogetonetea* (n=12), PHR – *Phragmito-Magnocaricetea* (n=112), MOL – *Molinio-Arrhenatheretea* (n=76), BID – *Bidentetea* (n=22), ART – *Artemisietea vulgaris* (n=14), POL – *Polygono-Poetea annuae* (n=10).

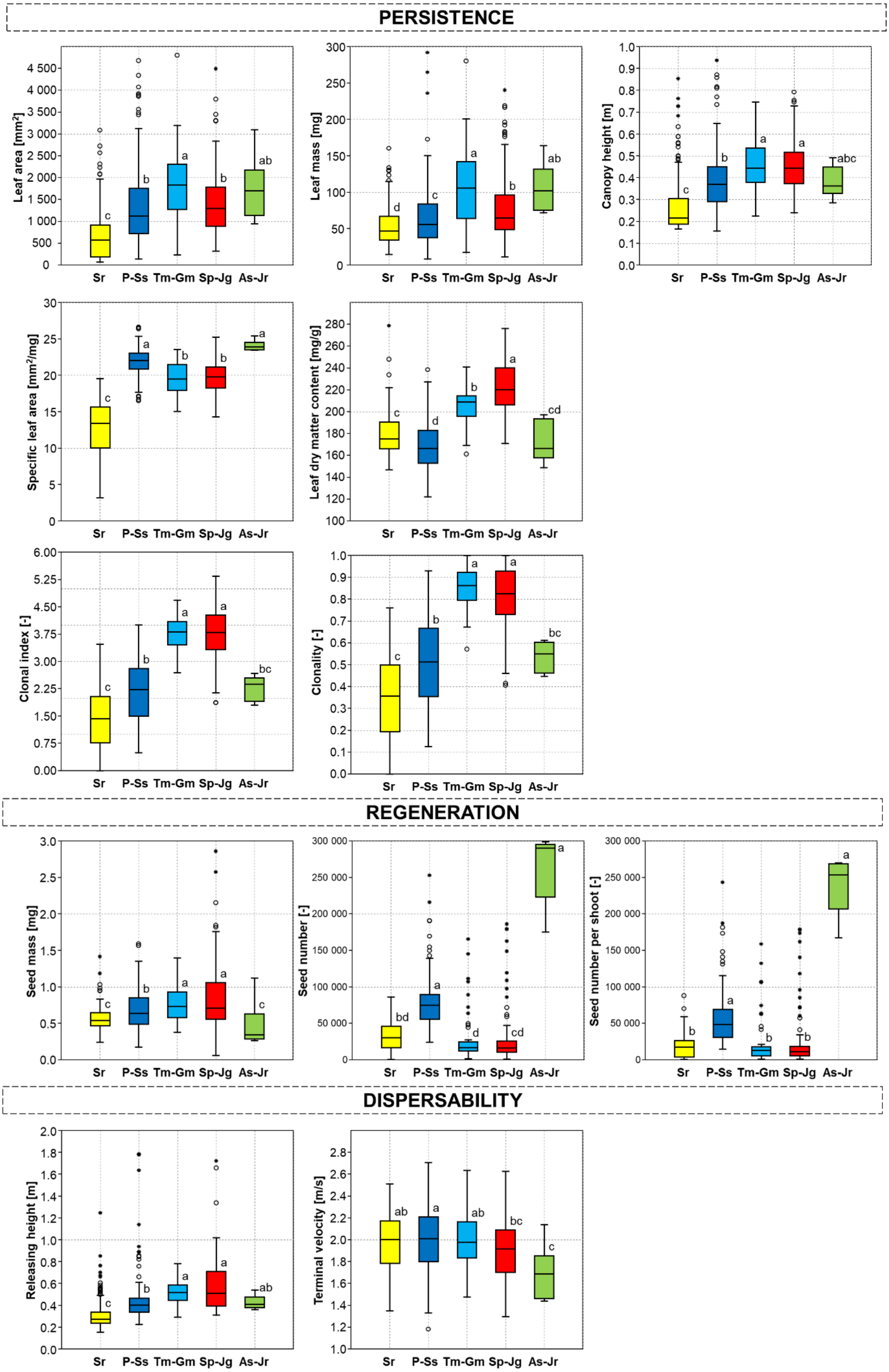
PERSISTENCE
Leaf area [mm²]
c b a b ab
Leaf mass [mg]
d c a b ab
Canopy height [m]
c b a a abc
Specific leaf area [mm²/mg]
c a b b a
Leaf dry matter content [mg/g]
c d b a cd
Clonal index [-]
c b a a bc
Clonality [-]
c b a a bc
REGENERATION
Seed mass [mg]
c b a a c
Seed number [-]
bd a d cd a
Seed number per shoot [-]
b a b b a
DISPERSABILITY
Releasing height [m]
c b a a ab
Terminal velocity [m/s]
ab a ab bc c
Sr P-Ss Tm-Gm Sp-Jg As-Jr

Figure 4. Comparison of functional traits for vegetation associations. Significantly different groups, according to the Kruskal-Wallis test with Dunn post hoc comparisons, are denoted by different letters at $p \leq 0.05$. Abbreviations of vegetation associations (n=450): Sr – *Salicornietum ramosissimae* (n=133), P-Ss – *Puccinellio-Spergularietum salinae* (n=134), Tm-Gm – *Triglochino maritimae-Glaucetum maritimae* (n=56), Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii* (n=121), As-Jr – *Agrostio stoloniferae-Juncetum ranarii* (n=6).

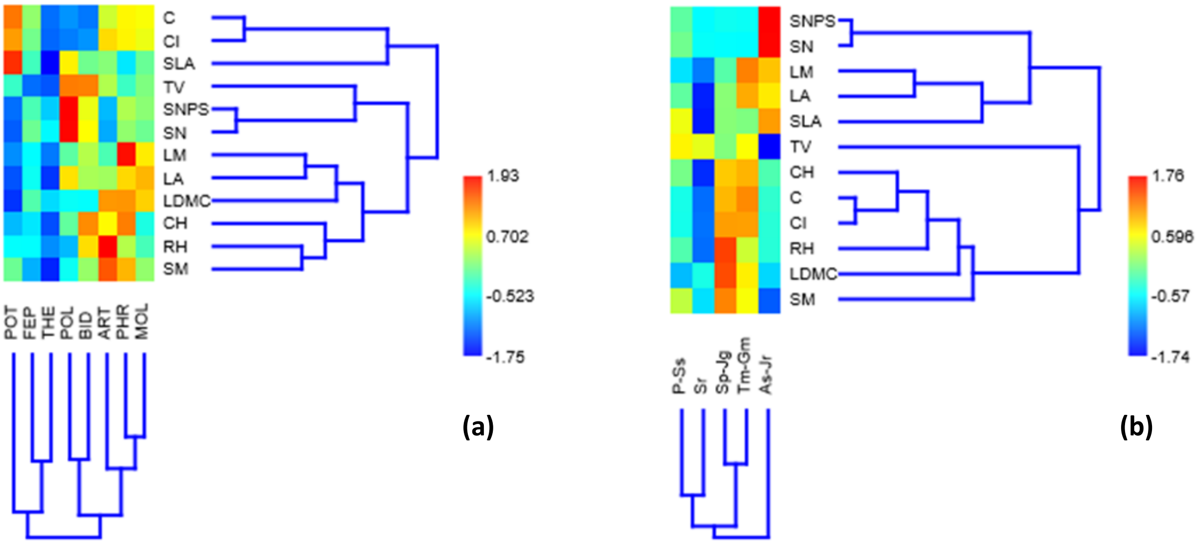

Figure 5. Results of two-way clustering with unweighted paired group (UPGMA) algorithm and Euclidean distance index, relations between analyzed functional traits and: (a) vegetation classes; (b) vegetation associations. Abbreviations of functional traits: C – clonality, CH – canopy height, CI – clonal index, LA – leaf area, LDMC – leaf dry matter content, LM – leaf mass, RH – releasing height, SM – seed mass, SN – seed number, SNPS – seed number per shoot, SLA – specific leaf area, TV – terminal velocity. Abbreviations of vegetation classes (n=868): POT – *Potamogetonetea* (n=12), FEP – *Festuco-Puccinellietea* (n=485), THE – *Therosalicornietea* (n=137), ART – *Artemisietea vulgaris* (n=14), BID – *Bidentetea* (n=22), PHR – *Phragmito-Magnocaricetea* (n=112), MOL – *Molinio-Arrhenatheretea* (n=76), POL – *Polygono-Poetea annuae* (n=10). Abbreviations of vegetation associations (n=450): As-Jr – *Agrostio stoloniferae-Juncetum ranarii* (n=6), Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii* (n=121), Tm-Gm – *Triglochino maritimae-Glaucetum maritimae* (n=56), P-Ss – *Puccinellio-Spergularietum salinae* (n=134), Sr – *Salicornietum ramosissimae* (n=133).

3.2. Relationships between functional traits and environment

Redundancy Analyses (RDA) showed that the functional traits of the vegetation were strongly related to environmental conditions (Figure 6). Regarding environmental variables based on the EIVs, functional traits differed for all indicators. The highest variation of 18.8% was explained by salinity, and the next highest variation of 4.5% was explained by moisture indicator values. Similar results were obtained based on the soil parameters for a smaller set of samples, with the highest variability explained by salinity (EC_e) at 9.8%, followed by soil moisture at 3.5%. We also included land use type data in the analysis. The results showed that the cessation of mowing or grazing (not used) also considerably affected the variability of functional traits (5.1% of the variation explained). The detailed results are presented in Table S5.

Analysis of the single effects of environmental parameters based on EIV using Spearman's correlation revealed that salinity reduced almost all vegetation traits (Table 1).

We found a strong negative correlation between salinity indicators and persistence traits (LA, LM, CH, SLA, LDMC, and CI), regeneration (SM), and dispersability (RH). In general, moisture positively correlated with most traits. A strong negative correlation was observed between moisture and SLA. The remaining correlation coefficients were low. The nitrogen indicator positively correlated with all traits except LDMC and had no effect on clonality traits. The reaction indicator, light availability, and temperature were negatively correlated with the analyzed functional traits of the vegetation.

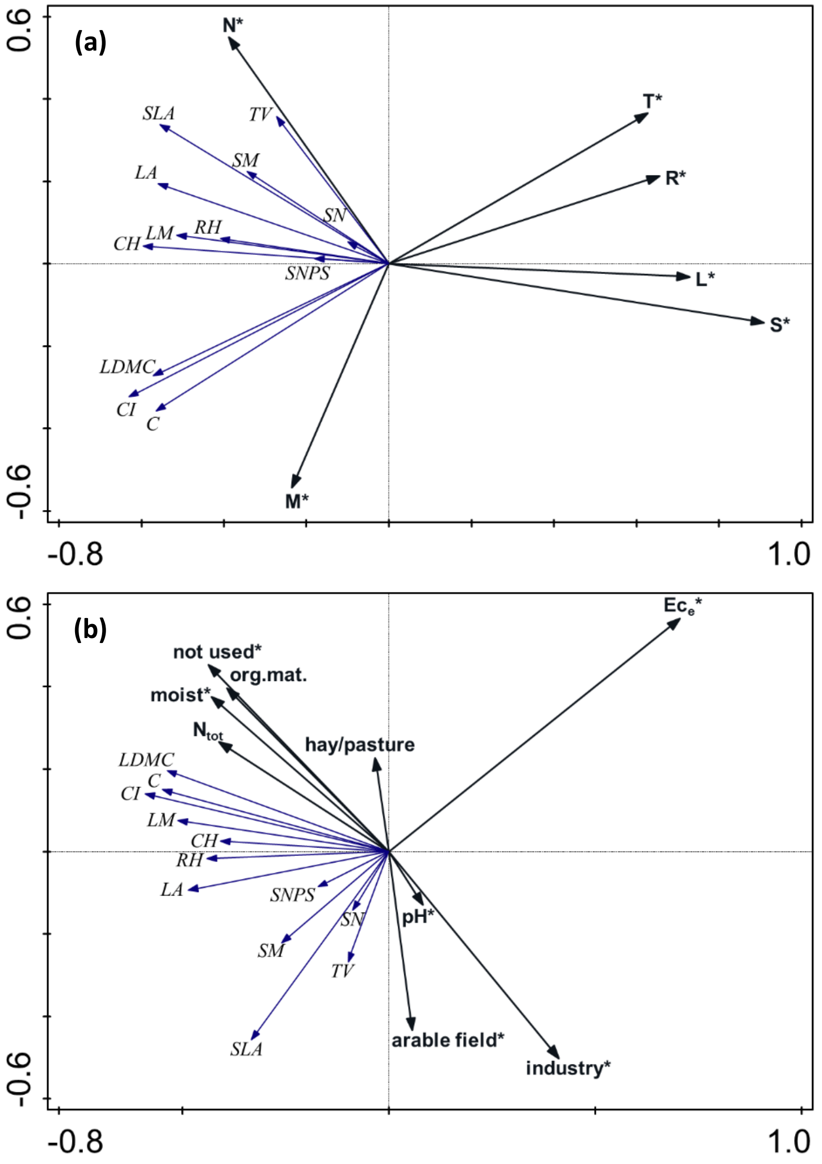

Figure 6. Results of Redundancy Analysis (RDA), relations between analyzed functional traits and: (a) environmental variables based on Ellenberg indicator values (EIV, n=868); (b) soil parameters and land use type (n=266). Statistically significant factors are marked by an asterisk ($p \leq 0.05$). Abbreviations of functional traits: C – clonality, CH – canopy height, CI – clonal index, LA – leaf area, LDMC – leaf dry matter content, LM – leaf mass, RH – releasing height, SM – seed mass, SN – seed number, SNPS – seed number per shoot, SLA – specific leaf area, TV – terminal velocity. Abbreviations of environmental variables: L – light availability, M – moisture, N – nitrogen content, R – reaction, S – salinity, T – temperature. Abbreviations of soil parameters: EC_e – salinity

measured as the electrical conductivity of saturated extract, moist – moisture, N_{tot} – total nitrogen, org.mat. – organic matter content.

The results from the soil data confirm the findings on salinity and moisture based on EIV. Soil salinity, expressed as EC_e was negatively correlated with trait values. A strong negative correlation was found between SLA and LA. Soil moisture negatively correlated with SLA, SN, and TV. The results for pH and nitrogen from the soil data differ from those based on EIV. Soil pH did not show any correlation with the functional traits. This difference can be attributed to the lack of a correlation between the reaction indicator and pH (Table S1). Nitrogen was negatively correlated with SLA, SN, and TV; however, these correlations were weak. These differences could be caused by the low correlation between the nitrogen indicator and the soil total nitrogen and organic matter content. Detailed correlation analysis results are presented in Table 1 (Figure S2).

Table 1. Spearman’s correlation coefficients between functional traits and environmental variables based on Ellenberg indicator values (EIV, n=874) and soil parameters (n=266). High correlations (r≥0.5) are marked in bold.

Variables\Traits	LA	LM	CH	SLA	LDMC	CI	C	SM	SN	SNPS	RH	TV
S	**-0.64********	**-0.56********	**-0.52********	-0.48****	**-0.60********	-0.49****	-0.41****	**-0.61********	ns	-0.29****	**-0.58********	-0.39****
M	ns	0.17****	0.20****	**-0.57********	0.30****	0.28****	0.26****	-0.08*	-0.30****	-0.19****	0.15***	-0.12***
N	0.40****	0.35****	0.44****	0.34****	-0.10**	ns	ns	0.37****	0.07*	0.12***	0.36****	0.09**
R	-0.46****	-0.36****	-0.27****	-0.49****	**-0.50********	-0.44****	-0.42****	-0.29****	-0.09**	-0.22****	-0.36****	-0.13***
L	-0.44****	-0.29****	-0.45****	-0.43****	-0.40****	-0.41****	-0.34****	-0.35****	ns	-0.19****	-0.48****	-0.17****
T	-0.49****	-0.42****	-0.41****	-0.25****	**-0.62********	-0.47****	-0.43****	-0.24****	ns	-0.21****	-0.48****	ns
EC_e	-0.46****	-0.39****	-0.37****	**-0.51********	-0.33****	-0.40****	-0.35****	-0.46****	-0.16**	-0.37****	-0.41****	-0.33****
moist	0.22***	0.34****	0.17**	-0.29****	0.31****	0.38****	0.43****	ns	-0.19**	ns	0.22***	-0.23***
pH	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
org.mat.	ns	0.21***	ns	-0.25****	0.28****	0.31****	0.35****	ns	-0.24***	ns	0.16**	-0.20**
N_{tot}	0.24***	0.33****	0.20**	-0.18**	0.40****	0.43****	0.45****	ns	-0.19**	ns	0.29****	-0.14*

**** p≤0.0001, *** p≤0.001, ** p≤0.01, * p≤0.05, ns – non-significant. Abbreviations of functional traits: LA – leaf area, LM – leaf mass, CH – canopy height, SLA – specific leaf area, LDMC – leaf dry matter content, CI – clonal index, C – clonality, SM – seed mass, SN – seed number, SNPS – seed number per shoot, RH – releasing height, TV – terminal velocity. Abbreviations of environmental variables: S, salinity; M, moisture; N, nitrogen content; R, reaction; L, light availability; T, temperature. Abbreviations of soil parameters: EC_e – salinity measured as the electrical conductivity of the saturated extract; moist, moisture; org.mat. is the organic matter content, and N_{tot} is the total nitrogen.

In the case of land use type comparisons, the high values of some persistent traits, especially those related to the leaves (LM, LDMC), clonality (CI, C), and light competing ability (CH), as well as regeneration (SM) and dispersability traits (RH), were related to abandonment (see Figures 6 and S3). In contrast, the vegetation of the abandoned sites was characterized by the lowest SLA (persistence), SN, SNPS (regeneration), and TV (dispersability). In samples collected from arable fields, the highest values were recorded of LM, CH, and SLA (persistence), SM, SN, and SNPS (all traits related to regeneration), and RH and TV (dispersability). Vegetation in the industrial areas was characterized by the lowest LM, CH, LDMC, CI, C (persistence), and RH (dispersability). Intermediate trait values characterized the hay/pasture management type (Figure S3).

4. Discussion

4.1. Functional pattern of salt marsh syntaxonomical units

Our results showed that SLA, CH, CI, LDMC, LM, and C, which are traits responsible for persistence (Kleyer et al., 2008), explained the most significant percentage of the variability between vegetation classes in salt marshes. Plant leaf traits, which are usually correlated with each other, are represented by the so-called leaf economics spectrum, which balances leaf construction costs against growth potential (Díaz et al. 2016; Wright et al, 2004). Plant leaves have already been recognized as critical sites for photosynthesis and evapotranspiration (Zhou et al., 2020), and are essential for material and energy exchange within the soil-plant-atmosphere system (Ackerly et al., 2002). Our results demonstrate that their roles are recognizable at the syntaxonomical level. SLA, which explains the highest variability among the analyzed vegetation classes, is directly influenced by LA, thickness, shape, and age (Zhou et al., 2020). It is linked to water use or survival strategies and is often applied to evaluate the performance of plants under water deficit (Boucher et al., 2017). It is generally believed that plants grown in resource-rich environments use higher SLA to enhance photosynthetic capacity and productivity (Yao et al., 2016). They adapt the strategy of smaller SLA to improve stress resistance and competitive ability in stressful environments (Long et al., 2011) because large leaves tend to require higher biomass investments per unit LA than small leaves (Milla et al., 2008). Our results reflect these relations because classes typical of salt marshes, i.e., *Therosalicornietea* and *Festuco-Puccinellietea* growing under the highest salt stress in the research area, represent the lowest values of all traits related to the leaves, including SLA, which indicates low productivity of this type of vegetation, except LDMC, which low value is related to the fast and acquisitive strategy (Poorter & de Jong, 1999; Reich, 2014). Lower SLA and LDMC in salt marsh vegetation are associated with reduced evapotranspiration and the maintenance of osmotic balance under salinity stress conditions (Richards et al., 2005). This is due to the largest proportion of salt-adapted halophytic species in the *Therosalicornietea* and *Festuco-Puccinellietea* classes. Halophytes are defined as plant species able to survive and reproduce under a salinity of approximately 200 mM NaCl (Flowers & Colmer, 2008), as confirmed by studies on individual species, for example, *Salicornia europaea* L. by Cárdenas-

Pérez, Rajabi Dehnavi et al. (2022), or *Tripolium pannonicum* (Jacq.) Dobrocz. (Ludwiczak et al. 2023). Less than 0.2% of the plants worldwide possess this ability (Flowers & Colmer, 2015). Halophytes adapt to water deficiency and excess salt, for example, by the reduction of LA (reduction of evapotranspiration), exclusion of excess salt in vacuoles, old organs, specially developed salt glands, and dilution of salts by water storage (Grigore & Toma, 2020; Pérez Cuadra et al., 2020). These adaptations affect morphological traits. The low values of most traits responsible for persistence recorded for *Therosalicornietea* and *Festuco-Puccinellietea* classes highlight the sensitivity of these vegetation units to environmental changes. This is indicated not only by the traits related to leaves but also by the low proportion of species with high clonality, which helps plants adapt to environmental disturbances (Klimešová et al., 2016). The most similar to *Therosalicornietea* and *Festuco-Puccinellietea* classes in terms of functioning is vegetation from *Potamogetonetea* class also adapted to extreme environments, that is, to grow in underwater conditions (Caldarella et al., 2021; Tuthill et al. 2023). Vegetation from this class has a higher SLA because of the low dry matter accumulation in the leaves (Ronzhina et al., 2009) and larger seeds for better dispersal under water conditions (de Jager et al., 2019). The remaining vegetation classes, i.e., *Polygono-Poetea annuae, Artemisietea vulgaris*, *Bidentetea*, *Phragmito-Magnocaricetea*, and *Molinio-Arrhenatheretea,* are characterized by higher values of the analyzed parameters. *Polygono-Poetea annuae* includes therophyte-rich vegetation in trampled habitats (Vassilev et al., 2022). It is characterized by high seed production by annual species (SN and SNPS) and low potential for effective wind dispersal because of its low RH and high TV. *Artemisietea vulgaris* class includes thermophilic and (sub)xerophytic ruderal vegetation, which mainly consists of biannual and perennial seminitrophilous to nitrophilous species widely distributed in the temperate and sub-Mediterranean zones of Europe (Vassilev et al., 2021). This class in salt marshes is characterized by high productivity, expressed as high LDMC (Polley et al., 2022), regeneration success, defined as high SM, and high dispersibility at high RH (Jansen et al., 2004; Wyse & Hulme, 2021). *Phragmito-Magnocaricetea* class of reeds and the *Molinio-Arrhenatheretea* class of meadow vegetation were the most similar among analyzed vegetation regarding functional traits. However, *Phragmito-Magnocaricetea* had significantly higher persistence traits, such as LM and CH, but a lower SLA, indicating a more stressed wetland environment. Both vegetation classes overlap under environmental conditions in inland saline habitats (Lubińska-Mielińska et al., 2023), which can explain their similarity in functioning. High CH values, traits unrelated to the economic spectrum of leaves (Díaz et al. 2016, Wright et al., 2004), in *Phragmito-Magnocaricetea* may be caused by adaptation to wetlands, where plants elongate to provide oxygen access to tissues (Colmer, 2003). The highest values of traits related to clonality among these classes, including *Potamogetonetea*, are related to adaptation to environmental disturbances (Klimešová et al., 2016) and also explain the large expansion potential of species belonging to these groups. For example, *Phragmites australis* expansion into meadow vegetation after abandonment of mowing and grazing has been reported (Burdick et al., 2001; Wilkoń-Michalska, 1970). The *Bidentetea* class of tall-growing, competitively potent annual wetland herbs (Stępień & Rosadziński, 2020) differs from

Phragmito-Magnocaricetea and *Molinio-Arrhenatheretea* classes by lower clonality traits because covers only temporarily available flooded sites, and lower LDMC, which however indicates also disturbed environment (Cornelissen et al., 2003).

The variability between the salt-adapted associations within *Therosalicornietea* and *Festuco-Puccinellietea* classes can be explained by the traits responsible for persistence (SLA, CI, and LDMC) and regeneration (SN and SNPS; Kleyer et al., 2008). The lowest SLA was noted in *Salicornietum ramosissimae* grown under the highest salt stress (Lubińska-Mielińska et al., 2023). *Salicornia europaea* dominates this association and is adapted to high soil salinity through almost total leaf reduction and high succulence (Cárdenas-Pérez et al., 2021). *Scorzonero parviflorae-Juncetum gerardii* and *Triglochino maritimae-Glaucetum maritimae* have the lowest SN values, indicating a low generative regeneration ability (Rosbakh et al., 2018). However, traits related to the mass and number of seeds affect not only the ability of plants to regenerate but also, to some extent, their dispersability and response to disturbances (Leishman, 2001; Westoby et al., 2002). The highest LDMC was recorded for *Scorzonero parviflorae-Juncetum gerardii*. This can be interpreted as higher productivity of this association but also lower acquisitive strategy (Polley et al., 2022; Reich, 2014). Moreover, Májeková et al. (2014) showed that higher LDMC values might be related to higher population stability. The soil salinity reported for *Scorzonero parviflorae-Juncetum gerardii* was higher than that reported for *Triglochino maritimae-Glaucetum maritimae* (Lubińska-Mielińska et al., 2023). The highest clonality parameters were recorded for both associations, indicating better adaptation to environmental disturbances (Klimešová et al., 2016). *Agrostio stoloniferae-Juncetum ranarii* and *Puccinellio-Spergularietum salinae* associations have the highest SLA and the lowest LDMC, which are related to the fast and acquisitive strategy (Reich, 2014). Both associations had the highest SN, which indicated the highest ability for generative regeneration.

4.2. Environmental pattern of functional traits

In our study, we used the functional traits of individual species to calculate the weighted means for vegetation patches and to better understand the functioning of temperate inland salt marsh vegetation. This approach for vegetation has been advocated in the literature, e.g., by McGill et al. (2006), as one to rebuild the view of community ecology. This ensures a better understanding of the processes governing the analyzed phenomena, including environmental gradients. We found a significant relationship between functional vegetation traits and environmental parameters, including management type. Batriu et al. (2015) also demonstrated the influence of land use and past use on the traits of salt marsh communities. However, the most limiting factors for salt marsh vegetation are salinity and moisture, which considerably influence its functional traits of species (Piernik, 2012; Lubińska-Mielińska et al., 2023; Minden et al., 2012; Minden & Kleyer, 2015). Our results show that these factors explain the most significant part of the variability in vegetation functional characteristics, which demonstrates the validity of our assumption that environmental parameters shape traits.

We found a negative correlation of salinity with the trait values resulting in different life strategies, e.g., decrease in SLA marking low photosynthetic capacity and productivity but also decrease in LDMC marking the fast and acquisitive strategy, as it was already mentioned. Similar results were obtained on coastal marshes by Minden and collaborators (Minden et al., 2012; Minden & Kleyer, 2015). Soil moisture is also stressed in coastal marshes (Minden et al., 2012). According to Ulrich et al. (2019), the strength of the compensatory mechanisms that stabilize assimilation rates in salt marsh environments depends heavily on soil conditions; for example, assimilation rates are negatively correlated with average moisture. Similarly, our results showed that an increase in moisture content was associated with a decrease in SLA. The correlations of soil nitrogen and organic matter content with vegetation functional traits were low, demonstrating their low importance in shaping strategies under saline conditions. In addition, Minden et al. (2012) showed that the SLA and LDMC of salt marsh plants were more constrained by a salt-waterlogging gradient than by a nutrient gradient.

According to Schöb et al. (2013), environmental conditions can contribute to the physiological and morphological states of plants expressed in their functional traits, which in turn can shape interactions between individuals. According to Larcher (1987), the presence of stress in this system is a selective power that contributes to adaptive evolution by improving resistance. In salt marshes, this has been confirmed by the multitude of halophyte adaptations to salinity (Pérez Cuadra et al., 2020).

We found a positive correlation between leaf traits and plant height, suggesting that they are interdependent and are not worth analyzing separately. However, according to Price et al. (2014), these traits are largely orthogonal, depending, for example, on the habitat, i.e., an inverse relationship has been found in plants in wet areas. This finding shows that the plants on salt marshes, although related mainly to high soil moisture, demonstrate the traits of dry habitats because of low water availability from the saline solution (Ludwiczak et al., 2021).

Moreover, Díaz et al. (1998) suggested a ‘filtering effect’ of climatic factors on essential plant functions, in which vegetative traits are filtered more often than those related to regeneration. This explains why, in our study, the smallest percentage of variance among the analyzed features was defined for vegetation classes based on seed-related traits. Moreover, we based on data from a single climate type. The research from dry areas by Soliveres et al. (2014) shows, that the environmental conditions and the functional traits themselves may be responsible for the co-occurrence of species from some groups of plants. Salt marsh vegetation remains a topic for future research.

4.3. Data and terminology

Despite the use of functional traits to understand the ecological processes occurring in plant communities, the Holy Grail has been considered in ecology for years (Funk et al., 2017; Suding & Goldstein, 2008), and this is the first study linking syntaxonomical and functional approaches based on the functional traits of inland salt marshes across temperate Europe. For years, there have been discussions in the literature on the proper understanding and use of the term functional traits (e.g., Caruso et al., 2020; Dawson et al., 2021; Violle et al., 2007). In our research, we decided to base the data already defined from professional ready-made CLO-PLA and LEDA trait bases, consistent for individual species and coming from the moment of full plant development according to LEDA Data Standards published on the website (Kleyer et al., 2008). The functional traits in the database provide a general view of individual species. By calculating weighted averages for plots, we decided to consider all species, that is, approximately 400, because it was essential to obtain a complete picture of the results (Pakeman & Quested, 2007). This approach provides satisfactory results for comparing individual vegetation groups instead of field measurements of the populations of approximately 400 species. This should also prevent differences in the analyzed data, as Garbowski et al. (2021) warn. They suggested using indicators based on multidimensional relationships between traits rather than individual traits for species comparisons, because they seem more ontogenetically stable, such as SLA. However, they admit that LDMC and several root parameters, which we did not consider in this study, are suitable for comparison, even at the seedling stage. In future research, it will be worth considering the root traits that perform essential functions in plants, such as obtaining nutrients or water. They also significantly affect the entire ecosystem (Freschet et al., 2021; Laliberté, 2017; Valverde-Barrantes et al., 2017). However, these are often overlooked (e.g., Chelli et al., 2019). A possible reason for this is that root traits are underrepresented in global databases; therefore, to address this lack, the Fine-Root Ecology Database was recently created (Iversen et al., 2017).

Another methodological issue worth discussing is the application of weighted averages of functional traits for each plot (relevè) and weighted averages of EIV for environmental assessments. These are the average trait values or EVI for plants at each site weighted by species cover/abundance (Jongman et al., 1987). In functional ecology, the weighted mean of functional traits is widely referred to as the community weighted mean (CWM) (Lavorel et al., 2008); Ricotta and Moretti 2011; Miller et al., 2019). However, this term relevant to functional ecology can confuse some plant sociologists because CWM refers to plot/relevè weighted mean, while the term ‘community’ in plant sociology can refer to a set of relevès representing similar species composition. To avoid this misunderstanding in the research merging the two different concepts of vegetation, we decided not to apply this terminology to the manuscript but to explain this issue in the discussion section.

Regarding the use of weighted means of EIV as environmental estimates, according to Zelený and Schaffers (2012), statistical conclusions should not be made in analyses combining mean EIV with other variables resulting from species composition because it may give inflated results and often leads to incorrect interpretations. However, these authors allowed the use of EIV, but with the implementation of specific methods. Undoubtedly, for a large dataset such as ours, this significantly facilitates the analysis. Therefore, we used the permutation p value instead of the classical p to avoid excessively high significance levels. In addition, we validate the EIV data using field measurements from a smaller dataset. Schaffers and Sýkora (2000) performed such a correlation analysis for a larger number of parameters and concluded that

EIVs are a valuable tool for habitat calibration but indicate the importance of selecting appropriate parameters. We obtained a high correlation between the most critical parameters in salt marshes: salinity and moisture. Analyses conducted by Schaffers and Sýkora (2000) regarding pH and reaction showed, similarly to our case, unsatisfactory results. The authors suggested that this indicator should be referred to as the calcium value. We also found a low correlation between the nitrogen indicator and soil total nitrogen and organic matter contents. This may be because of the modified availability of nutrients under saline conditions (Fageria et al., 2011).

4.4. Conservation and protection implications

According to Cadotte et al. (2015), communities can be predicted based on their functional traits. The results obtained can be used to create models for salt marshes in the future because we detected general relationships among the analyzed characteristics in the context of phytosociological classes and associations. Venn et al. (2011) presented results that should allow the creation of such a model for predicting vegetation response to climate change and the disappearance of snow cover. They analyzed Australian alpine snow patches using functional traits and showed that the emergence of strong environmental filters may favor the occurrence of specific plant communities that build species with more competitive traits. In salt marshes, the salinity gradient can be a strong filter that favors a high rate of halophytes rather than plant species that tolerate lower salinity. With a decrease in salinity, controlling the expansion of more competitive and taller glycophytic species with greater clonality abilities is crucial (Bosiacka et al., 2011).

Our results demonstrate that both vegetation classes typical of salt marshes, that is, *Therosalicornietea* and *Festuco-Puccinelietea* have low persistence potential and are thus sensitive to environmental changes. Considering specific salt marsh associations, sensitive seem to be *Salicornietum ramosissimae* of the lowest persistence potential and values of regeneration traits. Therefore, significant attention should be paid to protecting this typical of high soil salinity vegetation type (Lubińska-Mielińska et al., 2023). *Puccinellio-Spergularietum salinae* association has significantly lower stability (expressed by lower LDMC; Májeková et al., 2014) but higher regeneration ability (SN, SNPS). Therefore, regeneration should be made more easy. A similar situation was observed for the *Agrostio stoloniferae-Juncetum ranarii* association. *Triglochino maritimae-Glaucetum maritimae* and *Scorzonero parviflorae-Juncetum gerardii* associations have low generative regeneration abilities (low SN, SNPS; Rosbakh et al., 2018), but *Scorzonero parviflorae-Juncetum gerardii* has significantly higher stability (expressed by higher LDMC; Májeková et al., 2014).

Saatkamp et al. (2019) stressed that seed traits should be used to develop biodiversity conservation strategies, including the protection of endangered species, based on a more comprehensive set of traits. The regeneration parameters that we considered differentiated the analyzed vegetation classes of salt marshes to the slightest degree. However, the SN and SNPS, explained a large proportion (8.4%) of the variability among associations. In addition, salt marsh associations are built mainly through low plants without particular adaptations to disperse seeds over long distances. Erfanzadeh et al. (2010) demonstrated that dispersal traits are non-limiting factors for salt marsh plant colonization. However, research on the restoration of halophyte nature reserves by Lubińska-Mielińska et al. (2022) shows that at points far from halophytic vegetation, halophyte seeds do not occur in the soil seed bank. Additionally, associations typical of the most saline areas, *Salicornietum ramossissimae* and *Puccinellio distantis-Spergularietum salinae* (Lubińska-Mielińska et al., 2023) have the lowest SM, which may affect their instability in the soil seed bank. This makes restoration challenging. Another problem in inland salt marsh conservation and restoration is landscape fragmentation and the island structure of saline habitats, which affect the functional diversity of individual plant systems (Zambrano et al., 2019). Minden and Kleyer (2015) stated that the total pool of typical coastal salt marsh species is rather small. The loss of a few of them with their specific trait composition has the potential to considerably change the relationships between the environment and vegetation-based ecosystem properties, and therefore elicit profound effects on the functioning of the entire and adjacent ecosystems and other systems depending on it. In our opinion, this also applies to inland salt marshes and is why effective protection is important.

5. Conclusions

The results of our research show that the syntaxonomical units of inland salt marsh vegetation in temperate Europe have functional significance. The most important factors in separating vegetation classes and salt marsh plant associations are the functional traits responsible for plant persistence, which are generally negatively correlated with soil salinity and positively correlated with soil moisture and abandonment of mowing or grazing. Associations were also separated according to regenerative traits (SN and SNPS). Classes and associations differed the least in terms of traits related to dispersability. Based on functional traits, the most sensitive to environmental changes were vegetation classes typical of salt marshes. Regarding associations, *Salicornietum ramossissimae* had the lowest persistence and regeneration potentials. Therefore, significant attention should be paid to protecting this vegetation type. In our opinion, the functional pattern of the analyzed vegetation may play a crucial role in the effective protection and restoration of these endangered habitats.

CRediT authorship contribution statement

SLM – prepared the first draft of the publication, organized and managed data from the CLO-PLA and the LEDA databases, and performed vegetation-traits and traits-environment analyses; DK – managed plant species and vegetation nomenclature; JP – collected data from France; CE – collected data from Germany; AP – conceived the ideas, designed methodology, performed statistical traits-environment analyses, and supervised the project. All authors substantially contributed to the manuscript’s final version and approved publication.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Plant functional traits drive syntaxonomical units in temperate European inland salt-marsh vegetation

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Supplementary material

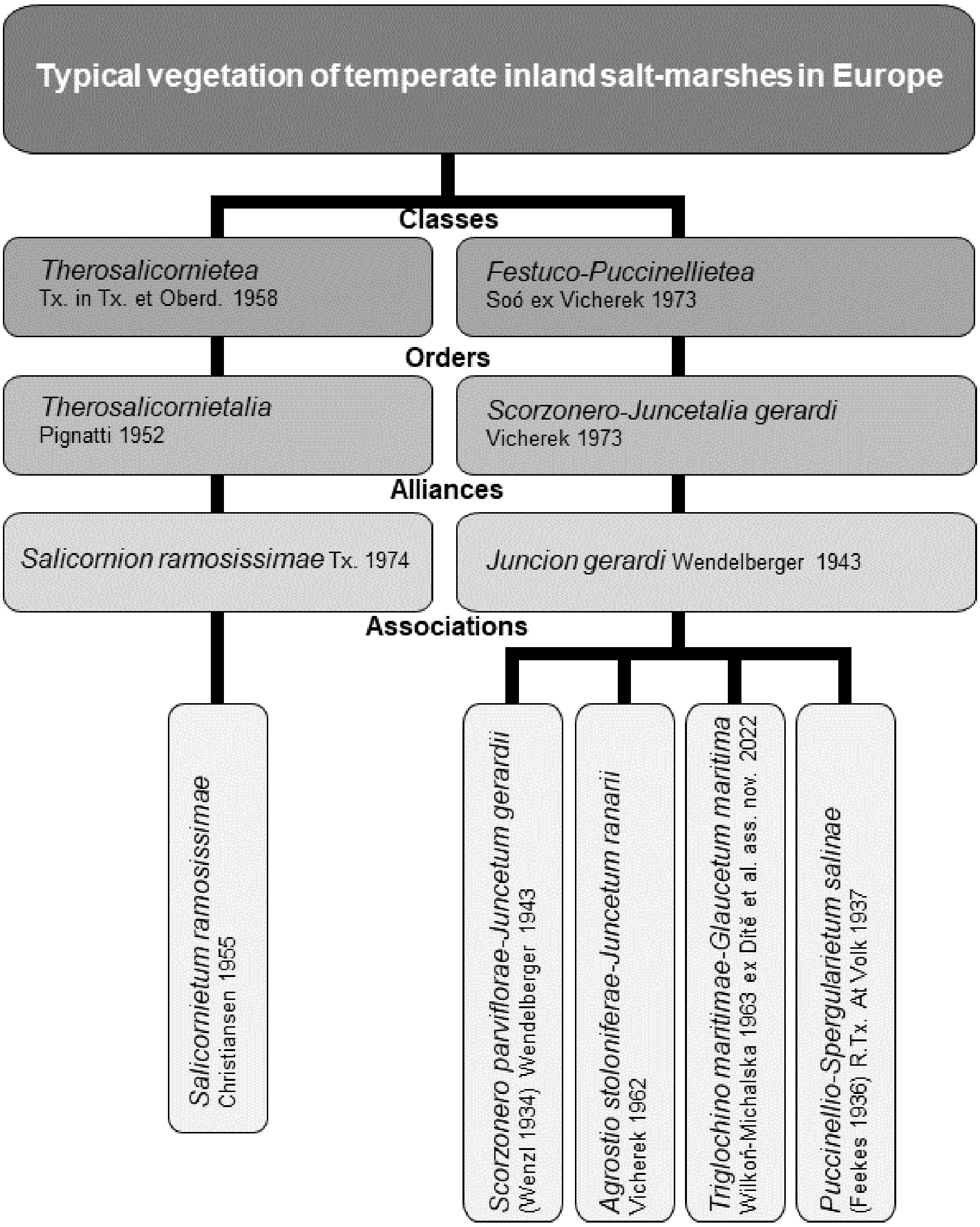

Figure S1. Diagram showing the syntaxonomical classification of two classes typical of the vegetation of temperate inland salt marshes in Europe. Prepared based on Lubińska-Mielińska et al. (2023).

Reference:
Lubińska-Mielińska, S., Kącki, Z., Kamiński, D., Pétillon, J., Evers, C., & Piernik, A. (2023). Vegetation of temperate inland salt marshes reflects local environmental conditions. Science of the Total Environment, 856, 159015. https://doi.org/10.1016/j.scitotenv.2022.159015

Table S1. Spearman's correlation coefficients between environmental variables based on Ellenberg indicator values and soil parameters (n=266). High correlations (r≥0.5) are marked in bold.

EIV\soil parameter	**EC_e**	**moist**	**N_{tot}**	**org.mat**	**pH**
S	**0.77******				
M		0.47****			
N			-0.14*		
N				-0.21***	
R					ns

**** p≤0.0001, *** p≤0.001, ** p≤0.01, * p≤0.05, ns – non-significant. Abbreviations of EVIs: S – salinity, M – moisture, N – nitrogen content, R – reaction. Abbreviations of soil parameters: EC_e – salinity measured as the electrical conductivity of saturated extract, moist – moisture, N_{tot} – total nitrogen, org.mat. – organic matter content.

Table S2. Conditional term effects of discriminant analysis (CVA) of functional traits and: vegetation classes (n=868); associations (n=450). Statistically significant factors are marked in gray ($p \leq 0.05$). Abbreviations of functional traits: C – clonality, CH – canopy height, CI – clonal index, LA – leaf area, LDMC – leaf dry matter content, LM – leaf mass, RH – releasing height, SM – seed mass, SN – seed number, SNPS – seed number per shoot, SLA – specific leaf area, TV – terminal velocity. Other abbreviations: pseudo-F – Fisher parameter, p – significance level. Conditional term effects exclude the effect of the most correlated variables.

Classes				**Associations**			
Variable	**% variation explained**	**pseudo-F**	***p***	**Variable**	**% variation explained**	**pseudo-F**	**p**
SLA	8.2	77.5	0.002	**SLA**	16.1	86	0.002
CH	5.7	57.7	0.002	**CI**	14.2	91.3	0.002
CI	3.9	41.2	0.002	**SN**	6.1	43.2	0.002
LDMC	1.8	19.3	0.002	**LDMC**	3	22	0.002
LM	1.9	21.1	0.002	**SNPS**	2.3	17.2	0.002
C	1.7	18.8	0.002	**C**	1.9	14.7	0.002
TV	0.9	10	0.002	**TV**	1.4	11.4	0.002
RH	0.8	8.7	0.002	**CH**	1.5	12.7	0.002
LA	0.6	7.2	0.002	**SM**	0.7	5.4	0.028
SN	0.5	5.9	0.002	**LM**	0.5	4.5	0.018
SNPS	1	11.9	0.002	**RH**	0.5	4	0.024
SM	0.2	2.1	0.092	**LA**	0.3	2.5	0.056

Table S3. Comparison of functional traits for vegetation classes (n=868). The ranges and means are given. Significantly different means are denoted by different letters at $p \leq 0.05$ according to Kruskal-Wallis test with Dunn post hoc comparisons. Abbreviations of vegetation classes: THE – *Therosalicornietea*, FEP – *Festuco-Puccinellietea*, POT – *Potamogetonetea*, PHR – *Phragmito-Magnocaricetea*, MOL – *Molinio-Arrhenatheretea*, BID – *Bidentetea*, ART – *Artemisietea vulgaris*, POL – *Polygono-Poetea annuae*.

Classes→ **Number of plots**	**THE** **137**	**FEP** **485**	**POT** **12**	**PHR** **112**	**MOL** **76**	**BID** **22**	**ART** **14**	**POL** **10**	**p**
Persistence									
Leaf area [mm^2]	73.6-9102 765^{c}	144-7843 1740^{b}	560-1284 903^{c}	784-8467 3032^{a}	939-10138 3192^{a}	1136-3599 2464^{a}	1342-4291 2425^{a}	539-6233 2985^{ab}	p<0.0001
Leaf mass [mg]	14.3-533 55.4^{e}	8.29-376 88.9^{cd}	34.2-85.1 60.5^{de}	56.7-657 216^{a}	43.7-581 159^{b}	58.3-356 136^{b}	53.4-245 109^{bc}	43.5-222 113^{bcd}	p<0.0001
Canopy height [m]	0.17-1.18 0.29^{d}	0.16-1.54 0.42^{c}	0.21-0.51 0.38^{c}	0.38-1.64 0.76^{a}	0.27-1.39 0.46^{bc}	0.45-1.16 0.75^{a}	0.49-0.80 0.66^{a}	0.33-0.61 0.52^{ab}	p<0.0001
Specific leaf area [mm^2/mg]	3.22-21.4 12.8^{e}	11.3-30.1 21.4^{c}	24.0-42.1 32.0^{a}	12.4-24.2 19.0^{d}	17.0-31.7 22.4^{b}	18.6-26.6 22.6^{bc}	21.2-25.5 23.2^{ab}	22.4-29.7 26.8^{a}	p<0.0001
Leaf dry matter content [mg/g]	139-279 179^{c}	122-277 195^{b}	129-180 155^{d}	153-314 234^{a}	190-280 226^{a}	137-237 184^{bc}	176-264 234^{a}	144-201 185^{bc}	p<0.0001
Clonal index [-]	0.00-3.48 1.44^{d}	0.50-5.35 3.09^{c}	4.17-4.89 4.55^{a}	1.74-5.27 4.01^{ab}	2.10-4.85 3.83^{b}	0.48-3.08 1.71^{d}	2.43-4.94 4.17^{ab}	0.88-2.27 1.58^{d}	p<0.0001
Clonality [-]	0.00-0.76 0.35^{d}	0.13-1.00 0.70^{c}	1.00-1.00 1.00^{a}	0.36-1.00 0.84^{b}	0.51-1.00 0.83^{b}	0.12-0.67 0.36^{d}	0.50-0.95 0.77^{bc}	0.22-0.60 0.39^{d}	p<0.0001
Regeneration									
Seed mass [mg]	0.24-1.42 0.58^{d}	0.06-5.97 0.85^{c}	0.78-1.73 1.21^{ab}	0.22-20.9 1.63^{b}	0.37-4.28 1.28^{b}	0.89-1.72 1.29^{ab}	0.85-2.41 1.82^{a}	0.34-1.84 1.02^{bc}	p<0.0001
Seed number [-]	709-86388 31489^{d}	479-322298 52829^{c}	268-10824 1771^{e}	54.5-858268 59907^{bd}	12891-291997 53041^{c}	14538-785214 80487^{abc}	2989-43435 16429^{e}	46493-714633 128029^{a}	p<0.0001
Seed number per shoot [-]	716-88102 17281^{c}	626-320781 37712^{b}	376-10913 1920^{d}	94.5-855075 54283^{b}	10493-282270 48459^{a}	6767-778915 64125^{ab}	3058-34017 14411^{c}	24678-699185 109356^{a}	p<0.0001
Dispersability									
Releasing height [m]	0.15-1.25 0.32^{f}	0.23-3.20 0.55^{de}	0.45-0.66 0.55^{bcd}	0.42-3.94 0.91^{a}	0.26-2.22 0.69^{c}	0.33-4.65 1.12^{ab}	0.63-4.48 1.57^{a}	0.26-0.53 0.41^{ef}	p<0.0001
Terminal velocity [m/s]	1.35-2.62 1.98^{d}	0.95-2.76 1.99^{d}	1.98-2.44 2.13^{acd}	1.13-3.58 2.14^{c}	1.50-2.70 2.18^{ac}	1.95-2.71 2.36^{b}	1.64-2.65 2.22^{abc}	2.17-2.66 2.37^{ab}	p<0.0001

Table S4. Comparison of functional traits for vegetation associations (n=450). The ranges and means are given. Significantly different means are denoted by different letters at $p \leq 0.05$ according to Kruskal-Wallis test with Dunn post hoc comparisons. Abbreviations of vegetation associations: Sr – *Salicornietum ramosissimae*, P-Ss – *Puccinellio-Spergularietum salinae*, Tm-Gm – *Triglochino maritimae-Glaucetum maritimae*, Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii*, As-Jr – *Agrostio stoloniferae-Juncetum ranarii*.

Associations→	**Sr**	**P-Ss**	**Tm-Gm**	**Sp-Jg**	**As-Jr**	**p**
Number of plots	**133**	**134**	**56**	**121**	**6**	
Persistence						
Leaf area [mm^2]	73.6-9102	144-5790	237-4802	315-6404	947-3099	
	764^{c}	1396^{b}	1879^{a}	1479^{b}	1751^{ab}	p<0.0001
Leaf mass [mg]	14.3-533	8.29-335	17.5-354	11.1-240	72.0-164	
	55.9^{d}	67.6^{c}	114^{a}	80.5^{b}	106^{ab}	p<0.0001
Canopy height [m]	0.17-1.18	0.16-1.54	0.22-0.75	0.24-0.79	0.29-0.49	
	0.29^{c}	0.39^{b}	0.46^{a}	0.45^{a}	0.38^{abc}	p<0.0001
Specific leaf area [mm^2/mg]	3.22-19.6	16.5-26.6	15.1-23.6	14.3-25.3	23.5-25.4	
	12.6^{c}	21.8^{a}	19.6^{b}	19.8^{b}	24.1^{a}	p<0.0001
Leaf dry matter content [mg/g]	147-279	122-239	161-241	171-277	149-197	
	179^{c}	169^{d}	206^{b}	224^{a}	172^{cd}	p<0.0001
Clonal index [-]	0.00-3.48	0.50-4.00	2.70-4.69	1.86-5.35	1.81-2.68	
	1.41^{c}	2.18^{b}	3.77^{a}	3.78^{a}	2.28^{bc}	p<0.0001
Clonality [-]	0.00-0.76	0.13-0.93	0.57-1.00	0.41-1.00	0.45-0.61	
	0.34^{c}	0.51^{b}	0.86^{a}	0.81^{a}	0.54^{bc}	p<0.0001
Regeneration						
Seed mass [mg]	0.24-1.42	0.18-4.89	0.38-1.40	0.06-2.86	0.26-1.12	
	0.57^{c}	0.73^{b}	0.77^{a}	0.86^{a}	0.47^{c}	p<0.0001
Seed number [-]	709-86388	24042-322298	1604-165450	912-320761	175505-298841	
	31669^{bd}	81322^{a}	28649^{d}	30007^{cd}	264810^{a}	p<0.0001
Seed number per shoot [-]	716-88102	14706-300567	1218-158806	987-320781	167415-270327	
	17514^{b}	58802^{a}	22822^{b}	24291^{b}	239048^{a}	p<0.0001
Dispersability						
Releasing height [m]	0.15-1.25	0.23-1.79	0.29-0.78	0.31-3.20	0.36-0.54	
	0.32^{c}	0.45^{b}	0.52^{a}	0.66^{a}	0.43^{ab}	p<0.0001
Terminal velocity [m/s]	1.35-2.51	0.95-2.71	1.48-2.63	1.29-2.63	1.44-2.14	
	1.97^{ab}	1.99^{a}	1.98^{ab}	1.92^{bc}	1.70^{c}	p<0.05

Table S5. Conditional term effects of forward selection and Monte Carlo permutation test (RDA analysis) of functional traits and: environmental variables based on Ellenberg indicator values (EIV, n=868); soil parameters and land use type (n=266). Statistically significant factors are marked in gray ($p \leq 0.05$). Abbreviations of environmental variables: L – light availability, M – moisture, N – nitrogen content, R – reaction, S – salinity, T – temperature. Abbreviations of soil parameters: EC_e – salinity measured as electrical conductivity, moist – moisture, N_{tot} – total nitrogen, org.mat. – organic matter content. Other abbreviations: pseudo-F – Fisher parameter, p – significance level. Conditional term effects exclude the effect of the most correlated variables.

Ellenberg Indicator Values				**Soil parameters and land use types**			
Variable	**% variation explained**	**pseudo-F**	***p***	**Variable**	**% variation explained**	**pseudo-F**	**p**
S	18.8	201	0.002	**EC_e**	9.8	28.6	0.002
M	4.5	50.4	0.002	**not used**	5.1	15.7	0.002
N	4.1	48.3	0.002	**moist**	3.5	11.3	0.002
R	3.3	40.6	0.002	**pH**	1.8	6	0.004
L	2.4	30.3	0.002	**industry**	1.8	5.9	0.002
T	0.9	12.3	0.002	**arable field**	1.2	4.2	0.024
				hay/pasture	0.5	1.8	0.100
				org.mat.	0.3	1	0.388
				N_{tot}	0.3	1.1	0.292

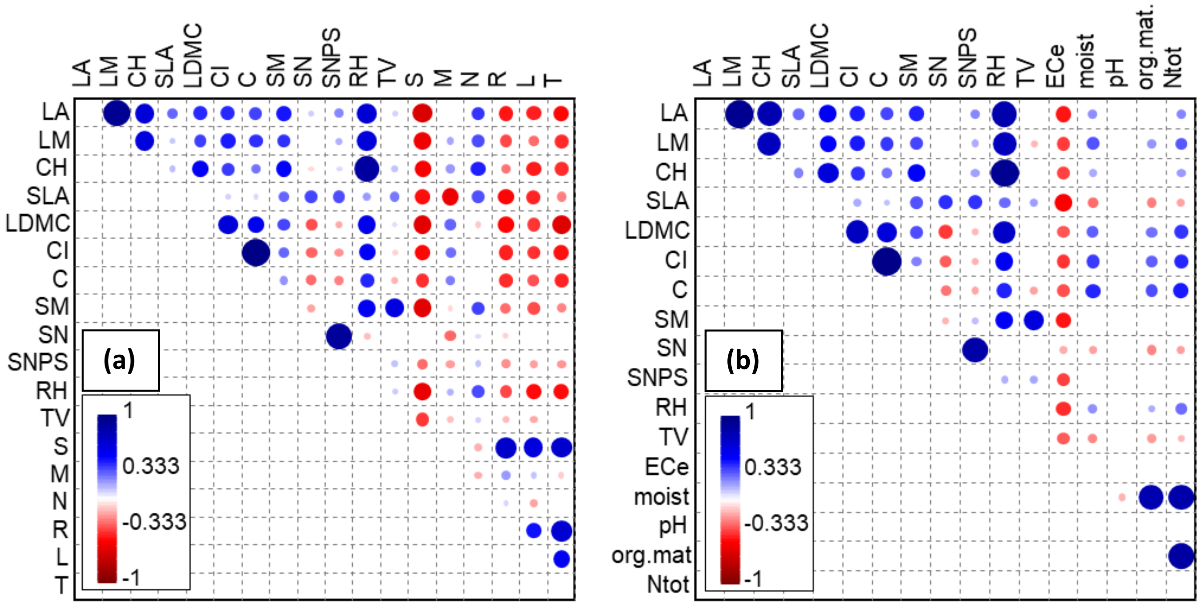

Figure S2. Results of Spearman's correlation analyses between functional traits and: (a) environmental variables based on Ellenberg indicator values (EIV, n=868); (b) soil parameters (n=266). Only significant correlations are presented (p≤0.05). Abbreviations of functional traits: LA – leaf area, LM – leaf mass, CH – canopy height, SLA – specific leaf area, LDMC – leaf dry matter content, CI – clonal index, C – clonality, SM – seed mass, SN – seed number, SNPS – seed number per shoot, RH – releasing height, TV – terminal velocity. Abbreviations of environmental variables: S – salinity, M – moisture, N – nitrogen content, R – reaction, L – light availability, T – temperature. Abbreviations of soil parameters: EC_e – salinity measured as electrical conductivity of saturated extract, moist – moisture, org.mat. – organic matter content, N_{tot} – total nitrogen.

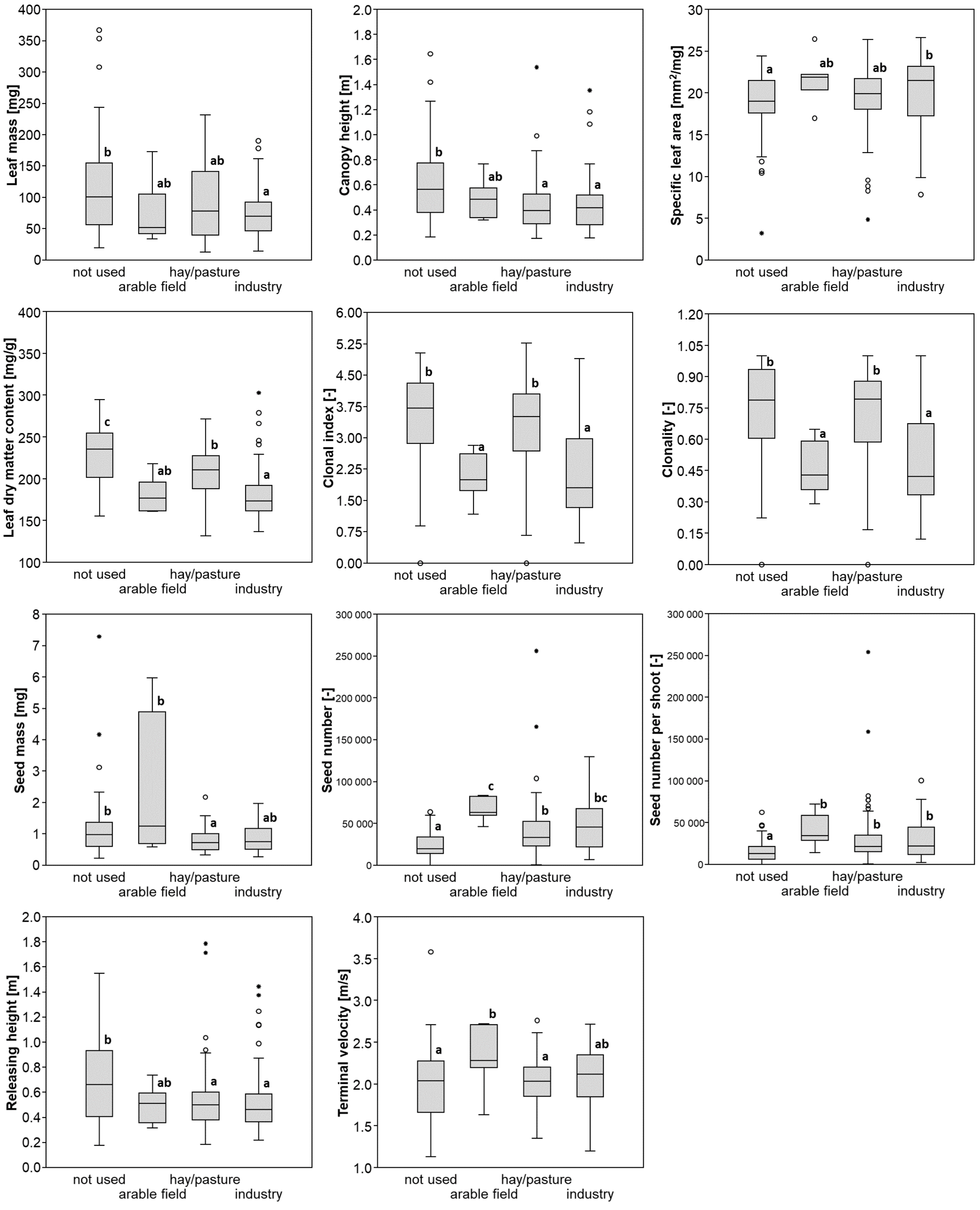

Figure S3. Relations between land use type and vegetation functional traits. Only traits with significant differences are presented. Significant differences between management types are denoted by different letters at p≤0.05 according to Kruskal-Wallis test with Dunn post-hoc comparisons.

4.3. *Diagnostic species are crucial for the functioning of plant associations in inland salt marshes*

Lubińska-Mielińska, S., Rajabi Dehnavi, A., Cárdenas Pérez, S., Kamiński, D., Piernik, A. – Diagnostic species are crucial for the functioning of plant associations in inland salt marshes

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Diagnostic species are crucial for the functioning of plant associations in inland salt marshes

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Abstract

Salt marsh vegetation is considered unique and valuable and has been legally protected in Europe for years but is still declining. Its protection is related to vegetation syntaxonomical units. The characteristic combination of diagnostic species is used to create this syntaxonomical system. The aim of our novel study was to assess whether diagnostic species are sufficient for characterizing vegetation functioning. Moreover, we included biochemical traits not considered to date in vegetation ecology. We hypothesized that 1) diagnostic species are crucial for the functioning of inland salt marsh vegetation and 2) their morphological and biochemical traits define the functioning of typical salt marsh associations. We chose three typical inland associations to test our hypotheses and measured the morphological and biochemical functional traits of their diagnostic plant species. Our research has shown that diagnostic species play a crucial role not only in distinguishing phytosociological units but also in determining their functioning. Among the analysed associations, *Salicornietum ramosissimae* was the most adaptable to osmotic and oxidative stress under soil salinity. *Triglochino maritimae-Glaucetum maritimae* showed the lowest salt resistance, as indicated by the highest osmotic and oxidative stress and stress responses. Our findings may facilitate practical application of new approaches and protection strategies for salt marsh habitats.

1. Introduction

The plant species that most effectively exhibit specific ecological relationships within a given community are used as indicators and are called diagnostic (Dg) species [1]. The characteristic combination of Dg species is used to create a hierarchical classification system of plant communities called phytosociological units. This system has been consistently developed and expanded based on the principle of maximal floristic and ecological similarity, with the association serving as the fundamental unit [2]. In fact, identifying individual communities is contingent upon the presence or absence of Dg plant species [3]. Within this selection framework, phytosociological fidelity, cover percentage, and frequency are clear pivotal indicators [1].

The development of the basic principles of vegetation classification facilitates the systematic description of all plant communities in large regions. Technological advancements have resulted in specialized software, such as TWINSPAN [4] or JUICE [5], to delineate syntaxonomical units. Although these programs help analyse large databases, the final decision on selection criteria is still in the hands of phytosociologists. However, the integration of specialized software ensures that these decisions are underpinned by statistical rigor, increasing the overall reliability of the classification process [4]. Currently, phytosociologists use Dg species based on the Phi coefficient as a statistical measure of the concentration and occurrence of species in phytosociological units [6,7]. An example of these recent developments is the study of European vegetation at the alliance level by Mucina et al. [8]. Ecological research shows that the species composition of such distinguished plant communities varies due to the availability of ecological niches and resource competition [9,10]. In addition to natural environmental factors that determine the species composition of phytosociological units, other processes are also critical, e.g., the influence of moving, grazing, and trampling by cattle [11,12].

Natural salt marsh habitats are critically important in the face of increasing salinity problems in agriculture worldwide [13]. They can serve as a source of natural, unique plant species adapted to high soil salinity that can be applied in future saline agriculture [14,15]. The most recent classification of European vegetation grouped inland salt marshes into two classes [8]. The class *Therosalicornietea* includes pioneer vegetation of annual succulent halophytes. The class *Festuco-Puccinellietea*, order *Scorzonero-Juncetalia gerardi* Vicherek 1973, and alliance *Juncion gerardi* Wendelberger 1943 include inland salt meadows of temperate salt marshes. Our recent research identified the association level within these classes together with their Dg species [16]. The main environmental drivers of this vegetation have already been identified [16,17,18]. A high-salt groundwater level, flooding, and management by moving and grazing are recommended for their conservation [17,19,20]. Although inland salt marshes in Europe have been protected for years and included in 1992 in the Natura 2000 network [21], they are still declining and are considered endangered [22]. Hence, it is imperative to explore novel approaches to address the question of which additional factors should be considered to prevent the depletion of salt marshes.

Recent investigations have demonstrated that syntaxonomical units and their functioning may be related to specific plant functional traits [23,24,25]. The functional traits of vegetation are increasingly used in the fight against invasive species and to predict the response of vegetation to climate change [23,26]. Therefore, an approach based on functional traits may also protect endangered habitats. Our recent research showed that syntaxonomical units of temperate inland salt marsh vegetation are functional, i.e., they differ in their functional traits [27]. Persistence traits, such as specific leaf area, canopy height, clonal index, leaf dry matter content, leaf mass, and clonality, are the most important for separating classes and associations. Additionally, regeneration traits, including seed number, play a significant role. We observed that the classes *Therosalicornietea* and *Festuco-Puccinelietea* and association with *Salicornietum ramosissimae* are the most sensitive to environmental changes due to their low persistence and regeneration potentials; therefore, special attention should be given to these units in the protection process.

Typically, such research on the functional traits of vegetation is based on data from large databases, which include many measurements or average values and a limited set of functional traits, e.g., by Kleyer et al. [28] or Lubińska-Mielińska et al. [27]. Biochemical traits related to salt stress responses were not included. Moreover, such research includes all recorded species, and whether Dg species have only syntaxonomical importance or functional meaning is not known. Therefore, we decided to concentrate only on Dg species in the current research and compare results based on the LEDA Traitbase [28]. The aim of this novel study was to ascertain whether including all species in vegetation trait analyses is essential or whether focusing solely on Dg species is sufficient. We hypothesized that 1) Dg species are crucial for the functioning of inland salt marsh vegetation and that 2) their morphological and biochemical traits define the functioning of typical salt marsh associations. To test our hypotheses, we chose three inland associations, the most common in Poland, and measured the functional traits of their Dg species. We used field-collected data from a single location with consistent salinity levels to include both morphological and biochemical traits, which are unavailable in functional trait databases. This approach allows for a detailed characterization of traits specific to individual associations and provides a partial validation of the relationships by leveraging morphological data from the LEDA Traitbase [28].

2. Results

2.1. Diagnostic species functional traits

The results concerning Dg species show that they differ significantly in measured persistence traits (see Tables 1 and S1). The highest values were found for Dg species of the *Triglochino maritimae-Glaucetum maritimae* association (*Tm-Gm*), i.e., *Phragmites australis* - shoot length (SL), shoots dry weight (SDW), leaves area (LA), leaves fresh and dry weight (LFW and LDW), and the leaf dry matter content (LDMC) of *Juncus compressus*. *Glaux maritima* had the highest specific leaf area index (SLA), while *Potentilla anserina* had the highest leaf mass (LM) and leaf weight ratio (LWR). In terms of the roots parameters, *P. australis* also had the greatest root length (RL) and roots fresh and dry weight (RFW and RDW), while *J. compressus* had the greatest root weight ratio (RWR). *Salicornia europaea*, a Dg species of the *Salicornietum ramosissimae* (*Sr*) association, had the highest shoots fresh weight (SFW) and shoot weight ratio (SWR), followed by the assimilation area (AA) of *P. australis. Atriplex prostrata*, *Puccinellia distans*, and *G. maritima* were characterized by the greatest number of leaves (NoL). The morphological traits of *Spergularia marina* and *Triglochin maritima* were intermediate.

For biochemical parameters, the highest contents of the photosynthetic pigments chlorophyll a (chla), b (chlb), total (chlt), and carotenoids (car), were found in *P. anserina, P. australis*, and *G. maritima,* which are the Dg species for the *Tm-Gm* association; *P. distans* and *A. prostrata,* which are the Dg species for the *Puccinellio-Spergularietum salinae* association (*P-Ss*) (Table S2). Among the substances involved in osmoregulation, proline (prol) was most abundant in *T. maritima* and *P. distans*, and carbohydrates (carbo) were most abundant in *G. maritima, J. compressus*, and *A. prostrata.* Substances acting as stress markers were also the most abundant in the Dg species of both associations. The highest hydrogen peroxide (H_2O_2) levels were detected in *G. maritima* and *A. prostrata,* while the highest malondialdehyde (MDA) levels were detected in *P. australis*, *J. compressus, P. anserina*, and *P. distans*. The highest antioxidant enzyme activities were observed in Dg species of the *Tm-Gm* association, i.e., catalase (CAT) activity in *G. maritima* and *P. anserina* and peroxidase (APX) activity in *T. maritima*, *P. australis,* and *P. anserina*.

2.2. Plant associations morphological traits

The results of trait comparisons weighted by species cover averages for associations demonstrated that the highest canopy (SL) was typical for *Tm-Gm* and the shortest for *Sr* (see Fig. 1). The *Tm-Gm* association was also characterized by the highest RL and belowground biomass (RFW and RDW), while the *Sr* association had the highest aboveground biomass (SFW and SDW). The *P-Ss* association had the shortest RL and the lowest RFW.

Among the parameters related to leaves (see Fig. 1), the *Tm-Gm* association had the highest LFW, LDW, single LM and LA. The highest NoL was recorded for the *P-Ss* association. Thus far, the lowest leaves parameter values were observed for the *Sr* association. However, the AA of this association was the highest. As mentioned, the Dg species of the *Sr* association is *S. europaea*, the entire shoots of which have assimilation functions.

Fig. 2 compares individual association indices calculated based on morphological parameters. The *Sr* association was characterized by the highest SWR, while the *Tm-Gm* association had the highest RWR, LWR, SLA, and LDMC. The *P-Ss* association had intermediate values in all cases except LDMC, which was similar to that of the *Tm-Gm* association.

The principal component analysis (PCA) and the correlation of traits with the ordination axes (Fig. 3a and Table 2) revealed differences between the analysed associations due to morphological traits. The first ordination axis (PC1) explained 54.3% of the trait variability. It was positively correlated with most leaves parameters, such as LM, LFW, LDW, LA, LDMC, SLA, LWR, and the SL and RWR characteristics of the *Tm-Gm* association. PC1 was also strongly negatively correlated with SFW and SWR, with the highest correlation occurring for the *Sr* association. The second axis (PC2) explained 29.7% of the variance and was positively correlated with AA, SDW, and RL; the correlations were stronger in the *Sr* and *Tm-Gm* associations than in the *P-Ss* association. PC2 was most strongly negatively correlated with NoL in the *P-Ss* association, for which the centroid was located in the lower part of the PCA graph.

2.3. Plant associations biochemical traits

Fig. 4 summarizes biochemical traits related to photosynthetic pigment contents – chla, chlb, chlt, and car; osmoregulation – prol and carbo; stress indicators – H_2O_2 and MDA; and antioxidant enzyme activities – CAT and APX. The parameters related to photosynthetic pigment content were the lowest for *Sr*, intermediate for *P-Ss*, and highest for the *Tm-Gm* association. The other parameters, except for MDA and prol, were highest for the *Tm-Gm* association. MDA was the highest for the *P-Ss* association, while prol was the highest for both of these associations. The lowest value for prol was obtained for the *Sr* association, and that for carbo was obtained for the *P-Ss* association. The lowest values of stress indicators and antioxidant enzyme activity were recorded for the *Sr* association. CAT activity was also low in the *P-Ss* association.

PCA (Fig. 3b) and the correlation of traits with the ordination axes (Table 3) revealed differences in the analysed associations due to biochemical traits. The first ordination axis (PC1) explained 70.5% of the variability. It was positively correlated with the prol, MDA, and car contents, which were highest in the *P-Ss* and *Tm-Gm* associations and lowest in the *Sr* association. The second axis (PC2) explained 24.0% of the variance. It was positively correlated with H_2O_2 content, APX activity, and chla, chlb, and chlt contents; the highest correlation was observed in the *Tm-Gm* association, for which the centroid was located in the upper right part of the graph, and the lowest was observed for the *Sr* association.

Table 1. Diagnostic species within three typical inland salt-marsh associations in temperate Europe according to Lubińska-Mielińska et al. [16]

Associations	Abbreviations	Diagnostic species
<u>Class:</u> *Therosalicornietea* **Tx. in Tx. et Oberd. 1958**	**THE**	(see association ↓)
Salicornietum ramosissimae Christiansen 1955	*Sr*	*Salicornia europaea* L.
<u>Class:</u> *Festuco-Puccinellietea* **Soó ex Vicherek 1973**	**FEP**	(see associations ↓)
Triglochino maritimae-Glaucetum maritimae Wilkoń-Michalska 1963 ex Dítě et al. ass. nov. 2022	*Tm-Gm*	*Triglochin maritima* L. *Glaux maritima* L. (= *Lysimachia maritima* (L.) Galasso, Banfi & Soldano) *Phragmites australis* (Cav.) Steud. *Juncus compressus* Jacq. *Potentilla anserina* L.
Puccinellio-Spergularietum salinae (Feekes 1936) R.Tx. at Volk 1937	*P-Ss*	*Spergularia marina* (L.) Besser *Puccinellia distans* (Jacq.) Parl. *Atriplex prostrata* Boucher ex DC.

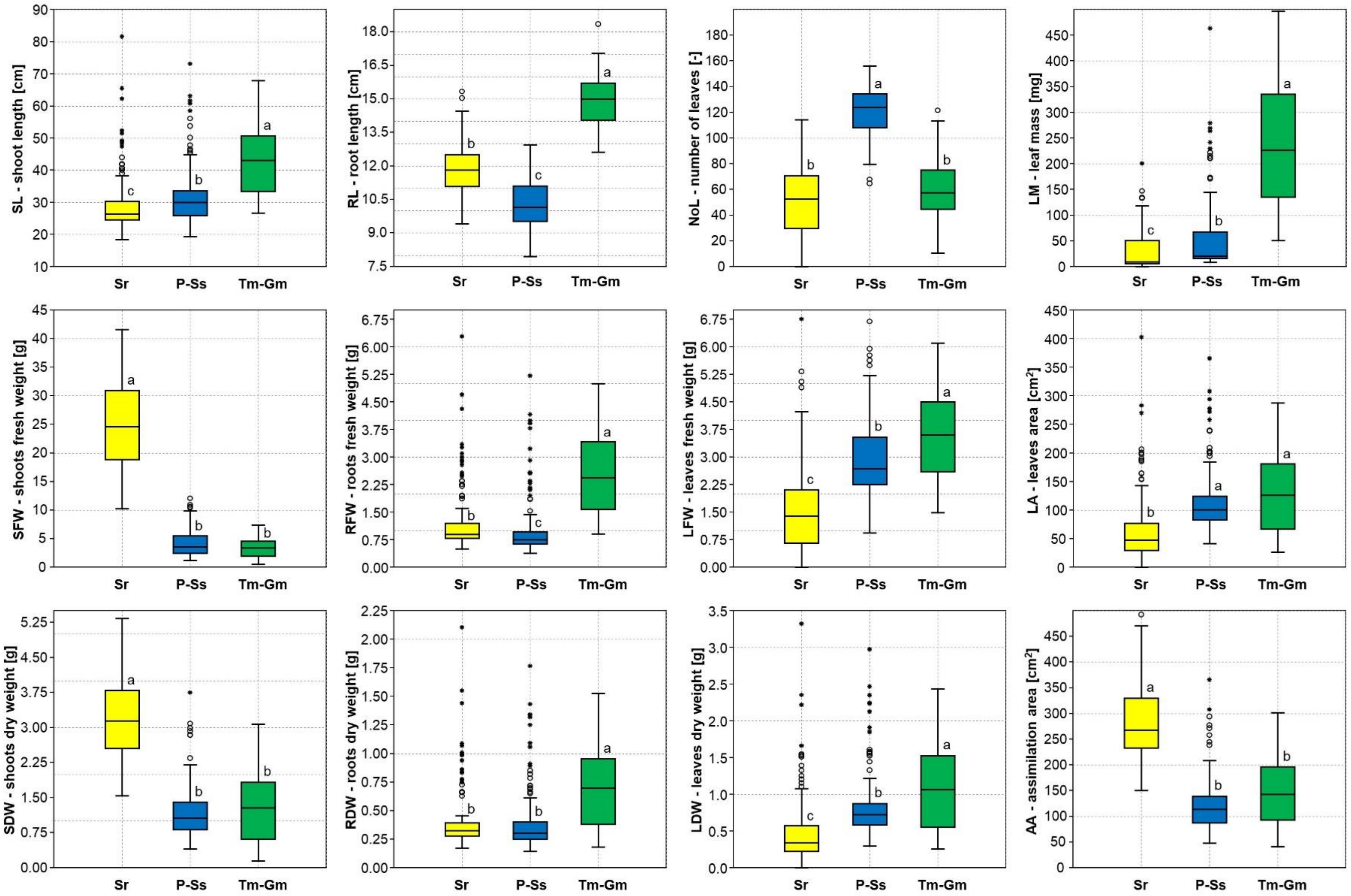

Figure 1. Comparison of morphological traits related to shoots, roots, and leaves parameters for vegetation associations. Significantly different groups (at p ≤ 0.05), according to the Kruskal–Wallis test with Dunn post hoc comparisons, are denoted by different letters. Abbreviations of associations: *Sr – Salicornietum ramosissimae* (n = 133), *P-Ss – Puccinellio-Spergularietum salinae* (n = 134), *Tm-Gm – Triglochino maritimae-Glaucetum maritimae* (n = 56).

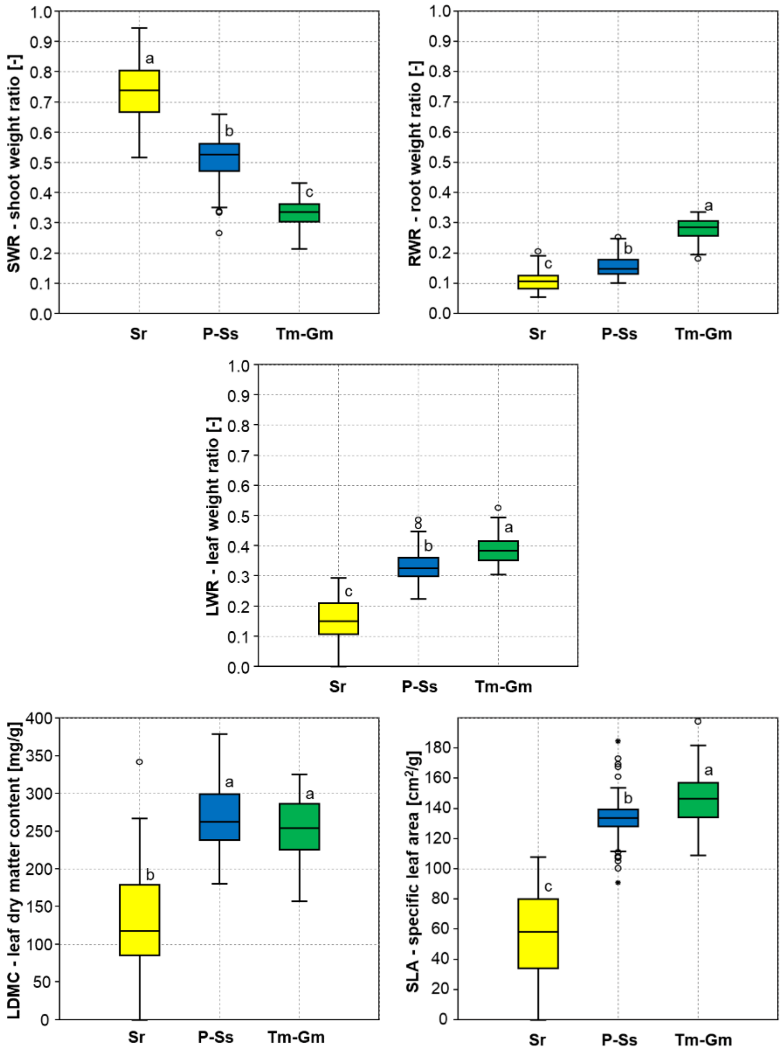

Figure 2. Comparison of indices calculated based on morphological traits for vegetation associations. Significantly different groups (at $p \leq 0.05$), according to the Kruskal–Wallis test with Dunn post hoc comparisons, are denoted by different letters. Abbreviations of associations: *Sr – Salicornietum ramosissimae* (n = 133), *P-Ss – Puccinellio-Spergularietum salinae* (n = 134), *Tm-Gm – Triglochino maritimae-Glaucetum maritimae* (n = 56).

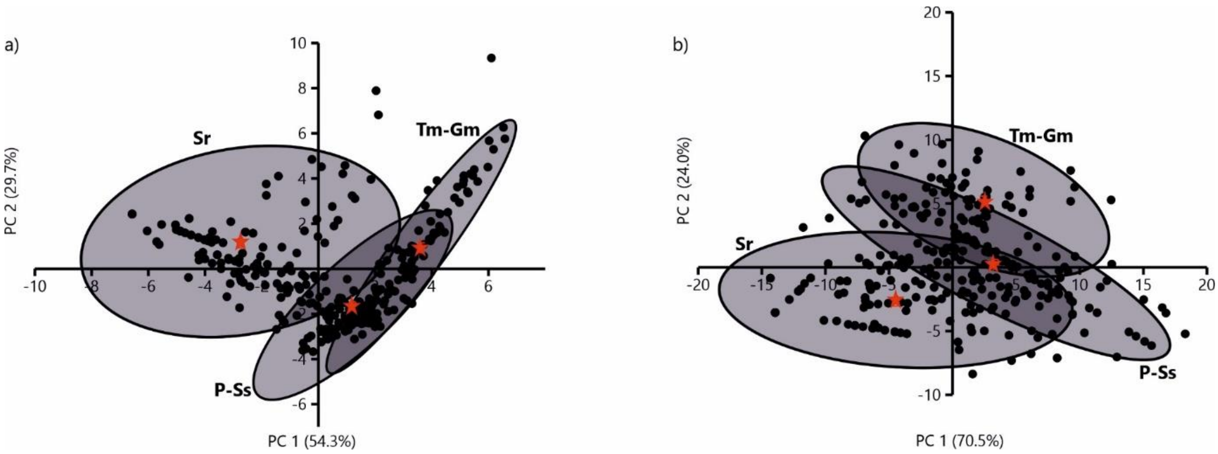

Figure 3. Results of principal component analysis (PCA) showing the relationships between the analysed associations and (a) morphological functional traits and (b) biochemical functional traits. The red star marks the centroid of each group. Abbreviations of associations: *Sr* – *Salicornietum ramosissimae* (n = 133), *P-Ss* – *Puccinellio-Spergularietum salinae* (n = 134), *Tm-Gm* – *Triglochino maritimae-Glaucetum maritimae* (n = 56).

Table 2. Results of Spearman's correlation (r_s) of morphological functional traits with the principal component analysis (PCA) ordination axes. Statistically significant values are marked by asterisks: * p≤0.05, ** p≤0.01, *** p≤0.001, **** p≤0.0001. Abbreviations of morphological functional traits: SL – shoot length, RL – root length, SFW – shoots fresh weight, SDW – shoots dry weight, RFW – roots fresh weight, RDW – roots dry weight, NoL – number of leaves, LM – leaf mass, LFW – leaves fresh weight, LDW – leaves dry weight, LA – leaves area, AA – assimilation area, LDMC – leaf dry matter content, SLA – specific leaf area, SWR – shoot weight ratio, RWR – root weight ratio, LWR – leaf weight ratio. Correlation coefficients greater than 0.7 are marked in bold, and the cells are grey.

	PC 1	PC 2	SL	RL	SFW	SDW	RFW	RDW	NoL	LM	LFW	LDW	LA	AA	LDMC	SLA	SWR	RWR	LWR
PC 1		-0.07	**0.79** ****	0.21 ***	**-0.73** ****	-0.54 ****	0.51 ****	0.54 ****	0.39 ****	**0.84** ****	**0.86** ****	**0.84** ****	**0.83** ****	-0.45 ****	**0.83** ****	**0.83** ****	**-0.94** ****	**0.87** ****	**0.92** ****
PC 2	-0.07		0.36 ****	**0.71** ****	0.66 ****	**0.82** ****	0.69 ****	0.59 ****	**-0.74** ****	0.16 **	0.07	0.13 *	0.10	**0.87** ****	-0.35 ****	-0.45 ****	0.27 ****	-0.16 **	-0.33 ****

Table 3. Results of Spearman's correlation (r_s) of biochemical functional traits with the principal component analysis (PCA) ordination axes. Statistically significant values are marked by asterisks: * p≤0.05, ** p≤0.01, *** p≤0.001, **** p≤0.0001. Abbreviations of biochemical functional traits: chla – chlorophyll a, chlb – chlorophyll b, chlt – total chlorophyll, car – carotenoids, prol – proline, carbo – carbohydrates, H_2O_2 – hydrogen peroxide, MDA – malondialdehyde, CAT – catalase, APX – ascorbate peroxidase. Correlation coefficients greater than 0.5 are marked in bold, and the cells are grey.

	PC 1	PC 2	chla	chlb	chlt	car	prol	carbo	H_2O_2	MDA	CAT	APX
PC 1		0.02	0.40****	0.48****	0.43****	**0.54******	**0.99******	-0.48****	-0.23****	**0.70******	0.02	0.37****
PC 2	0.02		**0.59******	**0.62******	**0.60******	0.50****	0.09	0.46****	**0.96******	0.00	0.16**	**0.62******

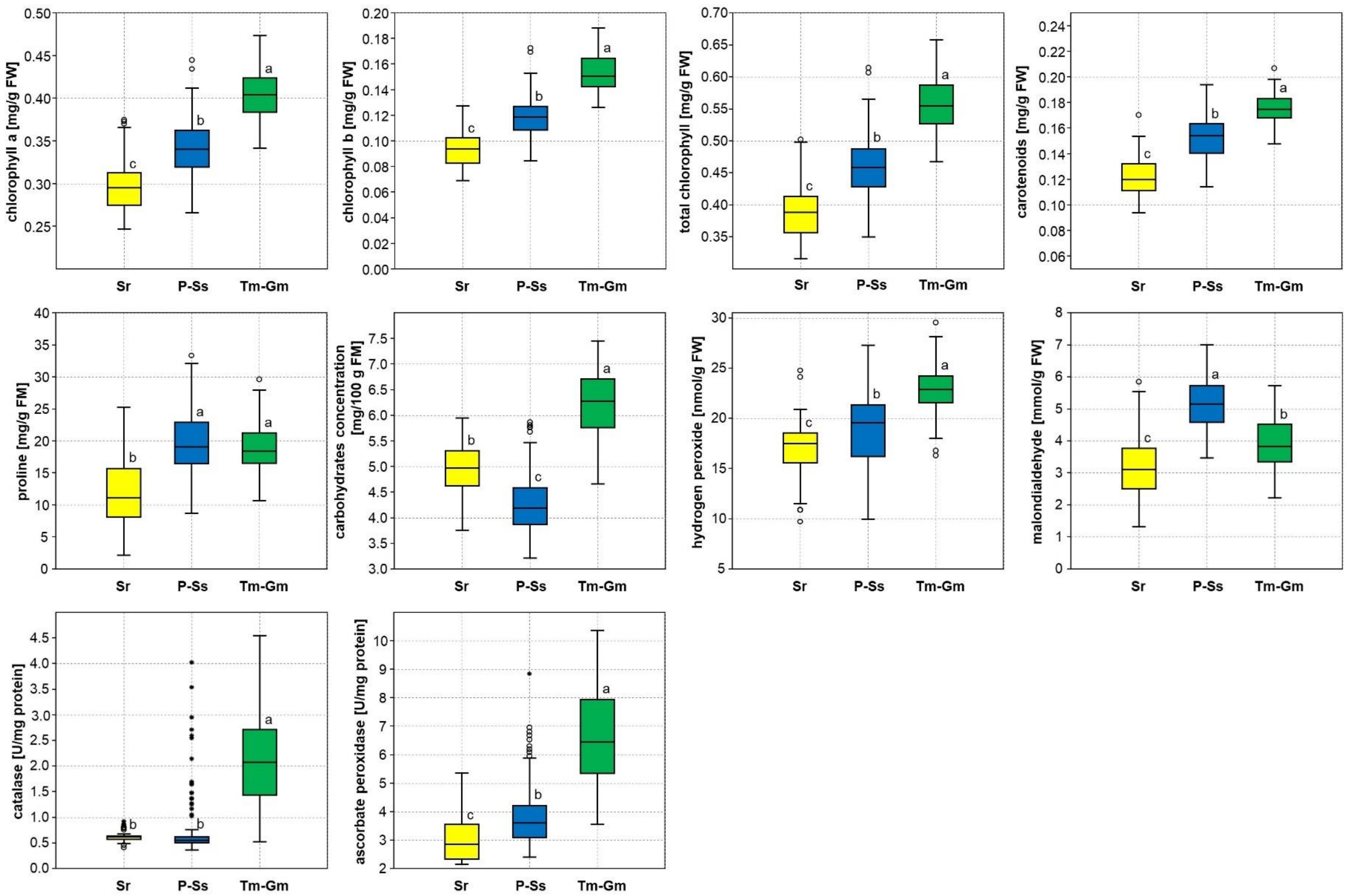

Figure 4. Comparison of biochemical functional traits for vegetation associations. Significantly different groups (at p ≤ 0.05), according to ANOVA with Tukey's post hoc comparisons, are denoted by different letters. Abbreviations of associations: *Sr – Salicornietum ramosissimae* (n = 133), *P-Ss – Puccinellio-Spergularietum salinae* (n = 134), *Tm-Gm – Triglochino maritimae-Glaucetum maritimae* (n = 56).

2.4. Key role of diagnostic species

To test the key role of Dg species, we compared data from the LEDA Traitbase [28] based on weighted means of nine Dg species with weighted means of all species recorded in the plots. We compared the five functional traits of the *Sr*, *P-Ss*, and *Tm-Gm* associations: canopy height (CH), leaf size (LS), leaf mass (LM), leaf dry matter content (LDMC), and specific leaf area (SLA). In all cases, except those involving LM, the results for the analysed associations were identical (see Fig. 5). The results for the *Sr* and *P-Ss* associations calculated using data for only Dg species showed no difference in LM, but when using data for all species, LM was clearly lower for the *Sr* association. Despite these slight differences, the results indicate the key role of Dg species in the functioning of plant communities in salt marshes.

We also validated the data from the LEDA Traitbase by comparing the results with those based on field measurements. The LEDA CH can be considered equivalent to our SL, and the LEDA LS is comparable to our 1LA. The other three parameters, LM, LDMC, and SLA, are the same. The comparison showed that the weighted means of species traits, in general, reflect differences in CH, LA, and LM between associations. The greatest differences between the results were found for LDMC and SLA (Fig. S1). For LDMC, the highest value was obtained for the *P-Ss* association based on measurements instead of the lowest, and for SLA, the *P-Ss* and *Tm-Gm* associations switched places.

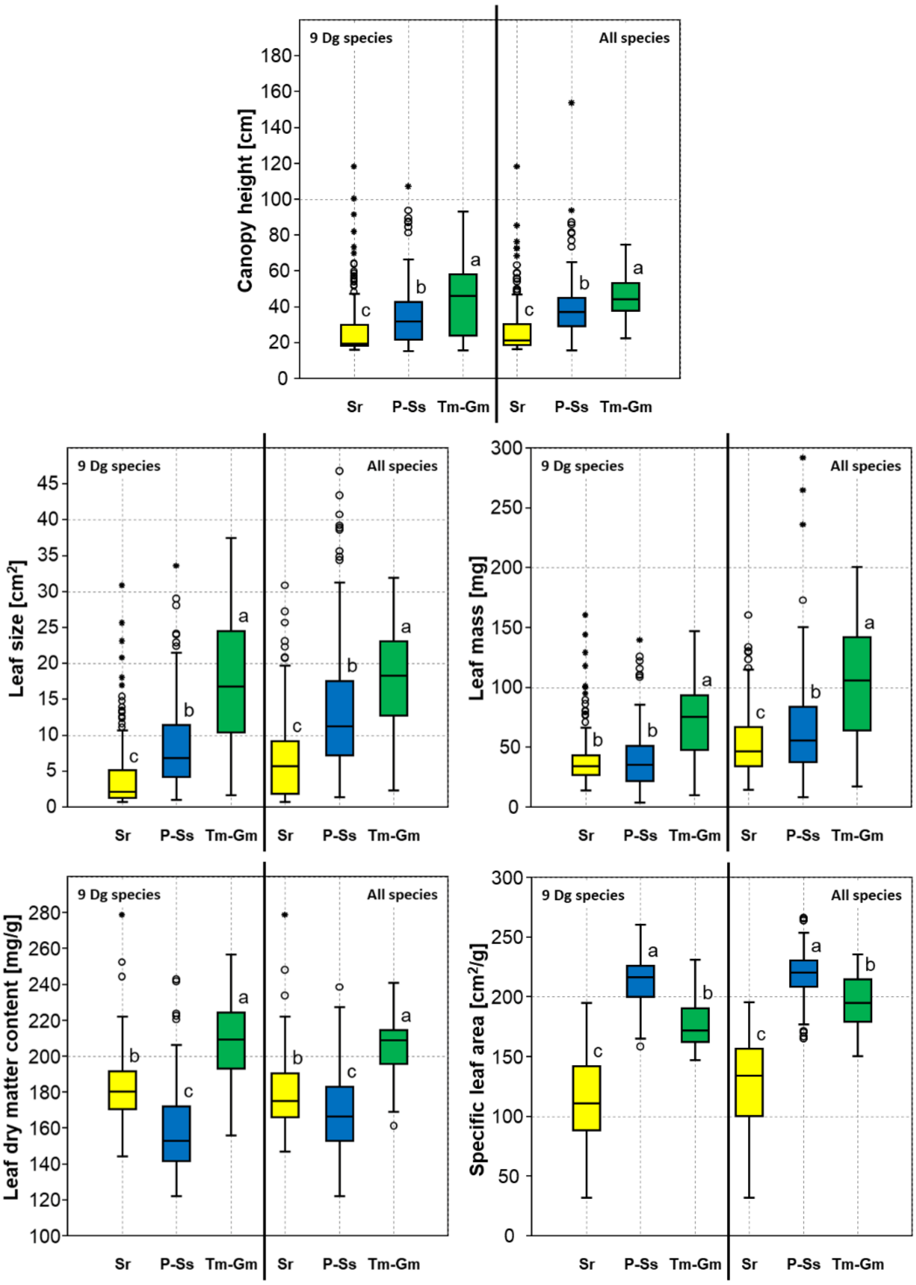

Figure 5. Comparison of functional traits based on LEDA Traitbase data [28] for vegetation associations. Significantly different groups (at p ≤ 0.05), according to the Kruskal–Wallis test with Dunn post hoc comparisons, are denoted by different letters. Abbreviations of associations: *Sr* – *Salicornietum ramosissimae* (n = 133), *P-Ss* – *Puccinellio-Spergularietum salinae* (n = 134), *Tm-Gm* – *Triglochino maritimae-Glaucetum maritimae* (n = 56).

3. Discussion

3.1. Adaptive strategies

Our previous results [27] showed that persistence traits are the most important for separating classes and associations among the vegetation of inland salt marshes in temperate Europe. Moreover, the classes specific to salt marshes, *Therosalicornietea* and *Festuco-Puccinelietea*, are the most sensitive to environmental changes due to their low persistence and regeneration potential and thus need special attention in the protection process. Therefore, we decided to take a closer look at the functional strategies of associations representing both salt marsh classes, expanding the group of analysed traits to include more of the most important traits responsible for persistence under salinity stress. We measured morphological functional traits, which are the focus for most scientists when creating databases with functional traits of plant species, e.g., the LEDA Traitbase [28] or the Clo-pla database [29], and parameters of roots that are missing in databases. In addition, we extended our research with biochemical parameters to better understand the relationships between these traits and the functioning of leaves, which play an essential role in differentiating associations in salt marshes [27]. Moreover, functional biochemical plant traits, which we included as the novelty of our study, are currently unavailable in databases and are novel in phytosociological studies. The results of the morphological trait analysis revealed significant differences among the three considered associations. These differences were particularly notable for various leaves parameters, including LWR, LFW and LDW, LM, SLA, LDMC, and LA, as well as RWR and SL. Remarkably, the *Tm-Gm* association exhibited the highest values for these parameters. The high dry and fresh weight values revealed relatively high biomass production in this association. Therefore, habitats occupied by *Tm-Gm* are frequently reported as pastures or hay meadows [30,31]. A high LA directly influences the highest SLA [32]. Plants grown in resource-rich environments can increase their photosynthetic capacity and productivity via higher SLAs [33]. SLA is linked to water use or survival strategies [34]. Plants adopt the strategy of smaller SLAs to improve stress resistance and competitive ability in stressful environments [35] because large leaves tend to require greater biomass investments per unit of LA than small leaves [36]. The relatively high LDMC in the *Tm-Gm* association confirms, on the one hand, the higher productivity of this association [37] but, on the other hand, the lower acquisitive strategy [38]. These results also prove the role of roots in association productivity. The highest RWR in the *Tm-Gm* association was related to the greatest ability to acquire water and nutrients from the soil [39]. An increase in roots parameters such as length and weight indicates the plasticity of the plant, which is adapted to salinity stress [40,41].

The highest values of AA, SFW, SDW, and SWR were characteristic of the *Sr* association. This association is dominated by the extreme halophyte *S. europaea*, whose reduced leaves and succulent shoots take over during the assimilation process [42]. The fresh weight can be affected by water accumulation, and a greater dry weight can be affected by ionic accumulation [43]. The leaves reduction of this Dg species affects the low SLA of the association, which proves that its stress resistance and competitive ability increase in stressful environments [35]. A low LDMC in the *Sr* association indicates a rapid acquisition strategy in leaves [38]. The *P-Ss* association was characterized by the greatest number of leaves related to the physiognomy of the Dg species *P. distans* and *S. marina* [44,45]. This association had an LDMC similar to that of the *Tm-Gm* association, which was lower than that of the *Sr* association, indicating an acquisitive strategy in leaves [38]. All differences in traits between associations could be related to the impact of salinity. It is well documented that an increase in salinity, depending on the species and even variety, has a negative correlation with all morphological traits of leaves, shoots, roots, and even flowers [46]. For example, Mohammadi and Kardan [47] reported a noticeable response to increasing salinity, manifested by a reduction in the dry mass of shoots and roots of selected halophytes.

The results of the biochemical trait analysis highlighted notable differences among the considered associations, particularly in the prol and MDA contents, which were greater in the *P-Ss* and *Tm-Gm* associations than in the *Sr* association. High prol accumulation is a physiological response of plants to abiotic stress factors, which may be due to its synthesis, reduced degradation, lower utilization, or protein hydrolysis [48]. In addition, under saline conditions, there is an increase in the activity of prol synthesis enzymes, including pyrroline carboxylic acid and glutamyl kinase [49]. A relatively high prol content can be due to plant defence against high osmotic pressure in the soil solution, which allows water absorption under high soil salinity. However, as shown in the example of *S. europaea*, the level of prol in halophytes may be stable even with increasing salinity [42]. Some halophytes produce prol analogues, e.g., glycine betaine, under salt stress to survive due to their ability to protect the protein turnover machinery, stabilize proteins, and prevent enzymes from denaturing [50]. For glycophytic species, an increasing level of prol is observed with increasing salinity [51]. MDA is used to evaluate lipid peroxidation in cell membranes induced by salt stress [52,53,54]. A high MDA level can indicate greater oxidative stress under saline conditions [55], which can be comparable for both the *Tm-Gm* and *P-Ss* associations in terms of lipid peroxidation and lower for the *Sr* association.

Another marker of oxidative stress is H_2O_2, a reactive oxygen species (ROS) produced in cells during normal aerobic metabolism. During the action of unfavourable external factors (such as salinity), H_2O_2 is overproduced in plants, which can damage cell components and lead to cell death [56,57,58]. A greater increase is observed in salt-sensitive plants than in salt-tolerant plants under salt stress [53]. Our results demonstrated that the lowest oxidative stress caused by H_2O_2 was present in the *Sr* association, the stress caused by H_2O_2 was greater in the *P-Ss* association, and the stress caused by H_2O_2 was greatest in the *Tm-Gm* association. One of the elements involved in the response to oxidative stress is the induction of CAT and APX, which are H_2O_2-metabolizing enzymes [56,57]. The highest activity of the mentioned enzymes in the *Tm-Gm* association indicates the highest defence against oxidative stress under salinity. Interestingly, APX activity was greater than CAT activity, demonstrating its greater role in salt marsh vegetation. Cárdenas Pérez et al. [42] reported similar results for the halophyte *S. europaea*.

The photosynthetic pigment concentration related to productivity was greatest in the *Tm-Gm* association, lower in the *P-Ss* association, and lowest in the *Sr* association. The different responses of photosynthetic pigments to soil salinity levels have been reported in the literature. In some species, a decrease in the level of chl or car was recorded under salt stress, e.g., by Taïbi et al. [59]. In others, an increase was observed but was not related to increased productivity [60,61]. A decrease in chl content is considered a symptom of oxidative stress [62]. This is related to the inhibition of chl synthesis and the activation of chl degradation [63]. The results for *S. europaea*, the Dg species of the *Sr* association, confirmed a decrease in chl content together with increasing salinity but not related to a decrease in biomass production [42]. Car not only acts as a pigment but also as an antioxidant, and its high content may indicate that its production is one of the most important protective mechanisms against salinity stress in the *Tm-Gm* vegetation type [59]. Carbo acts together with prol as an osmolyte responsible for the greater biochemical stability of cells. Research on various species shows that an increase in the level of carbo is associated with greater plant resistance to salinity [64,65]. Our results demonstrate that both prol and carbo play similar roles in the *Sr* and *Tm-Gm* association*s,* while carbo plays a minor role compared to prol in the *P-Ss* association.

PCA allows us to compare the functioning of the associations based on all analysed traits together. However, to make this comparison clearer, we separated morphological and biochemical traits. The first PCA axis of the morphological trait analysis can be interpreted as a negative salinity gradient with *Sr* at the most saline sites and *P-Ss* and *Tm-Gm* at the least saline sites, which has already been discussed. Such a sequence along the salinity gradient of these associations has already been reported [16,17,45]. The second PCA gradient separating the *P-Ss* association from the other two associations can be interpreted as a different strategy of receiving resources—related to high RL and AA – resulting in relatively high SDW in the *Sr* and *Tm-Gm* associations and, at the opposite axis end, the *P-Ss* association investing in higher NoL. Taking into account biochemical parameters, the main differences between the considered associations along the first PCA axis can be interpreted as a response to osmotic stress, the latter expressed in the *Sr* association, where dominant species are adapted to extreme salinity [42,66] and the most highly expressed in the *P-Ss* and *Tm-Gm* associations, where the Dg species are less adapted to salinity and demonstrate more intensive defences. This osmotic stress is most strongly related to the accumulation of prol but also to the oxidative damage of lipids in cell membranes (MDA) and the protective response of car. The biochemical factor related to the second PCA axis can be interpreted as a response to the oxidative stress marked by H_2O_2, and the defence by APX was the highest in the *Tm-Gm* association, where the Dg species are less adapted to salinity. A greater increase in H_2O_2 and APX in salt-sensitive plants than in salt-tolerant plants under salt stress has already been reported [53].

3.2. Validity of the databases

Our research indicated that results based on directly measured functional traits may differ from those obtained based on average values from the databases. According to Kattge et al. [67], plant traits are heterogeneous, have a low degree of standardization, and often require auxiliary data to interpret the results, particularly in the context of biotic and abiotic environmental stress. For habitats such as the analysed salt marshes, environmental factors such as substrate parameters (e.g., salinity level) can be crucial [42,68,69]. Cárdenas Pérez et al. [42] showed that changing only the substrate salinity concentration may influence fluctuations in both the morphological and biochemical traits of *S. europaea*. Such factors may result in differences even within plants of the same age and within the same research area, which may result in a mosaic of environmental parameters. Moreover, Cárdenas Pérez et al. [66] demonstrated that the local environment, i.e., maternal salinity, can determine trait responses in the same species. Additionally, trait values may depend on the genotype or ecotype of the plant species [13,70]. We found the greatest differences in the results based on our own measurements and data from the LEDA Traitbase referring to LDMC and SLA. The LDMC reflects an acquisitive strategy and may be related to population stability. Lower values of LDMC can be interpreted as lower productivity related to the site of species collection but a higher acquisitive strategy [37,38]. Májeková et al. [71] showed that higher LDMC values might be related to greater population stability. The SLA also reflects adaptation to the local environment. It is generally believed that plants grown in resource-rich environments use higher SLA to enhance their photosynthetic capacity and productivity [33]. Species adapt to smaller SLAs to improve stress resistance and competitive ability in stressful environments [35,72]. Therefore, the SLA may strongly depend on the salinity level of the site where the plants were collected. Independently of the trait data source, the results should be interpreted with caution. For large datasets, average trait values from databases can be even better, reflecting general differences and trends.

3.3. Syntaxonomical integrity

Our results indicate the syntaxonomical integrity of inland salt marsh vegetation in temperate Europe. The species composition of the syntaxonomical units distinguished based on phytosociological principles [1] and statistical measures [6,16,73] reflects the different strategies used by the analysed associations. Moreover, for the first time, we demonstrated the key role of Dg species in linking phytosociological and functional vegetation approaches. The Dg species, which reflect ecological relationships, constitute specific indicators of syntaxonomical divisions according to the assumptions of Braun-Blanquet [1]. Even at the lowest level of organization in the syntaxonomical hierarchy – associations – identifying Dg species can be difficult [2]. With the use of the Cocktail method [73,74] and an expert computer system [75], it is possible to obtain stable, repeatable, and consistent classification outcomes, including Dg species identification, e.g., by Landucci et al. [76]. Our results demonstrated that functional differences between associations are directly related to Dg species rather than the whole species composition. This can make progress in research focusing on association functioning by limiting measurements and calculations to a few Dg species instead of all species. Additionally, our concept of phytosociological units as functional units can be applied as a tool for the validation of existing phytosociological systems.

3.4. Conservation and protection implications

Our results highlight the importance of the legal protection of Dg species, which not only constitutes the basis for the separation of syntaxonomical units but also, as we demonstrated, plays a key role in the functioning of plant associations. Inland salt marshes are legally protected in Europe under the Natura 2000 network as two habitat types: 1310 - *Salicornia* and other annuals colonizing mud and sand and *1340 - Inland salt meadows *Glauco-Puccinellietalia* [31,77]. However, the protection of these two habitats and their key species should be integrated, which, unfortunately, is not always practised. An example is the protection of vegetation in inland salt marshes in Poland. Habitats are protected under the Natura 2000 network and as nature revers [20,78], but not all Dg species are legally protected. Only three Dg salt-adapted halophytes, *S. europaea*., *T. maritima*, and *G. maritima* (*Lysimachia maritima*) are protected by the law [79]. The other key halophytes in salt marsh associations, such as *S. marina,* are unprotected. Of course, only rare specialists should be considered. Although *P. australis* is included in a set of Dg species for the *Tm-Gm* association [16], it is a common and expansive species and does not require protection. In addition, its expansion may adversely affect more valuable and light-requiring species of typical halophytes, which has been widely reported in the literature [19,80].

Most of the functional traits we analysed concerned growth parameters and leaves dimensions, including these biochemical parameters, which are responsible for plant persistence, especially in the context of salt stress [28]. Therefore, our results show that the greatest attention when selecting protective treatments should be focused on sensitive associations, i.e., *Sr*, followed by *P-Ss* and *Tm-Gm*. This confirms our previous findings reported by Lubińska-Mielińska et al. [27]. In this way, an approach based on functional traits may facilitate the practical application of our research results to new protection strategies for endangered habitats.

4. Materials and Methods

4.1. Plant material

We included three of the most common associations: *Salicornietum ramosissimae* (*Sr*), *Puccinellio-Spergularietum salinae* (*P-Ss*), and *Triglochino maritimae-Glaucetum maritimae* (*Tm-Gm*), which belong to two syntaxonomical classes typical of inland salt marshes. The list of their Dg species, according to Lubińska-Mielińska et al. [16], is presented in Table 1 and includes nine species in total, i.e., *S. europaea*, *T. maritima*, *G. maritima* (*L. maritima*), *P. australis*, *J. compressus*, *P. anserina*, *S. marina*, *P. distans*, and *A. prostrata*. Plant samples were collected on August 10, 2023, from the inland salt marsh in Inowrocław, located in north-central Poland (52°45′N, 18°13′E; Central Europe). This site was chosen because the three selected associations are present in this relatively small area, forming a mosaic of small patches. Moreover, strong soil salinity (>16 $dS \cdot m^{-1}$) has been stable in this area for several years [81,82,83]. We dug out 15 individuals of each species together with a large layer of soil around the roots and transported them to the laboratory in plastic bags to prevent moisture loss. In the laboratory, leaves samples were immediately prepared for further biochemical analyses, frozen in liquid nitrogen, and placed in a freezer at -80 °C. Morphometric analyses were then carried out. Together with plants, soil samples (0-25 cm) were also collected, and parameters were analysed by external services (see supplementary materials Table S3). Because of the low saline groundwater table depth close to the surface, we reported the mean values of the soil properties at this site. During the sampling period, the salinity was approximately 36 $dS \cdot m^{-1}$. Three of the nine analysed species are legally protected in Poland: *S. europaea*., *T. maritima*, and *G. maritima* (*L. maritima*). Therefore, permission to collect and work with the plants was provided by the Regional Director of Environmental Protection in Bydgoszcz, number WOP.6400.9.2023.MWK. The voucher specimen of the plant material has been deposited in a publicly available herbarium of the Nicolaus Copernicus University in Toruń (Index Herbarium code TRN); the deposition number is not available (dr Dariusz Kamiński undertook the formal identification of plant species). Collection of plant material complies with relevant institutional, national, and international guidelines and legislation. All methods were carried out in accordance with relevant guidelines.

4.2. Vegetation data

We used data from a database by Lubińska-Mielińska et al. [16] with vegetation plots (relevés) for the three abovementioned syntaxonomical associations: *Sr* – 133 plots, *P-Ss* – 134 plots, and *Tm-Gm* – 56 plots, for a total of 323 plots. These data were used to calculate weighted averages of the functional traits (community weighted means, CWMs) [84] for each association based on the cover/abundance and measured parameters. To perform the calculations, we transformed the phytosociological data from the Braun-Blanquet [1] scale into the van der Maarel [85] ordinal scale as follows: r → 1, + → 2, 1 → 3, 2 → 5, 3 → 7, 4 → 8, 5 → 9. Only nine Dg species [16], as mentioned above, were considered (see Table 1). Data on the other species have been omitted. All species were considered only in comparisons based on data from the LEDA Traitbase [28].

4.3. Morphological analyses

To evaluate morphological characteristics, 10 plants were randomly selected from each species. Subsequently, measurements were taken for shoot length (SL) and root length (RL) in centimetres (cm). Additionally, the number of leaves (NoL) was counted. Shoots fresh weight (SFW), roots fresh weight (RFW), and leaves fresh weight (LFW) were assessed in grams (g). Leaf mass (LM) was expressed in milligrams (mg). The dry weights of the shoots (SDW), roots (RDW), and leaves (LDW) were determined after the samples were oven-dried at 80 °C for 72 hours, as reported in g. Leaves area (LA) and assimilation area (AA) were scanned and measured using digiShape 1.9 software [86], and the results are reported in square centimetres (cm^2). In the case of AA for *S. europaea*, the entire area of shoots was considered to be affected by the assimilation functions. For *T. maritima,* the AA value is the LA multiplied by two due to the double-sided structure of its leaves. A single ramet was measured as an individual plant for ramet-producing species such as *P. distans*, *T. maritima*, *P. australis*, and *J. compressus*. More details about the measurement methods are provided in Table S4.

Based on the measured parameters, five growth indices were calculated: shoot weight ratio (SWR), root weight ratio (RWR), leaf weight ratio (LWR), leaf dry matter content (LDMC) [mg/g], and specific leaf area (SLA) [cm^2/g] according to the following formulas:

$$SWR = \frac{\mathrm{SDW}}{\mathrm{DW}} \tag{1}$$

where SDW is the shoots dry weight [g], and DW is the total dry weight [g].

$$RWR = \frac{\mathrm{RDW}}{\mathrm{DW}} \tag{2}$$

where RDW is the roots dry weight [g], and DW is the total dry weight [g].

$$LWR = \frac{\mathrm{LDW}}{\mathrm{DW}} \tag{3}$$

where LDW is the leaves dry weight [g], and DW is the total dry weight [g].

$$LDMC = \frac{\mathrm{LDW}}{\mathrm{LFW}} \tag{4}$$

where LDW is the leaves dry weight [mg], LFW is the leaves fresh weight [g],

$$SLA = \frac{\mathrm{LA}}{\mathrm{LDW}} \tag{5}$$

where LA is the leaves area [cm^2], and LDW is the leaves dry weight [g].

Additionally, to compare the results based on our measurements with those based on the LEDA Traitbase data, we recalculated our data to obtain the single leaf area (1LA) expressed in cm^2 and the single leaf dry mass (1LDM) as the dry weight of one leaf according to the LEDA protocol expressed in mg.

4.4. Biochemical analyses

The biochemical traits related to photosynthetic activity, osmotic adjustment, oxidative stress, and enzymatic activities were measured. All biochemical analyses were performed with three replicates of 0.5 g fresh green leaves samples. In the case of *S. europaea*, instead of leaves that are reduced in this species, the assimilation tissue of shoots was used for measurements. Fresh plant material was frozen using liquid nitrogen and stored at -80 °C except for carbo, where 0.1 g of dried sample was used.

4.4.1. Photosynthetic pigment content

The content of photosynthetic pigments, i.e., chlorophyll a (chla), b (chlb), total (chlt), and carotenoid (car), was measured according to Lichtenthaler and Wellburn [87]. A total of 0.5 g of each fresh green leaves sample was ground in a liquid nitrogen mortar. Next, 10 ml of 80% acetone was added to the mortar with the ground sample and triturated until a green liquid was obtained. Then, the sample was transferred to a test tube and adjusted to a 10 ml volume with 80% acetone. All the samples were centrifuged for 15 minutes at 5,000 RPM. Absorption was measured at wavelengths of 663 nm, 646 nm, and 470 nm using a spectrophotometer and 80% acetone as a blank. The pigment contents were calculated using the following equations:

$$\mathrm{Chla} = \frac{\left(\left((12.21 \cdot \mathrm{Abs}\ 663) - (2.81 \cdot \mathrm{Abs}\ 646)\right) \cdot \mathrm{ml\ Acetone}\right)}{\mathrm{mg\ plant\ sample}}\ [\mathrm{mg/g\ FW}] \tag{6}$$

$$\mathrm{Chlb} = \frac{\left(\left((20.13 \cdot \mathrm{Abs}\ 646) - (5.03 \cdot \mathrm{Abs}\ 663)\right) \cdot \mathrm{ml\ Acetone}\right)}{\mathrm{mg\ plant\ sample}}\ [\mathrm{mg/g\ FW}] \tag{7}$$

$$\mathrm{Car} = \frac{\left(\left(\left((1000 \cdot \mathrm{Abs}\ 470) - (3.27 \cdot \mathrm{Chl\ a}) - (104 \cdot \mathrm{Chl\ b})\right) / 227\right) \cdot \mathrm{ml\ Acetone}\right)}{\mathrm{mg\ plant\ sample}}\ [\mathrm{mg/g\ FW}] \tag{8}$$

The sum of chla and chlb was taken as the chlt content. The results are reported as milligrams per gram of fresh weight [mg/g FW].

4.4.2. Proline content

The proline (prol) content was determined according to Bates et al. [88]. Each sample (0.5 g) was ground in a liquid nitrogen mortar. Then, 10 ml of 3% sulfosalicylic acid was added to the mortar with the crushed sample and further ground. Next, the sample was transferred to a test tube. All the samples were centrifuged for 10 minutes at 13,000 RPM at 4 °C. Later, 2 ml of supernatant from each sample was transferred to a new tube, and 2 ml of ninhydrin and 2 ml of glacial acetic acid were added. All the samples were placed in a water bath for one hour at 100 °C. After cooling on ice, 4 ml of toluene was added to the test tubes, and the samples were mixed. The absorbances of the samples were measured at 520 nm. Toluene was used as a blank. The prol content was determined using the standard curve in the 0.5-4 mg/l prol concentration range and equation $y = 0.1964x + 0.0143$, $R^2 = 0.9748$. The results are reported as milligrams per gram of fresh weight [mg/g FW].

4.4.3. Total soluble carbohydrate content

To determine the total soluble carbohydrate (carbo) content in our samples, we used the Sheligl method [89]. Plant materials (0.1 g of each sample) were used after oven-drying for 72 hours at 80 °C. Each sample was ground into powder using an electric grinder and mortar. The crushed samples were transferred to Falcon tubes, and 15 ml of warm 80% ethyl alcohol was added. After mixing the samples, they were placed in a centrifuge for 10 min at 3,000 RPM. The solution was poured into Petri dish lids (5 cm in diameter) and placed for 60/90 minutes (until the alcohol evaporated completely) in a dryer at 50 °C-70 °C. Next, each sample was rinsed from the bottom of the dish lid into a Falcon tube and 40 ml of distilled water. Next, 5 ml of 5% $ZnSO_4$ and 5 ml of 3% $Ba(OH)_2$ were added to the test tubes. The samples were centrifuged for 10 minutes at 3,000 RPM. Then, 2 ml of the supernatant was transferred to another Falcon tube, and 1 ml of 5% phenol and 5 ml of 96-98% H_2SO_4 were added. After 45 minutes of reaction, the absorbance was measured at 485 nm and mixture of 1 ml millilitre of phenol and 5 ml of H_2SO_4 was used as a blank. To obtain the results, a standard curve for glucose was used in the range of 0-90 mg, with the following equation: $y = 0.0091x + 0.0212$, $R^2 = 0.9808$. The results are reported in milligrams per 100 g fresh weight [mg/100 g FW].

4.4.4. Hydrogen peroxide (H_2O_2) content

The hydrogen peroxide (H_2O_2) content was determined according to the method of Velikova et al. [90]. The samples were ground in a mortar in liquid nitrogen. Next, 2 ml of 1% TCA was added to each sample, and then ground further. Later, the samples were poured into Eppendorf tubes and centrifuged for 10 minutes at 4 °C at 10,000 RPM. After that, 0.5 ml of supernatant, 0.5 ml of 0.1 M potassium phosphate buffer, and 1 ml of 1 M potassium iodide were added to new tubes. Potassium iodide was added in the dark. The samples were placed in the dark on ice for one hour. The absorbance of the samples was measured at a wavelength of 390 nm. We used 0.5 ml of 1% TCA, 0.5 ml of buffer, and 1 ml of potassium iodide as a blank. We used a standard curve in the 0–40 nM H_2O_2 concentration range and the equation $y = 0.0615x + 0.0287$, $R^2 = 0.9954$ to obtain the results. The results are reported as nanomoles per gram of fresh weight [nmol/g FW].

4.4.5. Malondialdehyde (MDA) content

The malondialdehyde (MDA) content was measured according to Velikova et al. [90]. After grinding the sample in a mortar in liquid nitrogen, 2 ml of 1% trichloroacetic acid (TCA) was added, followed by further grinding. Each sample was poured into Eppendorf tubes and centrifuged for 5 minutes at 4 °C at 10,000 RPM. Next, 0.5 ml of the supernatant was transferred to a new tube, and 1 ml of a mixture of 20% TCA and 0.5% thiobarbituric acid (TBA) was added. The samples were placed in a water bath for 30 minutes at 95 °C. After that, the samples were cooled on ice and placed in a centrifuge at 4 °C for 15 minutes at 10,000 RPM. The absorbance of the supernatants was measured with a spectrophotometer at two wavelengths – 532 nm for MDA and 600 nm – to determine changes caused by infection. A 1 ml mixture of 20% TCA, 0.5% TBA and 0.5 ml of 0.1% TCA was used as the blank. The MDA content was calculated according to the following formula:

$$MDA = \frac{Abs\ 532 - Abs\ 600}{155} \cdot \frac{sample\ volume}{sample\ fresh\ weight} \cdot 1000\ \text{[mmol/g FW]} \tag{9}$$

where the sample volume was 1.5 ml, and the sample fresh weight was 0.5 g. The results are given as millimoles per gram of fresh weight [mmol/g FW].

4.4.6. Soluble protein content

The protein content was measured according to the Bradford method [91]. The samples were crushed in a mortar with liquid nitrogen and transferred to Eppendorf tubes. Next, 1 ml of extraction buffer (consisting of a buffer and Tris, EDTA, Triton, and DDT) was added. The samples were subsequently centrifuged for 30 minutes at 12,000 RPM at 4 °C. The protein content was measured after adding 3 ml of Bradford’s reagent to new tubes and adding 100 µl of the supernatant. They were allowed to complete the reaction for 30-60 minutes. The absorbance was measured at a wavelength of 595 nm. Bradford's reagent was used as a blank. The results were used to express the enzyme activity (ascorbate peroxidase and catalase) in the samples. For this purpose, a standard curve was determined for protein concentrations in the range of 0-120 µg/ml, using the equation $y = 0.0088x + 0.0387$, $R^2 = 0.9906$. The protein content is expressed in milligrams of protein per millilitre [protein mg/ml].

4.4.7. Specific catalase (CAT) activity

For measurements of catalase (CAT), we used the same samples used for the protein measurements. The method of Aebi [92] was used. The absorbance was measured at 240 nm in 1.5 ml of phosphate buffer supplemented with 4.51 µl of H_2O_2 and 50 µl of the supernatant. The mixture of phosphate buffer and 30% H_2O_2 was used as a blank. The following formula was used to calculate the enzyme content in ml of the sample:

$$Enzyme = \frac{\Delta Abs \cdot Tv \cdot D}{\varepsilon \cdot Ev}\ \text{[u/ml]} \tag{10}$$

where:

ΔAbs – difference in absorbance (240 nm for CAT/290 nm for APX) of the sample after 30 seconds.
Tv – the volume of the spectrophotometer cuvette used for the measurement (2 ml).
D – possible dilutions of the measured sample.
E – extinction coefficient (39,4 for CAT/2,8 for APX).
Ev – sample volume used for measurement (0.05 ml).

The results of the protein content were used to report the results of CAT expressed in units per milligram of protein [u/mg protein].

4.4.8. Specific ascorbate peroxidase (APX) activity

The same samples prepared for protein and catalase activity measurements were used to measure ascorbate peroxidase (APX) activity according to the method of Nakano and Asada

[93]. Absorbance measurements were performed at 290 nm by mixing 2 ml of phosphate buffer, 100 µl of ascorbic acid, and 4.51 µl of 30% H_2O_2 and 50 µl of supernatant. As a blank, 2 ml of phosphate buffer, 100 µl of ascorbic acid, and 4.51 µl of 30% H_2O_2 were used. The same formula as for CAT (above) was used to calculate the enzyme content per ml of the sample [u/ml]. The results of the protein content were used to report the results of APX expressed in units per milligram of protein [u/mg protein].

4.5. Statistical and multivariate analyses

All nine Dg species based on individual morphological and biochemical functional traits were compared by one-way analysis of variance (ANOVA) with Tukey's post hoc comparisons due to the normal data distribution according to the Shapiro–Wilk test.

We compared trait weighted averages of three analysed associations using the nonparametric Kruskal–Wallis test with Dunn post hoc comparisons for morphological data and the parametric ANOVA test for equal means with Tukey’s post hoc comparisons for biochemical traits, depending on the distribution of the data with the proven Shapiro–Wilk test. We used the unconstrained ordination method to explore and visualize relationships between these analysed associations regarding functional traits. Due to the high value of the stress index (> 0.5) for biochemical data in the nonmetric multidimensional scaling (NMDS) analysis, we decided to use principal component analysis (PCA) separately for morphological and biochemical traits. We also correlated traits with the first two ordination axes using Spearman’s correlation coefficient (r_S) to determine the pattern of the main differences. Due to the large variability in the morphological trait values resulting from the use of many specific units, the data had to be standardized before ordination analysis, which was carried out using MVSP 3.1 software [94].

To determine the role of Dg species in association functioning, we compared the results of the CWMs calculated based on Dg species with the CWMs calculated based on all species in the plots. We included CH, LS, LM, LDMC and SLA from the LEDA Traitbase [28] and made comparisons via Kruskal–Wallis tests with Dunn's post hoc test.

To validate the results obtained from field measurements with the results based on the LEDA Traitbase data [28], we compared three associations for nine Dg species using the Kruskal–Wallis test with Dunn's post hoc comparisons. For all analyses, we used PAST 4.12 software [95].

5. Conclusions

Based on the morphological and biochemical functional trait analyses, we demonstrated the different salinity resistance strategies of associations typical of inland salt marshes in temperate Europe. The *Tm-Gm* association had the highest values of most measured morphological parameters related to biomass production but also had the lowest salt resistance, as indicated by the highest osmotic and oxidative stress and oxidative stress responses. The *Sr* association was the best adapted to both osmotic and oxidative stress. The lowest levels of prol, H_2O_2, MDA, and antioxidant enzymes indicated the prevention of their overproduction. The *P-Ss* association has the smallest biomass production. This association was similar to that of the *Tm-Gm* association in managing osmotic stress but more adaptable to oxidative stress under soil salinity. The Dg species of the investigated associations play key roles in the functioning of the associations because including all species does not change the main research findings. Validation of the results based on data from a trait database revealed differences in results referring to sensitive to the local environment parameters – photosynthetic strategies (SLA) and resources acquisition (LDMS). Therefore, an approach based on functional traits may facilitate the practical application of our research results to new approaches and protection strategies for endangered habitats.

Author contributions

S.L.M., A.R.D., and D.K. collected plant material samples. S.L.M. and A.R.D. performed morphometrical measurements of the plant's functional traits and biochemical analyses. S.L.M. organized and managed data including from the LEDA Traitbase, performed statistical and multivariate analyses, and prepared the first draft of the publication. A.R.D. and S.C.P. contributed to the interpretation of the results and critical revision of the manuscript for important intellectual content. A.P. conceived the ideas, designed statistical and multivariate methodology, substantially contributed to the manuscript’s final version, and supervised the project. All authors have read and approved the final version of the manuscript.

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Competing interests

The authors declare no competing interests.

Data availability

Data used during the research will be made available upon request from the corresponding authors: Sandra Lubińska-Mielińska (slm@umk.pl) or Agnieszka Piernik (piernik@umk.pl).

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Diagnostic species are crucial for the functioning of plant associations in inland salt marshes

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Suplementary materials

Table S1 Comparison of diagnostic species morphological functional traits measurements results. Significantly different values are denoted by different letters at $p \leq 0.05$ according to the ANOVA test with Tuckey's post hoc comparisons. Abbreviations of species names: Sal.eur – *Salicornia europaea*, Spe.mar – *Spergularia marina*, Puc.dis – *Puccinellia distans*, Atr.pro – *Atriplex prostrata*, Tri.mar – *Triglochin maritima*, Gla.mar – *Glaux maritima*, Phr.aus – *Phragmites australis*, Jun.com – *Juncus compressus*, Pot.ans – *Potentilla anserina*. Association diagnostic species for: *Salicornietum ramosissimae* is marked in yellow, *Puccinellio-Spergularietum salinae* are marked in blue, and *Triglochino maritimae-Glaucetum maritimae* are marked in green.

Traits\Species	**Sal.eur**	**Spe.mar**	**Puc.dis**	**Atr.pro**	**Tri.mar**	**Gla.mar**	**Phr.aus**	**Jun.com**	**Pot.ans**	**p value**
SL - shoot length [cm]	$22.3^{cde}\pm3.01$	$13.0^{e}\pm2.84$	$36.2^{bc}\pm7.97$	$42.4^{b}\pm10.5$	$40.5^{b}\pm5.22$	$21.1^{de}\pm6.13$	$150^{a}\pm23.4$	$35.3^{bcd}\pm9.60$	$23.50^{cde}\pm7.04$	$1.16\cdot10^{-46}$
RL - root length [cm]	$12.5^{abcd}\pm2.81$	$7.67^{d}\pm2.13$	$8.70^{cd}\pm1.94$	$15.9^{abc}\pm10.1$	$19.8^{a}\pm4.27$	$12.3^{bcd}\pm4.88$	$17.2^{ab}\pm7.04$	$10.9^{bcd}\pm3.52$	$14.9^{abcd}\pm4.41$	$5.64\cdot10^{-6}$
SFW - shoots fresh weight [g]	$41.6^{a}\pm38.5$	$0.85^{b}\pm0.41$	$2.58^{b}\pm1.73$	$9.08^{b}\pm7.19$	$2.14^{b}\pm0.87$	$0.40^{b}\pm0.13$	$19.0^{b}\pm8.55$	$0.27^{b}\pm0.15$	$0.02^{b}\pm0.05$	$3.18\cdot10^{-10}$
SDW - shoots dry weight [g]	$4.55^{b}\pm4.09$	$0.19^{c}\pm0.09$	$1.13^{c}\pm0.76$	$2.11^{bc}\pm1.64$	$0.67^{c}\pm0.28$	$0.07^{c}\pm0.03$	$8.74^{a}\pm4.37$	$0.12^{c}\pm0.07$	$0.01^{c}\pm0.01$	$3.36\cdot10^{-16}$
RFW - roots fresh weight [g]	$0.80^{b}\pm0.74$	$0.14^{b}\pm0.08$	$1.21^{b}\pm0.93$	$0.60^{b}\pm0.61$	$2.90^{b}\pm2.02$	$0.37^{b}\pm0.28$	$13.3^{a}\pm6.04$	$0.59^{b}\pm0.25$	$1.32^{b}\pm0.55$	$7.53\cdot10^{-24}$
RDW - roots dry weight [g]	$0.27^{b}\pm0.26$	$0.04^{b}\pm0.02$	$0.56^{b}\pm0.42$	$0.22^{b}\pm0.20$	$0.56^{b}\pm0.33$	$0.06^{b}\pm0.04$	$4.33^{a}\pm2.06$	$0.20^{b}\pm0.06$	$0.24^{b}\pm0.10$	$1.37\cdot10^{-23}$
NoL - number of leaves	0.00 ± 0.00	$107^{b}\pm41.2$	$141^{ab}\pm59.0$	$181^{a}\pm95.6$	$13.6^{c}\pm6.75$	$123^{ab}\pm52.5$	$36.3^{c}\pm21.5$	$4.40^{c}\pm0.84$	$3.70^{c}\pm0.82$	$1.05\cdot10^{-15}$
LM - leaf mass [mg]	0.00 ± 0.00	$5.98^{d}\pm6.70$	$20.4^{cd}\pm4.44$	$36.8^{cd}\pm14.2$	$263^{bc}\pm78.4$	$5.07^{cd}\pm1.61$	$452^{b}\pm218$	$43.8^{cd}\pm16.7$	$1026^{a}\pm471$	$1.59\cdot10^{-21}$
LFW - leaves fresh weight [g]	0.00 ± 0.00	$0.43^{c}\pm0.20$	$2.89^{bc}\pm1.24$	$7.38^{b}\pm5.70$	$3.63^{bc}\pm2.14$	$0.62^{c}\pm0.40$	$13.5^{a}\pm8.07$	$0.20^{c}\pm0.12$	$3.86^{bc}\pm2.00$	$6.07\cdot10^{-12}$
LDW - leaves dry weight [g]	0.00 ± 0.00	$0.06^{b}\pm0.03$	$1.13^{b}\pm0.49$	$1.08^{b}\pm0.81$	$0.62^{b}\pm0.33$	$0.09^{b}\pm0.03$	$6.87^{a}\pm4.46$	$0.10^{b}\pm0.05$	$0.64^{b}\pm0.33$	$1.56\cdot10^{-14}$
LA - leaves area [cm^2]	0.00 ± 0.00	$6.71^{b}\pm3.08$	$162^{b}\pm91.9$	$149^{b}\pm107$	$48.1^{b}\pm20.1$	$18.8^{b}\pm8.98$	$814^{a}\pm496$	$9.34^{b}\pm3.74$	$105^{b}\pm51.3$	$1.93\cdot10^{-15}$
AA - assimilation area [cm^2]	$376^{b}\pm321$	$6.71^{c}\pm3.08$	$162^{bc}\pm91.9$	$149^{bc}\pm107$	$96.2^{bc}\pm40.4$	$18.8^{c}\pm8.98$	$814^{a}\pm496$	$9.34^{c}\pm3.74$	$105^{bc}\pm51.3$	$4.64\cdot10^{-14}$
LDMC - leaf dry matter content [mg/g]	0.00 ± 0.00	$177^{c}\pm145$	$394^{b}\pm30.0$	$146^{c}\pm22.3$	$178^{c}\pm16.6$	$150^{c}\pm26.9$	$491^{a}\pm81.6$	$513^{a}\pm53.6$	$169^{c}\pm25.6$	$1.01\cdot10^{-26}$
SLA - specific leaf area [cm^2/g]	0.00 ± 0.00	$125^{bcd}\pm43.0$	$137^{bcd}\pm26.3$	$161^{bc}\pm52.6$	$82.9^{d}\pm19.6$	$242^{a}\pm99.0$	$122^{bcd}\pm17.4$	$100^{cd}\pm20.6$	$169^{b}\pm26.5$	$1.01\cdot10^{-9}$
SWR - shoot weight ratio	$0.95^{a}\pm0.02$	$0.67^{b}\pm0.06$	$0.38^{c}\pm0.08$	$0.60^{b}\pm0.06$	$0.37^{cd}\pm0.13$	$0.35^{cd}\pm0.08$	$0.44^{c}\pm0.06$	$0.27^{d}\pm0.08$	$0.00^{e}\pm0.01$	$1.02\cdot10^{-43}$
RWR - root weight ratio	$0.05^{d}\pm0.02$	$0.13^{cd}\pm0.05$	$0.18^{bcd}\pm0.06$	$0.06^{d}\pm0.01$	$0.30^{b}\pm0.15$	$0.25^{bc}\pm0.13$	$0.23^{bc}\pm0.08$	$0.50^{a}\pm0.10$	$0.29^{b}\pm0.14$	$4.74\cdot10^{-17}$
LWR - leaf weight ratio	0.00 ± 0.00	$0.20^{d}\pm0.02$	$0.44^{b}\pm0.09$	$0.33^{bc}\pm0.06$	$0.33^{bc}\pm0.11$	$0.41^{b}\pm0.06$	$0.33^{bc}\pm0.08$	$0.23^{cd}\pm0.05$	$0.70^{a}\pm0.14$	$1.04\cdot10^{-20}$

Table S2 Comparison of diagnostic species biochemical functional traits measurements results. Significantly different values are denoted by different letters at $p \leq 0.05$ according to the ANOVA test with Tuckey's post hoc comparisons. Abbreviations of species names: Sal.eur – *Salicornia europaea*, Spe.mar – *Spergularia marina*, Puc.dis – *Puccinellia distans*, Atr.pro – *Atriplex prostrata*, Tri.mar – *Triglochin maritima*, Gla.mar – *Glaux maritima*, Phr.aus – *Phragmites australis*, Jun.com – *Juncus compressus*, Pot.ans – *Potentilla anserina.* Association diagnostic species for: *Salicornietum ramosissimae* is marked in yellow, *Puccinellio-Spergularietum salinae* are marked in blue, and *Triglochino maritimae-Glaucetum maritimae* are marked in green.

Traits\Species	**Sal.eur**	**Spe.mar**	**Puc.dis**	**Atr.pro**	**Tri.mar**	**Gla.mar**	**Phr.aus**	**Jun.com**	**Pot.ans**	**p value**
chla - chlorophyll a [mg/g FW]	$0.26^{b}\pm0.05$	$0.23^{b}\pm0.05$	$0.36^{ab}\pm0.03$	$0.48^{ab}\pm0.02$	$0.33^{ab}\pm0.25$	$0.47^{ab}\pm0.03$	$0.45^{ab}\pm0.08$	$0.27^{b}\pm0.05$	$0.56^{a}\pm0.02$	$3.06\cdot10^{-3}$
chlb - chlorophyll b [mg/g FW]	$0.07^{c}\pm0.01$	$0.07^{c}\pm0.01$	$0.13^{bc}\pm0.01$	$0.17^{ab}\pm0.01$	$0.13^{bc}\pm0.06$	$0.17^{ab}\pm0.01$	$0.16^{abc}\pm0.04$	$0.09^{bc}\pm0.02$	$0.24^{a}\pm0.04$	$3.87\cdot10^{-5}$
chlt - total chlorophyll [mg/g FW]	$0.33^{bc}\pm0.06$	$0.30^{c}\pm0.06$	$0.49^{abc}\pm0.05$	$0.66^{ab}\pm0.04$	$0.47^{abc}\pm0.30$	$0.64^{abc}\pm0.04$	$0.61^{abc}\pm0.12$	$0.36^{bc}\pm0.06$	$0.80^{a}\pm0.06$	$6.94\cdot10^{-4}$
car - carotenoids [mg/g FW]	$0.09^{c}\pm0.02$	$0.09^{c}\pm0.02$	$0.18^{abc}\pm0.01$	$0.20^{abc}\pm0.00$	$0.13^{bc}\pm0.10$	$0.19^{abc}\pm0.01$	$0.20^{ab}\pm0.05$	$0.13^{bc}\pm0.02$	$0.25^{a}\pm0.02$	$9.76\cdot10^{-4}$
prol - proline [mg/g FM]	$2.20^{c}\pm0.83$	$13.2^{b}\pm7.44$	$34.9^{a}\pm0.54$	$2.26^{c}\pm1.74$	$36.6^{a}\pm2.08$	$16.8^{b}\pm3.81$	$8.83^{bc}\pm3.29$	$0.56^{c}\pm0.51$	$1.49^{c}\pm1.91$	$2.99\cdot10^{-11}$
carbo - carbohydrates concentration [mg/100 g FM]	$5.59^{abc}\pm0.83$	$3.65^{bc}\pm0.20$	$3.12^{c}\pm0.25$	$7.00^{ab}\pm1.61$	$6.18^{abc}\pm0.67$	$7.86^{a}\pm0.40$	$3.25^{c}\pm0.18$	$8.52^{a}\pm2.37$	$5.05^{abc}\pm1.98$	$1.46\cdot10^{-4}$
H_2O_2 - hydrogen peroxide [nmol/g FW]	$17.5^{d}\pm3.85$	$25.3^{c}\pm2.11$	$7.19^{e}\pm0.03$	$33.6^{a}\pm0.96$	$21.8^{cd}\pm2.66$	$31.0^{ab}\pm1.17$	$7.33^{e}\pm0.62$	$26.5^{bc}\pm0.70$	$26.6^{bc}\pm0.54$	$1.48\cdot10^{-12}$
MDA - malondialdehyde [mmol/g FW]	$1.32^{cd}\pm0.15$	$2.69^{bc}\pm0.58$	$7.90^{a}\pm0.30$	$4.13^{b}\pm0.93$	$1.92^{cd}\pm0.04$	$0.89^{d}\pm0.69$	$6.78^{a}\pm1.14$	$6.38^{a}\pm0.25$	$7.83^{a}\pm0.07$	$6.35\cdot10^{-12}$
CAT - catalase [U/mg protein]	$0.63^{b}\pm0.04$	$0.57^{b}\pm0.15$	$0.64^{b}\pm0.57$	$0.17^{b}\pm0.08$	$0.59^{b}\pm0.53$	$3.19^{ab}\pm2.62$	$0.43^{b}\pm0.11$	$1.38^{b}\pm0.61$	$8.32^{a}\pm6.14$	$6.47\cdot10^{-3}$
APX - ascorbate peroxidase [U/mg protein]	$2.27^{b}\pm1.51$	$5.21^{b}\pm3.36$	$2.53^{b}\pm0.97$	$1.59^{b}\pm0.19$	$8.04^{ab}\pm3.61$	$3.41^{b}\pm0.98$	$9.29^{ab}\pm1.66$	$4.73^{b}\pm5.41$	$15.8^{a}\pm4.63$	$3.65\cdot10^{-4}$

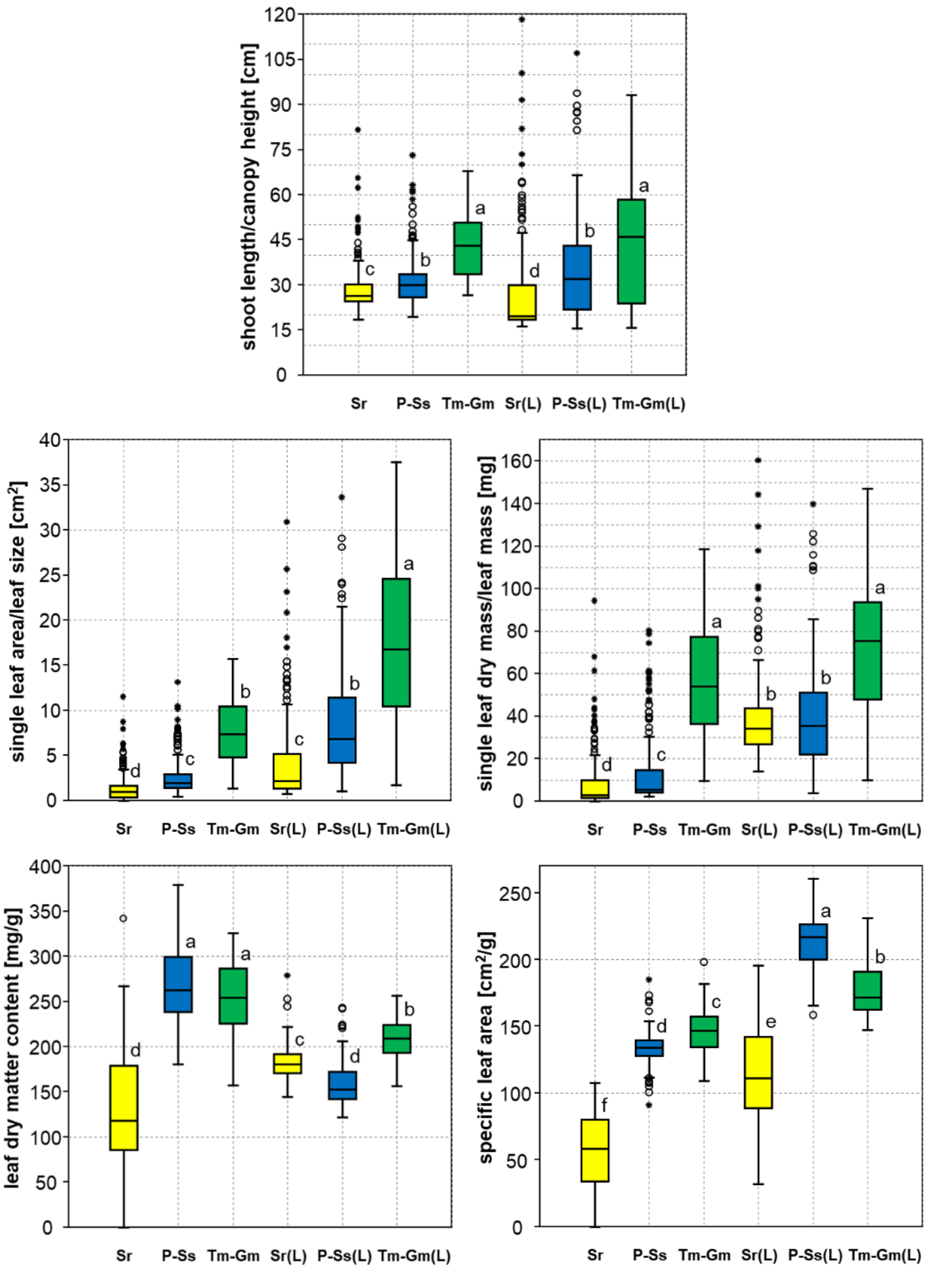

Figure S1 Comparison of functional traits based on own measurements and the LEDA Traitbase data (Kleyer et al., 2008) for vegetation associations with nine diagnostic species data only. Significantly different groups, according to the Kruskal-Wallis test with Dunn post hoc comparisons, are denoted by different letters at $p \leq 0.05$. Abbreviations of associations: *Sr* – *Salicornietum ramosissimae* (n = 133), *P-Ss* – *Puccinellio-Spergularietum salinae* (n = 134), *Tm-Gm* – *Triglochino maritimae-Glaucetum maritimae* (n = 56), (L) – means that the data comes from the Leda Traitbase.

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., et al. (2008). The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of ecology*, *96*(6), 1266-1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Table S3 The soil properties in the root zone in the sampling site (north-central Poland, Central Europe; 52°45′N, 18°13′E). Abbreviations of averaged soil sample properties: SP – moisture of soil saturated paste, EC_e – electrical conductivity of soil saturated extract, pH_e – reaction of soil saturated extract, C_{org} – organic carbon, N_t – total nitrogen.

Parameters	**Values**
Depth [cm]	0-25
Current soil moisture [%]	57.5
SP [%]	127.4
EC_e [mS/cm]	36.0
pH_e	7.3
C_{org} [%]	7.54
N_t [%]	0.555
C/N	14
$CaCO_3$ [%]	35.2

Table S4 Methods of measuring morphological traits

Abbreviation – Trait [Unit]	Measuring method	Tool
SL - shoot length [cm]	SL determines the height of the greatest shoot if there is more than one. This line connects the place where the shoot starts (above the root) and the top of the shoot/plant. There is a maximum length when straightened.	metric
RL - root length [cm]	RL determines the length of the greatest root fragment. This is the line connecting where the root starts (underneath the shoot) and the top of the roots. There is a maximum length when straightened.	metric
SFW - shoots fresh weight [g]	SFW is the weight of all fresh shoots after being collected from the field without leaves and separated from the roots; in the case of the presence of flowers, their weight is included in the weight of the shoots.	laboratory scale
SDW - shoots dry weight [g]	The weight of the SFW sample was used to measure SDW after drying in a laboratory dryer at 80 °C for 72 h.	laboratory scale
RFW - roots fresh weight [g]	RFW is the weight of all fresh roots after being collected from the field, stripped of the substrate, and dried; without leaves and separated from the shoots.	laboratory scale
RDW - roots dry weight [g]	The weight of the RFW sample was used to measure RDW after drying in a laboratory dryer at 80 °C for 72 h.	laboratory scale
NoL - number of leaves	Leaves were counted while removing them from the shoots, which constituted the preparation of samples for the remaining measurements (e.g. SFW).	–
LM - leaf mass [mg]	LM is the average value of the mass of single leaf, which was calculated for each individual leaf by dividing the mass of all leaves by their number.	–
LFW - leaves fresh weight [g]	LFW is the total weight of all leaves from the entire individual weighed after their separation from the shoot(s).	laboratory scale
LDW - leaves dry weight [g]	The weight of the LFW sample was used to measure LDW after drying in a laboratory dryer at 80 °C for 72 h.	laboratory scale
LA - leaves area [cm^2]	LA was calculated from the proportion based on the weight and area of a few leaves from each individual (usually five, sometimes 10 for smaller species, or three for larger) and the weight of all leaves of the individual plant. The leaf area was measured in the digiShape 1.9 software (Moraczewski, 2005). A single ramet was measured as an individual plant for ramet-producing species such as *P. distans*, *T. maritima*, *P. australis*, and *J. compressus*.	–
AA - assimilation area [cm^2]	AA was calculated the same as LA (see above), but in the case of AA for *S. europaea*, due to taking over the assimilation functions by shoots, the entire area of shoots was considered, and for *T. maritima* the AA value is the LA multiplied by two due to the double-sided structure of its leaves.	–

Moraczewski, I. R. (2005). digiShape. A software for automated morphometry; version 1. 9. Bydgoszcz: Cortex Nova.

5. Dyskusja – najważniejsze zagadnienia

5.1. Klasyfikacja syntaksonomiczna

W ramach niniejszej pracy doktorskiej (pierwsza publikacja) sklasyfikowano roślinność występującą na solniskach śródlądowych kierując się koncepcją Braun-Blanqueta (Braun-Blanquet, 1964). Oprócz znanej już z obszarów zasolonych roślinności reprezentującej klasy THE i FEP (Mucina i in., 2016), jako integralne części solnisk śródlądowych zidentyfikowano siedem klas reprezentujących inne typy roślinności (*Ruppietea maritimae* – RUP, *Polygono-Poetea annuae* – POL, *Artemisietea vulgaris* – ART, *Potamogetonetea* – POT, *Bidentetea* – BID, *Phragmito-Magnocaricetea* – PHR i *Molinio-Arrhenatheretea* – MOL). Jednak na solniskach klasy te wykazały się pewną specyfiką. Mianowicie, pulę typowych dla nich gatunków wzbogaciły rośliny uznane za gatunki Dg, stałe (Cs) i dominujące (Dm) dla roślinności charakterystycznej na solniskach, w tym halofity. Rośliny te uważane są za ograniczone do wąskiego spektrum warunków środowiskowych, a tymczasem mogą wykazywać stosunkowo szerokie reakcje ekologiczne. Przykładowo uzyskane wyniki pokazały, że gatunek o najwyższej tolerancji na zasolenie *S. europaea* występował w płatach roślinności trzech klas typowych dla terenów niezasolonych (ART, PHR i MOL). Takie szerokie spektrum reakcji gatunków jest zgodne z ustaleniami Piernik (2003a, 2012), która wykazała, że na glebach niezasolonych lub lekko zasolonych można zaobserwować nawet halofity obligatoryjne, do których właśnie należy *S. europaea* (Wilkoń-Michalska, 1963, 1970). Wynika to z dużej tolerancji tych gatunków na wahania poziomu zasolenia gleby i decyduje o specyfice badanej roślinności. Z drugiej strony powszechna obecność na solniskach klas roślinności typowych dla terenów niezasolonych spowodowana jest stosunkowo dużą odpornością na zasolenie wielu gatunków glikofilnych roślin. Na solniskach często spotyka się płaty roślinności o charakterze przejściowym, reagujące na lokalne warunki środowiskowe, które mają nieco odmienny skład gatunkowy niż uznany za charakterystyczny. Pomimo obecnego stosowania metod numerycznych, wpływa to na trudności w klasyfikacji przynależności syntaksonomicznej takich płatów, ponieważ ostateczne decyzje dotyczące jednostek roślinności pozostają nadal subiektywne. Jednak dzięki zaawansowaniu stosowanych narzędzi wszystkie te subiektywne decyzje mogą być sprawdzone i statystycznie uzasadnione (Tichý, 2002). Ponad 28% przeanalizowanych w pracy zdjęć fitosocjologicznych zostało zaklasyfikowanych do siedmiu klas uznanych za nietypowe dla obszarów zasolonych. Zatem w obliczu uzyskanych wyników trzeba te grupy roślinności wziąć pod uwagę jako integralną część solnisk podczas planowania ich zarządzania i ochrony.

5.2. Znaczenie czynników środowiskowych dla zróżnicowania roślinności

Wyniki uzyskane w ramach pierwszej publikacji pokazały, że o rozmieszczeniu płatów zróżnicowanej roślinności solnisk śródlądowych decydują gradienty czynników środowiskowych, z których najważniejszymi są zasolenie, wilgotność gleby oraz dostępność światła. Pozwoliło to pozytywnie zweryfikować hipotezę badawczą o zależności jednostek syntaksonomicznych roślinności śródlądowych solnisk od czynników środowiskowych. Uzyskane wyniki potwierdzają, że z najwyższym zasoleniem gleby najbardziej powiązana jest roślinność klasy THE, a następnie FEP. Ponadto pokazują, że klasa PHR może obejmować roślinność nie tylko odporną na wysoką wilgotność gleby, lecz również na dość wysokie zasolenie i preferuje stosunkowo wysoką zawartość azotu w glebie. Jest to ważne, ponieważ wysoka dostępność azotu może zwiększać tolerancję gatunków na zasolenie (np. Sikder i in., 2020). Klasę MOL reprezentuje roślinność o zdecydowanie mniejszej odporności na zasolenie, jednak na solniskach śródlądowych jej wymagania środowiskowe zdają się pokrywać z wymaganiami klasy PHR. Może to oznaczać, że grupa zdjęć zaklasyfikowana do klasy PHR obejmuje dawne łąki porośnięte przez *P. australis* w wyniku zaprzestania ich użytkowania (Bosiacka i in., 2011). W zróżnicowaniu zespołów roślinnych najważniejszą rolę odgrywają również zasolenie, dostępność światła i wilgotność, ale także odczyn i zawartość materii organicznej w glebie. Warto podkreślić, że wyniki analiz dyskryminacyjnych na bazie danych wykorzystujących EIV reprezentujących długoterminowe warunki środowiskowe oraz pomiary terenowe reprezentujących warunki czasowe w tym przypadku pokrywają się. Ponadto wyniki uzyskane dla poszczególnych zespołów na podstawie EIV znajdują potwierdzenie w literaturze z innych stanowisk śródlądowych w Europie (Dítě i in., 2021, 2022). Zespół *Sr* charakteryzował się najwyższym EIV zasolenia, wilgotności i odczynu gleby w porównaniu do pozostałych zespołów. Charakterystyczne dla tego zespołu wysokie zasolenie gleby zostało również potwierdzone analizami opartymi na pomiarach glebowych. Jako kolejny w gradiencie zasolenia znajdował się zespół *P-Ss*, który charakteryzowały również stosunkowo niskie wymagania wilgotności i preferencje do stosunkowo wysokiej zawartości azotu w glebie. *P-Ss* w gradiencie zasolenia często występuje po zespole *Sr* (Piernik, 2006; Piernik i in., 1996). Analizy na podstawie EIV pokazały różnice w preferencjach zawartości azotu wyższe u zespołu *Tm-Gm* oraz wyższe preferencje co do dostępności światła i temperatury w przypadku zespołu *Scorzonero parviflorae-Juncetum gerardii* (*Sp-Jg*). Wyjaśnia to występowanie tego drugiego zespołu w cieplejszym klimatcie Europy Zachodniej. Jendak inni badacze (Dítě i in., 2022) nie stwierdzili różnic pomiędzy *Tm-Gm* a znanym z Niemiec *Sp-Jg* w preferencjach środowiskowych na podstawie EIV. Natomiast porównania parametrów glebowych pokazały, że płaty *Tm-Gm* są typowe dla gleb o dużej zawartości materii organicznej i wysokiej zawartości azotu ogólnego, a zespół *Sp-Jg* preferuje gleby mineralne. Ponadto stwierdzono znacznie wyższe wartości zasolenia i pH gleby w płatach porastanych przez zespół *Sp-Jg*. Jest to zgodne z wynikami dotyczącymi składu gatunkowego, ponieważ stwierdzono wyraźne różnice pomiędzy tymi jednostkami, w tym większą liczbę gatunków Dg preferujących niższe zasolenie dla zespołu *Tm-Gm*.

5.3. Funkcjonalny wzorzec roślinności

Wyniki badań przeprowadzonych w ramach drugiej publikacji (manuskrypt) zweryfikowały pozytywnie hipotezę o odrębności poszczególnych jednostek roślinności ze względu na charakterystyczne zbiory ich cech funkcjonalnych. Stwierdzono, że znaczący procent zróżnicowania pomiędzy klasami roślinności na solniskach wyjaśniają cechy odpowiedzialne za trwałość roślin, takie jak SLA, CH, CI, LDMC, LM i C (Kleyer i in., 2008). Wiele z nich związanych jest z parametrami liści, które zwykle są ze sobą skorelowane i reprezentowane przez tzw. spektrum ekonomii liści równoważące koszty budowy liścia z potencjałem wzrostu (Díaz i in. 2016; Wright i in., 2004). Liście jako krytyczne miejsca fotosyntezy i transpiracji (Zhou i in., 2020) są niezbędne do wymiany materiałów i energii w układzie gleba-roślina-atmosfera (Ackerly i in., 2002). Otrzymane wyniki pokazują jednak, że ich role są rozpoznawalne nie tylko na poziomie funkcjonalnym gatunków, ale także na poziomie syntaksonomicznym. Obniżenie SLA ma pomagać w lepszej odporności roślin na stres i ich wyższej zdolności konkurencyjnej w środowiskach stresowych (Long i in., 2011), ponieważ duże liście zwykle wymagają większych inwestycji w biomasę na jednostkę LA niż małe (Milla i in., 2008). Z kolei niskie wartości LDMC związane są z szybką i zdobywczą strategią roślin (Poorter i de Jong, 1999; Reich, 2014). Zatem niższe SLA i LDMC u roślinności typowej dla solnisk są powiązane ze zmniejszoną transpiracją i koniecznością utrzymania równowagi osmotycznej w warunkach stresu solnego (Richards i in., 2005). Wynika to z największego udziału gatunków halofilnych przystosowanych do zasolenia w klasach

THE i FEP. Niskie wartości większości cech odpowiedzialnych za trwałość odnotowane dla klas THE i FEP podkreślają wrażliwość tych jednostek na zmiany środowiskowe. Wskazują na to nie tylko cechy związane z liśćmi, ale także niski udział gatunków o wysokiej klonalności, która wpływa na lepsze przystosowanie roślin do zaburzeń środowiskowych (Klimešová i in., 2016). Do klas THE i FEP wartościami cech funkcjonalnych nawiązywała najbardziej klasa POT, która charakteryzowała się również niskimi wartościami cech związanych z trwałością (LA, LM, CH, LDCM), zdolnością do rozprzestrzeniania (RH i TV), a nawet znacznie niższą wartością cech związanych z regeneracją (SN i SNPS). Jednak w przeciwieństwie do THE i FEP, ten typ roślinności charakteryzował się najwyższymi wartościami SLA, CI, C i SM. Klasy, POT i BID, zostały sklasyfikowane jako podobne do siebie ze względu na podobne wartości prawie wszystkich cech trwałości (LA, LM, CH, LDMC, CI i C), wszystkich cech regeneracji (SM, SN, SNPS) oraz wybranych cech związanych ze zdolnością do rozprzestrzeniania (TV). Różniły się jednak istonie dwiema cechami: POT charakteryzowała się wyższą wartością SLA a BID wyższą RH. Duże podobieństwo cech funkcjonalnych wykazały klasy PHR i MOL. Analizy zmiennych środowiskowych pokazały, że obie klasy na solniskach zajmują siedliska o podobnych właściwościach, co może wyjaśniać ich podobieństwo cech funkcjonalnych. Jednak PHR charakteryzują znacznie wyższe wartości LM i niższe SLA, co wskazuje na jej przystosowanie do środowiska bardziej podmokłego. Wysoka wartość CH u roślinności klasy PHR, cechy niezwiązanej ze spektrum ekonomicznym liści (Díaz i in. 2016, Wright i in., 2004), także stanowi typową adaptację do terenów podmokłych, gdzie rośliny wydłużają się, aby zapewnić dostęp tlenu do tkanek (Colmer, 2003). Najwyższe wartości cech związanych z klonalnością u roślinności klas PHR, MOL oraz POT są związane z adaptacją do zaburzeń środowiskowych (Klimešová i in., 2016) i świadczą również o dużym potencjale ekspansji gatunków charakterystycznych dla tych grup, np. *P. australis* po zaprzestaniu koszenia i wypasu łąk (Burdick i in., 2001; Wilkoń-Michalska, 1970).

Stwierdzono, że zróżnicowanie pomiędzy zespołami przystosowanymi do zasolenia w obrębie klas THE i FEP można w największym stopniu wyjaśnić cechami odpowiedzialnymi za trwałość (SLA, CI i LDMC) i regenerację (SN i SNPS; Kleyer i in., 2008). Najniższe SLA odnotowano dla zespołu *Sr*, w którym gatunkiem dominującym jest *S. europaea* przystosowana do dużego zasolenia gleby poprzez prawie całkowitą redukcję liści i dużą miąższość tkanek (Cárdenas-Pérez i in., 2021). Najniższe wartości

SN cechują zespoły *Sp-Jg* i *Tm-Gm*, co wskazuje na ich niską zdolność do regeneracji generatywnej (Rosbakh i in., 2018). Jednakże cechy związane z masą i liczbą nasion wpływają nie tylko na zdolność roślin do regeneracji, ale także w pewnym stopniu na ich zdolność do rozprzestrzeniania się i reakcji na zakłócenia (Leishman, 2001; Westoby i in., 2002). Najwyższą wartość LDMC odnotowano dla *Sp-Jg*, co można interpretować jako wyższą produktywność tego zespołu, ale także niższy potencjał zdobywczy (Polley i in., 2022; Reich, 2014). Ponadto Májeková i in. (2014) wykazali, że wyższe wartości LDMC mogą wiązać się z wyższą stabilnością populacji. Zespoły *Sp-Jg* i *Tm-Gm* wykazały najwyższe parametry klonalności, co wskazuje na ich lepszą adaptację do zaburzeń środowiskowych (Klimešová i in., 2016). Najwyższe SLA i najniższy LDMC cechują zespoły *Agrostio stoloniferae-Juncetum ranarii* (*As-Jr*) i *P-Ss*, co wiąże się ze strategią szybką i zdobywczą tych zespołów (Reich, 2014), a ich najwyższe SN wskazuje na najwyższą zdolność do regeneracji generatywnej.

5.4. Wpływ zmiennych środowiskowych na cechy funkcjonalne

Przeprowadzone analizy środowiskowego wzorca cech funkcjonalnych roślinności solnisk śródlądowych, wykonane w ramach drugiej publikacji (manuskrypt), wykazały istotny związek pomiędzy cechami funkcjonalnymi a parametrami środowiskowymi, w tym ze sposobem zarządzania terenu. Pozwoliło to na ustalenie jakie czynniki determinują cechy poszczególnych płatów roślinnych na solniskach śródlądowych. Wyniki pokazują, że czynnikami najbardziej ograniczającymi roślinność solnisk są zasolenie i wilgotność, które w istotny sposób wpływają na cechy funkcjonalne gatunków (Minden i in., 2012; Minden i Kleyer, 2015; Piernik, 2012). Czynniki te wyjaśniają największą część zmienności cech funkcjonalnych analizowanej roślinności, co wskazuje na słuszność przyjętego założenia, że parametry środowiskowe kształtują cechy. Wpływ użytkowania gruntów, w tym wcześniejszych form zarządzania, na cechy zbiorowisk solniskowych wykazali również Batriu i in. (2015). Stwierdzono, że zasolenie jest ujemnie skorelowane z większością cech funkcjonalnych, co skutkuje różnymi strategiami funkcjonowania płatów, np. spadkiem SLA oznaczającym niższą wydajność fotosyntezy, ale także spadkiem LDMC oznaczającym strategię szybszego i bardziej intensywnego pozyskiwania zasobów. Podobne wyniki uzyskano na solniskach nadmorskich (Minden i in. 2012; Minden i Kleyer 2015).

5.5. Rola funkcjonalna gatunków diagnostycznych

Hipotezę o odrębności funkcjonalnej analizowanych syntaksonów zweryfikowano pozytywnie również w oparciu o tylko gatunki Dg w ramach trzeciej publikacji (manuskrypt). Analizy bazujące na wykonanych pomiarach cech morfologicznych ujawniły istotne różnice pomiędzy trzema rozpatrywanymi zespołami roślinnymi, które były szczególnie widoczne w parametrach liści (LWR, LFW i LDW, LM, SLA, LDMC i LA), a także RWR i SL. Najwyższe wartości tych parametrów charakteryzowały zespół *Tm-Gm*. Siedliska zajmowane przez *Tm-Gm* są często określane jako pastwiska lub łąki kośne (Jarocińska i in., 2023; Nienartowicz i Piernik, 2004b), co znajduje odzwierciedlenie w relatywnie wysokiej produkcji biomasy wyrażonej wysokimi wartościami świeżej i suchej masy. Wysoka wartość LA w zespole *Tm-Gm* wpływa bezpośrednio na najwyższe SLA (Zhou i in., 2020), co może świadczyć o zajmowaniu przez ten zespół siedlisk bogatszych w zasoby, gdzie wyższy poziom SLA służy zwiększeniu wydajności fotosyntezy (Yao i in., 2016). Stosunkowo wysokie LDMC dla zespołu *Tm-Gm* potwierdza z jednej strony jego wyższą produktywność (Polley i in., 2022), a z drugiej oznacza niższy potencjał strategii zdobywczej (Reich, 2014). Wyniki potwierdzają także istotną rolę korzeni w produktywności poszczególnych zespołów. Najwyższy RWR u *Tm-Gm* można powiązać z największą zdolnością do pobierania wody i składników odżywczych z gleby (Lopez i in., 2023). Wysokie wartości parametrów korzeni (RL, RWR) świadczą o plastyczności, która jest przystosowaniem do funkcjonowania w warunkach stresu solnego (Alshiekheid i in., 2023; Arif i in., 2019). Zespół *Sr*, w którym dominuje halofit obligatoryjny *S. europaea* o zredukowanych liściach i pędach o dużej miąższości, które przejęły funkcje asymilacyjne (Cárdenas-Pérez i in., 2022b), charakteryzują najwyższe wartości AA, SFW, SDW i SWR. Na wyższą świeżą masę u *Sr* znaczący wpływ może mieć akumulacja wody w tkankach, natomiast na wyższą suchą masę akumulacja jonów (Pirasteh-Anosheh i in., 2023). Redukcja liści u tego gatunku Dg wpływa na niskie SLA całego zespołu *Sr,* co dowodzi jego odporności na zasolenie i świadczy o dużych zdolnościach konkurencyjnych w warunkach stresu (Long i in., 2011). Zespół *P-Ss* charakteryzował się najwyższą NoL, co związane jest z fizjonomią gatunków Dg tego zespołu – *S. marina*, *P. distans* i *A. prostrata* (Akcin i in., 2015; Piernik, 2006).

Wyniki analiz biochemicznych pokazały wyraźne różnice pomiędzy rozpatrywanymi zespołami roślinnymi, w tym szczególnie w zawartości proliny i MDA, które były wyższe dla zespołów *P-Ss* i *Tm-Gm* niż dla zespołu *Sr*. Wysoka zawartość proliny jest odpowiedzią fizjologiczną roślin na czynniki stresu abiotycznego, która ma na celu ochronę gatunku przed wysokim ciśnieniem osmotycznym roztworu glebowego i pozwala roślinie na wchłanianie wody w warunkach zasolenia roztworu glebowego. Zawartość MDA wskazuje na poziom peroksydacji lipidów w błonach komórkowych wywoływanej przez stres (Hnilickova i in., 2021). Wysoki poziom MDA w warunkach zasolenia może wskazywać na wyższy stres oksydacyjny (Wang i in., 2022). W analizowanych zespołach porównywalny poziom MDA odnotowano dla *Tm-Gm* i *P-Ss*, a niższy dla zespołu *Sr*. Innym markerem stresu oksydacyjnego jest H_2O_2 – reaktywna forma tlenu (ROS) wytwarzana w komórkach podczas normalnego metabolizmu tlenowego. Jednak podczas działania niekorzystnych czynników zewnętrznych (np. zasolenia) w roślinach dochodzi do jego nadmiernej produkcji, co może uszkadzać komponenty komórek i prowadzić do ich śmierci (Sofo i in., 2015; Ślesak i in., 2007). Wyższy wzrost zawartości H_2O_2 obserwuje się u roślin wrażliwych na zasolenie niż u tych tolerujących warunki stresu solnego (Kumari i in., 2013). Otrzymane wyniki pokazują, że najniższy stres oksydacyjny wyrażony przez niski poziom H_2O_2 odnotowano dla *Sr*, wyższy u *P-Ss*, a najwyższy dla zespołu *Tm-Gm*. Jednym z elementów odpowiedzi na stres oksydacyjny jest indukcja CAT i APX, które są enzymami metabolizującymi H_2O_2 (Sofo i in., 2015). Najwyższa aktywność wymienionych enzymów u roślinności zespołu *Tm-Gm* wskazuje na jej największą mobilizację do obrony przed stresem oksydacyjnym w warunkach zasolenia. Co ciekawe, aktywność APX była wyższa niż CAT, co sugeruje jej większą rolę w obronie przed stresem oksydacyjnym w przypadku roślinności solnisk (Cárdenas Pérez i in., 2022b). Z kolei najwyższe stężenie barwników fotosyntetycznych związanych z produktywnością odnotowano dla zespołu *Tm-Gm*, niższe u *P-Ss*, a najniższe w *Sr*. W literaturze opisano różną reakcję barwników fotosyntetycznych u poszczególnych gatunków na wzrost zasolenia gleby. U niektórych z nich w warunkach stresu solnego notowano spadek poziomu chl lub car, (np. Taïbi i in., 2016), a u innych wzrost, ale niezwiązany z wyższą produktywnością (Borghesi i in., 2011; Lim i in, 2012). Spadek poziomu chl uznawany jest za objaw stresu oksydacyjnego (Smirnoff, 1996), co wiąże się z hamowaniem syntezy chl i aktywacją jego degradacji (Santos, 2004). Car pełnią nie tylko rolę barwników, ale także przeciwutleniaczy, a ich wysoka zawartość może wskazywać, że stanowią one jeden z najważniejszych mechanizmów ochronnych podczas stresu zasolenia u roślinności zespołu *Tm-Gm* (Taïbi i in., 2016). Węglowodany działają wspólnie z proliną jako substancje osmoregulacyjne odpowiedzialne za większą stabilność biochemiczną komórek.

Badania różnych gatunków wykazały, że wzrost poziomu węglowodanów wiąże się z większą odpornością roślin na zasolenie (np. Almodares i in., 2008). Uzyskane wyniki pokazują, że zarówno prolina, jak i węglowodany odgrywają podobną rolę u zespołów *Sr* i *Tm-Gm*, podczas gdy węglowodany są mniej istotne w porównaniu z proliną dla zespołu *P-Ss*.

Główny gradient różnicujący cechy funkcjonalne analizowanych zespołów można interpretować na podstawie przeprowadzonych analiz ordynacyjnych jako gradient zasolenia. Analiza PCA cech morfologicznych pogrupowała poszczególne zespoły wzdłuż pierwszej osi ordynacyjnej w kolejności *Sr, P-Ss* i *Tm-Gm*, co wskazuje właśnie na gradient zasolenia zgodnie z wcześniej uzyskanymi wynikami analiz zróżnicowania poziomu zasolenia gleby w płatach tych jednostek roślinnych (pierwsza publikacja). Drugi gradient PCA oddzielający zespół *P-Ss* od dwóch pozostałych, można interpretować jako odmienną strategię pozyskiwania zasobów wyrażoną wysokimi wartościami RL i AA u tego zespołu, a także stosunkowo wysokim SDW u zespołów *Sr* i *Tm-Gm* oraz wyższą NoL u *P-Ss*. Analiza ordynacyjna cech biochemicznych pozwoliła zidentyfikować, że główną przyczyną zróżnicowania cech funkcjonalnych, wynikającą z zasolenia gleby może być stres osmotyczny. Pierwsza oś ordynacyjna analizy PCA wskazuje na silną reakcję na stres osmotyczny, związaną z akumulacją proliny, uszkodzeniami oksydacyjnymi lipidów w błonach komórkowych (MDA) i odpowiedzią ochronną ze strony car. Ten główny gradient wyraża się w najsłabszej odpowiedzi u zespołu *Sr*, którego gatunki Dg są przystosowane do ekstremalnego zasolenia (Cárdenas-Pérez i in., 2022a, 2022b) i najsilniejszej u zespołów *P-Ss* i *Tm-Gm*, których gatunki Dg są słabiej przystosowane do zasolenia i wykazują wyraźne strategie obronne. Za czynnik związany z drugą osią ordynacyjną można przyjąć odpowiedź na stres oksydacyjny wyrażony w wysokiej zawartości H_2O_2 i dużej aktywności APX u zespołu *Tm-Gm*, gdzie gatunki Dg są słabiej przystosowane do zasolenia (Kumari i in., 2013). Odnosząc to do drugiego gradientu różnicującego w wynikach analizy PCA cech morfologicznych, wykształcenie adekwatnej strategii pozyskiwania zasobów można powiązać z odpowiedzią na stres oksydacyjny.

Wyniki porównania wartości cech funkcjonalnych dla zespołów obliczone na podstawie wszystkich gatunków i wyłącznie gatunków Dg wykazały, że różnice funkcjonalne pomiędzy zespołami są bezpośrednio związane z gatunkami Dg, a nie z całym składem gatunkowym. Może to spowodować postęp w badaniach skupiających się na funkcjonowaniu zespołów roślinnych poprzez ograniczenie pomiarów i obliczeń do kilku gatunków Dg zamiast do wszystkich gatunków. Dodatkowo, zaprezentowaną koncepcję analizy jednostek syntaksonomicznych jako jednostek funkcjonalnych można zastosować jako narzędzie do walidacji istniejących systemów fitosocjologicznych.

5.6. Zastosowania w ochronie roślinności solnisk śródlądowych

Wyniki klasyfikacji syntaksonomicznej pozwoliły wyróżnić zespoły typowe dla solnisk, z których *Sr* można zaliczyć do podlegającego ochronie na terenie Europy siedliska 1310 (Nienartowicz i Piernik, 2004a), a pozostałe cztery zespoły reprezentujące klasę FEP (*P-Ss*, *Tm-Gm*, *Sp-Jg* i *As-Jr*) do siedliska *1340 (Nienartowicz i Piernik, 2004b). Jak potwierdzają przeprowadzone analizy, najważniejszymi czynnikami środowiskowymi kształtującymi ten typ roślinności są zasolenie i wilgotność podłoża, które są często ze sobą powiązane, ponieważ słone wody gruntowe mogą być źródłem zasolenia gleb zarówno na stanowiskach naturalnych, jak i przemysłowych (Piernik i Hulisz, 2011). Dlatego roślinność słonolubna jest wrażliwa na wszelkie regulacje wodne, które mogą wpływać również na pH gleby i zawartość materii organicznej w podłożu. Co więcej, badania Čížkovej i in. (2020) pokazały, że poziom wody może mieć wpływ na liczebność poszczególnych gatunków halofitów na solniskach. Kolejnym istotnym czynnikiem jest dostępność światła, co świadczy o konieczności odpowiedniego zarządzania solniskami, np. poprzez regularne koszenie, a także wypasanie zwierząt gospodarskich. Zgryzanie i wydeptywanie roślin powiązane z wypasem wpływają na tworzenie wolnych przestrzeni dla gatunków jednorocznych, np. *S. europaea* czy *S. marina* (Bakker i De Vries, 1992). Wypas jest najważniejszy w przypadku niskich gatunków halofitów takich jak *S. europaea*, *Suaeda maritima* (L.) Dumort. i *G. maritima* (Jensen, 1985).

Według Cadotte i in. (2015) zespoły roślinne można przewidywać na podstawie ich cech funkcjonalnych. Otrzymane wyniki analizy cech funkcjonalnych pozwalają stwierdzić, że klasy typowe dla solnisk, czyli THE i FEP, charakteryzują się niskim potencjałem trwałości. Z kolei biorąc pod uwagę zespoły, najniższy potencjał co do trwałości i regeneracji odnotowano dla *Sr* (Kleyer i in. 2008). Potwierdzają to zarówno analizy cech funkcjonalnych zespołów przeprowadzone w oparciu o dane z baz (Kleyer i in. 2008; Klimešová i in., 2017), jak i cech zmierzonych na materiale roślinnym zebranym w terenie. Jednostki te są zatem najbardziej wrażliwe na zmiany środowiskowe. Dużą część zmienności pomiędzy analizowanymi zespołami można tłumaczyć cechami związanymi ze wspomnianą regeneracją roślin, które opierają się na parametrach nasion. Zespoły roślinne na solniskach tworzą głównie niskie gatunki, których nasiona nie wykształciły szczególnych adaptacji do rozprzestrzeniania na duże odległości. Erfanzadeh i in. (2010) wykazali, że cechy rozprzestrzeniania się nie są czynnikami ograniczającymi kolonizację roślin na solniskach. Jednak warto zauważyć, że badania nad rekultywacją rezerwatu halofitów wykonane przez Lubińską-Mielińską i in. (2022) pokazały, że w miejscach oddalonych od płatów roślinności halofilnej nasiona halofitów nie występują w glebowym banku nasion. Dodatkowo niska SM roślinności zespołów *Sr* i *P-Ss*, charakterystycznych dla miejsc najbardziej zasolonych, może mieć wpływ na ich niestabilność w glebowym banku nasion. Może to generować problemy z rekultywacją tych zespołów. Na solniskach gradient zasolenia może być silnym filtrem sprzyjającym dużej liczbie halofitów i ograniczającym gatunki glikofilne. Jednak wraz ze spadkiem zasolenia kluczowe znaczenie ma kontrolowanie ekspansji wyższych i przez to bardziej konkurencyjnych gatunków o dużych zdolnościach klonalnych jak wspomniana wcześniej *P. australis* (Bosiacka i in., 2011). Kolejnym problemem w ochronie i odtwarzaniu roślinności solnisk śródlądowych jest fragmentacja krajobrazu i wyspowa struktura siedlisk, które wpływają na różnorodność funkcjonalną poszczególnych systemów roślinnych (Zambrano i in., 2019). Według Minden i Kleyer'a (2015) utrata kilku gatunków typowych dla solnisk nadmorskich z niewielkiej ich puli, może pociągnąć za sobą utratę ich specyficznego składu cech, co z kolei może znacząco zmienić relacje pomiędzy środowiskiem a właściwościami ekosystemów roślinnych danego terenu. Ta sama zależność dotyczy solnisk śródlądowych i dlatego tak ważna jest ich skuteczna ochrona. Podczas planowania działań ochronnych należy zatem zwrócić szczególną uwagę na jednostki najwrażliwsze pod względem funkcjonalnym.

Wyniki przeprowadzonych badań zwracają również uwagę na znaczenie ochrony prawnej gatunków Dg, które stanowią nie tylko podstawę wyodrębniania poszczególnych jednostek syntaksonomicznych, ale także, odgrywają kluczową rolę w funkcjonowaniu zespołów roślinnych na solniskach śródlądowych. Należałoby zintegrować ochronę siedlisk i ich kluczowych gatunków, co niestety nie zawsze jest praktykowane. Przykładem może być brak ochrony gatunkowej halofitu *S. marina* na terenie Polski (Dziennik Ustaw, 2014 – poz. 1409). Oczywiście należy brać pod uwagę tylko rzadkie i wyspecjalizowane gatunki, szczególnie zaliczane do halofitów. Przykładowo pomimo, że *P. australis* zaliczono do grupy gatunków Dg zespołu *Tm-Gm* to jest to gatunek pospolity i ekspansywny, który nie wymaga ochrony prawnej (np. Bosiacka i in., 2011; Burdick i in., 2001).

Na koniec warto podkreślić, że zarówno w zarządzaniu, jak i skutecznej ochronie roślinności europejskich solnisk śródlądowych najważniejsze jest odpowiednie zaangażowanie osób odpowiedzialnych za tereny chronione, które zapewnią systematyczne prowadzenie aktywnych zabiegów (np. Lubińska-Mielińska i in., 2022). Znane są od lat skuteczne działania imitujące tradycyjny sposób użytkowania gruntów, gwarantujące nie tylko utrzymanie, ale i poprawę kondycji roślinności solniskowej (Brandes, 1999). Podejście oparte na cechach funkcjonalnych może przynieść praktyczne zastosowanie zaprezentowanych wyników badań w tworzeniu nowych strategii zarządzania, ochrony i rekultywacji tych zagrożonych siedlisk.

6. Podsumowanie

Przeprowadzone w ramach niniejszej pracy doktorskiej badania pokazały, że oprócz klas typowych takich jak THE i FEP na solniskach śródlądowych klimatu umiarkowanego reprezentowana jest również roślinność klas typowych dla siedlisk niezasolonych. Stanowi ona integralną część solnisk i zawiera w swoim składzie gatunki halofilne. Zidentyfikowano w sumie siedem takich klas: RUP, POL, ART, POT, BID, PHR i MOL. W kwestii preferencji środowiskowych wyodrębnione klasy różnią się najbardziej pod względem zasolenia, wilgotności, dostępności światła oraz zawartości azotu w glebie. Natomiast typowe zespoły solniskowe (*Sr, P-Ss, Tm-Gm, Sp-Jg* i *As-Jr*) różnią się również preferencjami co do odczynu podłoża i zawartości materii organicznej w glebie. Otrzymane wyniki wskazują zatem na duże zróżnicowanie analizowanego typu roślinności. Ponadto uzyskane wyniki badań pokazały, że analizowane jednostki syntaksonomiczne mają także znaczenie funkcjonalne. Do najważniejszych cech funkcjonalnych decydujących o odrębności poszczególnych klas i zespołów solniskowych należą parametry odpowiedzialne za trwałość gatunków, które na ogół są ujemnie skorelowane z zasoleniem gleby i dodatnio z jej wilgotnością oraz z zaprzestaniem koszenia i wypasu. Dodatkowo dla zespołów istotne są również cechy związane z regeneracją. Pod względem analizowanych cech funkcjonalnych największą wrażliwość na zmiany środowiskowe wykazały jednostki typowe dla solnisk. Na podstawie pogłębionych analiz zarówno morfologicznych, jak i biochemicznych cech funkcjonalnych zespołów solniskowych (*Sr, P-Ss, Tm-Gm*) stwierdzono, że wykazują one zróżnicowane strategie odporności na zasolenie. Otrzymane wyniki zwracają uwagę na kluczową rolę gatunków Dg w funkcjonowaniu analizowanych zespołów. Wskazuje to na konieczność integracji ochrony całych siedlisk z ochroną gatunkową halofilnych gatunków Dg. Identyfikacja wymagań oraz nowe podejście oparte na cechach funkcjonalnych mogą posłużyć do stworzenia efektywniejszych strategii zarządzania, ochrony i rekultywacji solnisk śródlądowych istotnych dla zachowania różnorodności biologicznej w obliczu nowych globalnych zagrożeń.

7. Wnioski

1. Roślinność europejskich solnisk śródlądowych strefy umiarkowanej wykazuje duże zróżnicowanie, co odzwierciedla jej klasyfikacja syntaksonomiczna.
2. O rozmieszczeniu jednostek syntaksonomicznych w gradiencie środowiskowym decydują różne czynniki, z których dla klas najistotniejsze są: zasolenie, wilgotność, dostępność światła i zawartość azotu, a dla zespołów: zasolenie, dostępność światła, zawartość materii organicznej, odczyn oraz wilgotność podłoża.
3. Wyodrębnione jednostki sytaksonomiczne solnisk śródlądowych mają również znaczenie funkcjonalne.
4. Spośród analizowanych cech funkcjonalnych najistotniejsze dla odrębności wyróżnionych klas i zespołów są te odpowiedzialne za trwałość roślin. Wykazują one ujemną korelację z zasoleniem gleby, a dodatnią z wilgotnością podłoża oraz zaprzestaniem koszenia i wypasu. Na zróżnicowanie zespołów wpływ mają również cechy związane z regeneracją gatunków.
5. Niski potencjał trwałości i regeneracji klas THE i FEP oraz zespołu *Sr* wpływa na ich największą wrażliwość na zmiany środowiska i wskazuje na konieczność szczególnego zainteresowania pod kątem ich ochrony.
6. Poszczególne zespoły typowe dla solnisk śródlądowych wykazują zróżnicowane strategie adaptacyjne do warunków stresu zasolenia.
7. Gatunki diagnostyczne odgrywają kluczową rolę w funkcjonowaniu zespołów roślinnych solnisk śródlądowych, dlatego należy zintegrować ich ochronę gatunkową z ochroną siedlisk.
8. Zidentyfikowane wymagania i cechy funkcjonalne analizowanej roślinności należy wziąć pod uwagę przy tworzeniu nowych strategii zarządzania, ochrony i rekultywacji solnisk śródlądowych.

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