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RESEARCH ARTICLE

Habitat loss and isolation threaten specialist flora in Baltic coastal meadows

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Abstract

Questions: Baltic coastal meadows are ecologically unique habitats that have been severely impacted by habitat loss and environmental change. To determine the effects of habitat loss and isolation on their plant communities, we analysed the relationships between species richness and habitat size and amount. Because coastal meadows host species with a vast array of traits, we expected responses to vary between species groups.

Location: Swedish Baltic coast.

Methods: We inventoried the presence of vascular plant species in twenty-eight 1-m^2 plots placed along edaphically defined transects in fifteen coastal meadows. We determined the richness of three species groups: all species, halophytes and inland grassland specialists. We then mapped the habitat for coastal grassland plants using GIS overlay analysis. Using this habitat map, we calculated two variables: "habitat size" and "habitat amount". We tested correlations between species richness measures and habitat variables, as well as determining the distribution of species traits within meadows.

Results: We recorded 174 plant species, of which 6 were halophytes and 35 were inland grassland specialists. Species traits coincided with edaphic sea-to-land gradients. Halophyte and inland grassland specialist richness were significantly correlated with both habitat variables (r = 0.52–0.71). No correlations were found with total species richness. Our habitat map showed that there are 8,900 ha of managed Baltic coastal meadow left in Sweden, mostly in the south.

Conclusions: Species traits and distribution play a major role in determining persistence in the face of habitat loss and environmental change. This is especially true for some halophyte populations, which are more susceptible to habitat size and isolation because of their specialisation. Furthermore, they risk being squeezed between the dual threats of encroaching succession and sea-level rise. Preventing habitat loss, restoring meadows and increasing connectivity is crucial for the persistence of specialist plant species.

KEYWORDS

Baltic coastal meadows, biodiversity, environmental change, grassland, habitat amount, habitat isolation, habitat loss, land uplift, plant communities, sea-level rise

1 | INTRODUCTION

Baltic coastal meadows are semi-natural grasslands found in erosion-sheltered, low-lying and flat coastal areas. They have been largely influenced by isostatic land uplift since the last Ice Age, especially in the northern regions of the Baltic Sea where annual uplift of up to 1 cm still occurs (Vestøl et al., 2019). Today, the interplay between land uplift, sea-level rise and sedimentation determines the geomorphological development and extent of Baltic coastal meadows (Ward et al., 2016).

The Baltic Sea has brackish water and negligible tides, creating pronounced sea-to-land gradients in salinity, flooding and soil moisture in coastal meadows. In turn, these conditions create a unique habitat for, for example, plants, birds and amphibians (Rannap et al., 2007, 2017; Hulisz et al., 2016; Kaasiku et al., 2019). The plant communities of Baltic coastal meadows therefore differ from other grasslands in the region by hosting halophytes with adaptations to withstand saline conditions and high soil moisture. These species are generally found on the lower shore below the high-water mark and in highly saline depressions on the upper shore (Dijkema, 1990; Figure 1). Typical inland grassland plant species are instead successively found in more elevated areas that are rarely reached by seawater, where halophytes are outcompeted (Rautiainen et al., 2007; Figure 1). The plant species distribution also reflects a successional gradient driven by isostatic land uplift. The continuously lifted seabed is first colonised by halophytes, and then gradually populated by typical inland grassland species once the habitat becomes drier with the isostatic uplift and time (Auffret & Cousins, 2018, Ecke & Rydin, 2000; Figure 2).

The geomorphology of the Swedish coast allows only a scattered distribution of coastal meadows, which are bound to areas that are relative flat and sediment rich. Their distribution can thus be considered as naturally fragmented, with varying degrees of habitat patch size and isolation. However, the influence of these patterns on the ecology of Baltic coastal meadows has received little attention compared with other grasslands, even though habitat availability and arrangement have significant ecological responses on various spatial scales. For example, the risk of extinctions increases when habitat patches are small or habitat amount at the landscape scale is low (Lande, 1987; Ewers & Didham, 2005; Hanski et al., 2013); habitat isolation obstructs dispersal and can lead to loss of genetic diversity and further vulnerability to climate change (Jump & Peñuelas, 2005; Leimu et al., 2010; Saura et al., 2014); and the spatial configuration of habitat patches in fragmented landscapes has implications for species persistence (Fahrig et al., 2022). This is of particular concern regarding Baltic coastal meadows because they have been identified as being severely threatened by agricultural abandonment and environmental change.

During the past century, many Baltic coastal meadows stopped being grazed or mown, quickly becoming encroached by tall grasses, reeds and later shrubs, losing their typical plant community (Burnside et al., 2007; Sammul et al., 2012). Accordingly, they now require protection under the European Council Habitats Directive (92/43/EEC). In Estonia, the country with most Baltic coastal meadows, ca. 200 km^2 of meadows have been lost since the 1960s (Rannap et al., 2004). In 2018, 140 km^2 remained according to the Estonian assessment demanded by the Habitats Directive (European Environment Information and Observation Network, n.d.). In comparison, today there is 129 km^2 of coastal meadow in Sweden (European Environment Information and Observation Network, n.d.). There is no exact estimation of the extent of Swedish coastal meadows in the past, but Auffret and Cousins (2018) modelled the land uplift and potential for coastal meadows for a part of Sweden and concluded that only a fraction of their historical extent remains today.

Climate change further threatens this already endangered habitat by exacerbating habitat loss and inducing changes in environmental conditions and disturbance regimes. For example, sea-level rise can offset land uplift and by coastal squeeze contribute to habitat loss

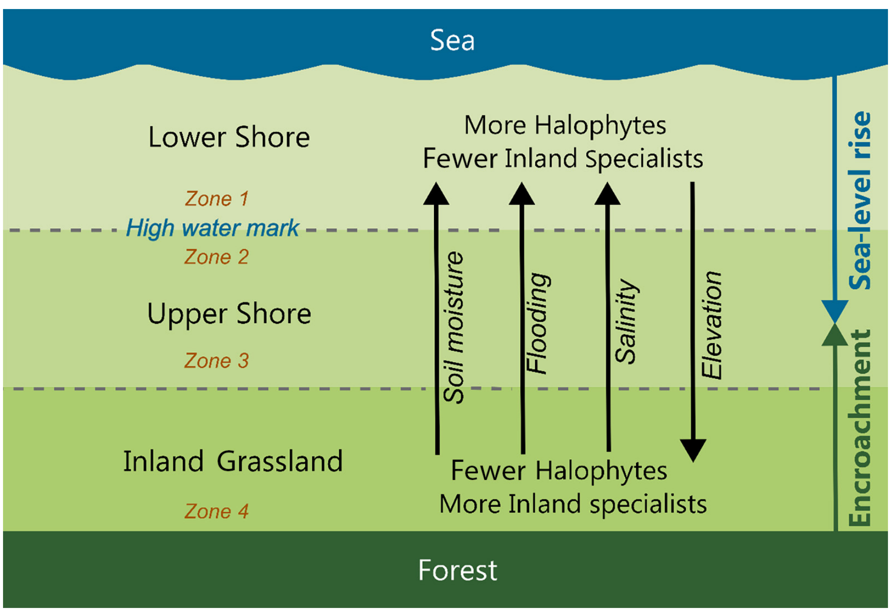

FIGURE 1 Conceptual model of plant species distribution in Baltic coastal meadows along their edaphic gradients (black arrows). The grey dashed line between the lower and upper shore designates the high-water mark. The grey dashed line between upper shore and inland grassland designates the limit where edaphic conditions switch character from typically coastal to inland. The blue and green arrows show the direction in which sea-level rise and encroachment will extend. Zones 1–4 designate the vegetation zones where plots were placed for plant inventories in this study, see Methods for further information.

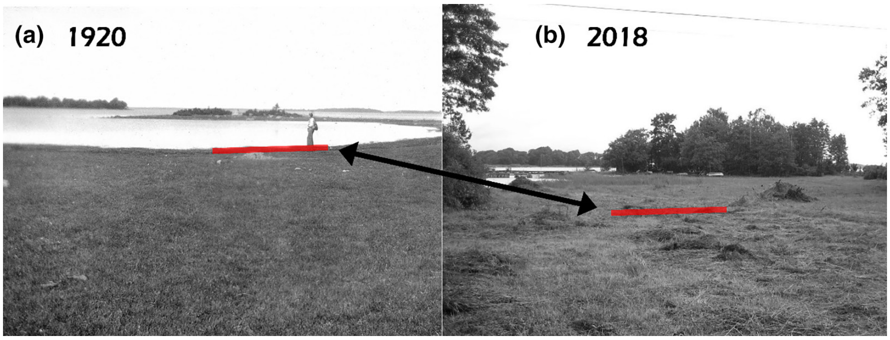

FIGURE 2 Pictures of the same meadow taken from approximately the same position in 1920 (a) and 2018 (b). The photographs show how a coastal meadow in southeastern Sweden has developed over 100 years. What was habitat for early successional species 100 years ago is now closer to the forest border and inhabited by species associated with drier or mesic grasslands. The land uplift is ca. 40 cm between the photographs. Photo credits: S. Sternberg (left), S. Cousins (right).

(Rautiainen et al., 2007; Moeslund et al., 2011). Furthermore, the increased frequency and magnitude of storm surges and droughts, as well as changes in salinity, alter plant community composition (Kont et al., 2007; Bergamo et al., 2022; Schibalski et al., 2022). Together, agricultural abandonment and climate change therefore threaten vulnerable populations of specialist flora, compromise habitat quality for other organisms such as birds and amphibians, and disrupt ecosystem services.

We hypothesise that plant species richness in Baltic coastal meadows is related to habitat size and habitat amount, because larger and less-isolated plant populations have a higher chance of surviving agricultural abandonment and environmental change. We expect that these relationships depend on the examined species groups, because highly specialised species like halophytes and grassland specialists are more dependent on meadow habitat than other, more generalist plant species. However, we believe that species typically associated with inland grasslands are less dependent on coastal meadow habitat, because they can utilise inland habitats and therefore exist as part of larger, more stable metapopulations. To test these hypotheses, we mapped Baltic coastal meadows along the east coast of Sweden. We coupled this map with plant inventories to investigate the relationships between plant species richness and "habitat size" (HS) and "habitat amount" (HA). These two variables represent the availability of coastal meadow habitat at the local and landscape scale, respectively. We explored the effects of HS and HA on plant species richness to understand how plant species in coastal meadows can be affected by future habitat loss and isolation.

2 | METHODS

2.1 | Study area

The study area in which we created a coastal meadow habitat map stretches for the whole Swedish east coast along the Baltic Sea (65°49′ N, 24°18′ E to 55°53′ N, 12°48′ E). This area lies on the border between the temperate and boreal climate zones, with a mean annual air temperature ranging between 2 and 8 °C and an annual precipitation of 400–800 mm (Swedish Meteorological and Hydrological Institute, 2009). The area is subjected to Glacial Isostatic Adjustment, resulting in a land uplift of up to 10 mm year^{-1} near the city of Umeå (Vestøl et al., 2019). Where the topography is relatively flat, this has had substantial effects, with large land areas rising above the sea-level in a century (Figure 2). However, land uplift is currently being offset by sea-level rise, with the southernmost regions being subject to coastal recession due to low or no land uplift (Kapsi et al., 2023).

We selected 15 coastal meadows, spaced evenly along a section of the Swedish east coast (57°35′ N, 16°30′ E to 59°10′ N, 18°22′ E; Figure 3), where we carried out plant inventories to obtain species richness data. The southern parts of this area currently have no relative sea-level rise because land uplift balances absolute sea-level rise. Instead, the northern parts have a relative sea-level rise of −1 mm^{-1} because land uplift exceeds absolute sea-level rise (Kapsi et al., 2023).

2.2 | Landscape data

Currently, there is no map of managed Baltic coastal meadows that we could use to test our hypotheses. To produce such a map, we used a GIS overlay analysis designed to retrieve Baltic coastal meadows as relatively flat and low-lying coastal areas subject to grazing or mowing.

This overlay analysis required two geodata sources: a LiDAR-based Digital Elevation Model (DEM) and a shapefile of areas managed by grazing or mowing. The DEM is originally produced by Lantmäteriet as a 2-m resolution national raster (Höjddata 2+ grid from Lantmäteriet), which we resampled to 10-m resolution. Managed grassland was extracted from the vector product Jordbruksblock 2021 by the Swedish Board of Agriculture.

The DEM was converted to a slope raster (Horn, 1981) that we used to map areas which are flat (slope ≤ 2%) and low-lying (elevation ≤ 1 m a.s.l.) Baltic coastal meadows were finally mapped as those with ongoing grazing or mowing as per the Jordbukblock 2021 layer,

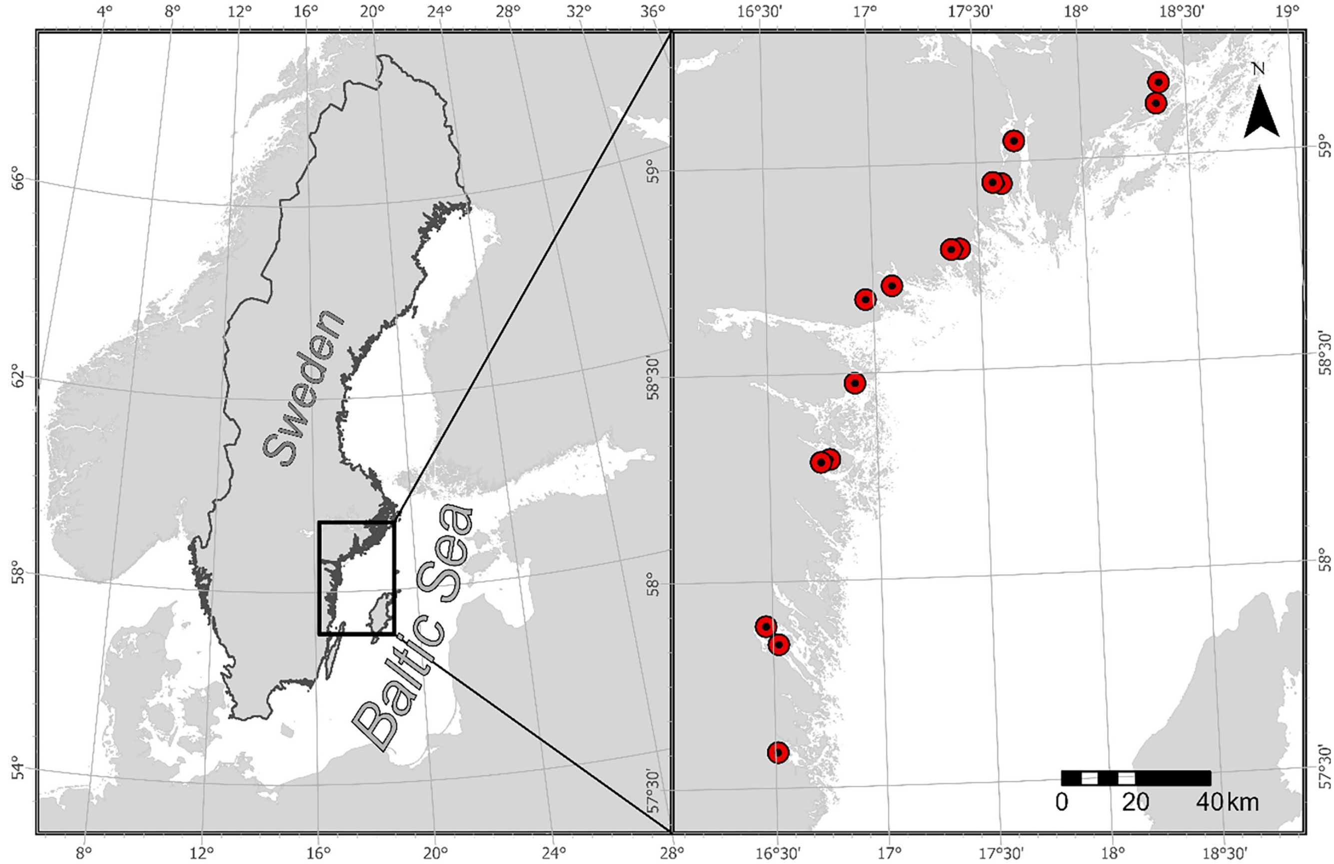

FIGURE 3 Map showing the Swedish coastline and the study area with the 15 Baltic coastal meadows in which plant inventories were carried out (red dots).

resulting in a binary raster layer (0 = non-coastal meadow, 1 = managed coastal meadow).

Processing was done at a national scale in Python code, utilising the packages: Fiona version 1.9.0, Geopandas version 0.14.0, Numpy version 1.22.3, Rasterio version 1.2.10 and RichDEM version 0.3.4. The coastal meadow map was used to obtain HS and HA for all meadows with plant richness data (hereafter called focal meadows). HS was defined as the area of each coastal meadow that we sampled. HA was defined as the total area of coastal meadows within a defined distance from the inventoried meadows, so-called buffer zones. These measures were chosen to represent the availability of coastal meadow habitat at the local and landscape scale, respectively.

Many focal coastal meadows have several grasslands of varying sizes in their immediate vicinity, which in some cases can be considered part of a grassland complex with the focal one. However, we disregarded the inclusion of surrounding grasslands when computing HS because of practical difficulties in delineating complexes. To delineate grassland complexes, it is necessary to define adequate and ecologically relevant distances within which complexes are formed and whether herds of livestock can roam between different grasslands. Livestock are an efficient way of connecting isolated grasslands (Plue et al., 2019). We therefore adopt the option of regarding only the sampled patches as focal ones. These arguments are also the basis for not including an isolation metric, defined as distance to nearest neighbouring habitat, often used in studies similar to this (Lindgren & Cousins, 2017; Melo et al., 2017). If we are not able to define meadow complexes and understand relationships between patches within them, we expect such a metric to be obfuscated and insignificant. HA on the other hand is a metric of isolation that is arguably free from these issues and adds the value of taking into account the whole landscape setting of the focal habitat patch.

We tested buffer zones with radii ranging from 1 to 15 km with 1-km increments to calculate HA, and we selected the buffer radius for which HA correlated most strongly with species richness, according to Fahrig (2013). That is, we computed a graph showing *r*-values between the richness measures and HA calculated with different buffer radii and selected the buffer radius that gave the highest *r*-value. HS was subtracted from HA, because the size of the focal patches becomes gradually more correlated to HA with smaller buffer sizes (MacDonald et al., 2021).

2.3 | Plant data

Plant inventories were carried out in August and September 2021 on 15 focal meadows. In these we placed inventory plots consisting of 1x1 m quadrats along transects ranging from sea to land. We aimed to make the plant data representative for whole meadows by placing the plots along the edaphically defined vegetation zones (Figure 1). First, the high-water mark in each meadow was identified visually using the occurrence of *Ranunculus* sp. and *Deschampsia cespitosa*, because they occur above the high-water mark but not below it (see Auffret & Cousins, 2018). Once the high-water mark had been identified, the sea–land transects of four plots were placed (Figure 1): one plot directly below the high-water mark (zone 1) and one directly above it (zone 2); one plot between the high-water mark and 1 m a.s.l. (zone 3) and one at ca. 1 m a.s.l. (zone 4). This was replicated seven times throughout each meadow, with evenly spaced transects. Twenty-eight plots were therefore placed per meadow in which all vascular plants were identified to species level (nomenclature: Mossberg & Stenberg, 2003).

We combined the species presence data from all quadrats in each meadow to define three meadow-scale species richness measures. These were: total number of plant species, number of halophytes and number of inland grassland specialists. To classify plant species into the specialist groups, we used the plant trait and ecological indicator database by Tyler et al. (2021) and its "Salinity" and "Grazing/mowing" columns. The salinity value indicates a species tolerance to saline conditions, and ranges from "not salt tolerant" (1) to "competitive only under high salinity" (5). The grazing/mowing value indicates a species response to grazing and mowing, and ranges from "does not endure any grazing/mowing" (1) to "demands repeated/continuous grazing/mowing" (8). Halophytes were defined as ≥4 salinity, thus selecting species that are only competitive under saline conditions. We selected this stricter salinity criterion to exclude typical ruderal species that thrive in Baltic coastal meadows, but are not restricted to them, e.g. *Plantago major* or *Argentina anserina*. Inland grassland specialists were defined as ≥6 grazing/mowing and <3 salinity. These criteria select species that are strongly favoured by regular grazing, but are not favoured by saline conditions. We separated the two specialist groups by applying the salinity criterion to the inland grassland specialists as well, because halophytes in coastal meadow are also favoured by grazing/mowing. We did this to be able test our hypotheses that coastal meadow HS and HA impact specialist groups differently.

2.4 | Data analysis

We computed boxplots of selected plant indicator values for the four inventoried zones 1–4 (Figure 1) because we hypothesise that species characteristics and distribution are crucial in determining their dependence on HS and HA. Also, we wanted to confirm that the sampling design effectively captured the sea-to-land plant community zonation and properly represented the plant communities of the meadows. The plant indicators that we tested were again extracted from the plant database by Tyler et al. (2021). These were: nectar production, light, moisture, salinity, grazing/mowing, soil disturbance, nitrogen, phosphorus and soil reaction (pH). Differences in mean values between zones were tested with one-way ANOVA tests. For significant ANOVA tests post-hoc Tukey's tests were performed.

To indirectly test the effects of habitat loss and isolation on species richness, we performed simple linear regression analysis between the richness measures and the habitat variables. The three species richness measures – total, halophytes and inland grassland specialists – were used as dependent variables in the data analysis, whereas the habitat variables, HS and HA were used as independent variables. Scatterplots with linear fits and correlation coefficients between the richness measures and the habitat variables were produced to show the effects of HS and HA on species richness. Because the examined habitat variables are often intercorrelated, complicating inferences on underlying ecological mechanisms, a correlation matrix reporting Pearson's correlation coefficient was generated and is available in Appendix S1.

3 | RESULTS

Mapping present-day managed coastal meadows (available as a raster data set, see Data Availability Statement below) shows that there are currently 8,900 ha of managed meadows on flat coastal terrain along the Baltic coast of Sweden with 2,000 ha in the study area (Figure 3). There are 21,401 individual coastal meadows in Sweden, with a maximum size of 190 ha. The median size of the inventoried meadows (HS) was 7.8 ha and the median amount of habitat surrounding them using a buffer zone with a 12-km radius (HA) was 165 ha. A 12-km buffer zone was used to calculate HA because it gave the strongest relationship between HA and specialist richness (Appendix S1).

In total, we found 174 different plant species on the inventoried meadows. Of these, 6 were halophytes and 35 were inland grassland specialists. The three most common halophytes encountered in the 420 one-metre plots were *Juncus gerardii*, *Centaurium littorale* and *Spergularia marina*. These species occurred in 11, 11 and 3 of the inventoried meadows, respectively. The 3 most common inland specialists were *Trifolium repens*, *Scorzoneroides autumnalis* and *Poa pratensis*, which occurred in 15, 14 and 14 of the meadows, respectively.

The full list of species, their frequency in each zone and the specialist groups to which they belong are given in Appendix S2. Per meadow, the mean "total species richness", halophyte richness and inland specialist richness was 67 ($SD=13.3$), 2 ($SD=1.1$) and 15 ($SD=3.9$), respectively. Mean halophyte richness decreased from 0.9 to 0.2 from sea to land (zone 1–4), whereas mean inland grassland specialist richness increased from 1.4 to 4.1; i.e. halophytes were more common closer to the sea, whereas inland specialists were more common inland.

There were significant differences between the vegetation zones in eight of the selected ecological indicator and trait values (Figure 4). Nectar production increased with distance from the shore. Realised niche regarding light, moisture, salinity, soil disturbance and soil reaction decreased with distance from the shore.

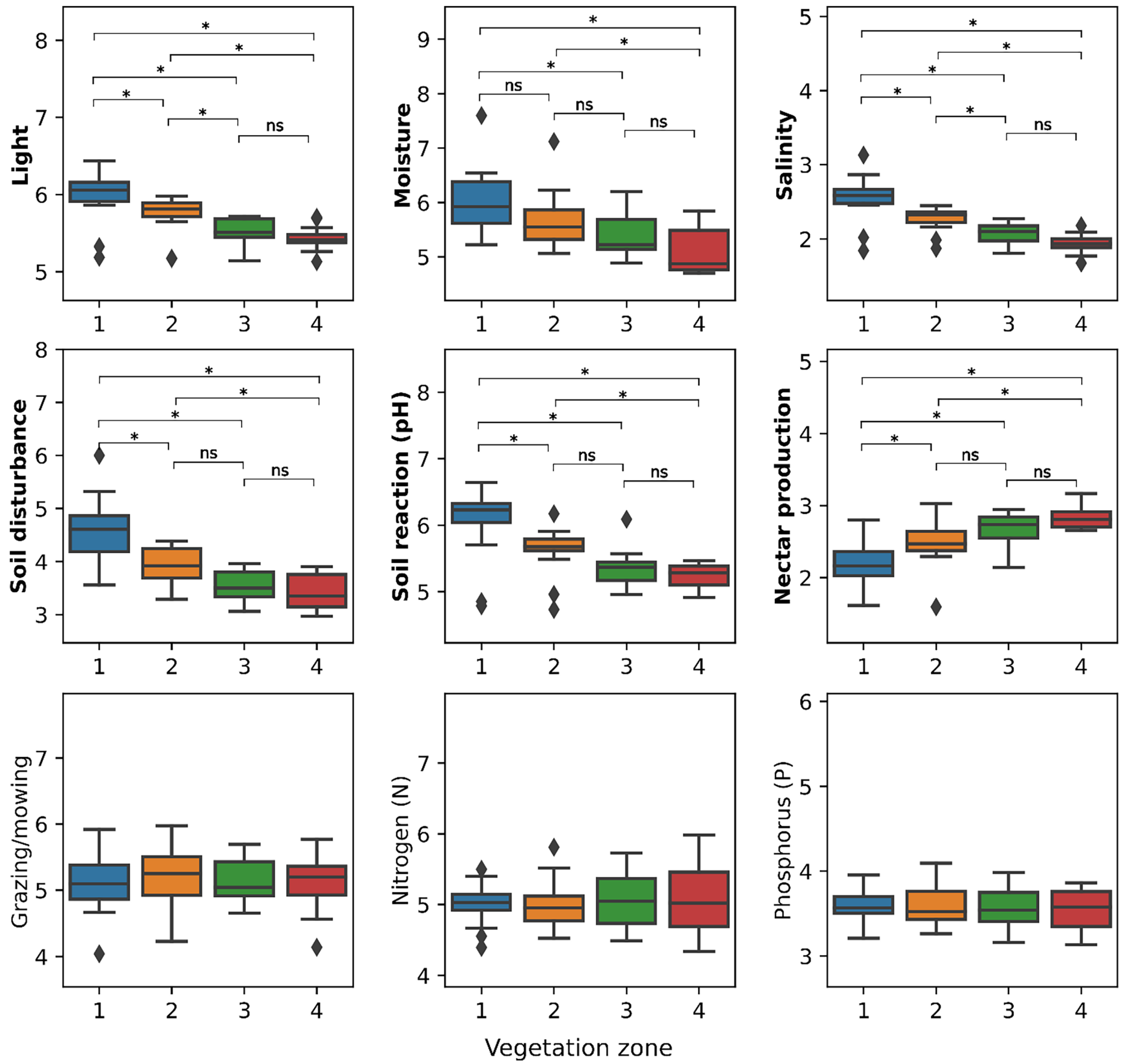

FIGURE 4 Boxplots of mean indicator values per site and zone from 1 to 4 in coastal meadows. Zone 1 is the closest to the sea and zone 4 is the farthest away. Indicator values on the *y*-axes are unitless. One-way ANOVA tests were significant for light, moisture, salinity, soil disturbance, soil reaction (pH) and nectar production, for which results from post-hoc Tukey's tests are shown (*$p<0.05$; ns, non-significant). See Tyler et al. (2021) for further information on the indicator values.

To visualise intercorrelations between the variables used in this study, we produced a correlation matrix reporting Pearson's correlation coefficient (*r*) (Appendix S3). The highest value was found between "total species richness" and richness of inland grassland specialists (0.79), followed by between HA and halophyte richness (0.71) and HS and HA (0.66). "Total species richness" was not found to be correlated with any habitat variable (Figure 5). Halophyte and inland grassland specialist richness were both positively correlated with HS ($r=0.52$ and 0.62; Figure 5) and HA ($r=0.63$ and 0.71; Figure 5).

4 | DISCUSSION

4.1 | The effects of habitat size and amount on species richness

We found positive relationships between the richness of both examined specialist groups and HS and HA (Figure 5). This means that plant species richness in Baltic coastal meadows is influenced by habitat availability at both local and landscape scales, but only if the different specialist groups are considered. The weaker relationships

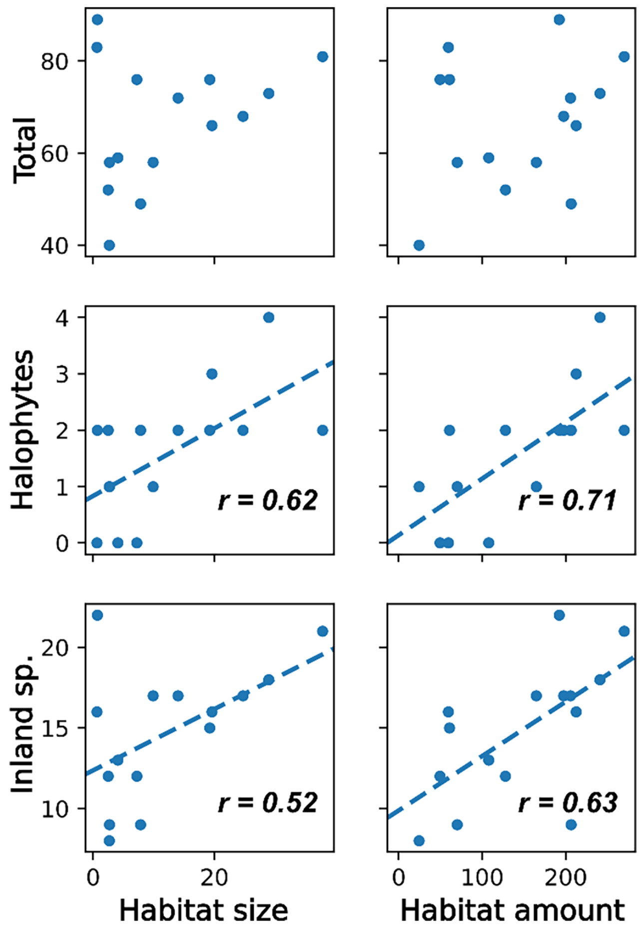

FIGURE 5 Scatterplots between species richness (total, halophytes and inland grassland specialists) and the habitat variables (HS and HA). The habitat variables are given in hectares. For significant linear regression tests ($p < 0.05$), Pearson's correlation coefficients (r) are reported with drawn regression lines.

between inland grassland specialist richness and the habitat variables may suggest that they are less dependent on coastal meadow habitat, probably because they are typically associated with inland habitats. This means that inland grassland specialists may form larger, more stable, meta-populations, indicating that they are less dependent on coastal meadow size and amount. Our map does not include managed grasslands further inland that are not in contact with the Baltic Sea. Halophytes, however, are restricted to coastal environments, making their relationships with the habitat variables comparatively strong.

Nevertheless, even though specialist richness responds to the examined habitat variables, no correlations were found with "total species richness". This could be an effect of generalists comprising the bulk of coastal meadow plant communities; of 174 species found in our inventory, 133 were neither halophytes nor inland grassland specialists. These species are generally not constrained to a coastal meadow habitat, and therefore their richness does not respond to variables derived from our habitat-specific map. This is a clear example of how examining the effects of spatial dependencies of community composition requires the selection of species groups that are delineated by the habitat in question (see, e.g. Fahrig, 2013).

In landscapes where coastal meadows are small, few and isolated, the richness of both examined specialist groups can be expected to be low (Figure 5). Habitat loss by partial or complete abandonment of meadows therefore threatens specialist flora by decreasing HS and HA. We believe that this inference, drawn from current plant and habitat data, may help us understand the pressures that Baltic coastal meadows have undergone in the past and will be subjected to in the future.

In the past century, grassland abandonment has led to severe habitat loss in the Baltic region, eliminating typical plant communities (von Numers & Korvenpää, 2007; Joyce, 2014; Pätsch et al., 2019). In many landscapes, meadow complexes that previously shared moving livestock have become more uniform and smaller leading to increasing isolation from their nearest neighbour and less habitat amount in the surroundings. Thus, habitat loss has affected HS and HA concurrently, probably leading to the important intercorrelations between them ($r = 0.66$). As an effect, in landscapes where habitat loss has occurred, coastal meadow specialists have experienced the joint effects of smaller populations, meta-populations and lower connectivity, leading to local and landscape-scale extinctions. In other words, landscapes that have experienced less habitat loss have been able to retain their specialists by maintaining their (meta-)population sizes and their connectivity.

4.2 | Sea-level rise and environmental change

Sea-level rise in the Baltic Sea has accelerated in past decades and is expected to do so even more in the future, exacerbating habitat loss. Depending on the climate change scenario and region, sea-level rise will either offset or exceed land uplift (Hieronymus & Kalén, 2020). This will slow, halt or reverse a millennial trend of coastal meadow habitat creation driven by land uplift, which has been identified as having important ecological implications (Auffret & Cousins, 2018). However, depending on local sediment accretion rates, sedimentation may mitigate the effects of sea-level rise and in some cases even exceed it, resulting in land accrual (Ward et al., 2016). Nonetheless, sea-level rise will significantly exceed land uplift in the south of Sweden where most managed Baltic coastal meadows are found. In meadows where sedimentation cannot offset sea-level rise, the inland movement of plant communities may be hindered, resulting in coastal squeezing (Moeslund et al., 2011). Ultimately, this will lead to further habitat loss with subsequent loss of specialist diversity. Further studies on current and future sediment accretion rates along the Baltic coast, which vary according to local conditions (Ward et al., 2014), are thus imperative to draw further conclusions on the magnitude of future coastal meadow habitat loss.

That Baltic coastal meadows are extensively affected by habitat loss, both by abandonment and sea-level rise, is concerning considering that they are especially threatened by environmental change

(Bergamo et al., 2022; Schibalski et al., 2022). Synergistic effects between habitat loss and environmental change increase extinction risk (Brook et al., 2008), and avoiding extinction is deeply dependent on genetic variation (Greenspoon & Spencer, 2021) and/or the possibility to migrate to new environmentally suitable areas (Vos et al., 2008). Highly isolated populations with low genetic variation and few possibilities of dispersal, which we believe applies to the specialists in this study, are therefore at risk (Jump & Peñuelas, 2005; Leimu et al., 2010).

Disturbance events like storm surges and droughts are also increasing in frequency and magnitude (Kont et al., 2007; Meier et al., 2022). This will have further deleterious effects on specialist flora in Baltic coastal meadow because they will not be able to recover or recolonise affected meadows owing to their isolation (Dornelas, 2010). Probably, the two specialist groups will also respond differently to future extreme weather events because of differences in their traits (Mouillot et al., 2013). For example, droughts caused by prolonged summer periods of high atmospheric pressure with low sea-levels and little to no precipitation may affect halophytes more owing to their adaptations to wetter areas. Instead, storm surges may affect inland grassland specialists more owing to their inability to withstand submersion, particularly by salty water. This means that even though specialists respond similarly to spatial patterns induced by habitat loss (Figure 5), their fate in Baltic coastal meadows may diverge significantly because of their differences in isolation and traits.

4.3 | Habitat mapping

We have found that there are 8,900 ha of managed coastal meadows left along the Baltic coast of Sweden. Their distribution is uneven, with an almost total lack in the north due to little or no management. The central and south parts of the country are instead characterised by patchiness, while the large islands of Gotland and Öland are partially encircled. We did not validate the map using any direct statistical methods; however, the strength of the relationships between the habitat variables obtained from it and the species richness values demonstrate that the habitat delineations are ecologically relevant (Figure 5).

Our estimate of Baltic coastal meadow area is comparable with the 2018 assessment report to the European Council Habitats Directive, in which 12,900 ha of Baltic coastal meadow are attributed to Sweden (European Environment Information and Observation Network, n.d.). By imposing a requirement on management such as grazing or mowing in our analysis, we excluded unmanaged meadows in northern Sweden, which have a sward that is kept open by ice scouring. Instead, mapping for the assessment report is based on aerial image interpretation and field surveys that include these unmanaged habitats.

Comparison of our map can also be made with the 3,000 km^2 total extent of valuable grasslands in Sweden (Swedish Board of Agriculture, 2023), meaning that coastal meadows constitute only a small fraction of the grassland habitats in the country. This underpins our argument that species that occur more strictly in coastal meadows are more sensitive to habitat loss than those also occurring inland.

4.4 | Plant indicators

We found distinct differences in plant indicators along the sea-to-land gradient that we sampled (Figure 4). These results relate to the distribution of specialist flora in coastal meadows along their edaphic gradients. Not surprising, halophytes and other species favoured by typical coastal conditions are more common closer to the sea, whereas inland grassland specialists are more common farther away. By showing the realised niches for the two examined specialist groups, these results further support our conclusions on how sensitivity to habitat loss and isolation is related to species traits. Inland grassland specialists are not restricted to coastal habitats and may thus be in a less precarious situation than halophytes regarding habitat loss, isolation and their synergies with environmental change.

Besides being in general more light-demanding and tolerant of higher soil moisture, salinity and soil disturbance, halophytes produce less nectar, probably because they often rely on vegetative reproduction (Jefferies & Rudmik, 1991). Because all typical coastal meadow species are dependent on management to keep the habitat from being encroached by high reeds and shrubs, there were no significant differences between the different zones regarding the grazing/mowing value. The nitrogen and phosphorous values indicate that the plants thrive in intermediate nutrient conditions regardless of vegetation zone (Tyler et al., 2021).

4.5 | Habitat management

In conclusion, to prevent loss of typical Baltic coastal meadow species, it is necessary to prevent further habitat loss, restore habitat and adapt the landscape management to enhanced connectivity. Furthermore, there is a need to investigate how much coastal meadow has been lost in the past to set up accurate and adequate restoration targets. Restoration initiatives may need to include land farther from the sea and uphill from present-day coastal meadows to combat the effects of future sea-level rise. Also, plans should proceed for at least 15 years in previously abandoned meadows, because shorter efforts have been shown to not be enough for the recovery of typical plant communities (Kose et al., 2021). As plant richness in coastal meadows is clearly affected by the amount of habitat in their surroundings, there is a need to adopt a landscape approach when devising management and restoration plans.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

The map of managed Baltic coastal meadows in Sweden produced in this study is available at https://doi.org/10.17045/sthlmuni.25196084.v1. A plant species list with information on distribution and occurrences at plot and site levels is available as Appendix S2.

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SUPPORTING INFORMATION

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

Appendix S1. The effect of buffer size on the relationship between "habitat amount" and species richness.

Appendix S2. Species list with number of presences at each vegetation zone and site as well as categorization into specialist groups.

Appendix S3. Correlation matrix reporting Pearson's correlation coefficient between all variables tested in this study.

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