

RESEARCH ARTICLE

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Plant diversity and community composition in temperate northeast Atlantic salt marshes are linked to nutrient concentrations

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Abstract

Question: Studies in the northwest Atlantic have shown that nutrient enrichment can severely impact salt marshes, undermining their broad range of high-value ecosystem services. However, biogeographical differences in plant communities may preclude extrapolation of these findings to other regions. The few investigations of such impacts elsewhere, including in Europe, have been strongly localised, restricting generalisations, and have not addressed community-level properties.

Location: South and east coasts of Ireland (northeast Atlantic).

Methods: We conducted a field survey of vascular plants and soil properties in fifteen salt marshes representing broad environmental gradients but comparable biogeographical settings, to test if salt marsh plant (a) diversity and (b) community composition are related to soil nutrients.

Results: Species richness and Shannon diversity were both negatively related to soil NO_x^- , and Shannon diversity had a hump-shaped relationship to labile P. Multivariate community composition was highly significantly related to NO_x^- , to a lesser degree to P, and marginally significantly to NH_4^+ . This was most clearly evident in the positive association of the ground cover of an evergreen dwarf shrub, *Atriplex portulacoides*, and a weaker negative association of a forb, *Plantago maritima*, with NO_x^- , indicating competition between these key and functionally contrasting mid-salt-marsh species. The relationship between community composition and P was most evident through the positive association of P with the invasive cordgrass, *Spartina anglica*.

Conclusions: Physiognomic and functional differences between the herb-rich *Pl. maritima* community and monospecific *A. portulacoides* stands likely have implications for ecosystem services, as would a continued expansion of *S. anglica*. Further studies to ascertain causality could determine whether such transitions can be driven by nutrient enrichment.

KEYWORDS

coastal wetland, community structure, ecological assessment, nitrogen, nutrient enrichment, phosphorus, Shannon diversity, species richness, Water Framework Directive

1 | INTRODUCTION

Salt marshes provide a broad range of high-value ecosystem services (de Groot et al., 2012), including dissipation of wave energy, sediment trapping, carbon storage, nutrient cycling and trophic subsidies to aquatic food webs (Weis, Segarra, & Bernal, 2016). Eutrophication is one of the most pervasive global pressures on both aquatic and terrestrial ecosystems (Smith & Schindler, 2009; Peñuelas et al., 2013) and has also been shown to impact salt marshes (Weis et al., 2016). In a long-term experiment in the Plum Island Estuary, Massachusetts, USA, eutrophication of tidal waters decreased root biomass and accelerated decomposition of organic matter, destabilising soil and leading to salt marsh loss along creeks (Deegan et al., 2012). Such an impact clearly leads to a localised loss of the ecosystem functions with which salt marshes are credited. At a less conspicuous level, but a broader scale, nutrient enrichment can alter species composition and reduce diversity in plant communities (Hautier, Niklaus, & Hector, 2009; Cleland & Harpole, 2010; Ceulemans et al., 2014), impairing important ecosystem functions such as resilience to environmental fluctuations (Hector & Bagchi, 2007; Isbell et al., 2013; Hautier et al., 2014; Prager et al., 2017). Experiments and observations in eastern-USA salt marshes have linked nitrogen enrichment with favouring species that are stress-tolerant but poor competitors under lower nutrient concentrations, such as the tall form of *Spartina alterniflora* (Gallagher, 1975; Teal, 1986; Levine, Brewer, & Bertness, 1998; Emery, Ewanchuk, & Bertness, 2001; Fox, Valiela, & Kinney, 2012; but see Johnson, Warren, Deegan, & Mozdzer, 2016). There is also limited evidence of a negative relationship between species diversity and N (Wigand, McKinney, Charpentier, Chintala, & Thursby, 2003), but a positive one with P availability (Theodose & Roths, 1999) in New England, USA. However, salt marshes in the north-western Atlantic are strongly dominated by *Spartina* spp., and contrast floristically and physiognomically with salt marshes in other regions (Adam, 2002). Thus, it is uncertain to what degree these findings can be generalised elsewhere.

The Water Framework Directive (European Parliament & Council, 2000) aims to restore and maintain all water bodies in the European Union to at least *good* ecological condition. Various metrics of salt marsh vegetation structure and function have been incorporated into assessments in some member states pursuant to this directive (Devaney & Perrin, 2015). However, the underlying ecological links with anthropogenic pressures, including nutrient enrichment, have not been established. Expansion of *Elymus athericus* in the Netherlands and northern France has been attributed to nitrogen enrichment (Rozema, Leendertse, Bakker, & Wijnen, 2000; Valéry, Radureau, & Lefeuvre, 2017), but this has weak empirical support (Bockelmann & Neuhaus, 1999; Davy, Brown, Mossman, & Grant, 2011). Experimental nutrient enrichment has consistently been shown to benefit *Suaeda maritima* (Jefferies & Perkins, 1977; Kiehl, Esselink, & Bakker, 1997; Sheehy Skeffington, 1983). Evidence for effects on other species is limited, typically restricted to a single salt marsh, and in some cases is apparently contradictory among studies (Appendix S1), which demonstrates

the importance of context. For example, salinity, tidal inundation regime, and the community composition of herbivores and competitors, all of which vary among salt marshes, are key determinants of salt marsh plant performance (Silliman & Zieman, 2001; Pennings, Grant, & Bertness, 2005; Janousek & Folger, 2014; Wong, Van Colen, & Airoldi, 2015; Schoolmaster & Stagg, 2018). Moreover, these factors can moderate plant responses to nutrients (Sheehy Skeffington & Jeffrey, 1988; Bertness, Crain, Holdredge, & Sala, 2008; Alberti et al., 2010). Field experiments are invaluable in establishing causality, but are laborious, and thus typically sacrifice spatial scale. Such localised studies may be inadequate to capture environmental gradients that obscure or alter plant responses to nutrient enrichment. Moreover, whole-community effects of nutrient enrichment, such as species composition and diversity, have not been investigated in Europe.

Using field surveys across fifteen Irish salt marshes, we tested if salt marsh plant (a) diversity and (b) community composition are related to soil nutrients. Nutrient enrichment is the most important pollutant of surface waters in Ireland (Fanning et al., 2017) and salt marshes are widely distributed around Ireland (Curtis & Sheehy-Skeffington, 1998). Thus, these surveys facilitated comparison

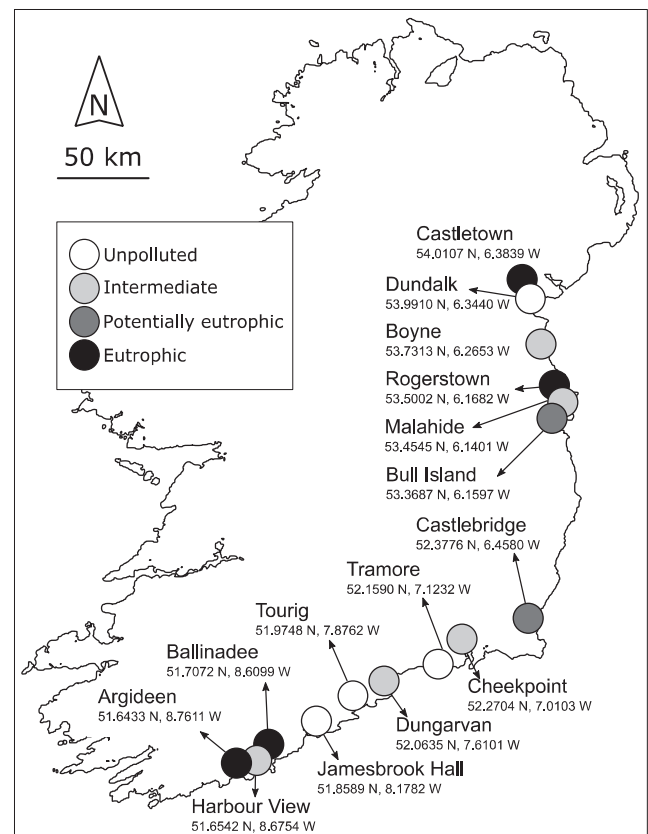


FIGURE 1 Surveyed salt marshes with latitude and longitude coordinates recorded from the centre of the sampling area. Circle shading gradient reflects Trophic Status Assessment Scheme ranking of water bodies by Environmental Protection Agency, Ireland, based on water quality data that were not collected for this particular project, and not used in any analyses (source: gis.epa.ie). See Appendix S2 for locations of sampling quadrats

across a broad gradient of trophic and other environmental conditions, but within comparable biogeographical settings.

2 | METHODS

2.1 | Site selection

Salt marshes were selected for this study with the intention of maximising the gradient of soil nutrient conditions, whilst minimising the potentially confounding effects of other variables. Fifteen sites were selected on the southern and eastern coasts of Ireland that represented a broad range of trophic conditions (Environmental Protection Agency, Ireland, gis.epa.ie) and were ungrazed by livestock (Figure 1). Water bodies in the north and west of Ireland generally have low trophic status compared with the broader range of those in the south and east (Fanning et al., 2017), and their inclusion could conflate biogeographic patterns and nutrient conditions. Furthermore, salt marshes on the northern and western coasts of Ireland are frequently grazed by livestock (McCorry & Ryle, 2009), which influences soil structure and vegetation (Davidson et al., 2017). As the majority of salt marshes in the selected region have muddy soils (Curtis & Sheehy-Skeffington, 1998), we also avoided sites with other soil types, to improve comparability within the dataset.

2.2 | Field survey

Our individual survey units were 2 m × 2 m quadrats. At each salt marsh, between three and five quadrats were placed along each of four transects perpendicular to the shoreline (12–20 quadrats per salt marsh, and 246 in total; Appendix S2). The purpose of these transects was to spread our sampling effort, rather than to create a spatial sampling hierarchy within salt marshes, and so distances among quadrats were not necessarily greater between transects than within transects. The quadrats were placed in different communities along those transects, akin to a stratified random sampling design where the strata are the plant communities along the transects, in order to sample the maximum range of communities, but without any regard to species diversity within the individual quadrats. Whilst the diversity of vegetation communities along the entire transect and at a site level was likely maximised by our selection procedure, the quadrat-level diversity metrics, which we use in the analysis, were unlikely to be affected in any systematic way.

Percentage ground cover of each plant taxon was estimated within each quadrat between July and August 2016, to coincide with peak standing biomass for most salt marsh species, generally to the nearest 0.1%, 1% and 5% at cover ranges 0%–1%, 1%–10% and 10%–100%, respectively, or at higher resolution when necessary. Species nomenclature throughout followed Hassler (2018). We assume our *Spartina* records all refer to the vigorous allotetraploid *S. anglica*, as

this is by far the most widespread taxon within this genus in Ireland, there being no recent records of *S. × townsendii* and with *Spartina maritima* having an extremely restricted distribution. Within a month of plant survey (in August 2016), at each quadrat, at low tide, we combined eight soil cores of 22 mm diameter to a depth of 10 cm for soil analyses. Samples were stored in polythene bags in a cold and dark container, and frozen at 20°C within three days of collection for up to seven months. Ground elevation was measured at the centre of each quadrat as an index of tidal inundation regime using a differential GNSS (Trimble R8 receiver with TSC3 logger) with a vertical inaccuracy of ≤2 cm. Elevation was expressed as a proportion of the highest astronomical tidal amplitude for each salt marsh (Environmental Protection Agency; unpublished data).

2.3 | Laboratory analyses

Soil samples were thawed at room temperature, sieved through a 2-mm sieve, homogenised and subsampled for analyses. Sand content was determined to the nearest 0.1 g using a VWR LP-2102i balance as a proportion retained on 63-μm mesh by wet-sieving after ignition at 550°C to incinerate organic matter. Samples with extracting solutions specified below were shaken for 30 min at 160 oscillations per min, and allowed to settle for 30 min. We used Milli-Q water throughout (Merck). Salinity and pH were measured from the supernatant of a 1:4 extract of field-moist soil in Milli-Q water, using a WTW Cond 197i electrical conductivity meter (Xylem) and a VWR pH 1100L probe, respectively.

From the thawed samples, we determined key plant-reactive forms of nitrogen and phosphorus, that is total oxidised nitrogen (NO_x^- , i.e. the sum of NO_2^- and NO_3^-), exchangeable ammonium (NH_4^+) and NaHCO_3 -extractable P. NO_x^- (after cadmium reduction of NO_3^- to NO_2^-) and NH_4^+ were determined spectrophotometrically using a Lachat Quikchem 8500 flow injection analyser (Hach), as azo dye and indophenol, respectively, formed from a 1:10 extract of field-moist soil in 2 M KCl, passed through Whatman 42 filters (GE Healthcare Life Sciences) (Maynard, Kalra, & Crumbaugh, 2008). Thirty samples with the highest NO_x^- concentrations were also analysed for NO_2^- using the above method without the cadmium reduction step, but all were below the detection limit, indicating that NO_x^- was mostly in the form of NO_3^- . P was determined using a Hach DR5000 spectrophotometer as phospho-molybdic blue complex formed from a 1:20 extract of field-moist soil in 0.5 M NaHCO_3 , buffered to pH 8.5 and passed through Whatman 40 filters (Schoenau & O'Halloran, 2008). Salinity data were expressed per weight of soil moisture, whereas all other data were expressed per weight of field-moist soil passed through 2-mm mesh.

2.4 | Statistical analyses

Statistical analyses were conducted in R v3.5.0 (R Core Team, 2018) using the default arguments of each function, unless specified.

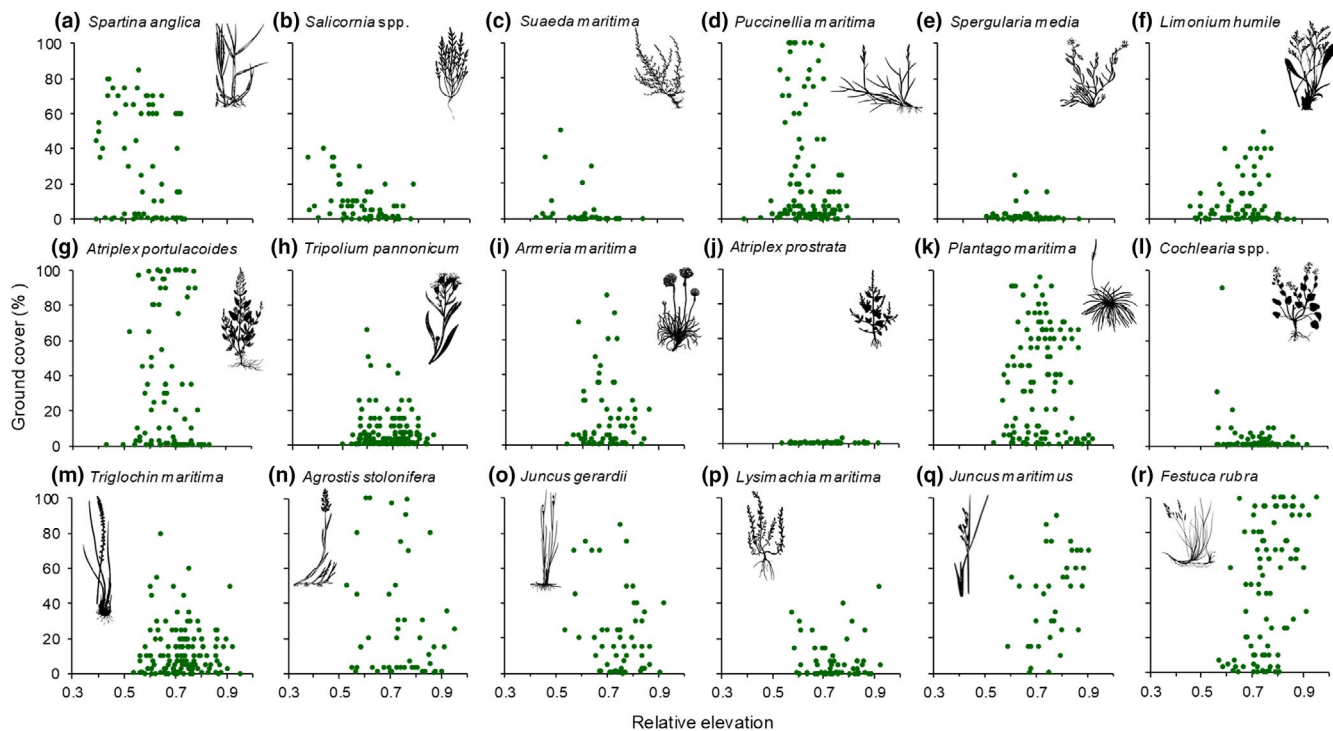


FIGURE 2 Ground cover (non-zero records only) of plant taxa used in multivariate community analyses across ground elevation gradient, ordered by increasing mean elevation. Plant silhouettes are not to scale [Colour figure can be viewed at wileyonlinelibrary.com]

Individual quadrats were our study unit. Salt marsh identity was included as a random variable in univariate models and a conditional term in community analyses to account for any spatial autocorrelation. Soil nutrient and sand data were $\log_{10}$ -transformed for all analyses to improve normality and homoscedasticity of model residuals. Ground cover of each species was transformed using a Hellinger transformation for multivariate analyses (Borcard, Gillet, & Legendre, 2011) and using square root for correlation coefficients.

2.4.1 | Diversity

We investigated the relationships of plant species richness and the Shannon diversity index ($\log_e$ base) with soil P, NO_3^- and NH_4^+ using generalised additive models (GAM) in the *mgcv* package (Wood, 2017). Soil salinity, pH, moisture and sand content, and ground elevation were included as covariates in the model because they were expected to influence plant community. All terms were included in the model as smoothers, with automated selection of the degree of smoothing. For visualisation, significant response variables were modelled on regression coefficients using the function *predict.gam* in package *mgcv* with all other fixed model terms set to their mean values and the salt marsh identity random term excluded. Model diagnostics were conducted visually using functions *plot.gam* and *gam.check* in package *mgcv* (Appendix S3). To support inference, relationships of richness and Shannon diversity with ground cover of each dominant taxon ($\geq 75\%$ ground cover in >1 quadrat) are presented in Appendices S4 and S5, respectively.

2.4.2 | Community composition

All multivariate analyses were conducted using the *vegan* package (Oksanen et al., 2017). The association of plant community composition with the same set of explanatory variables as for diversity was analysed using multivariate redundancy analysis (RDA). Elevation was included as first- and second-degree polynomial terms (computed using function *poly* to minimise correlation between them) because many species appeared to have a hump-shaped relationship with elevation (Figure 2). Nine plant species were omitted from the RDA analysis because there were insufficient data to accurately assess their associations with response variables. The omitted species occurred in ≤ 8 out of 246 quadrats across ≤ 5 out of 15 salt marshes, whereas the 18 species used in the analyses were recorded in ≥ 37 quadrats and ≥ 9 salt marshes. Significance of explanatory variables was tested by 999 Monte Carlo permutation using function *anova.cca*. Model diagnostics were conducted visually using function *ordiresids* (Appendix S6). RDA plots project multiple dimensions onto two dimensions, and thus, the magnitude and sign of associations with individual response variables are not always clear. To quantify variance in individual species associated with each variable and the sign of their correlations, we used partial RDA models (pRDA) with each variable individually as a constraint and all other variables, including differences among salt marshes, as conditions. This procedure produces a conservative estimate, because it excludes any variance overlaps between constraints and conditions.



3 | RESULTS

3.1 | Diversity

Species richness ranged from 1 to 12 species and Shannon diversity ranged from 0 to 1.99 among quadrats. Both generally increased with increasing elevation, albeit at a decelerating rate, and the highest richness was found at intermediate elevations (both $p < 0.001$; Table 1, Figures 3a, 4a, respectively). Both were negatively related to

soil NO_3^- ($p = 0.09$ and $p = 0.021$; Table 1, Figures 3b, 4b). They were not significantly related to NH_4^+ (both $p > 0.05$; Table 1). Shannon diversity had a hump-shaped relationship with P, whereas species richness was not related to P ($p = 0.005$ and $p > 0.05$; Table 1, Figure 4c). Species richness and Shannon diversity were positively related to salinity (both $p < 0.001$; Table 1, Figures 3c and 4d) and sand content ($p = 0.003$ and $p = 0.007$; Table 1, Figures 3d, 4e). Both also decreased over higher, but not lower, pH range (both $p < 0.001$; Table 1, Figures 3e, 4f).

TABLE 1 Generalised additive model of the relationship of species richness and Shannon diversity with ground elevation and soil properties

	Species richness			Shannon diversity		
	Estimated/reference df	F ratio	p	Estimated/reference df	F ratio	p
Elevation	4.2/5.2	11.70	<.001	1.9/2.4	6.68	<.001
NO_3^-	1.8/2.3	4.65	.009	1.5/1.9	3.71	.021
NH_4^+	1.9/2.4	0.66	.560	3.2/4	0.99	.415
Labile P	2.7/3.4	2.26	.078	2.8/3.6	4.10	.005
Salinity	1.1/1.3	15.14	<.001	1/1	20.81	<.001
Sand	1/1	9.06	.003	1/1	7.37	.007
pH	2.6/3.3	7.37	<.001	2.8/3.5	11.03	<.001

Note: Deviance explained: 58.9% and 56.7% for the two models, respectively. Estimated df = 1 denotes linear relationship.

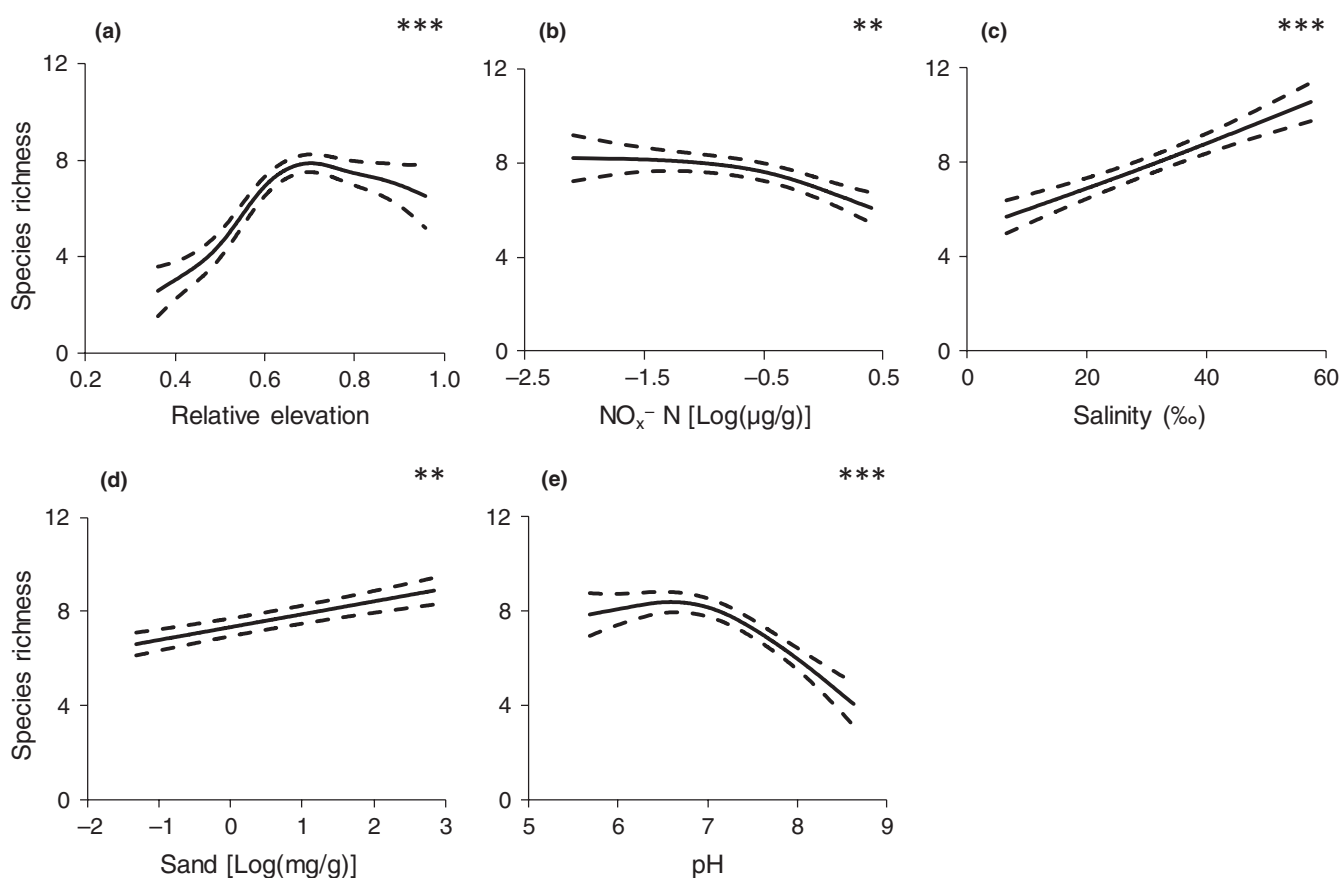


FIGURE 3 Significant relationships ($\pm \text{SE}$; $p \leq 0.05$) of species richness to (a) ground elevation, (b) soil nutrients and (c–e) other soil properties in a generalised additive model. Asterisks denote significance: **, $p \leq 0.01$; ***, $p \leq 0.001$

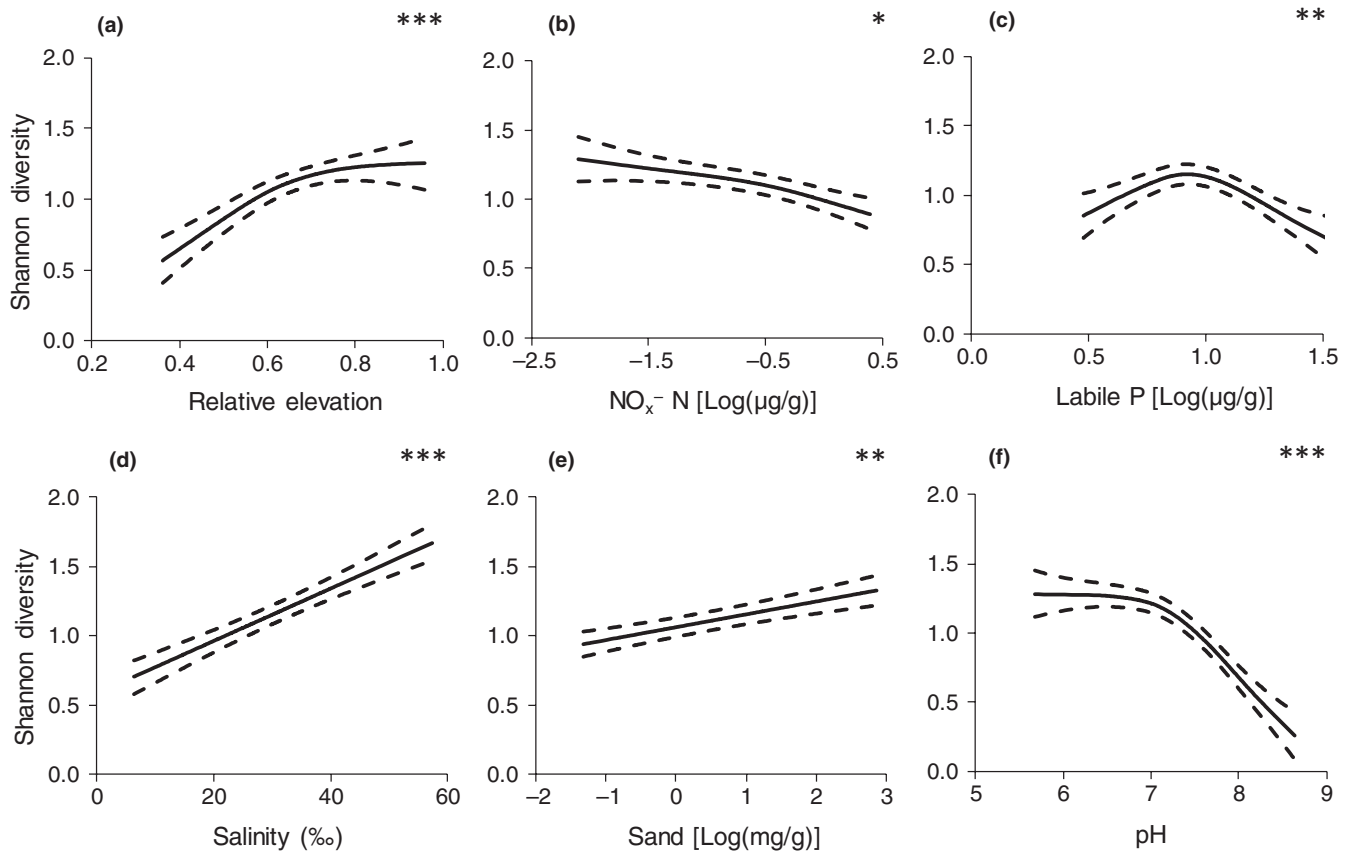


FIGURE 4 Significant relationships ($\pm$ SE; $p \leq 0.05$) of Shannon diversity to (a) ground elevation, (b, c) soil nutrients and (d, f) other soil properties in a generalised additive model. Asterisks denote significance: *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$

TABLE 2 Permutational test of a redundancy analysis model of the relationships of plant community composition with soil characteristics and elevation

Explanatory variable	Pseudo-F	P
Elevation	7.77	<.001
Elevation ²	8.81	<.001
NO _x ⁻	14.45	<.001
NH ₄ ⁺	2.27	.029
P	6.68	<.001
Salinity	20.01	<.001
Sand	4.90	<.001
pH	6.61	<.001

Note: Constrained variance: 31.0%, residual degrees of freedom: 223.

3.2 | Community composition

Multivariate community composition within quadrats was significantly associated with elevation and its quadratic term (both $p < 0.001$; Table 2, Figure 5a). It was also significantly related to soil NO_x⁻, which was among the most significant explanatory variables in the model, and to P (both $p < 0.001$; Table 2, Figure 5a), and marginally significantly related to NH₄⁺ ($p = 0.029$; Table 2). Community composition was also related to salinity, which was the

most significant explanatory variable, and to sand content and pH (all $p < 0.001$; Table 2, Figure 5).

The full set of explanatory variables explained between 4.8% and 45.8% of the variance in ground cover of individual species (Table 3). Partial RDA showed that, after accounting for all other explanatory variables and differences among salt marshes, ground cover of *Atriplex portulacoides* was most positively associated with soil NO_x⁻ (14.1% of marginal variance; Table 3). We also found some evidence for a positive association of *Suaeda maritima* and *Cochlearia* spp. with NO_x⁻ (1.5% and 1% of marginal variance, respectively; Table 3). Ground cover of *Plantago maritima* had the strongest negative association with NO_x⁻ (5.1% marginal variance), followed by *Armeria maritima* (3.8%), *Spartina anglica* (3.4%), *Juncus gerardii* (3.0%) and *Lysimachia maritima* (2.7%), and *Tripolium pannonicum* (1.0%; Table 3). *Salicornia* spp. was negatively associated with NH₄⁺ (2.3%) and there was some evidence of a positive association between *L. maritima* and NH₄⁺ (1.0%; Table 3). Ground cover of *S. anglica* had the strongest positive association with P (5.1%), followed by *Triglochin maritima* (2.1%), and more limited evidence for *J. gerardii* (1.1%). *Agrostis stolonifera* had the strongest negative association with P (3.5%), with more limited evidence for *Salicornia* spp., *Puccinellia maritima* and *Su. maritima* (1.7%, 1.7% and 1.1%, respectively; Table 3).

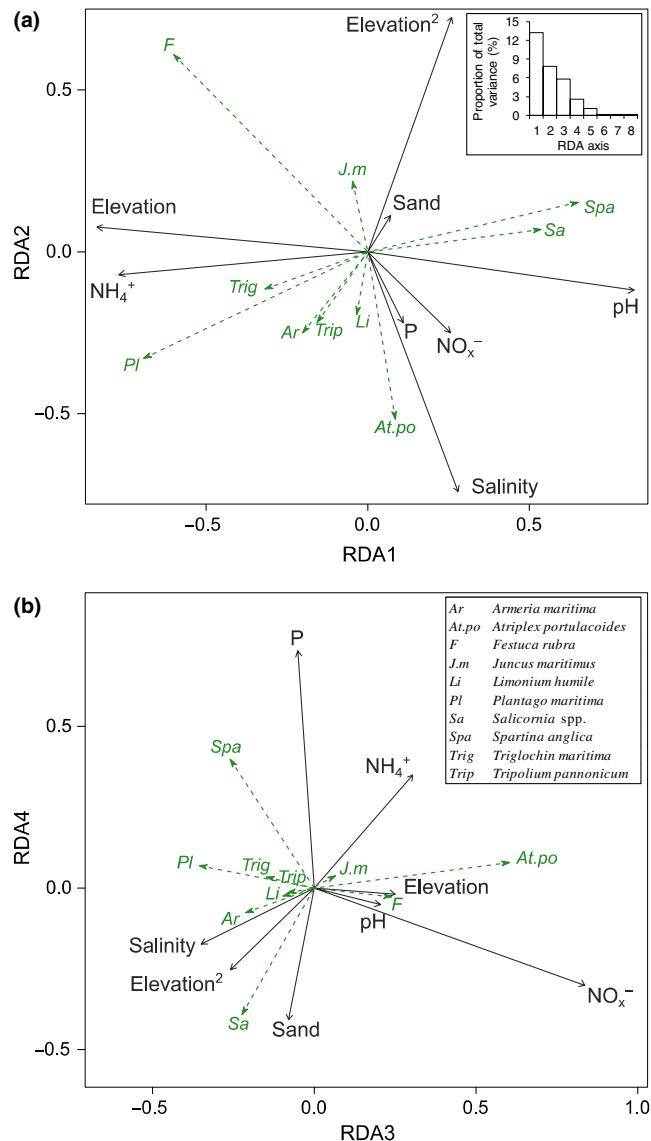


FIGURE 5 Associations between plant taxa and explanatory variables in a redundancy analysis model (RDA) approximated by similarity between vector angles along (a) RDA axes 1 and 2, best representing salinity, elevation and pH, and (b) RDA axes 3 and 4, best representing NO₃⁻ and P. For clarity, only taxa with ≥5% variance associated with any variable are shown. Insert (a) shows proportions of data variance represented by RDA axes and insert (b) shows full taxon names in both plots [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

We found inverse relationships of both species richness and Shannon diversity with soil NO₃⁻ and a hump-shaped relationship of Shannon diversity with labile P. Decreased diversity can diminish functional complementarity, with negative impacts on important ecosystem functions such as productivity and resilience to perturbations (Hector et al., 2010), but also nutrient uptake (Hooper & Vitousek, 1998). The negative relationship of diversity with N is in

line with observational findings from New England, USA (Theodose & Roths, 1999; Wigand et al., 2003). However, the functional implications of such relationships are likely to depend on the functional traits of individual species and underlying causalities, and the latter are yet to be established.

We found that salt marsh plant community composition was significantly related to nutrients, in particular to soil NO₃⁻. This was most clearly evident in the positive association of the ground cover of *Atriplex portulacoides*, and the weaker negative association of *Plantago maritima*, with soil NO₃⁻. Moreover, *A. portulacoides* was the only species strongly positively associated with NO₃⁻, whilst multiple species, e.g. *Armeria maritima*, *Spartina anglica*, *Juncus gerardii* and *Lysimachia maritima*, were negatively associated with NO₃⁻. These species-specific relationships may be at least in part driving the mechanism of the negative association of richness and diversity with the same nutrient. Dominance of *A. portulacoides* was associated with a sharp decline in species richness and Shannon diversity, in contrast to *Pl. maritima* (Appendices S4c, g and S5c, g). *Atriplex portulacoides* was frequently found in near-monospecific stands, whereas quadrats dominated by *Pl. maritima* were among the most species-rich in our survey. Furthermore, although the mean elevation range of *A. portulacoides* was lower than that of *Pl. maritima*, their elevation ranges strongly overlapped (Figure 2d, l) such that they frequently co-occurred in the field. These similarities are conducive to competition.

Stands of *A. portulacoides* have half the root biomass and an order of magnitude higher shoot-to-root ratio than *Pl. maritima* (Penk, Perrin, & Waldren, 2019a), which is conducive to poorer competitiveness for nutrients. However, where nutrients are not limited, competition for light is considered the main mechanism structuring plant species composition (Hautier et al., 2009). *Atriplex portulacoides* is an evergreen dwarf shrub forming a thicket of obliquely arranged branches, whereas *Pl. maritima* is a short rosette-forming forb. The former physiognomy appears more advantageous for competition for light. Thus, *A. portulacoides* may be benefiting from increased NO₃⁻ concentrations to outcompete *Pl. maritima*, with a knock-on effect on species diversity, but this hypothesis requires further experimental testing. Where present, *A. portulacoides* could lend itself well as an indicator of the underlying environmental gradient. It is easy to identify and map, even from aerial photographs, owing to its distinct physiognomy, and thus could be easily incorporated into assessment programmes, such as for the Water Framework Directive. Our findings support observational evidence of a positive, albeit weak association between ground cover of *A. portulacoides* and soil NO₃⁻ previously shown in the eastern UK (Davy et al., 2011), and experimental evidence of strongly enhanced shoot frequency, biomass and sexual investment of *A. portulacoides* in the same region following addition of inorganic nitrogen (Jefferies & Perkins, 1977). The latter study also reported a parallel suppression of a short rosette-forming forb, *Armeria maritima*, frequently found in association with *Pl. maritima* (Devaney & Perrin, 2015), whose ground cover in our study was also negatively, although weakly, related to soil NO₃⁻. *Atriplex portulacoides* used to be scarce at Bull Island salt marsh in Ireland in the

TABLE 3 Marginal variance (%) in ground cover of individual taxa associated with individual explanatory variables in partial redundancy analysis models, expressed as a proportion of total after accounting for all other explanatory variables and differences among salt marshes

Taxa	Elevation	Elevation ²	NO _x ⁻	NH ₄ ⁺	P	Salinity	Sand	pH
<i>Agrostis stolonifera</i> (12.1)					3.5 ⁻	3.7 ⁻	1.6 ⁻	
<i>Armeria maritima</i> (33.6)	2.2 ⁺		3.8 ⁻			18.7 ⁺		1.3 ⁻
<i>Atriplex portulacoides</i> (37.9)		5.7 ⁻	14.1 ⁺				1.6 ⁻	2.6 ⁺
<i>Atriplex prostrata</i> (9.5)						1.7 ⁻		
<i>Cochlearia</i> spp. (4.8)			1.0 ⁺					
<i>Festuca rubra</i> (45.5)	2.9 ⁺	3.7 ⁺				7.6 ⁻		
<i>Juncus gerardii</i> (15.9)			3.0 ⁻		1.1 ⁺	1.1 ⁻		2.1 ⁻
<i>Juncus maritimus</i> (11.6)						7.5 ⁻		
<i>Limonium humile</i> (15.7)		3.3 ⁻				5.5 ⁺		2.1 ⁻
<i>Lysimachia maritima</i> (18.9)			2.7 ⁻	1.0				
<i>Plantago maritima</i> (45.8)	1.9 ⁺		5.1 ⁻			10.0 ⁺	1.6 ⁺	4.8 ⁻
<i>Puccinellia maritima</i> (10.3)		3.5 ⁻			1.7 ⁻			
<i>Salicornia</i> spp. (38.2)	2.8 ⁻	1.7 ⁺		2.3	1.7 ⁻		3.0 ⁺	
<i>Spartina anglica</i> (34.9)	3.9 ⁻		3.4 ⁻		5.1 ⁺	1.9 ⁻	1.1 ⁻	1.2 ⁺
<i>Spergularia media</i> (8.7)		2.9 ⁻				1.5 ⁺	2.7 ⁺	1.0 ⁻
<i>Suaeda maritima</i> (15)			1.5 ⁺		1.1 ⁻	2.1 ⁺	1.3 ⁺	
<i>Triglochin maritima</i> (26.3)	1.6 ⁺				2.1 ⁺	5.6 ⁺		4.5 ⁻
<i>Triplolium pannonicum</i> (24.9)	1.7 ⁺	1.5 ⁻	1.0 ⁻			12.5 ⁺		

Note: Superscripts '+' and '-' denote positive and negative univariate correlations, respectively. For clarity, only values $\geq 1\%$ are shown. Numbers in parentheses denote variance in taxa associated with all explanatory variables combined after accounting for differences among salt marshes.

1950s (O'Reilly & Pantin, 1956), but has expanded to about one third of the salt marsh area at the expense of the *Pl. maritima*-dominated community, concurrent with nutrient enrichment from the growing Dublin conurbation (Wilson, 2004). The *A. portulacoides* community is typically found on the sea-ward side of the *Pl. maritima* community. Thus, this expansion appears to represent reverse succession, and potentially supports the nutrient-driven reversal of competitive outcomes demonstrated in eastern-USA salt marshes (Levine et al., 1998; Emery et al., 1998).

The environmental covariates considered in this study offer no evidence of an alternative explanation, for example in the form of clearly contrasting relationships of these two species with another environmental gradient. However, it is possible that some gradient unaccounted for in this study could promote higher abundance of *A. portulacoides*, to either the direct or competition-driven detriment of *Pl. maritima*. For example, sulphide is a common phytotoxin found in marine sediments (Bradley & Morris, 1990; Lamers et al., 2013), and redox potential can correlate strongly with the cover of some salt marsh plants (Davy et al., 2011), but neither of them was measured in this study. Such an alternative explanation, that higher soil N is a result and not a driver of the observed differences in the plant communities, would make an implicit assumption that the inherent traits of *A. portulacoides*-dominated communities result in poorer extraction efficiency of soil NO_x⁻ compared with species-rich *Pl. maritima*-dominated communities, for example through lower root

biomass of *A. portulacoides*, or lower functional complementarity of its associated community.

We also found a significant relationship of community composition with P, but the weak evidence for underlying relationships of individual species with soil P hampers biological interpretation. However, the positive relationship of the highly invasive *Spartina anglica* and the apparently negative relationships of the native *Salicornia* spp., *Pu. maritima* and *Su. maritima* with P leave open the possibility of a P-driven competitive advantage for *S. anglica* in lower salt marsh communities, given that all four species overlapped in their vertical distributions and were frequently found in the same quadrats. However, alternative causalities cannot be ruled out based on the results of this study, as noted in the preceding paragraph.

NO_x⁻ was generally a less abundant form of inorganic N than NH₄⁺ across our salt marshes (Penk, Wilkes, Perrin, & Waldren, 2019b), and yet the former, but not the latter, was related to plant community composition and diversity. Plants can generally utilise both NO_x⁻ and NH₄⁺, but the associated trade-offs in assimilation pathways can result in different uptake rates (Boudsocq et al., 2012). Moreover, even in an abundance of NH₄⁺, some plants need at least some NO₃⁻ for optimal growth (Falkengren-Grerup, 1995), particularly where nitrification is inhibited (Falkengren-Grerup & Lakkenborg-Kristensen, 1994).

Elevation and salinity were the two most significant non-nutrient correlates of plant community composition and diversity in

this study. Elevation determines the degree of tidal inundation, and thus waterlogging and the prevalence of marine vs terrestrial influences. This shapes a vertical gradient of plant succession (Devaney & Perrin, 2015). Such a gradient was also evident in our study in the elevation-specific distributions of multiple plant species, with an overall trend of generally increasing plant diversity with elevation. Salinity tends to decrease with elevation (Penk et al., 2019b), but can also vary among salt marshes, depending on the degree of freshwater influences. We found that when elevation was accounted for, plant diversity was positively related to salinity. We are uncertain what has driven this relationship. Brackish marshes tend to be strongly dominated by a few species, but we did not include such communities in our survey. After accounting for elevation, percent bare ground correlated positively with soil salinity (M. Penk, unpublished data), so perhaps salt stress is conducive to niche openings.

Our recorded NO_x^- concentrations were within the lower to mid-range of typical values reported from a review of 120 salt marshes globally (Lawrence, 2018), and thus do not seem exceptionally high, and yet we have found strong relationships of community composition with this nutrient. Ireland is currently on a trajectory of a growing population with targeted doubling of agricultural production. Global population is also predicted to grow, likely in concert with the food production sector. Therefore, nutrient enrichment pressures are likely to become aggravated. At the same time, sea-level rise may outpace salt marsh accretion (Horton et al., 2018), challenging the coastal resilience provided by salt marshes. In North American salt marshes, nutrient enrichment has been shown to undermine soil cohesion, which underpins salt marsh stability (Deegan et al., 2012). The link between plant diversity – a widely used proxy for ecosystem functionality – and N found in this study is likely to be spatially heterogeneous. For example, a stronger relationship could be anticipated at mid-marsh elevations, because this is where communities dominated by *A. portulacoides* and *Pl. maritima* can typically be found. Furthermore, because of physiognomic and functional differences between the herb-rich *Pl. maritima* community and monospecific *A. portulacoides* shrub stands, a shift between these communities could have implications for ecosystem services, such as wave attenuation and sediment trapping, as would expansion of *S. anglica*. Further studies to ascertain causality could determine whether our observed patterns are the result of nutrient enrichment.

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AUTHOR CONTRIBUTIONS

MP, PP, SW and RK conceived the ideas, MP, PP and FON collected data, MP analysed data and lead writing, and all authors contributed substantially to the manuscript.

DATA AVAILABILITY STATEMENT

All data used in this manuscript will be deposited in the EPA Secure Archive For Environmental Research Data (SAFER; <http://erc.epa.ie/safer/>).

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SUPPORTING INFORMATION

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

Appendix S1. Performance metrics of salt marsh plants in Europe in relation to nutrients

Appendix S2. Sampling quadrat locations

Appendix S3. Diagnostic plots for generalised additive models

Appendix S4. Species richness in relation to ground cover of dominant plant species

Appendix S5. Shannon diversity index in relation to ground cover of dominant plant species

Appendix S6. Diagnostic plots for Redundancy Analysis model

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