

Impacts of nutrients on saltmarsh: A rapid evidence assessment

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Foreword

Many of our estuarine and coastal marine protected areas are in unfavourable condition due to high levels of agricultural and wastewater discharges containing high nutrient loads. The impacts of elevated nutrients on marine ecosystems are variable depending on site specific conditions and, as such, we may see elevated nutrient impacts on more nutrient sensitive features before a eutrophic response is recognised in the wider environment.

Natural England's current approach for assessing water quality is based on data collected for waterbody scale assessments. This approach deviates from the feature-based assessments used for other attributes and as such, there is a risk that nutrient enrichment is not being assessed at an appropriate scale or sensitivity for protected features. There is a need to review the evidence and consider revising Natural England's conservation advice on water quality attributes so that these align with condition assessments and nutrient enrichment evidenced at the feature level.

To manage MPAs, and give appropriate advice, it is important for Natural England to understand the nutrient and water quality conditions that will lead to the favourable condition of protected features. This will enable conservation targets to be ecologically relevant at the appropriate scale. The results of this review will be used to improve our understanding of the impacts of elevated nutrients on saltmarsh species and update our conservation targets to reflect new understanding on the complex relationships between nutrient concentrations and ecosystem responses that have been evidenced in this review.

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Executive summary

Context

Natural England (NE) wish to understand the impacts of nutrients on saltmarsh vegetation so as to complement existing biological indicators of water quality, primarily to understand how water quality relates to the condition of saltmarsh habitat. This will allow NE to assess features at an appropriate scale.

The response of saltmarsh plant species and vegetation communities to increased nutrient availability, not only in relation to water quality, is expected to be context dependent. Nutrients can have complex impacts on systems depending on their source, the species present, and through multiple trophic levels. Response to nutrient enrichment may also depend upon biotic and other abiotic factors. Feedback and interactions among these different ecosystem properties can further complicate vegetation response to nutrients.

Here, we report the results of a rapid evidence assessment (REA) conducted on behalf of NE by UKCEH. The aim was to explore and interpret the complexity of saltmarsh response to nutrients through synthesizing relevant literature. This will aid NE in its desire to use feature-based assessments, while exposing potentially important knowledge gaps.

Objectives

The REA addresses 3 objectives in the context of species and vegetation communities found, or likely to be found, in UK saltmarsh systems:

Objective 1: Collate the evidence on the impact of nitrogen (N) and phosphorus (P) compounds on the condition of typical saltmarsh species present in the UK marine environment

Objective 2: Collate the evidence for environmental (abiotic) factors that can affect the impact of elevated nutrients on saltmarsh species present in UK waters

Objective 3: Collate the evidence for ecological (biotic) factors that can affect the impact of elevated nutrients on saltmarsh species present in UK waters

Key findings

Objective 1

There was robust evidence (i.e. multiple peer-reviewed sources) that nutrients, particularly N, altered the species composition of different marsh zones in the European context, with both 'winner' and 'loser' species. However, the identity of these species could depend upon abiotic and biotic context. In general, there was robust evidence that *Atriplex portulacoides* and *Elymus athericus* showed positive (or at least neutral) responses to increased nutrient availability. Species characteristic of upper to mid-marsh tend to

decrease with additional N, while combined high N and P addition sped up succession through increased biomass of late successional species.

There was limited evidence, from a non-UK context, that “saltmarsh squeeze” may be induced by additional nutrients: the pioneer zone can be smothered by *Ulva* species, and the upper marsh can be invaded by *Phragmites australis*. However, such responses depend upon context and may not be directly related to nutrient addition.

We did not assign critical levels of nutrient concentrations in the marine environment, or nutrient fluxes onto the marsh from terrestrial/atmospheric sources, at which compositional change occurred. This was due to lack of data, with studies not reporting nutrient additions, forms, and/or background availabilities, and/or conflicting results for particular species.

Objective 2

Few studies directly showed clear interactive effects in relation to nutrients and abiotic factors. Sediment type, salinity, deposition/accretion, temperature and pH appeared to co-vary with N and differences in vegetation communities. Relationships between salinity, P and vegetation was shown by multiple studies, including through residence time.

Objective 3

Some evidence showed grazers can change which species are dominant for a given set of environmental conditions, not always including nutrients. Dynamics of competing autotrophs e.g. *Ulva* spp. and *Enteromorpha* spp. at the pioneer zone appear more related to turbidity/bed stress as opposed to interactions with nutrients.

Caveats, knowledge gaps and future research

Some studies did not directly measure nutrients, referencing other work and/or using the vegetation itself to indicate environmental conditions. We did not follow-up such references. Follow-up may reduce uncertainty in the absolute and relative importance of nutrients in driving vegetation change, in relation to other factors e.g. sea level rise.

There is a lack of UK research on how environmental changes (e.g. in drought, temperature) could interact with nutrients and alter saltmarsh feature dynamics. There is a lack of evidence on how saltmarsh condition, life-stage, and surrounding vegetation affect response to nutrients.

There is a clear need for:

- Experimental and survey studies at appropriate scales in UK marshes to understand saltmarsh species and vegetation community response to nutrients (forms and amounts). This includes studies that consider how multiple trophic levels and marsh stability are affected directly and indirectly by increased nutrient availability over short/long timescales.
- Research to quantify nutrient drivers of change in saltmarsh ecosystems through consideration of all input pathways. This includes concentrations in the marine environment, and fluxes from terrestrial habitats and the atmosphere.

- Linked to this, there is a need to develop a metric of nutrient pressure that can account for different nutrient inputs to saltmarsh plants and vegetation communities.

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Introduction

Natural England context

Here, we report on the results of a Rapid Evidence Assessment (REA) regarding the impact of nutrients on saltmarsh vegetation. We briefly introduce the Natural England (NE) context to this research, before outlining *a priori* expectations as to how and why saltmarshes respond to nutrients, and the questions and objectives this context leads to. We then present our methodology, and the results, noting key take-home messages, caveats and knowledge gaps. This evidence synthesis aims to help NE assess water quality but at a scale that is relevant to features and using water quality targets that are based on feature-scale impacts, in relation to a vital habitat at the marine-terrestrial interface: saltmarsh.

Currently, the nutrient status of protected areas in the England, at the terrestrial-marine interface, is monitored through biological indicator responses e.g. expansion of opportunistic macroalgae. However, in some circumstances, such indicators are not reliable. For instance, macroalgae do not establish well in the Humber Estuary despite Environment Agency (EA) data classifying concentrations of inorganic nitrogen in the Humber as “moderate”, or worse, since 2011. In addition, the impacts of elevated nutrients on ecosystems are variable depending on site-specific conditions. This suggests a one-size-fits-all water quality indicator may not reflect when habitat features are threatened. Further, we may observe impacts on protected nutrient-sensitive features, such as saltmarsh plant species and/or communities, prior to an eutrophic response in the wider environment associated with a given water-quality indicator. This eutrophic response might be a rapid expansion of opportunistic macroalgae (a “macroalgal bloom”) or even organism die-off (dead zones) due to rapid oxygen depletion.

Natural England are interested in understanding the impact of nutrients on protected features such as saltmarsh for an additional reason. In general, NE uses a feature-based approach to assess condition of protected areas and defining conservation objectives that contribute to achieving Favourable Conservation Status (FCS). The current approach of using biological indicators of eutrophication does not satisfy this feature-based approach, and thus deviates from the methods used for other attributes. As such, there is a risk that nutrient enrichment is not being assessed at an appropriate scale or sensitivity for protected features, including seagrass meadows, kelp forests and the focus of this report, saltmarsh.

Natural England have therefore identified a need to review the evidence and consider revising NE’s conservation advice on water quality attributes. This should enable alignment with condition assessments and nutrient enrichment evidenced at the feature level. This report aims to satisfy the first component of this need, by providing a rapid evidence assessment of the impacts of nutrients on saltmarsh vegetation.

As we explore in the subsection *A priori* expectations: Saltmarsh response to nutrients, and the [Results](#) section, evidence suggests that saltmarsh habitats are sensitive to nutrient enrichment. It is important for NE to understand the nutrient and water quality conditions that will lead to the favourable condition of these features. Conservation targets can then be set that are ecologically relevant at the appropriate scale. To identify these targets, relationships between nutrient pressures and ecosystem responses need to be investigated.

This report provides the first step along this investigative pathway, by identifying those nutrient – vegetation community / plant species' relationships that have already been published in peer-reviewed and grey literature and interpreting their findings in the context of the UK marine-terrestrial interface. As we go on to show, much of the evidence pertains to saltmarsh in locations beyond the UK, making it uncertain as to the extent to which findings can be extrapolated to the UK context. As such, this report also highlights those approaches that have proved useful elsewhere to identify, sometimes complex, nutrient impacts on saltmarsh. Further, it suggests knowledge gaps that need to be addressed, potentially through the identified approaches, to fulfil NE's overarching aim to assess water quality alongside a feature-based assessment of conservation status.

***A priori* expectations: Saltmarsh response to nutrients**

Plant communities are structured by competitive and facilitative relationships. Such relationships play out on a stage of varied abiotic and biotic resources and conditions. These environments include the nutrient resources, especially nitrogen (N) and phosphorus (P), required for plants to function. However, other resources, such as light and water, and conditions, such as pH, temperature and salinity, can affect the extent to which nutrients structure plant community trajectories and determine successional pathways. The form of a given nutrient can also affect how plant communities respond due to preferential uptake of one nutrient source over another by different species (Falkengren-Grerup 1995). Further, short-term responses to nutrients may not relate to longer-term responses, especially where issues of scale add complication. For instance, as shown in North American systems, initial increases in growth across trophic levels may be lost if a system collapses due to loss of belowground structure (e.g. Nelson and others 2019). Indeed, other organisms (herbivores, predators, microbes) can further affect the dynamics of plant communities, as well as being affected in turn by vegetation responses. Community trajectories in response to environmental change, and thus the condition of habitat features, are expected to relate to the legacy of previous disturbances and management (Perring and others 2016).

Increasing N and/or P supply has been shown to interact with this long list of factors (other resources and conditions, organisms, historical legacies and baselines) and affect plant community dynamics (e.g. Perring, Bernhardt-Römermann, and others 2018; Segar and others 2022). This makes understanding and predicting system response to nutrient inputs a complex task.

A priori, we would expect saltmarsh vegetation communities to be structured by similar forces, including resource availability (Figure 1). However, traditionally, saltmarsh community structure was related to strong abiotic gradients in stress, and nutrient dynamics were considered secondary (e.g. see arguments in Ranwell 1964; Levine, Brewer, and Bertness 1998). Indeed, some considered nutrients to be unimportant in determining saltmarsh community dynamics (Ranwell 1964). Yet, more recent observations, associated with the large increases in nutrient availability in estuaries, point towards saltmarsh plant communities being affected by nutrients. Responses included total reversals in competitive hierarchies when investigated using fertilization experiments in New England, US saltmarshes (Levine, Brewer, and Bertness 1998; Emery, Ewanchuk, and Bertness 2001). In a UK/Irish context, observations include smothering of low marsh communities by opportunistic macroalgae (Bardsley and others 2020), changes in root structure (Penk, Perrin, and Waldren 2020), and increased dominance of species such as sea couch (*Elymus athericus*) (Natural England, personal observation). However, whether saltmarsh vegetation dynamics in the UK environment have actually been **caused** by increased nutrient availabilities, or by other changing environmental conditions (e.g. sea level rise, coastal development, rising temperatures, change in grazing or other management) alone, or in conjunction with changed nutrient dynamics, is uncertain. Further, the extent to which any changes in response to nutrients depends on other factors, and the extent to which saltmarsh vegetation community impacts are directly mediated by nutrients, or indirectly mediated through nutrient-induced changes in microbial communities or trophic relationships, requires elucidation.

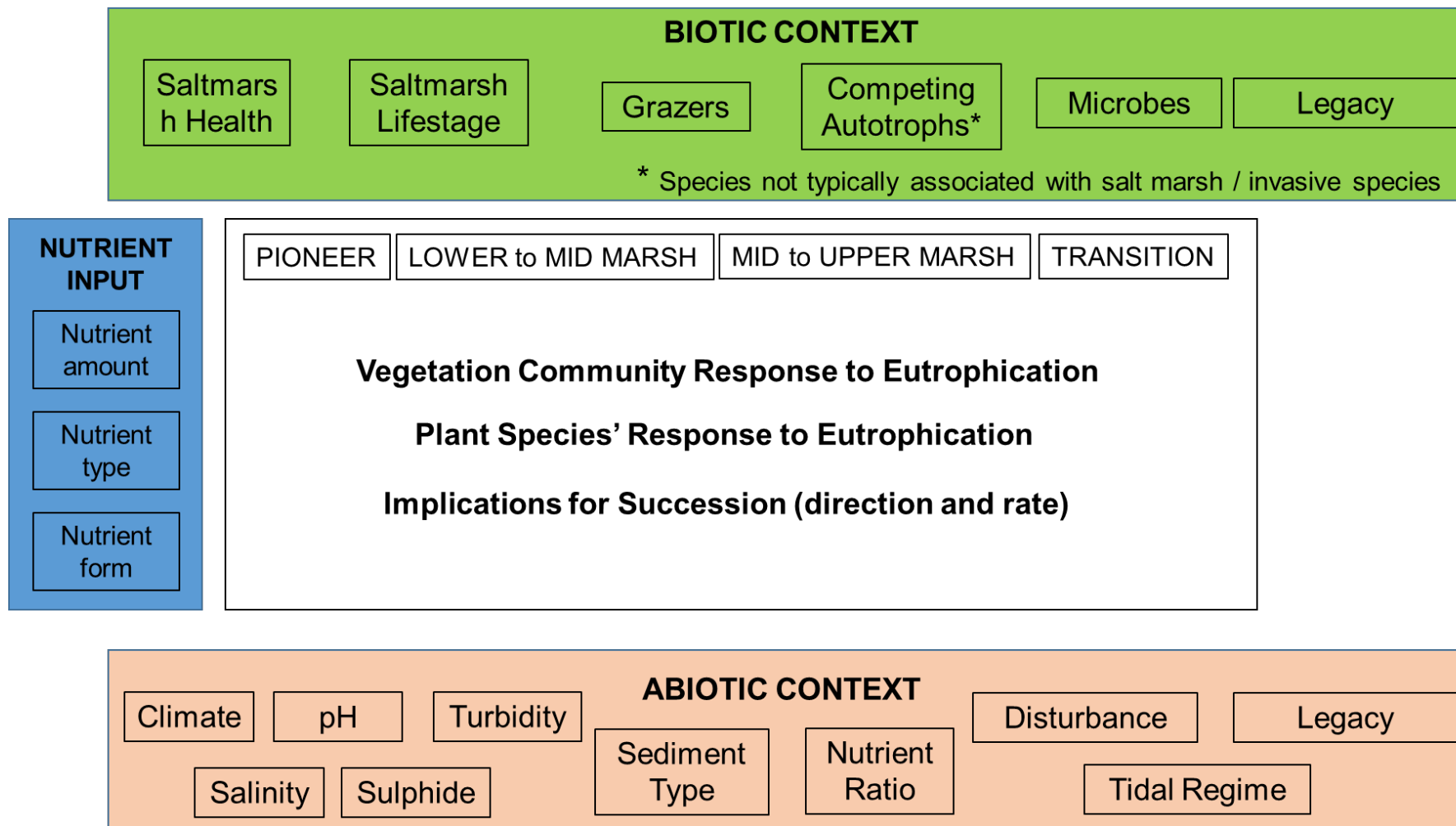


Figure 1. Factors that can influence saltmarsh response to nutrients. This report focuses on evidence for impacts of nutrients on saltmarsh species found in the UK environment, and the communities of which they are part. We amend this Figure in the Evidence gaps section, highlighting those areas where we have uncovered evidence, and those where there is no evidence. We highlight that “absence of evidence” is not “evidence of absence” given the mechanisms by which we expect elevated nutrients to affect saltmarsh habitat features. Where evidence is missing, this may suggest key knowledge gaps that need investigating

The saltmarsh context in UK marine waters

At temperate latitudes, saltmarshes generally occur between mean high-water spring tides and mean high-water neap tides (with transitional elements to Highest Astronomical Tide). The development of saltmarsh is largely controlled by physiography, where fine-grained sediments accumulate in relatively low-energy environments where wave action is limited. Consequently, salt-tolerant vegetation develops where there is an accumulation of mud in estuaries, inlets, behind barrier islands or spits, and occasionally via marine inundation of low-lying ground. Specialist 'perched saltmarsh' can also be found behind rocky outcrops or wave-cut platforms. The JNCC (2008) report gives a UK-wide figure of saltmarsh area of 45,500 ha, but this is likely to be greater given current work on national inventories in Northern Ireland, Scotland and Wales. Regardless of the precise figure, the largest areas of saltmarsh in the UK are concentrated in the major estuaries on low-lying land in eastern and north-west England (JNCC 2008). In England, the area is estimated at 35,500ha, based on extent and zonation mapping 2016-2019 (Environment Agency 2022). Four physical factors – sediment supply, tidal regime, wind-wave climate, and the movement of relative sea-level – primarily govern the character and dynamic behaviour of saltmarshes.

The composition of saltmarsh flora and fauna is traditionally considered to be determined by complex interactions between frequency of tidal inundation, salinity, suspended sediment content and particle size, slope, and biotic factors (e.g. herbivory) and other habitat management. In general, total species richness increases with elevation leading to a characteristic zonation of the vegetation. We considered this zonation when extracting evidence i.e. whether there was evidence for within- or across-zone response to nutrients. Transitions to mudflat occur at the seaward limit, while in the upper elevations of saltmarshes there may be further transitions to brackish or freshwater marsh, dune vegetation, or vegetation overlying shingle structures. The halophytic flora (i.e. plant species adapted to saline conditions) is relatively species poor, dominated by perennial grasses, rushes and dwarf shrubs. Annual species are poorly represented and restricted to the upper (terrestrial) and lower (mudflat) transition zones. Saltmarsh invertebrates are dominated by the high abundance of a few species and a high degree of adaptation to cope with the intertidal environment. Saltmarshes are important habitats for breeding, feeding, and roosting birds, many of them migratory.

There is considerable geographical variation between marsh types in England. This variation can be reflected in very local conditions; at the meso-scale where strong environmental gradients occur (e.g. between the head and mouth of an estuary or open coast); and at the regional scale where marshes on the west coast are subject to higher rain fall and exposure from prevailing westerly winds than east coast marshes. This results in higher energy environments and sandier sediments in the west, compared to south and east coast marshes which are on finer silts and clays. Creek systems on the west coast are relatively simple in comparison to the dendritic systems found in the south and east. The marshes of the south and east coast are characterised by a relatively low plant diversity of halophytic species. The mid and upper sections of marshes on the west coast

are predominantly grasslands dominated by glycophytes (plants that grow in low salinity soils).

The varied geographic distribution of saltmarshes in England can lead to different exposures to nutrient inputs. The large lowland rivers of the south and east drain extensive areas of agricultural land or run through large urban areas. The main source of nitrogen and phosphorus to the water environment in England is agriculture, comprising 69% of N inputs. The second largest source is wastewater, which contributes close to 25% of N inputs (Environment Agency 2023). These sources could influence the forms of nutrients that are present in the saltmarsh environment. In estuaries situated in more urban and industrial catchments, phosphorus can dominate the runoff, along with industrial contaminants. Contrary to the typically closed cycles of terrestrial environments (although note Hedin and others, (2003)) saltmarshes are considered to have an open nutrient cycle. This is due to their greater or lesser exposure to the marine environment depending on their location. This open cycle can make it harder to characterise input sources and amounts, and thus understand and quantify the amount of nutrient pressure that saltmarsh plant species and vegetation communities are exposed to.

Questions and Objectives

Questions

The contextual background led to NE posing two original questions:

- What is the response of saltmarsh to changing nutrient concentrations in estuarine ecosystems?
- How are these relationships affected by other factors?

The focus is on estuarine systems due to water quality issues being associated with these areas, but increasing nutrient amounts may also affect other marsh systems, such as marshes behind barrier islands, at the heads of sea lochs and on beach plains. This awareness affected the statement of the objectives below i.e. we did not only consider evidence from estuaries.

Objectives

To help NE transition towards water-quality assessment through understanding feature-based response to nutrients, the project identified the following objectives:

1. Collate the evidence on the impact of nitrogen (N) and phosphorus (P) compounds on the condition of typical saltmarsh species present in the UK marine environment
2. Collate the evidence for environmental (abiotic) factors that can affect the impact of elevated nutrients on saltmarsh species present in UK waters
3. Collate the evidence for ecological (biotic) factors that can affect the impact of elevated nutrients on saltmarsh species present in UK waters

Although the three objectives focus on UK waters, for obvious reasons, we also explored evidence from further afield, particularly Europe and North America. This was agreed with the Project Steering Group, especially when initial searches suggested a lack of UK-specific evidence.

Evidence from further afield provides important context as to the types of responses that may occur in UK saltmarshes with changed nutrient availabilities. However, especially for the east coast of North America, the environmental context of many saltmarshes is different e.g. low tidal ranges, a preponderance of organic sediment and low sediment inputs, and monodominance of species such as *Spartina alterniflora*, *S. patens* and *Juncus gerardii* depending on the marsh zone. As noted in the Rating approach subsection, we assigned lower confidence, in terms of their applicability to UK marine waters, to findings from those studies. However, these studies also provide useful lessons in regard to multi-trophic interactions and longer- vs short-term responses to changed nutrient availability. These studies therefore raise potential issues in relation to the impacts of nutrients on saltmarsh vegetation that NE need to be aware of going forward.

Metrics of nutrient change in saltmarsh systems

It is important to remember that changing nutrient concentrations in estuaries are not the only nutrient sources affecting the saltmarsh habitat (see also Bowen and others 2020). At higher elevations, with less frequent inundation, atmospheric deposition, grazing fauna, freshwater run-off and/or direct fertilization of the saltmarsh system can lead to changed nutrient availabilities. Thus, we expanded the focus of the two original research questions to consider altered nutrient inputs (typically measured in $\text{kg ha}^{-1} \text{yr}^{-1}$), as well as changing nutrient concentrations (e.g. mg l^{-1}).

Readers should note that we did not resolve these different metrics of nutrient availability/input into a single indicator at this time. This makes it difficult to answer supplementary questions posed by NE, in particular “At what nutrient [level] does damage to the feature condition occur?” Further, answering such a question requires a subjective judgement as to what constitutes ‘damage’, which may further depend on the policy environment. However, we do report, where available, nutrient values found in different literature sources to enable NE to form a judgement as to whether particular values can be associated with harm, in whatever manner that is decided upon.

Methods

Search approach

Preliminary searches and discussions with NE led to an agreed set of search terms for investigating the published peer-reviewed literature (see Appendix 1). This included a set of terms for the:

- species and community context;
- relevant (bio-)geographical area;
- target potential explanatory variables.

We conducted the search on Web of Science, across all available years with UKCEH access levels, on 23rd December 2022, exporting results to a spreadsheet. We retained relevant publication information, including authors, date, title, abstract, journal (or book/book chapter), journal volume number, page numbers and date of issue. Our initial search found 1812 literature sources.

Screening approach

We screened titles and abstracts between 23rd and 31st December 2022. Titles were excluded if they were clearly not relevant geographically (e.g. from Australia, New Zealand, west coast of North America) or from a terrestrial biome (e.g. freshwater wetlands or pasture) (flow diagram representing the systematic review process is available in Appendix 1 (Figure A1.1, Appendix 1)).

Although the report's primary focus is nutrient effects on saltmarsh vegetation, we retained titles that related to nutrient cycling in salt marshes / estuaries in general, other ecosystem compartments or functions (e.g. C sequestration), saltmarsh functions and/or saltmarsh restoration. We retained such titles in case their abstracts suggested consideration of vegetation responses to nutrients and/or if they could provide useful context for the final report. **530 records** were retained after title screening.

We then screened abstracts from these records. As with titles, we excluded abstracts that had an inappropriate geographical/biome context, or that did not investigate/discuss nutrient impacts on saltmarsh vegetation (or other target organisms that may be problematic for / relate to vegetation within saltmarshes). There was a general paucity of papers from UK waters, but some papers were found that related to Irish saltmarshes, as well as from European marshes around North Sea coastlines. A series of papers dealt with nutrient impacts on saltmarshes in the USA (in conjunction with other stressors such as coastal development and grazing), and these were retained for further examination in case lessons could be transferred to UK-waters. Papers were also retained if they could provide useful context for the final report e.g. in relation to the Water Framework Directive. **175 papers** were retained after abstract screening.

While screening titles, papers were coded as to whether they dealt with vegetation response (explicitly) or ecosystem response more generally, and whether they related to nutrients or other potential explanatory variables. We provided NE with tables of retained papers in regard to these different categorisations, and other papers that were of potential interest following abstract screening. We highlighted papers that we believed should be prioritised for evidence extraction, given information contained within their titles and abstracts.

Following additional literature recommendations from the NE coastal specialists, we agreed with NE to extract evidence, into a purpose-built spreadsheet (see Evidence extraction subsection) from a total of 81 references. These papers and reports included those papers found in the Web of Science search that we identified as having a high priority (based on their title and abstract), together with those papers and reports identified by experts. Evidence extraction showed that a subset of these articles was from North America, which was not initially clear from title and abstract. We assessed the evidence in these papers in relation to the North American context from which they arose (see also Rating approach).

Prior to evidence extraction, we had also highlighted to NE papers from the title and abstract screen that may have had relevant insight, but from North American marsh systems. NE requested that we read and synthesize salient points from these 40 papers, as presented in the [Results](#). Given the different context for these North American systems, we did not directly extract evidence into the spreadsheet from this *a priori* subset of North American papers, but we did rate their relevance where appropriate (see also Rating approach).

Evidence extraction

We created an evidence extraction spreadsheet to streamline the extraction of evidence from the final set of selected papers with a presumed UK-focus or with information of direct relevance to the UK-context.

In addition to columns already described, this spreadsheet had the following 'sections', each made up of multiple columns:

- **Nutrient summaries** – columns indicating whether N, P, other nutrients. Then columns with nutrient forms, and the concentrations or quantities recorded.
- **Methodology** – columns indicating whether field- or lab-based, and whether observational (i.e. survey) or experimental (or some other method e.g. modelling).
- **Geographical context** – columns indicating latitude, longitude, and, as a quick check, whether the study was conducted in the UK/Ireland, elsewhere in Europe or, if left blank, elsewhere on the globe. The Biogeographic zone was also recorded.
- **Marsh zone** – columns indicating whether the study was located in the pioneer, low to mid marsh, upper marsh or transition zone.
- **Abiotic context variables** – columns indicating whether sediment type, N:P, pH, salinity, turbidity, temperature or another abiotic variable was considered.
- **Biotic context variables** – columns indicating saltmarsh life stage, saltmarsh condition, competing autotrophs, other organisms, and other biotic context. "Competing autotrophs" means those organisms not typically considered salt marsh species but that may affect salt marsh vegetation through competition.
- **Human management variables** – columns indicating whether the saltmarsh had the presence of (agricultural) grazers or mowing, and/or whether it was created through managed realignment.

- **Species columns** – columns indicating whether a particular species was considered by a paper.
- **Main findings and caveats** – columns representing a take home message, author caveats, any caveats inferred by the person extracting evidence, and any other remarks.

Multiple columns were included for each 'section' so that multiple responses could be considered e.g. in multifactorial experiments, or where multiple explanatory variables had been measured in observational studies. These columns enabled a rapid summary of the evidence available, across nutrients, species and saltmarsh zone.

For the Species column, and given time constraints, we agreed with the Steering Group that this would be indicated for those papers that focused on individual species. Where communities were recorded, we could not record all species that may be present. However, if particular species were found to be sensitive to nutrients within a given reference, this would be recorded in the Main findings and caveats section of the spreadsheet.

This approach enabled us to address each of the Objectives 1 to 3 in an efficient manner (i.e. without the need for multiple searches), and via filtering on appropriate context variables. The spreadsheet is not included in the report but aided production of the Results section and all tables.

Rating approach

We first tabulated the evidence, to provide an overview of what evidence had been extracted. As expected, we sourced evidence from a range of approaches, including laboratory-based studies on single species, field-based experiments in non-UK marshes, and observational survey-type studies, from inside and outside the UK. Occasionally, studies used model-based approaches, often informed by observations (see Overall evidence summary). These different approaches have different strengths and weaknesses in relation to clearly linking vegetation responses to nutrient availability (see Perring and others (2018) for further discussion on this in relation to N). For instance, laboratory studies can isolate physiological mechanisms underlying vegetation responses, but potentially lack real-world applicability. Field-based experiments provide a means to isolate the impacts of nutrients on vegetation, whether direct or indirect, but tend to be carried out at small scales e.g. 1 m² plots and only using two or three treatment levels i.e. a control and one, perhaps two, additional nutrient amounts. **These latter facets potentially reduce their representativeness in terms of characterising responses at the feature-scale to nutrient addition.** Observational studies, on the other hand, provide realism at appropriate scales, and thus be considered to have high 'representativeness', but can make it hard to isolate causal drivers of observed change. Indeed, observational studies for nutrient effects typically rely on spatial gradients in available nutrients with the assumption that changes observed over space will match what occurs over time with the same magnitude of nutrient alteration. Studies from other systems cast doubt on such

assumptions (De Lombaerde and others 2018). However, if available, combining resurvey studies (i.e. plant communities that have been recorded at different instances in time) across relevant environmental gradients could provide robust and representative evidence of vegetation change in response to nutrients (Verheyen and others 2016).

As well as considering the different methodological approaches in evidence rating, we also need to consider their location. Bearing in mind NE's context for this work (i.e. using feature-based assessments of saltmarsh response to nutrients in England) we adopted a quantitative rating system to assess the confidence and robustness in the overall evidence we had extracted.

For rating confidence in an individual study, we multiplied two scores together: that for the method adopted, and that for the location of the study (Box 1). In general, our rationale was that evidence for impacts on whole systems in a UK/Irish-context carried greater weight, providing an individual study adopted robust methods, than evidence from laboratory studies on a single species. Laboratory studies were also considered to be in an 'other' location even when sited in the UK or Ireland, as we consider laboratory studies provide corroborative evidence for observations in the field, whether from surveys across gradients or experimental investigations.

We assigned greater confidence to well-designed observational studies as compared to plot-based field experiments, because we had confidence that causal factors had been appropriately identified through controlling for other variables. We assume that well-designed and analysed surveys provide greater representativeness than field-based experiments, and therefore greater confidence that findings of nutrient impact (or not) are robust. Again, we gave greater weight to those studies from the terrestrial-marine interface in the UK or Ireland. However, where it was less clear that observational studies had controlled for covariates, field-based experiments carry greater weight. This is because we have increased confidence that observed changes relate to nutrients, compared to observational studies with poor control of covariates. This is despite the fact that a field experiment's representativeness of response may be lower e.g. due to small plot sizes and/or nutrient additions beyond those typically observed.

Finally, for primary literature sources, we assigned greater robustness to our conclusions when multiple, independent, studies found the 'same' qualitative result. For instance, the same species responding in the same manner in different locations. Where studies reported conflicting results (and this could not be clearly related to context variables), or results were from a single peer reviewed paper, we considered the evidence to be somewhat robust. Where evidence was from the grey literature, we considered this to be corroborative (Box 2).

Box 1: Confidence and representativeness of findings within evidence sources

Confidence score = Study type score x Study location score. Note the confidence score, by considering the location and method, considers representativeness, as noted in the main text. Below, we provide a qualitative indication of representativeness alone, for ease of reference and to help interpret findings.

Study type scores

- Observational survey, control of covariates: 4
- Field-based experiment: 3
- Observational survey, covariation uncontrolled: 2
- Laboratory experiment: 1

Study location scores

- UK and Ireland: 3
- Elsewhere in Europe: 2
- Other location across globe: 1

Study Method and Location	Overall confidence in findings: Nutrient impact in UK context	Representativeness of findings: Nutrient impact on vegetation at appropriate scale (i.e. feature level)
Survey – covariates controlled – UK/Ireland	12	High
Field-based experiment – UK/Ireland	9	Medium
Survey – covariates controlled – Europe	8	High
Field-based experiment – Europe	6	Medium
Survey – covariates uncontrolled – UK/Ireland	6	Medium
Survey – covariates uncontrolled – Europe	4	Medium
Survey – covariates controlled – Other	4	Potentially high
Field-based experiment – Other	3	Medium
Survey – covariates uncontrolled – Other	2	Medium
Laboratory-based experiment – Any location	1	Low

Box 2: Robustness of findings across evidence sources

- | | |
|--|--------------------------|
| • Multiple peer-reviewed sources: | Robust evidence |
| • Single peer-reviewed source
or unexplained conflicting responses: | Somewhat robust evidence |
| • Grey literature only: | Corroborative evidence |

Results

Overall evidence summary

Primary studies on the impacts of nutrients on saltmarsh vegetation ranged from laboratory experiments on single species (Eller and Brix 2012) to field experiments in multiple marsh locations (e.g. Pennings, Stanton, and Stephen Brewer 2002) and survey studies where a single reference encompassed evidence from multiple vegetation communities across multiple saltmarshes (e.g. Penk and others 2020). We also uncovered evidence in review papers such as the empirical critical loads for N (Aazem and others 2022).

We extracted evidence from 25 studies that had been carried out in a UK/Irish context, ranging from early observations in 1964 (Ranwell 1964) to recent observational studies in Chichester (Bardsley and others 2020) and comprehensive observational studies across multiple marsh locations in Ireland (e.g. Penk and others 2020). A similar number of studies (24) were from estuaries (and other locations) from elsewhere in Europe, particularly Germany (e.g. Schröder, Kiehl, and Stock 2002), and a mix of observational and experimental studies from the Dutch Wadden Sea (e.g. Dormann, Van Der Wal, and Bakker 2000) (Figure 2).

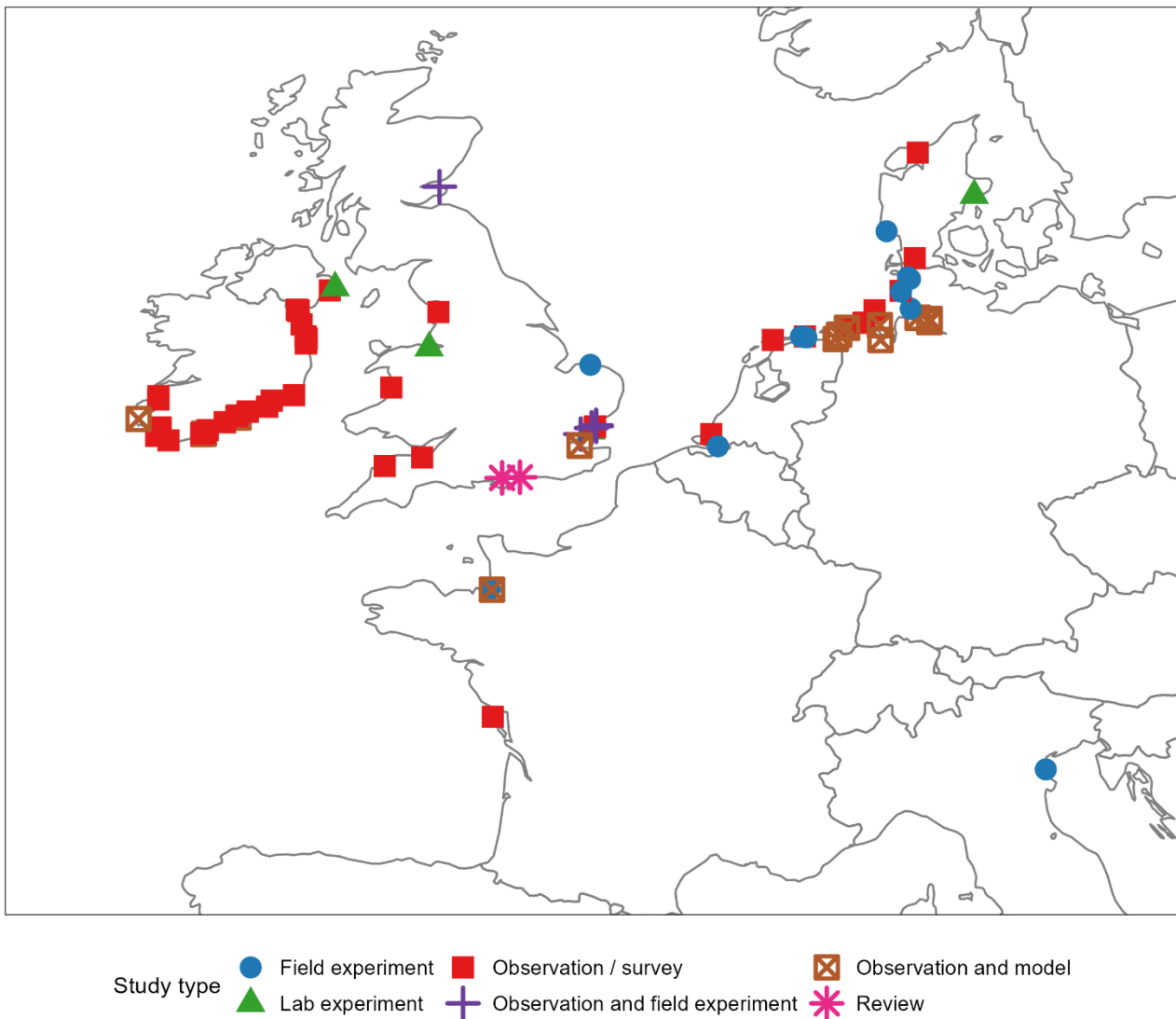


Figure 1. Locations and study type i.e. methodological approach across UK, Ireland and elsewhere in Europe where evidence on nutrient impacts on saltmarsh vegetation was extracted. Note that a single source reference could cover multiple sites.

Nutrient forms, methods and saltmarsh location

Studies considered nitrogen alone, or in combination with phosphorus (Table A2.1, Appendix 2). Only one study considered phosphorus alone (although nitrogen (and potassium) was added in other plots as mineral salts) (Jefferies and Perkins 1977). A few studies considered other ‘nutrients’, typically dissolved organic C. The vast majority of studies were based on observational survey evidence (70 instances across nutrient types), as opposed to field- or lab-based experimentation (31 instances). Note that we use the phrase ‘instances’ as a given reference could have multiple instances e.g. considering nitrogen and another nutrient. There was a reasonably even spread of studies across the different marsh zones, with 21 instances in the pioneer zone, 31 in the lower to mid marsh zone, 29 in the upper marsh, and 20 in the transition zone to terrestrial habitat. Again, a

single reference could consider multiple marsh zones. Not all papers specified the marsh zone, but we assigned one to the best of our knowledge given the species noted. Readers should be mindful that this can be difficult to infer, given variability in marsh position for many species relative to the tide, and likely dependent on other environmental conditions. **Indeed, we go on to show that one of the impacts of additional nutrients may be to allow species to move from the saltmarsh zone they are ‘typically’ considered to occupy.**

The forms of nutrients applied or investigated in the different studies showed some interesting contrasts. Dissolved organic N was never applied in field or laboratory experiments, but dissolved organic P was applied in two instances, once to the pioneer marsh and once to the lower marsh (Table A2.2, Appendix 2). Generally, inorganic forms of either N or P predominated over organic applications.

Frequency of species considered

Individual species, and their response to nutrients, were considered with varying frequencies (Table A2.3, Appendix 2). In contrast to other results in Appendix 2, we extracted no evidence that nutrient impacts on individual species to phosphorus supply alone was considered. This suggests that the results in Tables A2.1 and A2.3 for phosphorus relates to community responses.

Species missing evidence

We uncovered no references in a direct manner (see Methods) for the following species:

Althaea officinalis, *Arthrocnemum perenne*, *Blysmus rufus*, *Bostrychia scorpioides*, *Carex extensa*, *Carex flacca*, *Cochlearia anglica*, *Eleocharis parvula*, *Eleocharis uniglumis*, *Elytrigia farctus* (*Elytrigia juncea*), *Euphrasia foulaensis*, *Euphrasia heslop-harrisonii*, *Filipendula ulmaria*, *Frankenia laevis*, *Fucus cottonii*, *Inula crithmoides*, *Iris pseudacorus*, *Leontodon autumnalis*, *Limonium binervosum*, *Parapholis strigosa*, *Phalaris arundinacea*, *Puccinellia distans*, *Sagina maritima*, *Sarcocornia perennis*, *Schoenus nigricans*, *Spartina maritima*, *Suaeda vera*.

A key knowledge gap may be *Spartina maritima*, given it is a species component of the Annex 1 habitat “Spartina swards (*Spartinion maritmae*)” and is designated in Special Areas of Conservation (SAC). Other important knowledge gaps may be *Arthrocnemum perenne* / *Sarcocornia perennis* as they can be considered key species in the pioneer/low marsh.

Objective 1: Collate the evidence on the impact of nitrogen (N) and phosphorus (P) compounds on the condition of typical saltmarsh species present in the UK marine environment

Table 1, Table 2, Table 3 and **Table A2.3** (Appendix 2) show that a variety of species had evidence for the effect of N, alone or in combination with P (while some species did not respond). There was no evidence for the impact of P alone on individual species (but note associational responses within marsh zones outlined in detail in the subsections below). However, in the North American literature, reference is made to the fact that *Plantago maritima* responds strongly to P additions in European marshes (Tyler, 1967 in Theodose & Roths (1999)). We expanded on this objective by considering evidence of vegetation community, as well as plant species, responses to nutrients by marsh zone.

Pioneer zone

Some species, including *Spartina* sp., showed negative associations of e.g. ground cover, with ammonium concentrations (NH_4^+), which was more prominent in pioneer zones and peat-based systems (Penk and others 2020; Cott, Chapman, and Jansen 2013). This was not a universal response, as *Spartina*'s deep root systems can supply nutrients (Redelstein and others 2018) and there is little foliar ammonium uptake (Bouma and others 2002), rendering water column ammonium less important. In addition, when combined with high salinity, high ammonium loads can lead to decreased ammonium uptake in tissues and biomass of *Spartina alterniflora* (MacTavish and Cohen 2017). Interestingly, *Spartina* ground cover has a positive association with P supply (Penk and others 2020).

Lower to mid marsh

In the lower to mid marsh, there was evidence for positive relationships of marsh species' ground cover with nitrate (NO_3^-) (and NO_x more generally), including *Atriplex portulacoides*, *Suaeda maritima* and *Cochlearia* (Penk and others 2020). *Suaeda* has generally been shown to outcompete other species under high N conditions (e.g. Schröder, Kiehl, and Stock 2002), including through shading leading to declines in *Puccinellia* (Kiehl, Esselink, and Bakker 1997). *Puccinellia* is, however, capable of high rates of N assimilation (Aziz and Nedwell 1986) (which may be involved in maintaining salinity tolerance) and has a competitive advantage in low N levels (Huckle, Marrs, and Potter 2002) although the comprehensive survey of Irish marshes showed a negative association between its ground cover and P (Penk and others 2020). Interestingly, neither *Elymus athericus* nor *Atriplex portulacoides* showed a response to N fertilization during removal experiments (Bockelmann and Neuhaus 1999), despite *Atriplex* showing a

positive ground cover association with nitrate in Irish marshes. N fertilisation may also increase the salt tolerance of plant species typical for high marsh elevation allowing them to occur at lower elevations (Kuijper and Bakker 2012).

Negative associations between ground cover and nitrate were greatest for *Plantago*, followed by *Armeria*, *Juncus*, and *Tripolium pannonicum* (Penk and others 2020). Penk and others (2020) suggest that monodominant stands of *Atriplex* lead to a reduction in saltmarsh diversity: species-rich communities associated with *Plantago maritima* are lost, with potential functional consequences through a 6.6-fold increase in above- to below-ground biomass ratios across the N gradient (Penk, Perrin, and Waldren 2020). Overall, community composition in these Irish marshes (including quadrats within upper marsh areas), as analysed through redundancy analysis, showed a significant relationship with NO_x, which was the second-most important explanatory variable after salinity. Phosphorus also exhibited a significant correlation with community composition, while ammonium, despite dominating the total N pool, only showed a marginal significant relationship (Penk and others 2020).

Species' ground cover showing a negative association with ammonium in this marsh zone include *Salicornia* (Penk and others 2020) and *Atriplex portulacoides* in high ammonia peat-based saltmarshes (Cott, Chapman, and Jansen 2013). Species with positive association of ground cover with P include *Triglochin maritima* and *Spartina anglica* (Penk and others 2020).

Another *Spartina* spp. (*Spartina alterniflora*) can be found to a limited extent in UK saltmarsh systems. However, across a broad range of North American systems, with different tidal regimes and sediment types, this species has been experimentally shown to respond to increased N (and P and K) availability, becoming more dominant in upper marsh systems, at the expense of typical marsh species, as well as maintaining its dominance in low marsh (e.g. Pennings, Stanton, and Stephen Brewer 2002). However, in a Maine saltmarsh, which may have conditions more typical of UK saltmarsh, a survey study showed that areas with upland development, and therefore higher nitrate levels in the marsh, were associated with low abundance of *S. alterniflora*. Increased dominance of *Triglochin maritimum* was observed instead (Fitch, Theodose, and Dionne 2009). A lower primary production in *Spartina alterniflora* and *S. patens* in response to nitrate addition, as compared to ammonium, has also been found across other systems in North America (and China) (Bowen and others 2020).

Upper marsh and transition zone

In upper marsh / transition zone environments, N addition has been shown to increase *Spergularia* and *Festuca* shoot length to their self-shading limit (Kiehl, Esselink, and Bakker 1997). There were also some positive relationships with *Elymus athericus* abundance (Suchrow, Stock, and Jensen 2015; Valéry, Radureau, and Lefeuvre 2017) but other studies found no significant effect of nutrients and rather noted that surface elevation to be more important (Bockelmann and Neuhaus 1999; Kuijper and Bakker 2012; Nolte and others 2019; Veeneklaas and others 2013). As with the low to mid marsh, *Armeria*

and *Juncus* cover had negative ground cover relationships with NO_3^- , as did *Lysimachia maritima*. Intriguingly, NH_4^+ had a positive relationship with *Lysimachia maritima* cover although both these relationships only showed low marginal variance explained (approx. 1%) (Penk and others 2020). An early paper in the UK showed that species with low cover at the start of an experiment (*Atriplex portulacoides*, *Aster tripolium*, *Suaeda maritima*, *Spergularia marina*) responded positively to inorganic nitrogen (whether ammonium or nitrate) but not phosphate or potassium, while few differences were observed among nutrient treatments and the control for those species that were initially common (no difference for *Limonium vulgare*, *Puccinellia maritima* and *Salicornia europaea* agg. with nutrient treatments, a decrease in the shoot frequency of *Armeria maritima*, when either nitrate or ammonium was added) (Jefferies and Perkins 1977).

In a northern New England upper marsh, which may be considered as having conditions more similar to UK marshes than those marshes sited further south in North America, different plant communities were associated with available nutrients. Mixed forb zones, with the highest plant diversity, were associated with higher P availability, soil salinity and soil moisture than those zones dominated by graminoids. Ammonium had highest availability in *Juncus gerardii* patches which were also the patches with highest production, although there was no variation in nitrate-N among zones. This relationship with NH_4^+ , and lack of relationship with NO_3^- , contrasts with the general findings from the survey across multiple southern and eastern Irish saltmarshes (Penk and others 2020). Interestingly, plant tissue N concentrations were highest in the mixed forb zone, reflective of plant physiologies (Theodose and Roths 1999).

There are observations of increasing *Phragmites australis* abundance in some estuaries e.g. the Humber, with 'invasion' of the upper marsh from the terrestrial transition zone (Louise Denning, NE, pers. comm.). Although we did not uncover evidence relating this increase to nutrients from the UK or European context (although note findings reported in Objective 3: Collate the evidence for ecological factors that can affect the impact of elevated nutrients on saltmarsh species present in UK waters (Ranwell 1964)), North American studies suggest that *Phragmites*' success can be related to increased nitrogen availability (Bertness, Ewanchuk, and Silliman 2002; Legault, Zogg, and Travis 2018). Others highlight that physiological support from ramets located in more favourable habitats for the species (i.e. lower salinity with less waterlogging) can support the invasion of *Phragmites* ramets in higher salinity and more waterlogged conditions (Amsberry and others 2000). Amsberry and others termed this process 'clonal integration'. In this case, the role of nutrients was not discussed (Amsberry and others 2000). Some authors highlighted that *Phragmites*' success also depends upon reductions in salinity, as well as increased N availability, associated with shoreline development (Silliman and Bertness 2004). When in competition with *Spartina alterniflora*, additional nutrients led to *S. alterniflora*'s competitive displacement by *Phragmites*, including at elevated temperatures. This displacement does not occur with elevated temperature alone (Legault, Zogg, and Travis 2018).

Evidence for effects of nutrients on successional processes

The results for the different zones above point towards the fact that successional processes can be affected by nutrients, including the ability of high marsh species to invade the lower marsh through improved salinity tolerance (Kuijper and Bakker 2012). Dormann and others (2000) argue that it is probable that competition changes from nutrients to light in early to late successional stages, and increased fertility speeds this process up. In general, higher NO_3^- and NH_4^+ concentrations both result in increases in above-ground biomass with less investment in below-ground biomass (Penk, Perrin, and Waldren 2020). However, evidence from a North American marsh in southern Maine, with some species shared with UK saltmarshes, also suggests that less salty marshes (i.e. later in the successional sequence) may be co-limited by N and P (Crain 2007).

The recent review of empirical critical loads (Aazem and others 2022) corroborates these findings. Additional N increased the dominance of graminoids and decreased indicator species in the upper to mid marsh, while it increased late successional species in the pioneer zone. Combined high N and P application also increased biomass of late successional species and decreased floristic differences between young and old saltmarshes. However, P application alone led to insignificant changes (Aazem and others 2022).

In the US, as well as changed competitive hierarchies (Levine, Brewer, and Bertness 1998), evidence suggests that macroalgal smothering can shade and smother grasses, leading to bare spots on the marsh which compromises the saltmarshes' ability to intercept and retain nutrients - although macroalgae can also intercept and retain nutrients (references cited in Oczkowski and others 2016). There is also considered to be a general increase in saltmarsh loss in response to increased N availability, but some systems appear more resilient to this loss (Crosby and others 2021). There is also evidence, at least for young *Spartina alterniflora* marshes in the US, that high N loading will increase the rate of marsh development. These observations came from saltmarsh areas with underlying sandy sediment after a storm event (Tyler, Mastronicola, and McGlathery 2003) which may have some relevance to certain UK systems e.g. on the west coast.

A long term (40-year) N addition study at Cape Cod also shows how successional processes may be changed by altered nutrient availabilities. Corroborating a response described elsewhere (Pennings, Stanton, and Stephen Brewer 2002), *S. alterniflora* was replaced, in some areas, by *Distichlis*. Of particular note was loss of some rarer species in fertilized compared to control plots (e.g. *Aster tenuifolius* and *Limonium carolinianum*), with stimulation of other species, notably *Atriplex patula* and *Iva frutescens*. For the latter species in particular, it may have been an indirect effect of N fertilization that provided the foundation to the response: N addition was associated with increased elevation that then allowed *I. frutescens* to colonise (Fox, Valiela, and Kinney 2012).

Beyond vegetation dynamics, evidence from North America also suggests that sustained increases in nutrient availability can lead to creek bank collapse (e.g. Deegan and others 2012 cited in Nelson and others (2019)). This included disruption to the natural ramp form

of the creek bank through the development of large cracks between the creek and the marsh platform, as well as low-marsh slumping and loss. Such changes have multi-trophic implications and emphasize the importance of considering long- as well as short-term implications of nutrient enrichment. Thus, in the short term, an omnivorous fish – the mummichog (*Fundulus heteroclitus*), that plays an important role through a trophic relay in connecting the saltmarsh habitat to the wider marine-scape, increased in biomass with more nutrient input due to greater prey abundance. However, when the creek bank collapsed after sustained nutrient increase, the mummichog could no longer access its preferred prey and suffered biomass decline. Such a response, if replicated for e.g. species of conservation concern in UK waters, could be important to bear in mind for NE, if feature assessment is in relation to other trophic levels.

Evidence that suggests how different forms of nutrients are a threat to saltmarsh, at which concentrations in the marine environment

There is some evidence that different forms of nutrients can have different impacts on saltmarsh species, for instance that *Lysimachia* has different relationships with NH_4^+ and NO_3^- (Penk and others 2020). However, we did not find unequivocal evidence, from the focal literature extraction, of how particular forms of nutrients, at what concentrations in the marine environment, are a threat to UK saltmarsh plant species or plant communities (Table 1). It was rare that addition of nutrients was reported together with background concentrations. As well as being difficult to integrate these different metrics in an overall measure, lacking one or the other metric prevents straightforward assessment of the total nutrient pressure a particular species or vegetation community is exposed to. This prevents quantification of the level(s) at which a particular species was lost from a saltmarsh and/or the level at which species gain/loss leads to vegetation change that alters the integrity of the saltmarsh feature.

Table 1. Range of background N and P availabilities and nutrient addition amounts (note different units), where available, and associated confidence (based on study type and study location (see Box 1) in nutrient impact in UK waters at which no significant vegetation responses are reported in the evidence assessed. Table 2 reports evidence for positive relationships (i.e. an increase in response) and Table 3 reports evidence for negative relationship (i.e. a decrease in response) with nutrients. Note that studies and species can appear across tables. The use of ‘positive’ and/or ‘negative’ does not carry any connotation of good and/or bad in relation to what constitutes ‘harm’ to saltmarsh features. Where cells are left blank, this is intentional.

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
156-242 $\mu\text{mol L}^{-1}$ NO_3 + 8.1-21 $\mu\text{mol L}^{-1}$ NH_4 (Westerschelde)		1-50 μM NO_3 1-50 μM NH_4		<i>Spartina anglica</i> has a weakly positive (not significant) leaf and stem growth rate	6	(Bouma and others 2002)
5.3-26.3 $\mu\text{mol L}^{-1}$ NO_3 + 5.7-8.1 $\mu\text{mol L}^{-1}$ NH_4 (Easterschelde)						
		1.5 mg l^{-1} (Dengie) 5 mg l^{-1} (Dengie)	0.02 mg l^{-1} (Dengie) 0.07 mg l^{-1} (Dengie)	No effect on <i>Puccinellia maritima</i> and <i>Suaeda maritima</i>	1	(Reef and others 2017)
Clay thickness as a proxy				No – grazing more important than nutrients	6	(Chen and others 2021)

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
		20 g m ⁻² yr ⁻¹		No – grazing more important than nutrients	6	(Van Der Wal and others 2000)
16 kg ha ⁻¹ y ⁻¹ NH ₄ NO ₃ input 0.0092 g kg ⁻¹ NO ₃ -N + 0.0076 g kg ⁻¹ NH ₄ -N (low marsh) 0.0018 g kg ⁻¹ NO ₃ -N + 0.0116 g kg ⁻¹ NH ₄ -N (upper marsh)		40 kg ha ⁻¹ yr ⁻¹		No effect on <i>Elymus athericus</i> or <i>Atriplex portulacoides</i>	6	(Bockelmann and Neuhaus 1999)
		20 g m ⁻² yr ⁻¹ and 40 g m ⁻² yr ⁻¹		No effect on <i>Elymus athericus</i>	6	(Nolte and others 2019)
12.4-14.34 mg kg ⁻¹ N (soil) 1.02-1.24 mg kg ⁻¹ NO _x + 33.9-61.58 mg kg ⁻¹ NH ₄ (soil)	543-742 mg kg ⁻¹ P (soil)			Non-significant weak negative relation for species richness with P, and a non-significant weak positive relation for	4	(Andersen and others 2020)

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
				species richness with N		
5.8-13.6 g m ⁻² N (soil)	62.4-92.4 g m ⁻² P (soil)			No significant effect over range of nutrients	4	(Schulte Ostermann and others 2021)
		250 kg ha ⁻¹ yr ⁻¹	80 kg ha ⁻¹ yr ⁻¹	No significant effect, although a slight increase, for <i>Spergularia</i> and <i>Festuca</i>	6	(Kiehl, Esselink, and Bakker 1997)
1.9 – 31.6 µg cm ⁻³ ammonia-N; 0.009 – 3.213 µg cm ⁻³ NOx-N	3.2 – 40.2 µg cm ⁻³ labile P			Species richness and Shannon diversity not related to NH ₄ ⁺ . Species richness not related to P.	12 (although sulphide and redox potential not accounted for)	(Penk and others 2020)
1.9 – 31.6 µg cm ⁻³ ammonia-N; 0.009 – 3.213 µg cm ⁻³ NOx-N	3.2 – 40.2 µg cm ⁻³ labile P			No relationship with biomass and NH ₄ ⁺ across assemblages. Biomass	12 (although sulphide and redox potential not accounted for)	(Penk, Perrin, and Waldren 2020)

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
				and labile P relationships also weak and varied across whole P gradient and among individual assemblages.		
		10.05 g NaNO ₃ per 50 x 50cm subplot 7.95 g (NH ₄) ₂ SO ₄ per 50 x 50cm subplot (nutrients added separately)		No relationship of shoot frequency and inorganic nitrogen addition with species already common in plots at beginning of experiment i.e. <i>Limonium vulgare</i> , <i>Puccinellia maritima</i> , <i>Plantago maritima</i> , <i>Salicornia europaea</i> agg.	9 (but note very limited replication and paper mentions a number of experimental artefacts that compromise inference)	(Jefferies and Perkins 1977)
			5.58 g NaH ₂ PO ₄ .2H ₂ O per 50 x	No relationships reported	9 (but note very limited)	(Jefferies and

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
			50cm subplot	amongst plots with P addition and shoot frequency response	replication and paper mentions a number of experimental artefacts that compromise inference)	Perkins 1977)

Table 2. Range of nutrient values at which ‘positive’ impact on vegetation response and associated confidence (see Table 1 legend and Box 1 for further detail). Where cells are left blank, this is intentional.

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
		1.5 mg L ⁻¹ NO ₃ -N		<i>Spartina anglica</i> – positive impact on shoot biomass at low inundation	6	(Wong, Van Colen, and Airoldi 2015)
0.256 – 7.777 mg L ⁻¹ DIN	21 – 103 µg L ⁻¹ HPO ₄			Positive relationship with <i>Ulva</i> species.	Review so no confidence assigned	(Bardsley and others 2020)
50 – 200 kg N ha ⁻¹ yr ⁻¹ (floodwater) 30 kg N ha ⁻¹ yr ⁻¹ (atmospheric)				Positive abundance relationship for <i>Elymus athericus</i>	Review so no confidence assigned	(Rozema and others 2000)

Background concentration s / deposition (N)	Background concentration s / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
85.54 (NH ₄) + 6.87 (NO ₃) mg kg ⁻¹ (Peat sediment)	4.05 mg kg ⁻¹ P (Peat sediment) 7.14 mg kg ⁻¹ P (Sand sediment)			Positive abundance relationship with N for <i>Juncus maritimus</i> , <i>Armeria maritima</i> , <i>Triglochin maritima</i> , <i>Juncus gerardii</i> , <i>Plantago maritima</i>	6	(Cott, Chapman, and Jansen 2013)
21.63 (NH ₄) + 11.93 (NO ₃) mg kg ⁻¹ (Sand sediment)	4.58 mg kg ⁻¹ P (Mud sediment) 5.84 mg kg ⁻¹ P (Sand/Mud sediment)					
32.19 (NH ₄) + 11.59 (NO ₃) mg kg ⁻¹ (Mud sediment)						
16.38 (NH ₄) + 1.16 (NO ₃) mg kg ⁻¹ (Sand/Mud sediment)						
	100 kg P ha ⁻¹ (soil Mellum Island) 185 kg ha ⁻¹ (soil mainland) Potassium and carbonate also recorded			Positive relationship for specific leaf area (SLA) and stem biomass at the community-weighted mean level	4	(Minden and Kleyer 2011)
5 - 42 mg L ⁻¹ (Cousenon) 9 - 33 mg L ⁻¹ (Sélune) 9 - 30 mg L ⁻¹ (Sée)				Positive abundance relationship for <i>Elymus athericus</i>	4	(Valéry, Radureau, and Lefeuvre 2017)

Background concentration s / deposition (N)	Background concentration s / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
7592.4 t y ⁻¹ or 29.3 umolL ⁻¹ d ⁻¹ (Blackwater) 509.7 t y ⁻¹ or 11.9 umolL ⁻¹ d ⁻¹ (Argideen)	120.3 t y ⁻¹ (0.21 umolL ⁻¹ d ⁻¹) Blackwater 7.6 t y ⁻¹ (0.08 umolL ⁻¹ d ⁻¹) Argideen			Positive relationship (modelled) with nutrient loads for macroalgae in Blackwater and Argideen estuaries	6	(Ní Longphuirt and others 2016)
		12 umol L ⁻¹ NO ₃ + 0.2 umol L ⁻¹ NH ₄ 3 umol L ⁻¹ NO ₃ ⁺ + 0.05 umol L ⁻¹ NH ₄	0.75 umol L ⁻¹ PO ₃ 0.185 umol L ⁻¹ PO ₃	Positive relationship with growth for <i>Fucus vesiculosus</i> (under low salinity)	1	(Nygård and Dring 2008)
		250 kg ha ⁻¹ yr ⁻¹	80 kg ha ⁻¹ yr ⁻¹	Positive total biomass response for <i>Suaeda</i>	6	(Kiehl, Esselink, and Bakker 1997)
		0.9 g kg ⁻¹ NPK with 14% N, 13% P and 13% K	0.9 g kg ⁻¹ NPK with 14% N, 13% P and 13% K	Positive aboveground biomass response of <i>Puccinellia maritima</i> and <i>Spartina anglica</i>	1	(Huckle, Marrs, and Potter 2002)
149.4 kg m ⁻² N (soil low marsh) 64.9 kg m ⁻² N (high marsh)		25 g m ⁻²		Positive response of high marsh species because they have greater	6	(Kuijper and Bakker 2012)

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
				salt tolerance at lower elevation		
		15 g m ⁻² yr ⁻¹ 30 g m ⁻² yr ⁻¹		Positive biomass response of <i>Puccinellia maritima</i> and <i>Suaeda maritima</i>	6	(Tessier and others 2003)
Vegetation used as an indicator of environmental conditions				<i>Elymus athericus</i> had a positive abundance response to presumed nutrient availability.	4	(Suchrow, Stock, and Jensen 2015)
1.9 – 31.6 µg cm ⁻³ ammonia-N; 0.009 – 3.213 µg cm ⁻³ NOx-N	3.2 – 40.2 µg cm ⁻³ labile P			<i>Atriplex portulacoides</i> positively related to NOx (also <i>Suaeda maritima</i> and <i>Cochlearia</i> spp. to a lesser extent). Evidence for a slight positive association for <i>Lysimachia maritima</i> with NH ₄ ⁺ . Positive association of <i>Spartina</i>	12 (although sulphide and redox potential not accounted for)	(Penk and others 2020)

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
				<i>anglica</i> with P, followed by <i>Triglochin maritima</i> and <i>Juncus gerardii</i> . Shannon diversity hump-shaped relationship with P.		
1.9 – 31.6 $\mu\text{g cm}^{-3}$ ammonia-N; 0.009 – 3.213 $\mu\text{g cm}^{-3}$ NO _x -N	3.2 – 40.2 $\mu\text{g cm}^{-3}$ labile P			Above ground biomass and above to below ground biomass positively related to NO _x - across and within assemblages. 6.6 fold increase in this ratio across N gradient. Within assemblages there was a positive relationship with NH ₄ ⁺ .	12 (although sulphide and redox potential not accounted for)	(Penk, Perrin, and Waldren 2020)
		10.05 g NaNO ₃ per 50 x 50cm subplot 7.95 g (NH ₄) ₂ SO ₄ per 50 x		Increased shoot frequency with inorganic nitrogen addition for species rare at beginning	9 (but note very limited replication and paper mentions a number of experimental artefacts)	(Jefferies and Perkins 1977)

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
		50cm subplot (nutrients added separately)		of experiment e.g. <i>Atriplex portulacoides</i> , <i>Aster tripolium</i> , <i>Suaeda maritima</i> , <i>Spergularia marina</i>	that compromise inference)	

Table 3. Range of nutrient values at which ‘negative’ impact on vegetation response and associated confidence (see Table 1 legend and Box 1 for further detail). Where cells are left blank, this is intentional.

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
85.54 (NH ₄) + 6.87 (NO ₃) mg kg ⁻¹ (Peat sediment)	4.05 mg kg ⁻¹ P (Peat sediment) 7.14 mg kg ⁻¹ P (Sand sediment)			Negative abundance relationship with N for <i>Spartina anglica</i>	6	(Cott, Chapman, and Jansen 2013)
21.63 (NH ₄) + 11.93 (NO ₃)mg kg ⁻¹ (Sand sediment)	4.58 mg kg ⁻¹ P (Mud sediment) 5.84 mg kg ⁻¹ P (Sand/Mud sediment)					
32.19(NH ₄) + 11.59 (NO ₃)mg kg ⁻¹ (Mud sediment)						
16.38 (NH ₄) + 1.16 (NO ₃) mg kg ⁻¹ (Sand/Mud sediment)						

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
		250 kg ha ⁻¹ yr ⁻¹	80 kg ha ⁻¹ yr ⁻¹	Negative aboveground biomass response for <i>Puccinellia</i>	6	(Kiehl, Esselink, and Bakker 1997)
149.4 kg m ⁻² N (soil low marsh) 64.9 kg m ⁻² N (high marsh)		25 g m ⁻²		Negative response by <i>Atriplex portulacoides</i> in the low marsh when subjected to herbivory	6	(Kuijper and Bakker 2012)
		6.1 mM NO ₃ and 0.9 mM NH ₄	1.3 mM P	Negative belowground biomass response of <i>Phragmites australis</i>	1	(Eller and Brix 2012)
13.91-29.82 mg kg ⁻¹ N (soil Spiekeroog) 21.1-33.64 mg kg ⁻¹ N (soil Westerhaver)	44.83-84.46 mg kg ⁻¹ plant available P (soil Spiekeroog) 94.77-224.77 mg kg ⁻¹ plant available P (soil Westerhaver)			Negative fine root biomass response to nutrients	4	(Redelstein and others 2018)
Vegetation used as an indicator of environmental conditions				Negative overall species richness response to presumed nutrient availability	4	(Suchrow, Stock, and Jensen 2015)

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
1.9 – 31.6 µg cm ⁻³ ammonia-N; 0.009 – 3.213 µg cm ⁻³ NOx-N	3.2 – 40.2 µg cm ⁻³ labile P			Species richness and Shannon diversity negatively related to NOx. Driven by strong negative associations for <i>Plantago maritima</i> , then <i>Armeria maritima</i> , <i>Spartina anglica</i> , <i>Juncus gerardii</i> , <i>Lysimachia maritima</i> and <i>Tripolium pannonicum</i> . <i>Salicornia</i> spp. negatively related to NH ₄ ⁺ . Shannon diversity hump-shaped relationship with P, with <i>Agrostis stolonifera</i> then <i>Salicornia</i> spp., <i>Puccinellia maritima</i> and <i>Suaeda maritima</i> having a	12 (although sulphide and redox potential not accounted for)	(Penk and others 2020)

Background concentrations / deposition (N)	Background concentrations / deposition (P)	Nutrient addition (N)	Nutrient addition (P)	Vegetation affected	Confidence	Reference
				negative association with P.		
1.9 – 31.6 $\mu\text{g cm}^{-3}$ ammonia-N; 0.009 – 3.213 $\mu\text{g cm}^{-3}$ NO _x -N	3.2 – 40.2 $\mu\text{g cm}^{-3}$ labile P			Below ground biomass negatively related to NO _x ⁻ , across and within assemblages	12 (although sulphide and redox potential not accounted for)	(Penk, Perrin, and Waldren 2020)
		10.05 g NaNO ₃ per 50 x 50cm subplot 7.95 g (NH ₄) ₂ SO ₄ per 50 x 50cm subplot (nutrients added separately)		Decreased shoot frequency with inorganic nitrogen addition for species common at beginning of experiment i.e. <i>Armeria maritima</i> .	9 (but note very limited replication and paper mentions a number of experimental artefacts that compromise inference)	(Jefferies and Perkins 1977)

One study from North America (Logan 2018) suggested that two dominant species (*Spartina patens* and *Spartina alterniflora*) showed different responses in terms of stem density, height and biomass to nitrogen loadings and also whether the nitrogen was in the water column or from upland sources. However, general additive models had relatively low percentage deviance explained, which the authors attributed to a lack of consideration of relationships with additional variables, such as salinity and competition (Logan 2018).

Comparison of two studies from an interior marsh in North Carolina, North America neatly showed how nutrient form can be important in determining vegetation response. Use of ammonium sulphate ((NH₄)₂SO₄) as the N source found no response in belowground biomass to fertilization (Davis and others 2017 as cited in Czaplá and others (2020)). In contrast, ammonium nitrate (NH₄NO₃) led to decreasing belowground biomass (Czaplá, Anderson, and Currin 2020). Indeed, according to Johnson and others (2016) (as cited in

Crosby and others 2021), the domination of nitrate in coastal waters may cause different responses than those seen in earlier fertilization experiments [in North America] that had primarily used ammonia-based fertilizers. These different forms may also have an impact on saltmarsh feature integrity as a whole: Geoghegan and others (2018) note that nitrate is a strong electron acceptor that has stimulated denitrification, increased litter respiration and decreased soil organic matter stabilisation (see also Bowen and others 2020).

As suggested above, it is not just marine concentrations of nutrients that can threaten saltmarsh feature integrity. In the recent review of empirical critical loads for N, Aazem and others (2022) suggest a new range for nutrient inputs to Atlantic salt marshes of 5-10 kg N ha⁻¹ yr⁻¹ (see also Aherne, Wilkins, and Cathcart 2021). This is well below the range previously set (20-30 kg N ha⁻¹ yr⁻¹) and indicates a change in the range by 15-20 kg N ha⁻¹ yr⁻¹ for both lower to mid and mid to upper saltmarshes. These critical load values are intended to protect marsh features from harm over the long-term and are generally set based upon experimental additions to vegetation communities (although recent updates for some systems e.g. forest understoreys have incorporated findings from gradient studies). Load values contrast with critical levels, which typically denote exposure over shorter periods of time, where exposures above the critical level cause harm to the organism.

Caveats and knowledge gaps

Beyond the caveats mentioned earlier in relation to different study approaches, we also note the following: in some instances, nutrients have not been directly measured but referred to other studies which have characterised local conditions (e.g. Dormann, Van Der Wal, and Bakker 2000). Furthermore, although we focus on nutrients for obvious reasons, the literature also noted that other factors can be more important (as further explored in Objectives [2](#) and [3](#)). In particular, salinity was sometimes a variable more strongly related to community composition (Cott, Chapman, and Jansen 2013; Suchrow, Stock, and Jensen 2015) and plant traits (e.g. biomass allocation in *Spartina alterniflora* MacTavish and Cohen 2017) than nutrient conditions. Inundation also had a greater effect on plant traits than nutrients in some cases (Cebrián-Piqueras and others 2021; Schulte Ostermann and others 2021).

Box 3: Objective 1 Summary

- Elevated nutrient levels, particularly nitrate, are associated with species compositional change. The identity of ‘winner’ and ‘loser’ species can depend on context and nutrient form (see Objectives 2 and 3) (robust evidence).
- In general, and in a community context, *Atriplex portulacoides* and *Elymus athericus* benefit from additional nitrate. *Plantago maritima* and *Armeria maritima* decline in response to additional nitrate (somewhat robust evidence).
- Additional nitrogen appears to improve salinity tolerance, allowing some species to move to lower marsh zones than they would typically be associated with (somewhat robust evidence).
- Addition of both N and P appears to speed up succession (somewhat robust evidence).
- Nutrient addition may also lead to ‘saltmarsh squeeze’. In this scenario, pioneer communities are smothered by macroalgae and upper marsh becomes dominated by terrestrial species, such as *Phragmites australis*. Evidence for squeeze being due to additional nutrients is lacking in the UK context (corroborative evidence).
- We could not assign fluxes/concentrations of nutrients at which compositional change occurred. This may partly be due to context dependency in response, but likely also due to background levels not being reported, a lack of causal pathway identification, and analyses not reporting threshold responses, were they to exist.

Objective 2: Collate the evidence for environmental (abiotic) factors that can affect the impact of elevated nutrients on saltmarsh species present in UK waters

We uncovered some evidence that suggested the impact of elevated nutrients, particularly N, depended on, or related to, other abiotic environmental context variables (Table 4). In general, there were few clear interactive effects i.e. few instances where the impact of elevated nutrients depended upon the level of other abiotic context variables. Instead, there were inter-relationships among variables, particularly covariation and association of vegetation communities with particular nutrient (and other abiotic) properties, much of which has been presented and discussed in regards to Objective 1: Collate the evidence of impact of nitrogen and phosphorus compounds on the condition of typical saltmarsh species present in the UK marine environment. The lack of interaction effect may be due to the fact interactions simply do not exist. However, it may also be due to many studies being survey-based rather than experimental, and not designed to test for such eventualities, even where theory suggests they may be expected.

Vegetation relationships with nutrients and other environmental factors

For N, inter-relationships, and occasional interactions, were uncovered for sediment type and deposition/accretion, temperature, salinity and turbidity/light. For P, its interaction and/or interdependence with salinity for determining vegetation response was shown to be important, across multiple studies (e.g. Penk, Perrin, and Waldren 2020). This included a relationship with residence time, such that fucoid biomass was sensitive to P dynamics in a river-dominated estuary in Ireland (the Blackwater) but not in an estuary open to a large marine P influence (the Argideen) (Ní Longphuirt and others 2016). However, in some instances, vegetation dynamics were shown only to relate to N and not P – for instance, the distribution of macrophytes in coastal pasture and arable ditches was strongly related to dissolved inorganic N and salinity, but not phosphate (Hinojosa-Garro, Mason, and Underwood 2008). Sometimes nutrients were added in combination and revealed potential interactions: in a laboratory experiment, Eller and Brix (2012) found that a *Phragmites australis* clone from a warmer climate (Algeria) showed greater plasticity in response to nutrient addition (N, P and potassium) than the clone from a Danish saltmarsh. The clone from the cooler Danish climate showed greater plasticity in response to elevated temperature (Eller and Brix 2012) (Table 2).

With sediment type, few studies directly compared responses to nutrients across types; rather the sediment type was often recorded by different references and this co-varied with vegetation, across and within saltmarsh vegetation zones (Redelstein and others 2018; Schröder, Kiehl, and Stock 2002; Cott, Chapman, and Jansen 2013; Penk and others 2020). For instance, Cott (2013) showed that some common saltmarsh species are absent on an ammonium-rich, but nitrate-poor peat substrate i.e. *Atriplex portulacoides* and *Spartina anglica*, whereas they were present in sand, mud and sand/mud sediment types. On the other hand, some species were only found on the ammonium-rich peat substrate e.g. *Juncus gerardii*. Vegetation zonation as a whole was far more marked on sandy substrate than those more species-rich communities found on peat substrate (Cott, Chapman, and Jansen 2013).

In addition, the type of sediment may interact with vegetation to influence when nutrients may affect vegetation dynamics. For instance, more clayey intertidal sediment is less stable for algal growth suggesting nutrient inputs will have a more limited impact (Ní Longphuirt and others 2016). For turbidity, this was only investigated in relation to seaweed species at the pioneer zone and showed that light limitation had a larger impact than available nutrients on seaweed growth of *Ulva* and *Enteromorpha* species in the Medway estuary (Aldridge and Trimmer 2009). The importance of turbidity was likely related to bed stress. The seaweed species were likely to be found in areas of low tidal energy, with this result suggested to be applicable to a range of relatively turbid, meso- and macrotidal estuaries (Aldridge and Trimmer 2009).

Sediment accretion may also be more important than the nutrients it brings in, in determining the invasion success of *Elymus athericus* in upper marsh or those areas that were previously pioneer marsh. Although van Wijnen and Bakker (1999) (cited in Nolte and others 2019) suggested that N addition sped up the succession of *Elymus*, Nolte and

others (2019), in an experiment that disentangled the impacts of nutrient addition from the sediment accretion, showed there was no impact of N fertilization except on biomass. This complements the suggestion by Ranwell that rate of nutrient supply was unimportant in determining vegetation response in salt marshes of southern England (Ranwell, 1964). Veeneklaas and others (2013) came to a similar conclusion when considering *Elymus* invasion in the Wadden Sea, suggesting natural spatio-temporal dynamics related to the age of the marsh had more to do with localised conditions of sediment accretion than regional-level atmospheric nutrient inputs.

Allred and others (2017) provide important arguments as to why you would expect interactions among salinity and nitrogen, for instance that salinity directly inhibits ammonium assimilation by plants and increasing ammonium fluxes to porewater from sediments. However, they also highlight that field evidence for such interactions are sparse (particularly in relation to belowground growth) (Allred, Liberti, and Baines 2017).

In other instances, the impact of nutrients on saltmarsh geomorphic processes was highlighted while noting the importance of plant response in determining geomorphic outcomes. Thus, in North America, Wigand and others (2009) suggested that accumulation of sediment in mineral soils will not be affected as much by the reduction in belowground biomass resulting from increased nutrient availability, as compared to organic soils. This is because the volume occupied by the mineral matter is high or because greater aboveground biomass will trap more sediments to compensate for the volume lost by diminished belowground organic C content. Wigand and others (2018) later suggested that further research is needed to better understand the interactions of nutrient enrichment with sea level rise, and the consequences for soil shear strength and stability, and thus indirect impacts on marsh vegetation beyond direct fertilization-N concentration effects.

Spatial context and wave action

Additional factors that can affect vegetation response to increased nutrient supply include the spatial context of marsh patches. For the latter, there was a clear interaction between location of the vegetation within the patch and relationships with nutrients on a tidal flat in a marine bay in the southwest Netherlands. Thus, sediment N and P concentrations (not pore water concentrations, which are typically variable) explained 84 % of the variation in aboveground biomass in centre zones but no such relationship existed with edge zones for *Spartina anglica*. Further analysis suggested these centre-patch relationships were driven by allochthonous organic matter deposition (Hemminga, van Soelen, and Maas 1998). Interestingly, North American evidence suggests that pore water concentrations of hydrogen sulphide (H₂S) can influence saltmarsh system response to nutrient enrichment. Thus, about 80% of variation in response of net ecosystem exchange (NEE) to fertilization was explained by H₂S. This study argued that highly sulfidic marshes, which tend to be those with low elevation, long inundation and residence times, and limited pore water exchange, may be more resilient to the negative impacts of increasing N availability (Czapla, Anderson, and Currin 2020).

Wave action was a variable which highlighted inter-relationships between it and nutrients, and the response in terms of saltmarsh feature status. Thus, Rogers (2019) found wave action and nitrate levels had the strongest correlation to losses of saltmarsh with the correlation to winter nitrate levels stronger than that to summer nitrate (in Bardsley and others 2020). Increased wave height (and inundation period) at lower elevation has also been associated with increased standing biomass and decomposition, but a reduction in stiffness and specific leaf area (Schulte Ostermann and others 2021).

Wave action may be associated with mass sediment deposition (e.g. in storm events) and therefore high nutrient inputs. Such disturbance events can have a large impact on succession. For instance, favouring the growth of more resilient species such as *Suaeda maritima* in the upper marsh (Tessier and others 2003), and/or creating conditions for the invasion of lower-mid marsh species to the upper marsh, such as *Atriplex portulacoides* (Suchrow, Stock, and Jensen 2015). In other words, a storm event may set succession back towards the pioneer stage. This contrasts with a response where upper marsh species appear able to tolerate the increased salinity of the lower marsh through increased N. The latter response may therefore depend on a lack of storm disturbance and thus no reset of succession.

Future environmental changes

Future environmental changes, beyond sea level rise, may affect how UK saltmarsh responds to nutrient addition. Although not direct evidence, Pennings and others (2002) discuss the fact that there was less change in vegetation in response to nutrient addition in those sites with longer growing seasons, suggesting that warmer temperatures could ameliorate the response to nutrients. On the other hand, climate change effects may be exacerbated by nutrient addition due to associated acidification, although this idea has not been clearly evidenced (Crosby and others 2021). Theodose and others (1999) corroborate the importance of temperature, noting that lower temperatures in more northern saltmarsh sediments leads to lower salinities which could make nutrient impacts more apparent.

Indeed, altered climate has been investigated in the US through multiple mesocosm experiments (e.g. Oczkowski and others 2016; Hanson and others 2016). Results from these mesocosm experiments suggested that when eutrophication (or inundation) has a damaging effect on belowground structures, the presence of an additional stress (such as drought) can exacerbate changes in belowground structure. Furthermore, the decline in *Ulva lactuca* in an American estuary was related to carbon imbalance triggered by warming temperatures and its inability to store N when available, in comparison to *Gracilaria tikvahiae* (Rivers and Peckol 1995).

Table 4. Relationships between abiotic context variables and saltmarsh vegetation response to increased nutrient availability. Not shown here but discussed in the main text are relationships between saltmarsh location within a patch and nutrients, and between wave action, sediment deposition events, elevated nutrients and succession.

Key abiotic environmental factor	Saltmarsh zone	Context dependency with / relationships e.g. covariation with N/P	Example species showing these responses	Confidence	Reference
Temperature	Upper / Transition Zone	Different populations from different climates can have variable growth plasticity in response to temperature and nutrients	<i>Phragmites australis</i>	1	(Eller and Brix 2012)
Sediment Type	Pioneer	More clayey intertidal sediment is less stable for algal growth. This could influence where nutrients have an impact.	<i>Ulva</i> spp.	6	(Ní Longphuirt and others 2016)
Sediment Type	Pioneer to upper marsh	Sandy marshes have lower nutrient levels and therefore tend to have larger fine root mass and particularly surface area root systems. Unclear what the response is to nutrient addition.	<i>Spartina anglica</i> dominated pioneer marsh; <i>Atriplex portulacoides</i> dominated lower marsh; <i>Elytrigia atherica</i> dominated upper marsh	4	(Redelstein and others 2018)
Sediment Type	Lower and Upper	After cessation and/or reduction in grazing, species composition depended upon	<i>Atriplex portulacoides</i> ; <i>Suaeda maritima</i>	4	(Schröder, Kiehl, and Stock 2002)

Key abiotic environmental factor	Saltmarsh zone	Context dependency with / relationships e.g. covariation with N/P	Example species showing these responses	Confidence	Reference
		whether sandier and low N (<i>Atriplex</i>) or clayier and high N (<i>Suaeda</i>). Sandy areas also less intensively grazed. Note only small proportion (5%) of variation in community composition attributed to these conditions; 47% depended on elevation i.e. salinity and hydrological gradient.			
Sediment Type	Transition	Peaty soils have higher water and organic matter content than sandy or mud sediment. Peat also associated with twice as high ammonium concentration, although nitrate was lower on the peat as compared to sand substrates. Greater forb and rush diversity and richness in such areas.	Multiple	6	(Cott, Chapman, and Jansen 2013)
Sediment Accretion	Pioneer to Upper	Contrasting results: Gradual, nutrient rich sedimentation causing elevation gain can create	<i>Elymus athericus</i>	6 4	(Nolte and others 2019)

Key abiotic environmental factor	Saltmarsh zone	Context dependency with / relationships e.g. covariation with N/P	Example species showing these responses	Confidence	Reference
		favourable conditions for <i>Elymus athericus</i> . But others have found this not to be significant.			(Veeneklaas and others 2013)
Sediment Accretion	Unclear – referred to all areas as ‘high marsh’	Sediment accretion changes seasonally and this is associated with changes in mineralisation of organic N which then leads to plant growth effects.	<i>Puccinellia maritima</i> ; <i>Atriplex portulacoides</i>	6	(Aziz and Nedwell 1986)
Sediment Accretion	Lower-Mid Marsh	As sediment is accreted <i>Puccinellia</i> may establish and gradually replace <i>Spartina</i> due to allocations of more resources to root production in low nutrient conditions. In this pot experiment, <i>Spartina</i> was shown to have a positive (facilitative) effect on <i>Puccinellia</i> growth at low nutrient concentrations, while <i>Puccinellia</i> was always competitive.	<i>Puccinellia maritima</i> ; <i>Spartina anglica</i>	1	(Huckle, Marrs, and Potter 2002)
Turbidity	Pioneer	Light limitation has a larger effect than available nutrients on seaweed growth,	<i>Ulva</i> spp. <i>Fucus</i> spp.	6	(Aldridge and Trimmer 2009)

Key abiotic environmental factor	Saltmarsh zone	Context dependency with / relationships e.g. covariation with N/P	Example species showing these responses	Confidence	Reference
		which could otherwise smother typical saltmarsh vegetation. Bed stress increases turbidity			
Salinity	All zones	Salinity often linked to moisture content, and this strongly explained zonation and biomass. Plots with low moisture, low salinity and low N have higher richness. However, drier and more saline conditions are associated with less N limitation in some instances.	Community response	6 6 4 4	(Cott, Chapman, and Jansen 2013) (Penk, Perrin, and Waldren 2020) (Suchrow, Stock, and Jensen 2015) (Andersen and others 2020)
Salinity	Upper	Observational surveys and structural equation modelling across coastal ecosystems (not just saltmarsh) shows groundwater to affect N dynamics that then impacts on plant growth traits, related to land use change	Community response	4	(Cebrián-Piqueras and others 2021)
Salinity	Transition	Macrophyte distribution in coastal pasture and arable ditches is strongly related to salinity and dissolved inorganic	Community response	9	(Hinojosa-Garro, Mason, and Underwood 2008)

Key abiotic environmental factor	Saltmarsh zone	Context dependency with / relationships e.g. covariation with N/P	Example species showing these responses	Confidence	Reference
		N concentrations. The higher the salinity, then richness, biomass and growth rate decline. Note that these dynamics are not related to phosphate.			
Salinity	Pioneer	Modelled reductions in phosphate led to a decrease in fucoid biomass in a river-dominated estuary (the Blackwater Estuary), as compared to the Argideen that has a large marine P influence.	Fucoids	6	(Ní Longphuirt and others 2016)
Salinity	Lower to mid and upper marsh	Under variable salinity and moisture conditions relationships between biomass and labile P weaker. Direction could vary depending upon location along P gradient.	Community response	6	(Penk, Perrin, and Waldren 2020)
Salinity	Upper	Ground water salinity and P availability affect growth allocation to specific leaf area and stem biomass at community level.	Community response	4	(Minden and Kleyer 2011)

Caveats and knowledge gaps

There was no research on the impact of heatwaves (either alone, or in interaction with eutrophication), but seasonal changes in succession are well-known while other impacts of climate change have been examined, at least in North America. Another knowledge gap is the impact of background N:P ratios on the response of saltmarsh to eutrophication. This was highlighted as particularly important in North American literature (e.g. Alldred, Liberti, and Baines 2017): “The nutrient-loading context of Long Island marshes may explain why the responses of plant root variables differed from those observed in some other studies. While DIN [dissolved inorganic nitrogen] had an effect on belowground biomass, we found no evidence of phosphate effects. This difference may result from low N:P ratio in sediment porewater, which never exceeded 15 for any of the sites included in our study, making it extremely unlikely these marshes are phosphorus limited (Verhoeven and others 1996). In marshes with lower phosphorus availability, nitrogen enrichment may cause plants to become phosphorus limited, and they may allocate more growth to roots to scavenge for phosphate (Turner 2011). The background nutrient supply ratios should be taken into context when comparing results of studies relating eutrophication to marsh vegetation.”

Box 4: Objective 2 Summary

- No UK or Irish empirical studies directly showed clear interactive effects in relation to nutrients and abiotic factors. A modelling study suggested that fucoid biomass dynamics in response to P could depend upon the estuary type i.e. whether it was open to a large marine influence or not (somewhat robust evidence).
- Sediment type, salinity, deposition/accretion, pH and temperature often co-varied with nutrients and differences in vegetation communities (robust evidence).
- In some cases, presumed impacts of nutrients on vegetation dynamics have actually been shown to be driven by accretion alone, rather than the nutrients (somewhat robust evidence)
- Together, these environmental responses suggest that altered nutrient conditions in certain contexts could lead to community change that affects the favourable conservation status of saltmarsh features - but this interpretation is speculative in the absence of further evidence
- Studies from elsewhere in Europe and North America highlight the potential for interactive effects, especially in relation to spatial patchiness, temperature and drought (robust to somewhat robust evidence)
- A key knowledge gap is how background nutrient ratios could affect saltmarsh response to additional nutrients, as well as interactions with future environmental changes

Objective 3: Collate the evidence for ecological (biotic) factors that can affect the impact of elevated nutrients on saltmarsh species present in UK waters

Competing autotrophs

Evidence was uncovered that suggested that the impact of elevated nutrients, particularly N, depended on, or related to, biotic environmental context variables (Table 5). We did not, however, find clear evidence from a UK context in relation to saltmarsh condition, saltmarsh life stage or surrounding vegetation. One reference from North America did suggest that northern New England saltmarshes respond differently to nitrogen runoff, as compared to those from further south along the eastern seaboard of the US, because of an inherently greater species diversity (Fitch, Theodose, and Dionne 2009) – but there was no direct test of this contention.

Evidence from Chichester Harbour suggests that competing autotrophs, through growth of macroalgae, putatively linked to sustained increases in nutrient loads, have led to the smothering of the pioneer marsh (Bardsley and others 2020). However, other than that report and advice from the Steering Group in relation to Langstone Harbour (also in the Solent), we did not find clear evidence in relation to effects of competing autotrophs on saltmarsh dynamics. Indeed, evidence from Ireland suggests that macroalgae dominance was strongly related to hydrological and substrate conditions rather than nutrients. Thus, lower residence time can reduce light competition from phytoplankton and lower proportions of silt and clay in the sediment provide a better substrate for algal growth (Ní Longphuirt and others 2016). These types of dynamics were also supported by Aldridge and Trimmer (2009) who found low bed stress and high turbidity, rather than nutrients, were the main limiting factors for estuarine growth of *Enteromorpha* and *Ulva* species. The Steering Group consider this to reflect the situation noted in the Introduction in relation to the Humber i.e. poor water quality with high nutrient loads but a lack of macroalgae response.

Grazers

We did uncover evidence that suggested that vegetation response to nutrients depended on grazers. However, in general and as with abiotic context, there were few clear interactive effects at least in the focal UK and European literature i.e. where the impact of increased nutrient availability depended upon the level of the biotic factor. Instead, inter-relationships among variables were more common. Examples of the importance of biota contributing to nutrient impacts can be seen with detritus, and with nutrient deposition by wading birds and (other) grazing fauna (Tessier and others 2003; Penk and others 2019). For instance, *Spartina* spp. detritus has been shown to encourage invasion by *Phragmites* (Ranwell 1964), potentially through increased elevation. Interestingly, the importance of grazers influencing ecosystem response to additional nutrients (specifically N) has recently

been highlighted in forest understoreys, as well as tundra ecosystems (Segar and others 2022 and references therein).

Across the focal evidence, and in the pioneer zone, it appeared that grazers had a stronger impact on vegetation dynamics than nutrient input. In the lower- to mid-marsh, grazers affected some species regardless of nutrient dynamics (e.g. *Salicornia*) (Schröder, Kiehl, and Stock 2002) while in others, N fertilization interacted with below-ground herbivory to slow down succession involving *Atriplex portulacoides* (Kuijper and Bakker 2012).

The presence of grazers can change which species are dominant for a given set of environmental conditions, sometimes related to nutrients. Thus, in the lower to mid marsh, grazing allows domination of *Puccinellia* and *Salicornia*. If grazing ceases, and in highly productive i.e. nutrient-rich conditions, *Suaeda maritima* replaces *Salicornia*. In well-drained marsh and upon grazing exclusion, *Atriplex portulacoides* quickly outcompetes *Puccinellia*, whose growth is also promoted by low nutrient enrichment of 15g (compared to *Suaeda* being promoted by 30g) (Tessier and others 2003). In the upper marsh, similar dynamics are observed, with a reduction in grazing pressure increasing species richness but decreasing evenness (i.e. certain species become more dominant at the expense of others whereas previously the distribution of species was more even). Thus, *Tripolium pannonicum*, *Atriplex portulacoides*, *Artemisia* and *Elymus athericus* increased in abundance while *Salicornia* decreased with grazing decline. Interestingly, and in distinction to the findings from south and east Ireland, *Atriplex* was favoured under low N conditions. Under high N conditions it was *Suaeda* (Schröder, Kiehl, and Stock 2002) and *Elymus athericus* (Suchrow, Stock, and Jensen 2015).

Multiple lines of evidence in North American studies did show clear evidence of interactions between nutrient levels and grazers. Using a combination of field experiments (including through insect removal and nitrogen addition) and surveys, Bertness and others (2008) showed that fertilisation initially increased plant productivity but eventually led to reduced plant biomass due to insect herbivory. Marsh nitrogen supply was a good indicator of herbivore damage to plant, with insects having minimal effect in marshes of low nutrient supply but suppressing primary productivity in nutrient-enriched saltmarsh (by up to 75%). Primary production could be underestimated in many sites if the pattern of increased consumption under high nutrient levels has been happening cryptically (Bertness and others 2008). Sala and others (2008) reinforced these findings, showing that insects reduced biomass increases under N addition by 45% while not affecting biomass in unfertilized control treatments (Sala, Bertness, and Silliman 2008). The potential underestimation of productivity could be of particular relevance to NE if the delivery of primary productivity is considered an important habitat function, and were insects or other grazers to play a role in UK marshes.

Grazers can also be important in influencing response to other abiotic conditions, as suggested for drained marshes. Clay thickness and topographic variation affected trait variation of *Elymus athericus* at an early successional stage, and herbivores promoted variation in height and flowering (Chen and others 2021).

Across trophic levels

Interestingly, Sala and others (2008) discuss how the impacts of top-down control of vegetation are complex, and may even be triggered by N. They note that a mass vegetation die-off in a south-eastern US marsh was triggered by grazers (and drought) – but not directly by the herbivores. Instead, the snail herbivore involved (*Littoraria irrorata*) opened up wounds in the plant tissue that allowed secondary fungal infection (see references cited in Sala and others 2008). Sala and others's (2008) work in a more northern saltmarsh failed to find such die off, or fungal-mediated pathways. This suggests that this process may be of limited relevance in UK waters. Indeed, Sala and others (2008) state that the intensity of disease mediated top-down control by small grazers may be regulated by climate and/or grazer identity that could co-vary with latitude. However, awareness of the potential impact for UK saltmarsh features of across-trophic level response to nutrient addition, especially in the light of climate change e.g. increased frequency and/or severity of droughts and/or changes to potential for fungal growth, could be important.

Although not directly involving nutrient manipulation, another experimental study across North American saltmarsh systems showed that predator impacts on vegetation and ecosystem function are not ubiquitous (Moore and Schmitz 2021). This could suggest that the triggering of top-down control of saltmarsh vegetation dynamics by increased nutrient availability is not going to occur across all systems.

Table 5. Key biotic factors found in the evidence review to affect saltmarsh response to nutrients

Key biotic environmental factor	Saltmarsh zone	Context dependency with / relationships with N/P	Example species showing these responses	Confidence	Reference
Grazers	Lower- to mid-Marsh	N fertilization interacted with herbivory to slow down succession	<i>Atriplex portulacoides</i>	6	(Kuijper and Bakker 2012)
Grazers	Lower- to mid-Marsh	Species replacement if nutrients are high and grazing ceases	<i>Suaeda</i> replaces <i>Salicornia</i> in highly productive marshes once grazing ceases	6	(Tessier and others 2003)

Caveats and knowledge gaps

We uncovered no evidence in relation to how saltmarsh condition, saltmarsh life stage or surrounding vegetation affect saltmarsh response to additional nutrients. The lack of information on current saltmarsh condition could be particularly important in regards to saltmarsh restoration. Prior conditions can be very important in determining system response to elevated nutrients.

Box 5: Objective 3 Summary

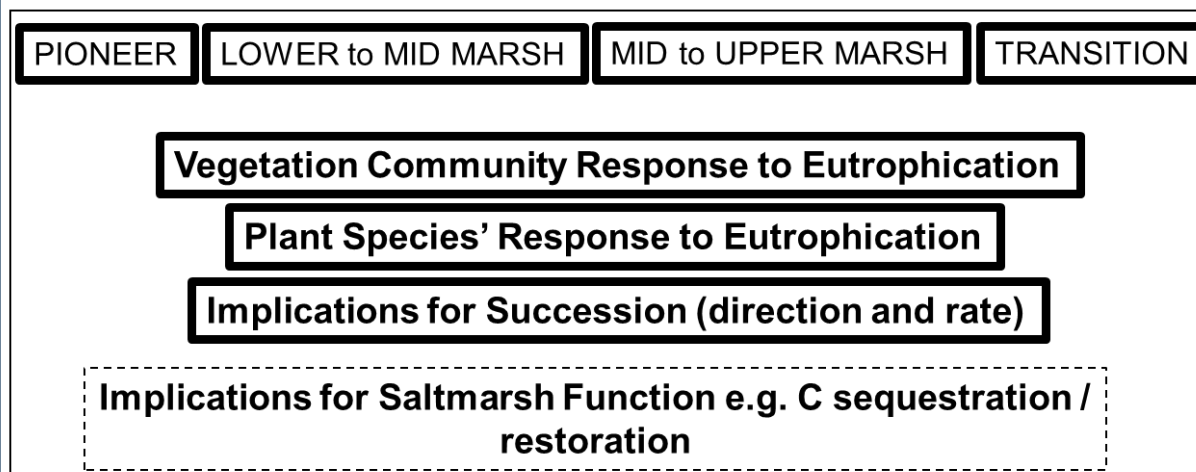
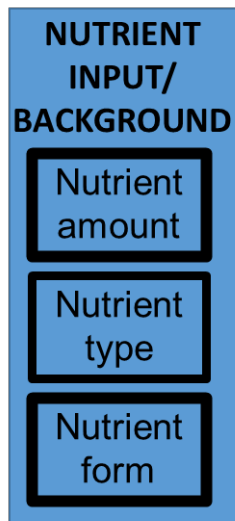
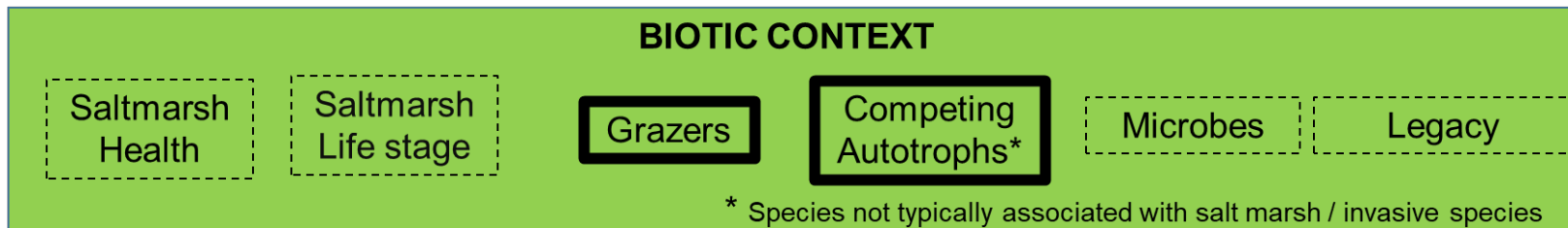
- Grazers can change which species are dominant for a given set of environmental conditions, not always including nutrients (robust evidence).
- Grazers may slow down the succession that would otherwise be induced by additional nutrient inputs - when the nutrient input is not due to e.g. a large scale deposition event that may otherwise reset succession (somewhat robust evidence).
- Dynamics of competing autotrophs e.g. *Ulva* spp. and *Enteromorpha* spp. at the pioneer zone appear more related to turbidity/bed stress as opposed to interactions with nutrients (somewhat robust evidence).
- Evidence from North America suggests that the presence of grazers can lead to a cryptic response to N. In other words, primary production could be underestimated in sites if a pattern of increased consumption under high nutrient levels has been happening without monitoring (somewhat robust evidence).
- Evidence from North America also suggested that addition of nutrients may cause a trophic cascade and affect vegetation indirectly e.g. through grazers introducing fungal pathogens (somewhat robust evidence). However, this pathogenic mode of action may be less relevant to the (currently) cooler climate of UK marshes (speculative).
- There is a lack of evidence as to how saltmarsh condition, saltmarsh lifestage and/or surrounding vegetation affect saltmarsh response to additional nutrients

Evidence gaps

Based on the literature we have assessed, we note the following evidence gaps (as also highlighted in Figure 3).

- The effect of biotic context variables on saltmarsh response to increased nutrient availability, especially saltmarsh condition, saltmarsh life stage, and surrounding vegetation.

- Studies based in the UK in general, particularly experiments, and especially those which consider other recent potential drivers of change and any interactions with nutrient availability. For instance, drivers such as temperature change, drought, and sea level rise. Understanding of saltmarsh vegetation response to marine acidification and altered atmospheric CO₂ is also lacking.
- Studies in the UK context that consider how multiple trophic levels (including decomposers, herbivores, predators) can be affected by increased nutrient availability to saltmarsh, over short- and long-time scales. Interactions between vegetation and these other ecosystem 'compartments' may have a strong bearing on feature-scale assessment, including successional processes and saltmarsh topographic change (e.g. bank collapse).
- Studies in the UK context that consider nutrient forms, background nutrient availabilities and nutrient input sources, including supply ratios. We also found few studies that considered the application of P alone, or considered the implications of additional dissolved organic N which may or may not be important depending on nutrient sources.
- The impact of nutrients on key species of the two Annex 1 saltmarsh habitats: *Sarcocornia perennis* (H1420 Mediterranean and thermo-Atlantic halophilous scrubs) and *Spartina maritima* (H1320 *Spartina* swards, *Spartinion maritimae*).
- Relative importance of nutrients in comparison to other potential drivers of vegetation change.



Long vs short term response

Multi-trophic response

Cryptic response
e.g. eutrophication shows no apparent vegetation growth response because of increased herbivory

Complex causal pathways
e.g. eutrophication causes marsh die-off through fungal infection from snail herbivory (US example)

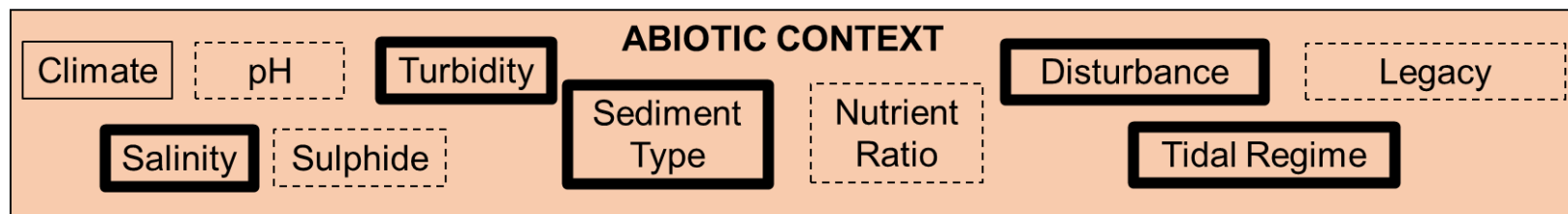


Figure 2. An amendment to Figure 1 highlighting evidence gaps (boxes with dashed lines), and evidence from the UK, Irish or other European context (solid wide continuous black lines). Evidence that we uncovered only in relation to the North American context is shown through normal text in boxes with thin continuous black lines i.e. in relation to climate. As noted in the main text, clear interactive effects were rare. Instead, some of the evidence denoted by these boxes shows where there was covariation in nutrient properties, vegetation response and abiotic/biotic context variables, hence why the blue box has been amended to read “Nutrient input / background”. We have also added an “Important Dimensions” box, which highlights evidence, mainly from experiments in the North American context, that long vs short-term, multi-trophic, cryptic, and/or complex causal pathway responses to nutrient addition may also be involved in plant species’ and vegetation community trajectories of change. Although not reviewed herein, our evidence screening suggested that additional nutrients may affect ecosystem response (e.g. carbon sequestration) through direct and indirect pathways (dashed outline box).

Targeted future research

Suggestions for targeted future research neatly follow the evidence gaps revealed by our rapid evidence assessment. In no particular priority order, we would recommend that future research in the UK Natural England context of saltmarsh vegetation response to nutrients consider the following aspects:

- The interactions of nutrient enrichment with sea level rise and consequences for soil-shear strength and stability, and thus indirect impacts on marsh vegetation beyond direct nutrient fertilization / concentration effects (see also Wigand and others 2018)
- Consideration of biotic context variables and how they influence response to nutrient enrichment. This may be particularly important in the context of saltmarsh restoration as the extent of degradation in an existing site could influence how restoration progresses in the context of nutrient inputs and other potential drivers of change.
- Related to the above, research on multiple trophic level responses to nutrient enrichment.
- Alldred and others (2017) identified that the interaction between salinity and nutrient enrichment is poorly known, especially for belowground growth. Understanding this could be very important, in the context of saltmarsh feature stability.
- Additional research is needed to explore the spatiotemporal repercussions of multiple stressors, especially across different salt marsh typologies e.g. differing elevation capital, those with peat- or sediment-based predominant elevation gain mechanisms, macrotidal or microtidal, and others (Crosby and others 2021).

- Quantification of nutrient stress to saltmarsh ecosystems through consideration of all input pathways i.e. concentrations in the marine environment and fluxes from terrestrial habitats and the atmosphere.
- Linked to the above point, development of a metric of nutrient pressure that can account for different nutrient inputs to saltmarsh plants and vegetation communities, as well as consideration of background environmental and ecological conditions at any given marsh.

We would also recommend that any observational surveys try to maximise gradient length and orthogonality in possible driving variables (including through the adoption of multi-country work where necessary) so as to accurately assess the direction and magnitude of nutrient impacts.

In the same vein, ideally experiments need to be conducted at appropriate scales to elucidate feature-scale impacts of nutrient addition while revealing mechanisms of change. It was noticeable that the UK has a lack of experiments relating to nutrient impacts on saltmarsh systems, compared to parts of Europe and especially North America. Experiments could also consider species removal treatments to understand interactions among species within the frame of nutrient enrichment. Inspiration for these could be gained from North American research e.g. Tyrrell and others (2015) examined the impact of saltmarsh fucoids on *Spartina alterniflora* abundance, production and decomposition, and sediment dynamics.

The sooner appropriate experiments can be implemented the better, given observations in North America point to the importance of differences between short- and long-time scales in response of saltmarsh to nutrient enrichment.

Natural England, and other interested parties, could also consider how co-ordinated approaches may shed light on saltmarsh response to nutrients. Thus, Watson and others (2014) combined inundation experiments, field surveys and LiDAR (Light detection and ranging) datasets to develop elevation – productivity relationship and ask what happens with changing water column nutrients, precipitation and elevation. In their North American case, they found that nutrient enrichment adversely affects peat formation (Watson and others 2014).

Overall, the targeted future research needs to be aimed at achieving NE's objective of moving towards a feature-based assessment of saltmarsh in the light of estuarine water quality conditions. However, we emphasize that saltmarsh feature condition will be affected by more than water quality conditions. In other words, nutrient inputs from terrestrial and atmospheric sources, and other driving variables need to be considered.

Beyond the scope of the assessment, but an important area of research, is understanding nutrient impacts on other aspects of saltmarsh ecology and function (e.g. carbon sequestration, water filtration, marsh elevation processes (e.g. Anisfeld and Hill 2012)), and the absolute and relative importance of direct and indirect impact pathways on these

processes (e.g. through vegetation or microbial community composition change) (see Suding and others 2008).

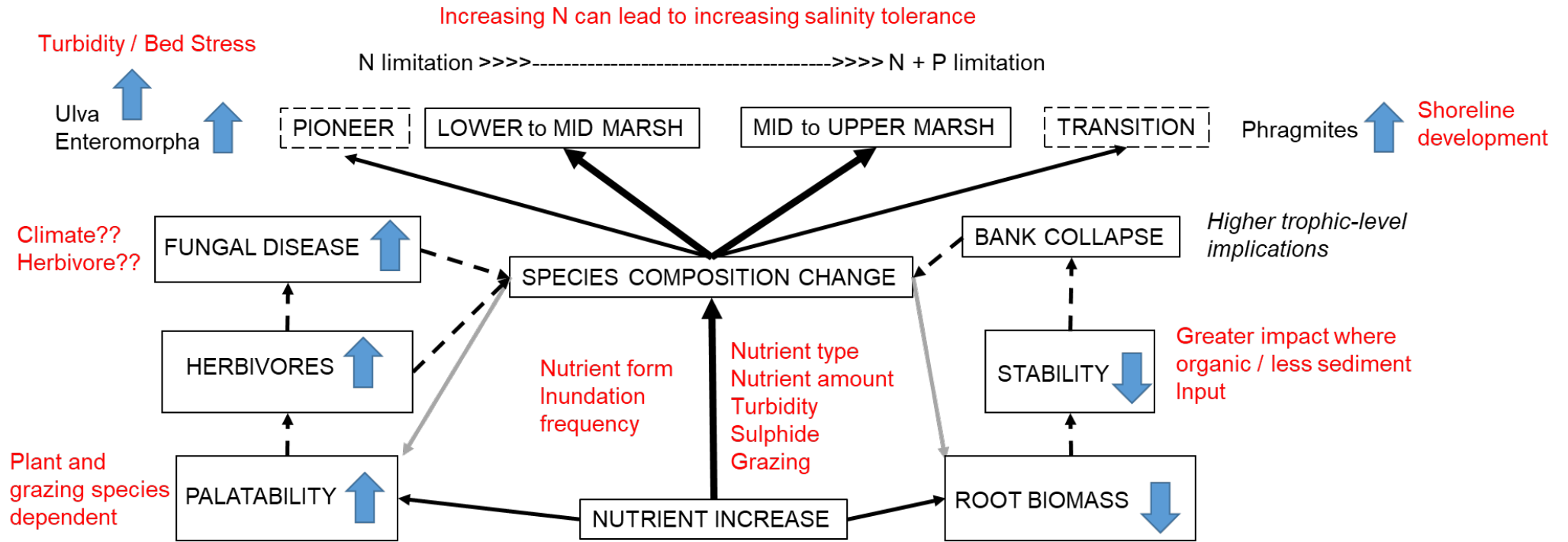
Ultimately, the goal of NE appears to align with the conclusion of Fitch and others (2009) in their consideration of nitrogen dynamics: “Continued monitoring of soil and plant nitrogen variables and aspects of plant community structure should occur in tandem with future estuarine eutrophication assessments. Water column nitrogen availability and utilization can then be linked with that of the saltmarsh, providing an integrated view of marsh estuarine response to eutrophication”

Conclusion

This rapid evidence assessment suggests the context of a given saltmarsh will potentially influence its response to additional nutrients. The response may further depend on what nutrient forms are present in the marine and terrestrial environment, and the sources from where they derive. However, the bulk of evidence from a UK-context at this time is observational survey-based, often without clear investigation of additional covariates which could influence vegetation dynamics. This means that although there can be clear associations between vegetation communities, some individual species and nutrients, causality of the relationships remains unquantified and uncertain.

The evidence we have uncovered, not just from a UK context, suggests that the processes through which saltmarsh features could respond to nutrients can be complex (Figure 4).

EUTROPHICATION EFFECTS ON SPECIES & VEGETATION COMMUNITIES



LEGEND	
<p>————→ Direct nutrient effect on vegetation</p> <p>- - - - - Indirect nutrient effect on vegetation</p> <p>————→ Feedbacks of species composition on other processes</p>	<p>----- Nutrient-induced saltmarsh "squeeze"</p> <p>XXXX Context dependent variables influencing magnitude of compositional change</p>

Figure 3. Species composition change in different saltmarsh zones in response to nutrient increase can be direct (centre of diagram, continuous arrows), and evidence from across the globe suggests it can depend on other variables (red text). Nutrients can also influence species properties (e.g. root biomass, palatability) that then influence other ecosystem properties with consequences for communities and saltmarsh feature integrity. This is an indirect pathway by which nutrients affect species composition (dashed arrows). The magnitude of impacts (indicated with blue arrows) likely also depends on context variables (red text). Note that nutrients have also been implicated in ‘saltmarsh squeeze’ (grey dashed box in the pioneer and transition zone).

The available evidence, from a UK-context, does not allow a clear quantification of the levels and forms of nutrient at which different vegetation zones in the saltmarsh will be adversely affected, and under what abiotic and biotic conditions. However, evidence available from elsewhere suggests nutrients can affect the favorable conservation status of this important habitat feature, over short- and long-timescales. Although not reviewed by this assessment, vegetation change can indirectly affect saltmarsh functional response to nutrients. Nutrient increase can thus affect the delivery of ecosystem services derived from these vegetation communities, such as carbon sequestration, water filtration and habitat provision. Based on the evidence gaps revealed by our assessment, a number of valuable lines of research have been suggested. Successful implementation of these research lines, through targeted experiments and representative observational surveys, should help Natural England achieve its aim of understanding nutrient impacts on saltmarshes at an appropriate scale, over the short- and long-term.

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Appendix 1

Agreed search terms

Species and community context

TOPIC = (saltmarsh* OR "salt marsh*" OR "pioneer zon*" OR "low-mid marsh*" OR "low* mid* marsh*" OR "upper marsh*" OR "transition zon*" OR Salicornia OR glasswort OR samphire OR "Spartina maritima" OR "cord-grass" OR "Spartina anglica" OR "common cord-grass" OR "Spartina alterniflora" OR "smooth cord-grass" OR "Sarcocornia perennis" OR "Arthrocnemum perenne" OR "perennial glasswort" OR "Suaeda maritima" OR "annual sea-blite" OR "Suaeda vera" OR "shrubby sea-blite" OR "Puccinellia maritima" OR "common saltmarsh-grass" OR "Puccinellia distans" OR "Northern saltmarsh-grass" OR "Aster tripolium" OR "Tripolium pannonicum" OR "sea aster" OR "Triglochin maritima" OR "sea arrowgrass" OR "Plantago maritima" OR "sea plantain" OR "Atriplex portulacoides" OR "sea-purslane" OR "Spergularia maritima" OR "Spergula marina" OR "lesser sea-spurrey" OR "Festuca rubra" OR "red fescue" OR "Juncus gerardii" OR "saltmarsh rush" OR "Armeria maritima" OR "thrift" OR "Agrostis stolonifera" OR "creeping bent" OR "Limonium vulgare" OR "common sea lavender" OR "Limonium binervosum" OR "rock sea-lavender" OR "Limonium humile" OR "lax-flowered sea lavender" OR "Parapholis strigosa" OR "sea hard-grass" OR "Glaux maritima" OR "sea-milkwort" OR "Seriphidium maritimum" OR "Artemesia maritima" OR "sea wormwood" OR "Juncus maritimus" OR "sea rush" OR "Blysmus rufus" OR "saltmarsh flat-sedge" OR "Eleocharis uniglumis" OR "common spike-rush" OR "Eleocharis parvula" OR "dwarf spike-rush" OR "Leontodon autumnalis" OR "autumn hawkbit" OR "Carex flacca" OR "glaucous sedge" OR "Carex extensa" OR "long-bracted sedge" OR "Frankenia laevis" OR "sea-heath" OR "Inula crithmoides" OR "golden samphire" OR "Sagina maritima" OR "sea pearlwort" OR "Elytrigia atherica" OR "Elymus athericus" OR "sea couch" OR "Elytrigia repens" OR "Elymus repens" OR "couch" OR "turf fucoids" OR "Fucus cottonii" OR "Schoenus nigricans" OR "black bog-rush" OR "black sedge" OR "Filipendula ulmaria" OR meadowsweet OR "Althaea officinalis" OR "marsh mallow" OR "Iris pseudacorus" OR "yellow iris" OR "Phragmites australis" OR "common reed" OR "Bolboschoenus maritimus" OR "sea clubrush" OR "Scirpus tabernaemontani" OR "Schoenoplectus tabernaemontani" OR "grey club-rush" OR "Euphrasia heslop-harrisonii" OR "Euphrasia foulaensis" OR "Phalaris arundinacea" OR "reed canary grass" OR "Elytrigia juncea" OR "Elytrigia pungens" OR "Elytrigia farctus" OR "sand couch" OR "Cochlearia officinalis" OR "common scurvygrass" OR "scurvy-grass" OR "spoonwort" OR "Cochlearia anglica" OR "English scurvygrass" OR "long-leaved scurvy grass" OR "Bostrychia scorpioides" OR "macroalgae" OR "Enteromorpha")

Relevant (bio-)geographical area

TOPIC = ("UK" OR "United Kingdom" OR "England" OR "English" OR "Wales" OR "Welsh" OR "Scotland" OR "Scottish" OR "Northern Ireland" OR "Northern Irish" OR "British" OR

“Britain” OR “Great Britain” OR “Eire” OR “Ireland” OR “Irish” OR “German” OR “Germany” OR “France” OR “French” OR “Netherlands” OR “Dutch” OR “Holland” OR “Belgium” OR “Belgian” OR “Denmark” OR “Danish” OR “Norway” OR “Norwegian” OR “temperate”)

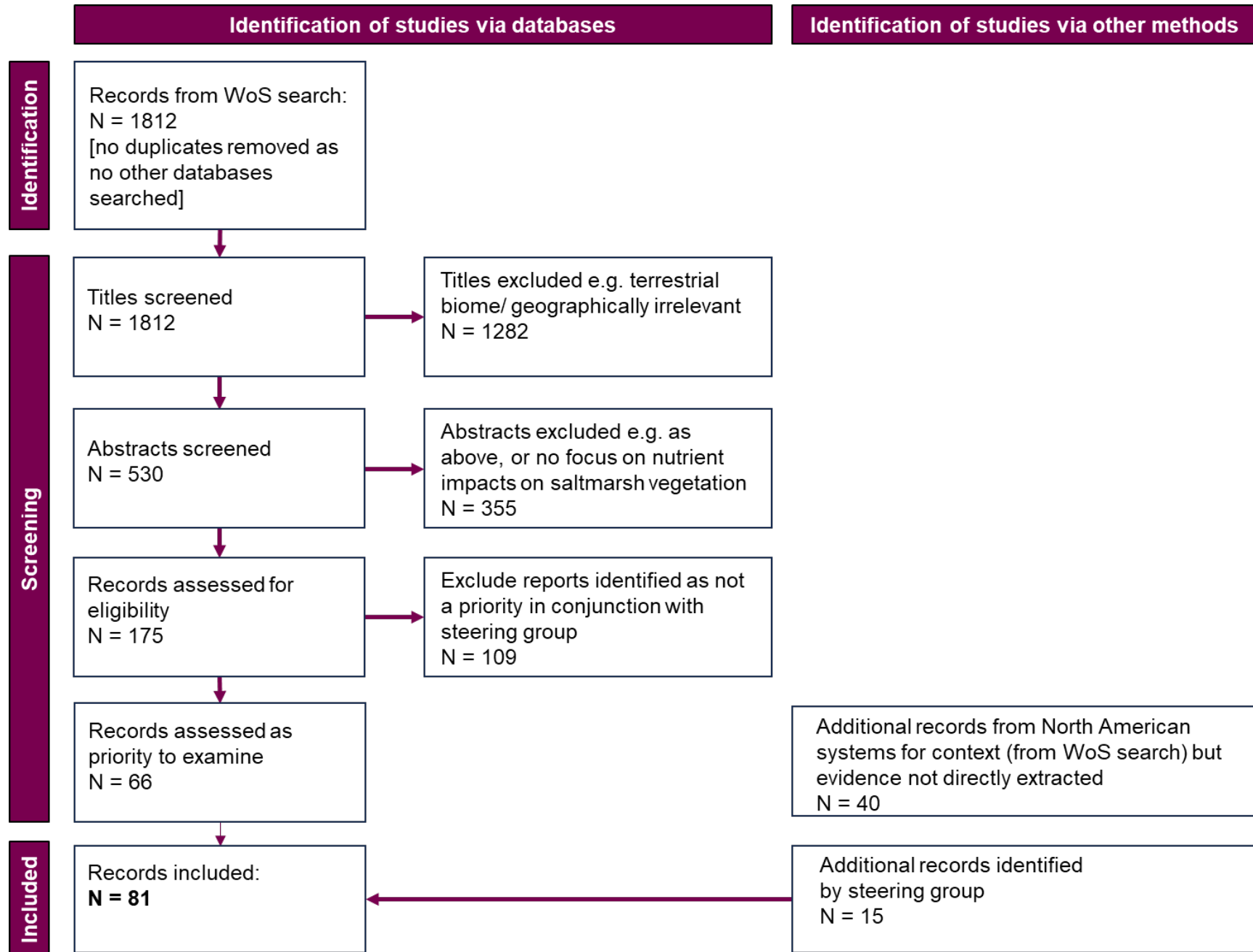
Target explanatory variables

TOPIC = (“nutr* enrichment” OR “nutr* load*” OR eutroph* OR “DIP” OR “DIN” OR nitr* OR phos* OR nutr* OR “water quality”)

As noted in the main text, we conducted the search, across all available years (our earliest result was from 1964) and with UKCEH access levels, on 23rd December 2022, exporting results to a spreadsheet. Please note that different access levels may mean that repeat searches by other organisations may lead to earlier/other results being uncovered, while the latest date above allows searches to be repeated to uncover new sources of evidence.

Process for identifying and screening studies

Figure A1.1: Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) diagram showing the process for identifying and screening potentially relevant studies



Appendix 2

Evidence summary tables

Table A2.1: Nutrients and methods across the different saltmarsh zones from the extracted evidence

Zone	N not P	N not P	N not P	P not N	P not N	P not N	N and P	N and P	N and P	Other	Other	Other	TOTAL
METHOD	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab	
Pioneer	1	6	2	0	0	0	0	8	0	0	4	0	21
Lower to mid marsh	6	7	4	0	0	0	1	7	1	0	5	0	31
Upper marsh	7	6	2	1	0	0	1	6	0	1	5	0	29
Transition zone	0	5	1	0	0	0	2	6	1	0	5	0	20
TOTAL	14	24	9	1	0	0	4	27	2	1	19	0	101

Table A2.2: Number of instances in which nutrient forms were applied or measured across saltmarsh zones and methodological approaches

Zone	Nitrate	Nitrate	Nitrate	Ammonium	Ammonium	Ammonium	DON	DON	DON	DIP	DIP	DIP	DOP	DOP	DOP	TOTAL
METHOD	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab	
Pioneer	1	7	2	0	6	1	0	3	0	0	5	0	1	3	0	29
Lower to mid marsh	5	7	2	2	6	1	0	3	0	2	5	0	1	3	0	37
Upper marsh	6	5	2	3	5	1	0	2	0	3	4	0	0	2	0	33
Transition zone	1	6	2	1	6	1	0	2	0	1	5	1	0	2	0	28
TOTAL	13	25	8	6	23	4	0	10	0	6	19	1	2	10	0	127

Table A2.3: Number of instances where references considered saltmarsh species' response to nutrients. Note these species (and some additional species referred to in the main text Species missing evidence subsection) may have been noted/involved in references that considered vegetation community response to nutrients. Due to time constraints, such evidence was not extracted in this table. Where cells are left blank, this is intentional.

Species name (focal species)	N only			P only			N + P		N+P	Other		Other
	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab	Field-exp	Field - survey	Lab
<i>Agrostis stolonifera</i>								2				
<i>Armeria maritima</i>								2				
<i>Aster tripolium</i> or <i>Tripolium pannonicum</i>	2	1					1	2			1	
<i>Atriplex portulacoides</i> or <i>Halimione portulacoides</i>	4	4					1	2	1		1	
<i>Bolboschoenus maritimus</i>								1			1	
<i>Cochlearia officinalis</i>								2				
<i>Elytrigia atherica</i> or <i>Elymus athericus</i>	4	3	1				1					
<i>Elytrigia pungens</i> or <i>Elymus pungens</i>	1											
<i>Elytrigia repens</i> or <i>Elymus repens</i>		1									1	
<i>Enteromorpha</i> or <i>Ulva</i>			1				1	1	3			1
<i>Festuca rubra</i>	2	2					2	2		1	1	
<i>Glaux maritima</i> or <i>Lysimachia maritima</i>	1						1	2				
<i>Juncus gerardii</i>	1	1						2			1	
<i>Juncus maritimus</i>								2				
<i>Limonium humile</i>								2				
<i>Limonium vulgare</i>	1											
<i>Phragmites australis</i>		1					1	3	2		3	1

Species name (focal species)	N only	N only	N only	P only	P only	P only	N + P	N + P	N+ P	Other	Other	Other
<i>Plantago maritima</i>	1							2				
<i>Puccinellia maritima</i>	2	4	1				2	2		1	1	
<i>Sagina maritima</i>									1			
<i>Salicornia</i>	2	1					1	2				
<i>Scirpus tabernaemontani</i> or <i>Schoenoplectus tabernaemontani</i>							1	2	1		1	
<i>Seriphidium maritimum</i> or <i>Artemesia maritima</i>		1									1	
<i>Spartina alterniflora</i>		2									1	
<i>Spartina anglica</i>	2	2	2					3				
<i>Spergularia maritima</i> or <i>Spergula marina</i> or <i>Spergularia media</i>	2						1	2		1		
<i>Suaeda maritima</i>	2	1					2	2	1	1	1	
<i>Triglochin maritima</i>	4		1					2				
turf furoids		1									1	

