

**Unravelling Ecological Connectivity and Natural Capital in
Essex's Salt Marshes**

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A thesis submitted for the degree of Master of Science (by Dissertation) in
Biological Sciences

School of Life Sciences

University of Essex

Date of submission for examination July 2026

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Abstract

Temperate estuarine salt marshes provide important ecosystem services, including carbon storage, carbon sequestration, nutrient removal, flood protection and biodiversity support. While natural capital assessments commonly consider habitat extent and condition, the influence of habitat connectivity on ecosystem service provision remains poorly understood, particularly within temperate estuarine systems. Furthermore, it is unclear how the spatial framework used to define the landscape influences estimates of structural connectivity.

This thesis investigated the relationships between structural connectivity and natural capital within the Blackwater and Colne estuaries, Essex, UK, using salt marshes as a case study. Structural connectivity was quantified using landscape metrics describing habitat area, patch isolation, patch cohesion and patch geometry. These metrics were compared with spatially explicit natural capital indicators representing carbon storage, carbon sequestration, nitrogen removal, wave attenuation and species richness. A second analysis examined how connectivity metrics varied across four spatial frameworks: the whole estuary, Water Framework Directive water bodies, nutrient management zones and Shoreline Management Plan policy units.

Habitat area showed the strongest and most consistent positive relationships with carbon storage, carbon sequestration and wave attenuation under current conditions, while greater patch isolation was generally associated with lower ecosystem service provision. In contrast, patch cohesion and shape exhibited weaker and less consistent relationships with natural capital indicators. Under a future habitat creation scenario, these relationships largely disappeared, reflecting reduced spatial variability and the

assumptions underlying projected ecosystem service estimates. Structural connectivity metrics were also highly sensitive to analytical scale, with finer spatial frameworks revealing greater heterogeneity than broader landscape-scale assessments.

These findings demonstrate that habitat extent remains the strongest predictor of several natural capital indicators, while structural connectivity provides complementary information regarding habitat configuration and fragmentation. The study highlights the importance of considering analytical scale when quantifying connectivity and demonstrates how landscape ecological approaches can strengthen natural capital assessment, habitat restoration planning and coastal management within temperate estuarine ecosystems.

Chapter 1

Literature Review

1. Introduction

Temperate estuaries represent dynamic and highly productive interfaces between land and sea. These seascapes are important for global biodiversity and provide many valuable benefits to human societies. This first chapter specifically sets the scene for analyses focused on the Blackwater and Colne estuaries in Essex, UK (a temperate seascape). By exploring the concept of ecosystem services and natural capital, outlining the history of landscape habitat connectivity, and examining current measurement methodologies for seascape-scale habitat connectivity, this review seeks to highlight the current knowledge base on seascape-scale habitat connectivity and natural capital accounting, particularly in the context of understanding the relationship between habitat connectivity and natural capital in temperate estuaries.

1.1. Ecosystem Services

1.1.1. The Concept of Ecosystem Services

Ecosystem services are defined by Natural England (2012) as ‘the benefits society gets from the natural environment’. More recently, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019) defines ecosystem services - or "nature's contributions to people" - as the diverse benefits that nature provides to people, which are shaped by social, cultural, and ecological contexts. These services encompass a wide range of contributions, including clean water, food production, climate regulation, and recreational opportunities that support mental wellbeing. Before the ecosystem service concept, the environment and people were considered separately

- this concept not only shows a change in thinking, but it brings to the forefront the interconnectedness of human well-being with the natural environment. The Millennium Ecosystem Assessment, a United Nations initiative, codified ecosystem services and categorised the benefits into four main groups: provisioning, regulating, cultural, and supporting services (Parliamentary Office of Science and Technology, 2007). More recently, the development of the Common Classification of Ecosystem Services (CICES), led by the European Environment Agency (version 5.2 was released in 2023), aimed to create a unified and globally accepted classification of ecosystem services. Notably, the CICES framework integrates and refines the Millennium Ecosystem Assessment (2003) and The Economics of Ecosystems and Biodiversity (TEEB 2010) classifications, grouping ecosystem services into three main categories: provisioning services, regulation and maintenance services, and cultural services. Provisioning services include tangible resources like food and water, while regulating services involve processes such as climate control and flood protection. Cultural services offer non-material benefits such as recreation and spiritual fulfilment. Ecosystem functions (or supporting services if using the Millennium Ecosystem Assessment), such as nutrient cycling and soil formation, underpin the other three categories. It's important to note that some ecosystem services may span multiple categories. For instance, water filtration can be considered both a provisioning service (providing clean water) and an ecosystem function (maintaining water quality for other processes). This is where the Millennium Ecosystem Assessment came under scrutiny as the inclusion of supporting services as a parallel category risked double-counting service contributions, since these processes (e.g., nutrient cycling) enable the other services; CICES addressed this by reclassifying supporting services as

ecosystem functions (Haines-Young and Potschin, 2009). The three CICES categories of ecosystem services provide a framework for understanding nature's contributions to humanity.

Ecosystem services are often confused with ecosystem functions, but there is a crucial distinction: Ecosystem functions are the underlying ecological processes and interactions that occur within an ecosystem, such as nutrient cycling, primary production, and trophic interactions (Paterson et al., 2012) (Table 1.1). Ecosystem functions can be described as the core ecological interactions that keep ecosystems operating (the “working parts”), such as energy flow, nutrient cycling, habitat formation, and species interactions. Ecosystem services, in contrast, are the human-relevant outcomes that arise when those functions support things people value. For example, primary production (an ecosystem function) by seagrass meadows contributes to the ecosystem service of carbon sequestration. Similarly, the filtering capacity of salt marsh plants (an ecosystem function) directly provides the ecosystem service of water purification. Therefore, ecosystem functions are the biophysical processes that underpin the delivery of all ecosystem services. Understanding this relationship is vital for effective management, as degrading functions inevitably diminishes the services they support. Ferraro et al., (2025) criticize the ecosystem service framework, illustrating how its human-centric perspective can raise ethical concerns and diminish the value of conservation efforts that do not directly result in service provision. Instead, they advocate for an ‘ecosystem functions’ framework, which more effectively captures the intricacies and complexities of the natural world and enables holistic consideration in management and policy.

Table 1.1. CICES categories of ecosystem services and their relevance to temperate estuaries.

Ecosystem Service Category	Definition	Examples in Temperate Estuaries	Key Measurement Approaches
Provisioning	Tangible products obtained from ecosystems.	Seafood, edible salt marsh plants, genetic resources for aquaculture.	Catch statistics, resource inventories, biomass assessments, habitat suitability models (Barbier, 2013).
Regulating & Maintenance	Benefits from the regulation of ecosystem processes.	Water filtration by salt marshes, shoreline stabilisation, flood and storm surge protection, carbon sequestration in sediments.	Water quality monitoring (pollutant levels, nutrient loads), hydrological modelling, flood attenuation, carbon flux measurements.
Cultural	Non-material benefits from ecosystems.	Recreational fishing, boating, swimming, birdwatching, aesthetic value of coastal landscapes, cultural heritage associated with estuaries, tourism.	Visitor counts, surveys of perceived value, economic valuation of tourism, mapping recreational areas.
Ecosystem Functions	Processes and habitats necessary to	Nutrient cycling, primary production, nursery grounds for fish and	Biomass production, nutrient cycling rates, biodiversity indices,

	produce all other services.	invertebrates, habitat for migratory birds.	habitat mapping, species abundance surveys (European Environment Agency, 2020).
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1.1.2. The Scale of Ecosystem Services

Ecosystem services can be considered across a range of spatial scales, from the local scale - such as the carbon sequestering ability of a single patch of salt marsh - to the global scale, where the global ocean supports the carbon cycle. Understanding the spatial scale of ecosystem services is critical for identifying beneficiary communities, accurate service valuation, and accounting. This is especially true in dynamic environments like wetlands, estuaries and marine ecosystems, where sediment transport and water exchange create heterogeneous environments and service provision varies across local and regional spatial scales, as well as temporal scales (Koch et al., 2009; Messié et al., 2023). Adopting landscape or seascape-scale thinking is essential to capture these spatial variations and their socio-ecological linkages.

1.1.3. The Measurement of Key Ecosystem Services

In temperate estuaries, approaches to measuring key ecosystem services differ across the estuarine system, reflecting variation in habitat type, position along the estuarine gradient, assessment scale, data accessibility, and available resources (including funding, equipment, and expertise).

1.1.3.1 Flood Protection

Salt marshes are among the most important temperate estuarine habitats for providing natural flood protection and mitigating storm surges (Möller et al., 2014). One method to effectively assess their protective potential is to quantify wave exposure across the estuary (using both historical and projected maximum water levels); then estimate maximum wave heights by measuring key variables such as fetch distance, wind speed, wind direction, and wind duration. Once wave exposure is calculated, wave attenuation can be calculated by comparing wave heights at the back (landward edge) of the salt marsh with those that would be present if the marsh were absent. This ratio provides a quantitative measure of wave attenuation, reflecting the proportion of wave energy dissipated by the marsh (Rogers and Möller, 2019). This method offers a practical and scientifically robust approach to evaluating the flood defence function of salt marshes. Additionally, the vegetative structure of the marsh could be considered; Möller et al. (2014) demonstrated that during storm conditions at high tide, salt marsh vegetation can reduce wave heights by up to 60% more than unvegetated areas, highlighting the physical role of vegetation in dissipating wave energy and stabilising sediment.

Salt marshes that protect a coastal town or village are likely more valuable to society than those that protect low agricultural quality fields, as the presence of the marsh directly benefits people and infrastructure. Recognising this, Gilbertson et al. (2020) developed an index to identify areas across the UK where salt marshes provide the greatest protection for infrastructure. According to their findings, the most significant protective benefits are offered by salt marshes located in the East and South of the UK, where these coastal habitats safeguard densely populated or strategically important areas. This

approach underscores the importance of considering both ecological function and human context when evaluating the value of individual salt marshes for coastal protection.

1.1.3.2 Carbon Storage and Sequestration

The measurement of carbon storage and sequestration in coastal habitats such as salt marshes, seagrass beds, and mudflats involves a series of methodologies designed to quantify both carbon stocks and ongoing sequestration rates. The most common approach for determining carbon stocks is the collection and analysis of sediment cores at representative sites within each habitat. Sediment cores are typically sectioned or subsampled at defined depth intervals, with samples analysed for dry bulk density and organic carbon content, typically assessed as percentage organic carbon or total organic carbon. Carbon stock is then calculated using bulk density, carbon concentration and the thickness of the sampled sediment interval, with measurements integrated across the depth of the core to estimate carbon stored per unit area (Howard et al., 2014; Legge et al., 2020; Ladd et al., 2022; Smeaton et al., 2022).

To estimate carbon sequestration rates, radiometric dating can be used to establish the rate of sediment accumulation. By combining this information with organic carbon concentration from sediment layers, annual rates of carbon burial are calculated. Above and below ground biomass in vegetated habitats like seagrass and salt marsh are also sampled, dried, and analysed for carbon content, though the majority of stored carbon in these systems is typically found in the sediments (Howard et al., 2014).

For a more in-depth assessment of carbon exchange - including both carbon uptake and emission - researchers deploy gas flux towers, also known as eddy covariance towers.

These towers continuously measure the exchange of greenhouse gases, including

carbon dioxide and sometimes methane, between the ecosystem and the atmosphere, providing highly detailed data on actual sequestration and emission rates over time (Adams et al., 2012; Howard et al., 2014).

These measurements are directly relevant to the regulating ecosystem service of climate regulation, where coastal habitats act as carbon sinks that help mitigate climate change by removing CO₂ from the atmosphere. Quantifying sequestration rates allows policymakers and conservationists to assess the contribution of these ecosystems to national greenhouse gas inventories, carbon offset markets, and climate mitigation targets. As such, robust measurement underpins both scientific understanding and the economic valuation of this critical ecosystem service.

1.1.3.3 Nutrient Storage and Cycling

Salt marshes and mudflats play a vital role in the storage and cycling of nutrients, particularly nitrogen and phosphorus, which are essential for ecosystem productivity but can cause environmental problems like eutrophication when present in excess. In temperate estuaries, the ecosystem service of nutrient storage and cycling (or remediation) is delivered through burial in sediments, microbially-mediated denitrification, and storage in biogenic material (e.g., biomass and shell material) (Watson et al., 2020). These processes underpin a key regulating ecosystem service: the natural filtration and purification of water bodies, contributing to improved water quality in estuarine and coastal systems (Watson et al., 2016). Measuring nutrient storage in these habitats typically begins with the collection of sediment cores, like those used for carbon assessments. These cores are analysed in the laboratory to determine concentrations of nutrients such as total nitrogen, ammonium, nitrate, and total phosphorus in the sediment

layers (Windham-Myers et al., 2018). Nutrient content is often expressed per unit of dry sediment mass (e.g., mg/kg) and combined with bulk density measurements to calculate nutrient stocks per square meter.

To understand nutrient storage and cycling, researchers study both biotic (plant uptake and microbial processing) and abiotic (burial in sediments) factors. Porewater sampling (the water found in-between sediments in the ground) is used to measure dissolved nutrient concentrations within the sediment, while oxidation-reduction potential and pH measurements provide information on the chemical conditions that influence nutrient transformations (Deegan et al., 2007). In salt marshes, the role of plants is crucial - vegetation takes up nutrients from the soil and stores them in above and below-ground biomass. Measuring nutrient concentrations in plant tissues provides additional insights into nutrient retention.

Flux measurements - both in situ and in controlled chambers - are used to determine the rate at which nutrients like nitrate or ammonium are taken up or released from the sediment. These techniques can help identify key processes such as denitrification, where microbes convert nitrate into nitrogen gas, removing nitrogen from the ecosystem (Nedwell et al., 2016).

Collectively, these biogeochemical processes represent a critical ecosystem service by regulating nutrient levels in estuarine waters, reducing eutrophication risk, supporting biodiversity, and attenuating the riverine loads of dissolved nutrients, potentially lowering the need for expensive engineered water treatment infrastructure. Thus, nutrient cycling in salt marsh and mudflat systems provides both ecological function and direct societal benefits.

1.1.3.4 Biodiversity

Biodiversity underpins ecosystem service delivery through its role in supporting ecosystem functioning. Diverse assemblages of salt marsh plants, benthic invertebrates, and microbial communities drive the processes that enable services such as carbon sequestration, nutrient storage, and flood protection.

Biodiversity in temperate estuarine habitats is typically assessed using a suite of habitat specific survey methods, which aim to capture both species richness and community composition. In intertidal habitats such as salt marshes and seagrass beds, biodiversity is commonly measured using transect and quadrat surveys, which allow for the systematic recording of plant and macrofaunal species within standardised areas (Davies et al., 2001). In benthic habitats such as mudflats and European flat oyster reefs, core and grab sampling methods are often used to collect infaunal organisms from the sediment, while epifaunal assemblages may be recorded using field observations or photographic surveys (Foster et al., 2014). Survey data is then typically analysed using diversity indices such as the Shannon-Wiener or Simpson's index, providing insight into species richness, distribution, and community structure.

Emerging techniques such as environmental DNA (eDNA) are increasingly used to detect species present from water or sediment samples, enabling the identification of species without the need for capture (Harrison et al., 2019). Acoustic seabed mapping and remote sensing techniques, including satellite and aerial imagery, can help delineate habitat areas and structural complexity, particularly for subtidal seagrass beds and oyster reefs (Mason et al., 2018).

The condition of the habitat plays a critical role in supporting biodiversity. Healthy estuarine habitats tend to support a higher diversity and abundance of species due to better habitat structure, water quality, and ecological function (Barbier et al., 2011). Degraded or fragmented habitats often show reduced biodiversity and a shift to more opportunistic or stress-tolerant species (Elliott and Quintino, 2007). Long-term monitoring and the use of standardised methods - such as those laid out in the Joint Nature Conservation Committee's Marine Monitoring Handbook or those of the Water Framework Directive Salt Marsh Tool - are essential for tracking changes over time and assessing the outcomes of conservation and restoration efforts (Davies et al., 2001).

1.2. Ecosystem Services to Natural Capital

1.2.1. Integrating Ecosystem Services into Natural Capital Approaches

The ecosystem services framework provides a foundation for valuing the environment by identifying the benefits ecosystems provide to people. Once these services are understood and, where possible, measured, they can be assessed in socio-economic terms to inform decision-making. Natural capital refers to framing ecosystems as assets and applying approaches that support the valuation and accounting of ecosystem services and the underlying ecological stocks that generate them (Natural Capital Committee, 2015) (Figure 1.1). Natural capital accounting is a structured approach that aims to systematically measure and report on the stocks and flows of ecosystem services they produce. In this context, natural capital refers to environmental assets - such as salt marshes, seagrass meadows, and estuaries - that give rise to the flows of ecosystem

services, such as climate regulation, water purification, and food production. Ecosystem services are essentially the "flows of materials, energy, and information" that emerge from these natural capital stocks (Costanza et al., 1997). It enables policymakers to incorporate the value of natural systems into national accounts, business strategies, and sustainability indicators. For instance, the UK's Natural Capital Committee and the UN's System of Environmental-Economic Accounting (SEEA) advocate such frameworks to better reflect environmental contributions to economic performance.

Furthering the ecosystem service concept with the natural capital concept reflects a growing recognition that healthy natural systems, play a key role in sustaining ecological processes that human well-being relies upon (European Environment Agency, 2020). This understanding elevates nature from a resource to a core, indispensable asset, emphasising that the ecological integrity of habitats directly underpins the sustained provision of vital services. Integrating natural capital into decision making frameworks is therefore a critical step towards achieving true sustainability and societal resilience, ensuring that the intrinsic value and function of coastal ecosystems are recognised, restored and protected.

The sustainable management of natural capital is critical to ensure the continued flow of these ecological services (Fairbrass et al., 2025). These include the role of coastal ecosystems in mitigating coastal flood risks, supporting jobs and livelihoods through fish stocks, and reducing the need for costly engineering solutions for storm surge mitigation and for carbon sequestration (Fairbrass et al., 2025). When natural capital is poorly managed, it becomes not only an ecological liability but also a significant social and economic burden.

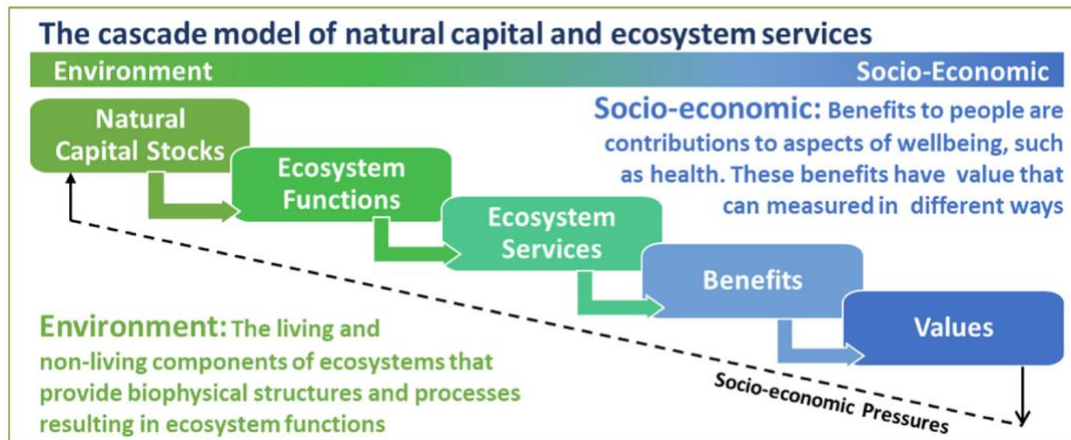


Figure 1.1. A simplified cascade model showing how natural capital is recognised from ecosystem services and how those services provide value for society (Neill et al., 2020).

1.2.2. Accounting and Monetising Natural Capital Assets

While the intrinsic ecological value of habitats is paramount to society, the quantification of ecosystem services, particularly through monetary valuation, serves as a useful tool to communicate their importance to a broader range of stakeholders (Selivanov and Hlaváčková, 2021). The natural capital approach is not designed to sell nature, but it is a lens in which the ecological contributions of natural systems are made accessible and understandable to different audiences (such as politicians and economists), thereby facilitating the integration of environmental considerations into decision-making processes (van den Belt et al., 2011; Bateman and Mace, 2020). Crucially, accounting frameworks must incorporate habitat condition alongside extent, as degraded assets deliver reduced service flows (Watson et al., 2022).

The Total Economic Value framework (TEV), used in the UK, is a conceptual framework that categorises the diverse benefits derived from ecosystems, encompassing both their

utility and their existence value (Selivanov and Hlaváčková, 2021). This framework helps to comprehensively assess the ecological contributions of habitats and species:

Use Values:

- **Direct Use Values:** These are benefits obtained through direct interaction with or use of an ecosystem. They can include consumptive uses, such as harvesting fish, and non-consumptive uses, such as recreation, wildlife watching and tourism (Selivanov and Hlaváčková, 2021).
- **Indirect Use Values:** These are benefits derived indirectly from ecosystem functions and processes, such as water filtration provided by salt marshes or carbon sequestration by seagrass meadows (Selivanov and Hlaváčková, 2021).
- **Option Value:** This represents the value placed on retaining the possibility of using an ecosystem or its services in the future, even if they are not currently being used. For example, conserving a salt marsh may retain the option of benefiting from its future recreational, flood protection or carbon sequestration services (Selivanov and Hlaváčková, 2021).

Non-Use Values:

- **Bequest Value:** This is the value attributed to maintaining something for the benefit of future generations (Selivanov and Hlaváčková, 2021).
- **Existence Value:** This refers to the satisfaction derived from simply knowing that something exists, regardless of direct use or future intent (Selivanov and Hlaváčková, 2021).

Monetary valuation techniques are broadly categorised into market-based, revealed preference, and stated preference methods (Pacifico et al., 2025) (Table 1.2). These

methods aim to quantify the ecological benefits in terms that can inform policy and management decisions:

Market-Based / Cost Approach:

- **Avoided Damage Cost Method:** This estimates the value of an ecosystem service as the monetary damages avoided because the ecosystem reduces risk or impacts for example salt marshes can attenuate waves and storm surge reducing potential flood damage (Mehvar et al., 2018).
- **Replacement Cost Method / Substitute Cost Method:** This values a service by the estimating the least-cost human-made alternative that would provide an equivalent level of benefit, for example, valuing natural water filtration vs the cost of building a water treatment plant (Mehvar et al., 2018).
- **Restoration Cost Method:** This values the cost of reconstructing or restoring a degraded ecosystem (or habitat) to a condition that reinstates the service, such as estimating the cost to restore a degraded salt marsh or oyster reef (Ignatyeva, Yurak and Dushin, 2022).
- **Factor Income Method:** This estimates the value by the change in net income (value added) from a marketed output attributable to that ecosystem service's presence, for example, improved water quality increasing commercial fisheries income (Balbar and Metaxas, 2019).
- **Shadow Pricing Method:** Assigns an accounting (shadow) price to a non-marketed ecosystem service to reflect its marginal social value/opportunity cost. In estuarine contexts, this is commonly estimated using the marginal cost of achieving a water-quality target (e.g., the least-cost measures required to deliver an additional unit of

nutrient reduction or water-quality improvement), which can then be linked to benefits such as recreational fishing (Balbar and Metaxas, 2019).

- **Stated Preference Methods:** These directly elicit values from individuals through surveys, asking their willingness to pay for a service or accept compensation for its loss. Examples include Contingent Valuation and Choice Experiment methods, such as asking people's willingness to pay for improved water quality in an estuary for recreation (Pacifico et al., 2025).

Despite the use of these methods, significant challenges persist in their application - particularly in marine and coastal environments. The inherent ecological complexity, temporal variability, and cross-scale dynamics of ecosystem services make scientific estimates of their value inherently uncertain (van den Belt et al., 2011). There is also difficulty in directly linking changes in ecosystem structure and function to the production of valuable goods and services (Barbier, 2013). One of the most pressing issues is data availability (Watson et al., 2020). Mapping coastal and marine ecosystem services often suffers from a lack of biophysical, quantitative, and geo-referenced data on ecosystem functioning and condition, especially across wide and dynamic spatial scales (Pacifico et al., 2025; Townsend et al., 2018). Furthermore, the valuation methodologies themselves are still evolving. Most tools have been developed with terrestrial systems in mind, meaning that existing models and metrics are often poorly suited to represent the fluid, interconnected, and submerged nature of marine environments (Pacifico et al., 2025). This has hindered the incorporation of marine ecosystem services into natural capital accounts, cost–benefit analyses, and decision-support tools.

The valuation of ecosystem services, particularly within the TEV, is an essential and increasingly adopted tool for integrating ecological considerations into policy and management. It provides a standardised unit of measurement that can inform trade-offs, highlight the ecological consequences of habitat modification, and ultimately promote more sustainable socio-ecological development (Pacifico, et al., 2025).

Table 1.2. Common methods for valuing ecosystem services.

Method Category	Specific Method	Description of Method	Example in Coastal / Estuarine Context	Key Advantages	Key Challenges
Market-Based / Cost Approach	Avoided Damage Cost	Estimates value by calculating costs avoided due to the service.	Valuing coastal wetlands for storm protection by assessing avoided property damage from floods.	Directly links to tangible economic savings; intuitive.	Requires accurate damage assessment; may not capture all benefits.
	Replacement Cost / Substitute Cost	Values a service by the cost of replacing it with a	Valuing natural water filtration by the cost of building a water	Provides a concrete, measurable cost; easy to understand.	Assumes perfect substitutability; may overestimate

	human-made alternative.	treatment plant.		value if natural service is superior or cheaper.
Restoration Cost	Values the cost of reconstructing or restoring a degraded ecosystem.	Estimating the cost to restore a degraded salt marsh or oyster reef.	Provides a direct cost for recovery efforts; useful for planning.	May not reflect the full value of lost services; reconstruction may not achieve full identity (Ignatyeva, Yurak and Dushin, 2022).
Factor Income Method	Estimates value by the increase in income obtained due to the service.	Improved water quality leading to increased commercial fisheries income.	Directly links ecosystem health to economic productivity.	Requires clear causal link between service and income; difficult to isolate factors (Balbar and Metaxas, 2019).

	Shadow Pricing Method	Uses adjusted market prices for non-market products, accounting for market failures.	Valuing clean water for recreational fishing where no direct market exists for water quality.	Can estimate values for non-market goods; accounts for policy distortions.	Complex to calculate; requires significant data and economic expertise (Balbar and Metaxas, 2019).
Stated Preference Methods	Contingent Valuation / Choice Experiment	Directly elicits values from individuals through surveys.	Asking people's willingness to pay for improved water quality in an estuary for recreation.	Captures non-use values (existence, bequest); flexible for various services.	Hypothetical bias; depends on survey design and respondent understanding (Pacifico et al., 2025).

1.3. Importance of Seascape Scale for Natural Capital

1.3.1. Seascape-Scale Management for Ecosystem Functioning and Biodiversity

Preston et al. (2025) define a seascape as “*The mosaic of habitats occupying the coastal environment across time and space that are ecologically and physically connected via*

water through which living organisms (e.g., phytoplankton, larvae, fish), genetic material (e.g., seeds, spores, and gametes), non-living matter (e.g., sediment, carbon, nutrients, pollutants) and energy flow". This connectivity operates at scales of metres to kilometres and extends from the intertidal zone to the shallow coastal shelf seas. The coastal seascape therefore, acts as a dynamic boundary, where social, marine, terrestrial and atmospheric processes interact, and offers an opportunity to restore and enhance coastal ecosystem integrity and resilience for the benefit of people and planet. This definition encapsulates the fact that effective restoration and conservation of temperate coastal and estuarine ecosystems require moving beyond isolated, site-specific interventions to capture the whole seascape to restore ecosystem functionality. This broader viewpoint should incorporate spatial patterns, ecological connectivity, ecosystem processes, and socio-cultural dimensions, helping to design and implement nature-based solutions that regenerate ecological functions and support biodiversity across entire coastal systems (Wedding et al., 2025; Blondel, 2006).

A valuable guiding principle for seascape-scale thinking is the "5 C's" of seascape ecology (developed by the Oxford Seascape Ecology Lab): Context, Configuration, Connectivity, Consideration of scale, and Culture. These five elements operate synergistically across spatial and temporal scales (Wedding et al., 2025). For example:

- Context considers the historical, environmental, and ecological background of a site, such as the legacy of coastal development, land-use change, or historical tidal regime modifications - which can affect the restoration potential of habitats like salt marshes.

- Configuration refers to the spatial arrangement of habitat patches e.g., fragmented versus continuous mudflat systems, which can influence both ecological processes and species movement.
- Connectivity highlights the importance of ecological linkages, such as larval dispersal between oyster reefs and seagrass beds or energy flows from tidal flats to salt marshes (Preston et al., 2025).
- Consideration of scale ensures that actions taken match the ecological and biological processes they aim to support - such as managing migratory fish that use multiple habitats over large distances.
- Culture integrates social values, uses, and stewardship into restoration - essential for ensuring community engagement and the long-term success of interventions (Wedding et al., 2025).

1.3.2. How Seascape-Scale Aids Natural Capital Understanding

When accounting for natural capital, decision-making often suffers from a scale mismatch - a misalignment between the spatial, temporal, or jurisdictional scales at which ecological processes operate and the levels at which economic and policy decisions are made. This leads to situations where the full costs and benefits of environmental impacts are frequently not captured, especially when the impacts are shifted to other countries or operate at broader, more diffuse scales (European Environment Agency, 2020). This highlights a disconnect, while ecological processes and their impacts (e.g., pollution, climate change) operate at large, interconnected scales, traditional economic and policy decisions often remain confined to smaller, isolated units or sectors. This mismatch

prevents comprehensive understanding of cumulative impacts and benefits, leading to suboptimal or counterproductive management outcomes.

Natural capital assessment must move beyond narrow, site-specific approaches and adopt a multi-scale, systems-oriented perspective. This is particularly important in marine and estuarine environments, where hydrological and ecological connectivity links habitats and human beneficiaries across broad spatial extents. Seascape-scale thinking—integrating ecological function, spatial configuration, and socio-political context—is thus essential for delivering more holistic, equitable, and resilient ecosystem management.

Seascape-scale management must also balance multiple ecosystem services, not treat them in isolation. Focusing on a single ecosystem service - such as carbon storage alone - can result in management outcomes that undermine other critical functions. For example, conifer plantations, while effective carbon sinks, often support low levels of biodiversity and disrupt native soil and hydrological processes (Brown et al., 2019). Similar trade-offs may occur in coastal salt marshes, where modifying hydrology to maximise carbon sequestration may reduce habitat suitability for wading birds or juvenile fish.

In contrast, multi-functional systems like restored salt marshes or seagrass meadows often provide co-benefits: they store carbon, support diverse species, stabilise sediments, and enhance water quality (Suykerbuyk et al., 2016). A multi-ecosystem services approach is therefore essential for assessing trade-offs, identifying synergies, and ensuring that management enhances ecosystem resilience and long-term sustainability. Restoration at the seascape scale is finding its way into global policy frameworks, such as the Kunming–Montreal Global Biodiversity Framework, which calls for achieving

restoration targets that enhance ecosystem integrity, connectivity, and the capacity to deliver multiple ecosystem services across landscapes and seascapes (CBD, 2022).

1.4. Connectivity in a Seascape

1.4.1. Defining Ecological Connectivity in Ecosystems

Ecological connectivity refers to the degree to which landscapes, seascapes, or habitats allow for the unimpeded movement of species and the flow of ecological processes that are essential for sustaining biodiversity and ecosystem function (Hilty et al., 2020). Connectivity can occur across different habitat types and at multiple spatial and temporal scales, facilitating key processes such as migration, reproduction, colonisation, and gene flow (Watson et al., 2018). Barbier (2017) highlighted the need to consider the connectedness of habitats within a seascape due to the transfer of life, energy and nutrients between those habitats and the cumulative impact this connectivity has on the ecosystem services being provided by that seascape. Without sufficient connectivity, populations can become isolated, genetic diversity may decline, and essential ecological functions like nutrient cycling or flow of water can be disrupted (McRae et al., 2012).

Habitat connectivity science originated in terrestrial landscapes and is far more advanced for terrestrial landscapes than it is for marine and coastal seascapes. Landscape connectivity was defined by Merriam (1984) as “the degree to which absolute isolation is prevented by landscape elements which allow organisms to move among habitat patches”. Stemming from MacArthur and Wilson’s 1967 theory of island biogeography (whereby core areas of habitat are surrounded by hostile environments), the terrestrial

field broke connectivity into two frameworks: structural connectivity, which focuses on the physical arrangement and spatial configuration of habitats (for example, the distance between habitat patches and if they are connected by corridors of similar habitats) (NatureScot, 2023); and functional connectivity (see Table 1.3) , which measures how organisms respond to these structures through movement or ecological processes (Taylor et al., 1993; Kindlmann and Burel, 2005) - a functionally connected landscape allows dispersal of individuals between discrete habitat patches (Briers, n.d.).

Structural connectivity provides the potential pathways for movement, while functional connectivity represents the actual movement and its ecological consequences. A physically connected habitat (structurally) does not automatically guarantee biological flow (functional connectivity) as other factors (e.g., environmental barriers or species behavioural traits) may inhibit it, but a lack of structural connection will limit functional connectivity – highlighting the hierarchical relationship between structural and functional connectivity (Agiadi et al., 2024). Effective marine conservation and management strategies must therefore adopt a dual approach, considering both the physical arrangement of habitats (structural connectivity) and the actual movement of species and resources between them (functional connectivity). Levels of functional and structural connectivity within a seascape may differ between species, depending on species characteristics, behaviours or life stages. Restoring physical connection is a necessary first step but understanding and facilitating the biological and energetic flows is crucial for achieving desired ecological outcomes such as ecosystem functioning.

Seascape connectivity as a concept was first explored in scientific literature in the early 2000's, with growing prominence and application in marine science, conservation, and

policy since the mid-2000's (Selkoe et al., 2016; Preston et al., 2025; Engelhard et al., 2017).

Table 1.3. The differences between structural and functional connectivity.

	Structural Connectivity	Functional Connectivity
<i>Focus</i>	Physical landscape or seascape configuration	Species' ability to move through the landscape
<i>Measurement</i>	GIS mapping, habitat fragmentation indices	Species dispersal data, movement modelling
<i>Dependence</i>	Independent of organisms	Species-specific (e.g., dispersal range, behaviour)

1.4.2. Scales of Connectivity

Connectivity within ecosystems operates across a wide range of spatial and temporal scales - from the vertical movement of microbes in mudflats, to the long-distance migrations of fish and birds across ocean basins. Among these scales, the seascape scale is particularly important for understanding and managing estuarine and coastal systems. The seascape scale is particularly relevant for processes like local larval dispersal, sediment transport (including identifying source and sink locations), and hydrological mixing. These processes often operate over spatial extents that are larger than a single habitat patch but smaller than the entire ocean, making the seascape scale

an effective lens for study and management (Endangered Landscapes and Seascapes Programme, 2024).

Research has shown that without connection between various marine habitats, populations may struggle to persist, since both larval dispersal and the movement of individuals at different life stages rely on such connectivity (Olds et al., 2016; Weeks, 2017; Virtanen et al., 2020). Maintaining connectivity is essential for allowing species to migrate, disperse, and adapt to changing environmental conditions which means it is critical for species' if they are to adapt to environmental stressors like climate change (Thompson and Fronhofer, 2019). In the face of climate change and its impacts on marine environments, understanding and actively managing seascape connectivity should be a priority for conservation.

Seascape connectivity helps to maintain biodiversity, promote ecological balance, and directly supports human well-being by sustaining ecosystem services such as fisheries, shoreline protection, and tourism (Wedding et al., 2025). Integrating connectivity into marine protected area design and management is important for their success in safeguarding marine biodiversity and ecosystem services (Balbar and Metaxas, 2019). A seascape approach that restores connectivity and ecosystem function is crucial for successful ecosystem restoration, ensuring that interventions are effective across broader areas (Preston et al., 2025).

1.5. Measuring Connectivity

1.5.1. Measuring Structural Connectivity

Structural connectivity can be assessed by measuring the physical arrangement and extent of habitat patches (Battisti et al., 2022). Methods include mapping the distribution, shape, and extent of habitats across a seascape, which can involve identifying the spatial patterns of patchiness, perimeter shape (meaningful in the context of the edge effect for fish), proximity to each other, and area.

Methods for measuring structural connectivity between patches of habitats, focus on the physical contiguity and proximity of habitat patches (Battisti et al., 2022). Remote sensing technologies, such as satellite imagery (e.g., Sentinel-2) and aerial surveys, are increasingly used to map habitat distribution and extent and track changes over time, providing crucial data for structural connectivity assessments of large areas of habitats like salt marshes or mudflats.

The physical properties of the seascape, such as estuary shape and mouth width, can influence the energy and flows (e.g., volume of water, wave energy and organic matter) coming into and exiting the estuary (Alvera-Azcárate et al., 2025). This highlights that the morphological characteristics of the seascape itself dictate the potential for structural linkages between diverse habitats as different environmental conditions and levels of exposure will affect morphology.

Spatial Analyses

Structural connectivity can be measured using Geographical Information System (GIS) tools such as QGIS and landscape pattern analysis software like FragStats. FragStats is freely available software that provides numerous metrics for measuring habitat

fragmentation. For example, the Aggregation Index can be used to quantify the degree of aggregation or clumping of salt marsh habitat, with higher values indicating greater spatial aggregation (McGarigal et al., 2023). Two commonly used metrics of salt marsh connectivity are distance between patches and patch size, which can both be calculated using FragStats. Equally relevant, FragStats allows users to compute the regularity of the shape of patch perimeters; Green et al. (2012) showed that salt marsh patch shape (increased circularity) highly influenced fish species richness and diversity. Salt marsh to intertidal proportion is another spatial method used to measure salt marsh connectivity. This metric calculates the proportion of the current salt marsh area to the total intertidal area, with higher proportions indicating better connectivity to the surrounding coastal environment (Water Framework Directive UK, 2012).

Limitations of Spatial Analyses

Structural connectivity metrics are purely spatial - they do not account for actual organism movement or ecological flows e.g. sediment source and sink points. Used in isolation, they may overestimate connectivity if physical barriers or unsuitable conditions exist between patches (Preston et al., 2025). Additionally, frequently updated spatial data is essential to accurately capture dynamic coastal habitats that may change rapidly due to natural and anthropogenic forces – this data may not always be available or may come at a high cost.

1.5.2. Measuring Functional Connectivity

Functional connectivity goes beyond spatial arrangement to quantify the actual ecological exchanges (organism movements, gene flow, energy, or matter) among habitat patches (Agiadi et al., 2024; Preston et al., 2025). Because functional connectivity can rarely be

directly observed, it is often inferred through various field based and modelling approaches outlined below (NatureScot, 2023).

Methods

- **Genetic Analyses:** Genetic studies infer functional connectivity by examining genetic similarities and differences between populations, providing insights into gene flow and population structure (Tanner et al., 2025). This can reveal how connected populations of a specific species are across patches of the same habitat type (e.g., genetic exchange between different salt marsh patches) or how species move between different habitat types if they utilise multiple habitats during their life cycle.
- **Oceanographic and Particle Tracking Models:** Particle tracking models simulate ocean currents and other physical processes to predict the dispersal of marine organisms and connectivity patterns between locations. These models can be used to predict larval dispersal pathways from spawning grounds in one habitat (e.g., offshore waters) to nursery habitats like seagrass beds or oyster reefs within an estuary. These models have proven effective for showing hydrodynamic connectivity in systems like the Pearl River Estuary, where tidal and fluvial forces dictate organism and sediment movement (Chu et al., 2022).
- **Direct Observation and Tagging:** Tagging (including acoustic telemetry and mark–recapture) directly tracks individual movement, this can be used to show how fish migrate between mudflats, creeks, and seagrass or oyster reef nurseries (Cooke et al., 2016). While powerful for certain species and scales, it can be limited by sample size and study duration.

- **Stable Isotope Analysis:** By tracing isotopic signatures (e.g., carbon, nitrogen) in migratory species, researchers can trace the origin of organic matter and clarify trophic connections or energy flows between estuarine and coastal habitats. For example, a study investigated the origin of organic matter (estuarine vs coastal) in the diet of the migratory spotfin mojarra fish (*Eucinostomus argenteus*) to understand flows between morphologically distinct estuaries and their adjacent coastal areas (Alvera-Azcárate et al., 2025).
- **eDNA Analysis:** eDNA can reveal presence of species, allowing inferences about recent movements and functional links, especially for scarcely seen or migratory species (Harrison et al., 2019). However, DNA persistence and flow can complicate any inferred movement paths.
- **Network and Graph Theory Modelling:** Functional connectivity is often represented as a network. Applying graph theory, with habitat patches as nodes, allows for quantification of direct and indirect connections, and highlights “hub” habitats or critical stepping stones for multispecies assemblages (Saura and Pascual-Hortal, 2007; Dou et al., 2014). These models have been applied in marine and estuarine systems to identify key subpopulations, stepping-stone habitats, and community-level exchange. For example, graph-theory modelling approaches have been applied to the marine realm to assess functional habitat connectivity for two reef fish species who utilise near-shore mangrove forests, seagrass beds and off-shore reefs (Stuart et al., 2023). Graph theory allows for further complex analysis such as “total probability of connectivity” - the probability that two points randomly placed in a landscape fall into habitat patches that are reachable from each other - and the “fortress ratio” - which

calculates the role of a habitat patch in upholding connectivity to other patches within the landscape (Lippi et al., 2024; Saura and Rubio, 2010).

- **Circuit Theory and Least-Cost Path Analysis:** Circuit theory considers all possible pathways and resistance surfaces across the landscape, providing a probabilistic approach to connectivity assessment; least-cost path models are similar but focus on optimal routes (McRae et al., 2008). These approaches are increasingly used in estuarine management to prioritise restoration and conservation of habitat corridors (McRae et al., 2008).

Limitations

Functional connectivity is inherently challenging to measure; genetic and tag-based data require extensive effort and are constrained by marker resolution or technological cost. Modelling approaches rely on ecological realism and up-to-date physical and biological data and may not always capture real population or flow dynamics (Cooke et al., 2016; Preston et al., 2025).

1.6. Gaps in Measuring Connectivity

Existing Studies

Studies have successfully quantified connectivity between different habitat types at the seascape scale, such as the linkages between coral reefs and mangrove habitats (Weeks, 2017). However equivalent data and evidence are still lacking for temperate seascapes. Studies have successfully quantified connectivity between different habitat types at the seascape scale, such as the linkages between coral reefs and mangrove

habitats (Weeks, 2017). Although approaches to incorporating functional connectivity into conservation management have been demonstrated in tropical seascapes, including in data-poor contexts by combining the spatial configuration of habitat patches with species movement ability (e.g., ontogenetic migration distance), equivalent evidence remains limited for temperate seascapes (Weeks, 2017). Evidence also suggests that proximity to nursery habitats can significantly enhance the effectiveness of marine protected areas by increasing fish abundance, density or biomass (Weeks, 2017). Advances in genetic tools and oceanographic modelling are improving the resolution of larval connectivity assessments (Quigley et al., 2022). Kang et al. (2024) demonstrated how circuit theory can be applied to coastal systems without requiring a species-specific focus, mapping seascape resistance based on factors such as fishing pressure, development and marine protected areas.

Challenges

Despite these advancements, frameworks for seascape connectivity often remain "aspirational" due to significant data and resource requirements (Weeks, 2017). There is a lack of biophysical, quantitative, and geo-referenced data which can be used to assess ecosystem function, which poses a main challenge for mapping coastal and marine ecosystem services and connectivity (Pacifico, et al., 2025). Long-term changes in marine ecosystems are difficult to quantify due to anthropogenic impacts and a lack of scientific records of previous states, leading to a "severely shifted baseline" that hinders historical comparisons (Preston et al., 2025). Although connectivity is widely recognised in MPA network theory (particularly larval dispersal), seascape connectivity linked to multi-habitat use and ontogenetic movements has historically been underrepresented (Weeks, 2017)

and remains inconsistently incorporated in applied MPA design and management. There is also a lack of progress in developing tools and methodologies for better valuation of marine and coastal ecosystem services, which hinders comprehensive integrated assessments (Pacífico., 2025).

Current methods for measuring seascape connectivity face several significant limitations:

- **Spatial Data Availability:** Spatial datasets useful for assessing structural connectivity are increasing due to the growing number of freely accessible national databases and catalogues of satellite imagery e.g. Emodnet. However, obtaining the detailed environmental and biological information required to accurately model functional connectivity remains challenging. Furthermore, most existing connectivity models focus on a single species, which raises concerns about whether the scale of functional connectivity being represented adequately captures the complexity of multi-species interactions and the ecosystem as a whole.
- **Spatial Resolution:** While traditional ocean colour satellites (e.g., Sentinel-3) provide daily images, the sensors on board these satellites do not measure at the necessary high spatial resolution to capture coastal dynamics (Alvera-Azcárate et al., 2025). High-spatial-resolution sensors (e.g., Sentinel-2) can capture small scales (10–60 m resolution) but have less frequent temporal revisit times (e.g., about 5 days), and both types of datasets are frequently hindered by cloud cover, resulting in large amounts of missing data (Alvera-Azcárate et al., 2025). Sentinel-2 satellite imagery, despite its relatively high resolution, may still lack the fine spatial detail needed to detect small-scale features within estuarine ecosystems, such as salt marsh creek networks or seagrass density. Additionally, distinguishing seagrass from green algae, particularly

Ulva species that bloom simultaneously, can be challenging when using satellite or remote sensing imagery.

- **Integration with Natural Capital Assessments:** Better integration between natural capital assessment and connectivity analysis is needed because many marine ecosystem-service benefits are delivered through linked habitat mosaics and cross-boundary flows (of organisms, water, sediments, nutrients, and people). Yet natural capital appraisals often treat habitats as discrete units, while connectivity studies frequently focus on biotic dispersal without translating connections into service delivery and beneficiary outcomes (Pacifico et al., 2025). This contributes to persistent evidence gaps for key services such as water quality regulation provided by marine habitats, along with limited attention to indirect cultural values (such as spiritual connections to nature) in marine decision-making processes (Fairbrass et al., 2025). Critically, the specific mechanisms and empirical evidence linking ecological connectivity to the provision of ecosystem services in temperate coastal systems remains underexplored, limiting the ability to capture cumulative benefits and avoid displaced or downstream impacts in appraisal and planning (Preston et al., 2025).

Balbar and Metaxas (2019) found that globally across 44 countries only a small proportion (11%) of marine protected areas explicitly incorporated connectivity as an ecological criterion in their design. While policymakers and practitioners increasingly acknowledge the importance of ecological connectivity, significant challenges remain in integrating it into policies, planning, and conservation efforts (Tanner et al., 2025). These challenges are exacerbated by the inherent variability and dynamic nature of temperate estuarine systems. Consequently, even when the scientific understanding of connectivity is well

established, translating this knowledge into effective, actionable policy may be constrained by the heterogeneous characteristics of different temperate systems and the large demand for data that comes with representing such complex environments.

1.7. Impact of Connectivity on Natural Capital

Evidence indicates that ecological connectivity influences ecosystem functioning, shaping species composition, productivity, population dynamics, and resilience and, in turn, the capacity of ecosystems to generate services and benefits for people. From a natural capital perspective, this positions connectivity as a key attribute of the underlying asset that helps determine how effectively habitat extent and condition translate into sustained service flows and societal benefits. Data show that connectivity influences ecosystems, affecting species composition, productivity, dynamics, resilience, and their capacity to generate services for humans (Carr et al., 2017). In natural capital terms, these connectivity-driven effects shape the condition and functional integrity of the ecosystem asset, thereby influencing both the magnitude and reliability of benefits delivered over time. It is the primary process by which one ecosystem interacts with and influences another, facilitating essential transfers that maintain ecological balance (Carr et al., 2017).

Ecosystem Service Provision

The delivery of ecosystem services fundamentally requires a "healthy mosaic of coastal habitats, maintained by the exchanges of matter and energy between them" (Preston et al., 2025). Connectivity ensures these exchanges, thereby enhancing overall biodiversity and ecosystem functions, which are the very basis for service provision (Preston et al.,

2025). Individual coastal habitats provide critical services - for example, climate regulation through carbon storage by salt marshes; water quality support via nutrient cycling by oyster reefs; fishery production through providing nursery habitats; and coastal protection via natural defences (Preston et al., 2025). Connectivity links these individual contributions into a larger, more robust system (Boström et al., 2011).

Challenges

- Geographical variability: Service provision varies geographically, requiring site-specific biophysical data (e.g., local carbon stocks, wave attenuation measurements) from the study location to test connectivity-service relationships.
- Habitat maturity / successional stage and trajectories: Ecosystem services vary within the same habitat type across "successional" stages, necessitating species linked time-series data on habitat development and service delivery.
- Spatial scale and accounting: Evidence is lacking on how connectivity metrics at different spatial scales relate to service provision, and how decision-makers can avoid double-counting services across connected habitat patches.

Relationship between Habitat Connectivity, Extent and Condition

A healthy, well-connected seascape allows for the free movement of species, genetic exchange, and the flow of essential nutrients and energy, all of which contribute to the robust condition and ecological integrity of individual habitats and the broader ecosystem (Preston et al., 2025). In natural capital terms, this means connectivity increases the functional value of habitat extent by ensuring that habitat patches operate as an integrated asset, rather than isolated fragments, thereby supporting the processes that

underpin condition. Conversely, disrupted or severed connections across habitats and trophic webs in temperate coastal seascapes lead to fragmented ranges and incomplete trophic webs, thereby reducing overall ecosystem resilience and degrading habitat condition (Preston et al., 2025). As a result, a seascape can retain the same mapped habitat extent while experiencing a decline in effective extent (i.e., the proportion of habitat that is accessible, usable, and able to support recruitment and recovery), reducing the capacity of the natural capital stock to generate sustained ecosystem service flows. Maintaining connectivity is crucial for preserving the "healthy mosaic of coastal habitats" necessary for sustained ecosystem functioning and service delivery (Preston et al., 2025). This reinforces that extent alone is insufficient for natural capital assessments: connectivity and condition jointly determine whether the asset base can reliably deliver benefits over time. However, it is also important to recognise that connectivity can facilitate the spread of detrimental impacts, such as pollutants or invasive species, which can negatively affect habitat condition. Accordingly, connectivity also shapes the risk profile of coastal natural capital, because the same pathways that support beneficial ecological exchange may also transmit pressures that erode condition and diminish service provision. Overall, the relationship between habitat connectivity, extent, and condition can be conceptualised as a mechanism that determines how much of the habitat stock is functionally available and resilient, and therefore how effectively the natural capital asset can deliver ecosystem services now and into the future.

Challenges

- **Interdependence:** Condition, connectivity, and extent cannot be treated independently; changes in one can alter the others, affecting predicted ecosystem service delivery (Mace et al., 2015).
- **Uncertain interactions:** The degree to which connectivity, extent, and condition interact remains unclear e.g., whether increasing structural connectivity improves habitat condition, whether poor condition limits the benefits of connectivity.
- **Proxy limitations:** It is uncertain how well structural connectivity metrics may be able to be used as a proxy for functional connectivity (and thus ecosystem functionality), physical patch arrangement does not guarantee biological or energetic flows between habitats.
- **Beyond single habitat and species-based assessments:** Species- and habitat-specific analyses can miss wider ecosystem processes; seascape-scale assessments should prioritise connectivity of ecological processes (e.g., nutrient, energy, propagule flows) rather than individual species movements.

Ecosystem Resilience

As Preston et al. (2025) pointed out, a seascape approach that restores connectivity and optimal structure-function relationships is crucial for successful ecosystem restoration. Connectivity underpins resilience by enabling dispersal and recolonisation after disturbance, supporting demographic and genetic exchange (“rescue effects”), and maintaining trophic and biogeochemical flows that sustain ecosystem functioning. Integrating landscape ecology concepts and methods into coastal restoration efforts enables the effective scaling up of restoration initiatives, which are vital for building

resilience against environmental changes (Wedding et al., 2025). Connectivity helps achieve global restoration targets by promoting more strategic, inclusive, and effective marine restoration across coastal seascapes (Wedding et al., 2025). It allows for the persistence and recovery of populations, which are key indicators of ecosystem resilience (Balbar and Metaxas, 2019). Connectivity-informed marine protected areas and marine protected area networks are better equipped to address ecological changes induced by climate change, enhancing the adaptive capacity of marine systems by facilitating species' range shifts and genetic adaptation (Carr et al., 2017). However, connectivity can also transmit pressures (e.g., invasive species or pathogens, or excess nutrients), so resilience benefits depend on local context and the balance of beneficial versus harmful flows.

Challenges

- Shifting and uncertain baselines: Unknown or degraded baselines, combined with climate-induced changes, create uncertainty in defining resilient ecosystem states that can adapt while maintaining service provision.
- Linking connectivity to outcomes: Evidence is needed to establish whether connectivity enhances ecosystem functionality and resilience, and how these relationships translate to sustained service delivery under changing conditions.

1.8. Aims and Objectives

Summary

Ecosystem services are widely recognised as fundamental to human well-being, yet the ecological mechanisms that underpin their delivery remain incompletely understood. In particular, the role of structural connectivity in influencing ecosystem service provision and natural capital within temperate estuarine systems has received comparatively little attention (Preston et al., 2025). Although ecological connectivity is increasingly recognised as an important component of coastal ecosystem functioning, there remains limited understanding of how structural connectivity can be quantified, how it varies across different spatial frameworks, and whether connectivity metrics provide meaningful insight into ecosystem service delivery.

Structural connectivity is more than a descriptor of habitat pattern; it influences the spatial organisation of ecological assets and has the potential to affect the movement of organisms, sediments, nutrients and energy throughout estuarine landscapes. Consequently, changes in habitat connectivity may alter ecological functioning and the capacity of ecosystems to provide services such as carbon storage, nitrogen removal and coastal protection. Despite this, natural capital assessments continue to focus primarily on habitat extent and condition, with comparatively little consideration given to habitat configuration or the influence of analytical scale on estimates of connectivity.

Addressing these knowledge gaps would improve understanding of the relationship between landscape structure and ecosystem functioning, while providing a stronger evidence base for natural capital assessment, habitat restoration and coastal management. In particular, evaluating whether structural connectivity metrics provide

complementary information to conventional measures of habitat extent could support more spatially informed conservation planning and restoration design within temperate estuarine ecosystems.

This study addresses these knowledge gaps through the following aim, research questions and objectives.

Aim

To quantify the structural connectivity of salt marsh habitats and investigate how structural connectivity and analytical scale influence natural capital assessment within temperate estuarine ecosystems.

Research Questions

1. How can structural connectivity within salt marsh habitats be quantified using landscape metrics at spatial scales relevant to coastal management?
2. What relationships exist between structural connectivity metrics and natural capital indicators within temperate estuarine salt marshes?
3. How does the spatial framework used to define the landscape influence estimates of structural connectivity?

Research Objectives

1. Map and quantify spatially explicit natural capital indicators representing key regulating ecosystem services, including carbon storage, carbon sequestration, nitrogen removal and wave attenuation, across the Blackwater and Colne estuaries.
2. Quantify structural connectivity within salt marsh habitats using landscape metrics calculated with the landscapemetrics package in R and evaluate relationships

between connectivity metrics and natural capital indicators within Shoreline Management Plan (SMP) policy units.

3. Evaluate how estimates of structural connectivity vary across alternative spatial frameworks, including the whole estuary, Water Framework Directive (WFD) water bodies, nutrient management zones and Shoreline Management Plan (SMP) policy units.

This research investigates how structural connectivity and analytical scale influence the assessment of natural capital within temperate estuarine salt marshes, using the Blackwater and Colne estuaries as a case study. By integrating landscape ecology with natural capital assessment, the study examines how habitat configuration and the spatial framework used for analysis influence estimates of structural connectivity and their relationship with natural capital indicators. The findings provide evidence to support more spatially informed approaches to habitat restoration, coastal management and natural capital assessment by demonstrating how structural connectivity metrics can complement conventional measures of habitat extent. More broadly, the research contributes to understanding how landscape ecological principles can be incorporated into decision-making for the conservation and sustainable management of temperate estuarine ecosystems.

Chapter 2

From Structure to Value: The relationship between salt marsh structural connectivity and natural capital in the Blackwater and Colne estuaries.

Chapter 2 represents original analysis undertaken by the author, with contributions from collaborators as outlined below. Structural connectivity metrics were calculated by the author using QGIS and RStudio, including all spatial analyses and statistical correlation testing. Connectivity analyses were developed and implemented independently by the author.

Natural capital metrics were derived using a combination of existing datasets and collaborative analyses. Wave attenuation estimates were calculated by the author using fetch and effective fetch data provided by Gilbertson et al. (2020). Net sediment flux was calculated by the author using Ladd et al. (2019) data. Denitrification rates were calculated collaboratively between the author and Professor Graham Underwood. Carbon sequestration, carbon storage, and species richness metrics were calculated by Dr Stephen Watson and Charlotte Worrall. Habitat datasets were collated and mapped in QGIS by Dr Stephen Watson prior to connectivity analysis. The integration, interpretation, and discussion of all connectivity and natural capital relationships presented in this chapter were undertaken by the author.

2.1 Introduction

Temperate estuaries represent complex ecological mosaics where multiple habitats interact to sustain ecosystem functioning and the provision of ecosystem services (Preston et al., 2025). Salt marshes are among the most valuable of these habitats, supporting biodiversity while delivering a range of regulating ecosystem services including carbon sequestration, nutrient removal, and coastal protection (Barbier et al., 2011; Möller et al., 2014). In natural capital terms, these habitats represent ecological assets that generate flows of benefits to society through the ecological processes they support.

Understanding how these ecosystem services are distributed spatially within estuarine systems is increasingly important for coastal management and restoration planning (Preston et al., 2025). Traditional natural capital assessments often focus on the extent and condition of habitats, yet the spatial configuration of habitats within the wider seascape may also influence ecosystem functioning and service delivery (Boström et al., 2011; Carr et al., 2017; Preston et al., 2025). Habitat connectivity, defined as the degree to which landscapes facilitate ecological flows such as organism movement, sediment transport, and nutrient cycling, has therefore emerged as an important concept within coastal ecosystem management (Preston et al., 2025).

Most research exploring the relationship between connectivity and ecosystem services has been conducted in terrestrial systems, where landscape ecology metrics are widely used to assess habitat fragmentation and connectivity. In marine and coastal systems, however, the application of connectivity metrics remains less developed, particularly in temperate estuaries (Preston et al., 2025). As discussed in Chapter 1, this represents an

important knowledge gap in understanding how spatial habitat configuration influences the delivery of natural capital within coastal seascapes.

Salt marshes provide a useful coastal habitat for investigating these relationships. These habitats are structurally complex and spatially dynamic, with patterns of marsh expansion, erosion, and fragmentation influencing their spatial distribution within estuaries (Allen, 2000; Temmerman et al., 2013). At the same time, salt marshes support several ecosystem services that can be quantified and mapped, including “blue carbon” storage, nitrogen removal through denitrification, storm protection through wave attenuation capacity, and biodiversity.

The Blackwater and Colne estuaries in Essex (Figure 2.1), UK provide an ideal case study for exploring connectivity relationships between salt marshes. These two estuaries contain extensive intertidal habitats and have been the focus of long-term ecological monitoring and restoration initiatives. At the same time, they are subject to coastal management policies under the Environment Agency’s Shoreline Management Plans (SMP), which divides the coastline into policy units used for flood and erosion risk management. The Blackwater and Colne estuaries fall into the Essex and South Suffolk SMP.

This chapter therefore aims to investigate how the structural configuration of salt marsh habitats relates to the spatial distribution of natural capital indicators within the Blackwater and Colne estuaries. Specifically, it examines whether structural connectivity metrics derived from landscape analysis correspond with measures of ecosystem service provision at the scale of SMP policy units.

Research questions

1. How can structural connectivity be quantified for salt marsh habitats within the Blackwater and Colne estuaries?
2. How do structural connectivity metrics relate to natural capital indicators across the estuarine system?

To address these questions, spatial habitat data were analysed using four landscape connectivity metrics (FragStats) and compared with mapped natural capital indicators for key ecosystem services including carbon sequestration and storage, nitrogen removal through denitrification, wave attenuation capacity, and species richness as a proxy for biodiversity. Analyses were conducted for both present-day conditions and a projected 2055 scenario whereby salt marshes are restored - incorporating potential habitat creation sites as detailed by the Environment Agency Restoring Meadows, Marsh and Reef programme (ReMeMaRe) (ECSA., 2026).



Figure 2.1 Location of the Blackwater and Colne estuaries study area in Essex, England, outlined in red.

2.2 Methods

2.2.1 Study Area

The study focused on the Blackwater and Colne estuaries, located on the Essex coast in south-east England. These estuaries are characterised by extensive intertidal mudflats and salt marsh systems and form part of a wider coastal complex that includes internationally important habitats designated under several conservation frameworks; The Blackwater and Colne estuaries contain two Sites of Special Scientific Interest (Blackwater Estuary SSSI and Colne Estuary SSSI), two Special Protection Areas (Blackwater Estuary SPA and Colne Estuary SPA), two National Nature Reserves

(Blackwater Estuary NNR and Colne Estuary NNR), two Ramsar sites (Blackwater Estuary Ramsar site no. 543 and Colne Estuary Ramsar site no. 665), and one Marine Conservation Zone (the Blackwater, Crouch, Roach and Colne Estuaries MCZ) (Defra, 2013).

This work formed part of the wider 'Source 2 Sea: Blackwater and Colne Natural Capital project' (Underwood et al., 2025) which was commissioned by the Environment Agency to support the Defra Natural Capital Ecosystem Assessment initiative (NCEA). Because of this, the study area was restricted to the Essex and South Suffolk Shoreline Management Plan (SMP). The SMP area is divided into policy units which represent coastal management divisions used to guide flood and erosion risk management strategies along the coastline; SMP policy units are delineated by shared characteristics of coastal processes. The following analysis quantified salt marsh structural connectivity within each SMP policy unit, with each unit treated as a separate landscape for analysis. This allowed evaluation of whether SMP policy units provide an appropriate spatial framework for linking patterns of salt marsh connectivity to natural capital metrics relevant to coastal management.

2.2.2 Map Preparation and Habitat Data

Spatial habitat layers for the Blackwater and Colne estuaries were obtained from the EUNIS habitat classification dataset and imported into QGIS version 3.44.5 (Solothurn). The intertidal habitat dataset included several core habitat types including salt marsh which were used to represent current habitats within the two estuaries (Figure 2.2). The salt marsh within this dataset included vegetated and unvegetated areas of marsh - it was

inclusive of small creek systems and areas of bare mud; this habitat layer will be termed 'salt marsh full' from hereon.

The SMP shapefile (including individual policy units) was downloaded from the UK Government coastal management database and clipped in QGIS to include only the Blackwater and Colne estuary region (Figure 2.3). Habitat layers were subsequently clipped to the same spatial boundary, hereafter referred to as the project area (Figure 2.3).

For the future scenario (2055), projected salt marsh areas were mapped using the ReMeMaRe habitat potential dataset (ECSA, 2026), this included vegetated and unvegetated areas of salt marsh combined. This dataset was developed through the ReMeMaRe programme and identifies areas where salt marsh creation may occur through coastal realignment or restoration initiatives by 2055 (ECSA, 2026) (Figure 2.4). Future scenario 2055 salt marsh and current scenario 2 salt marsh shapefiles were converted to raster format for each SMP policy unit to enable the connectivity analysis.

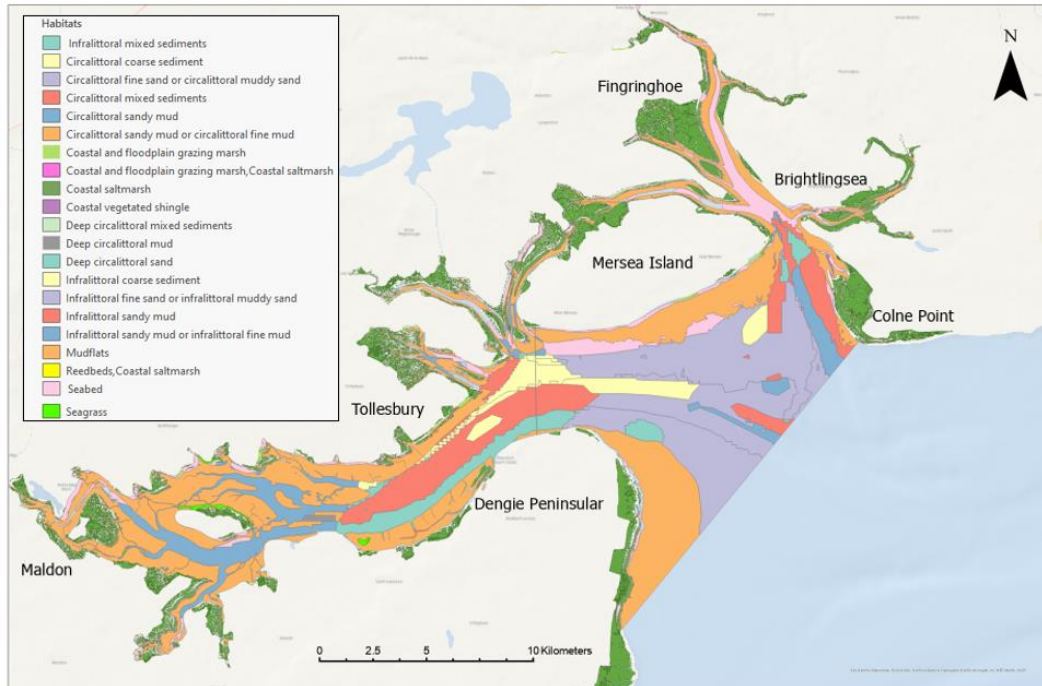


Figure 2.2. Blackwater and Colne estuaries showing the EUNIS habitat classification data within the project area (Underwood et al., 2025).

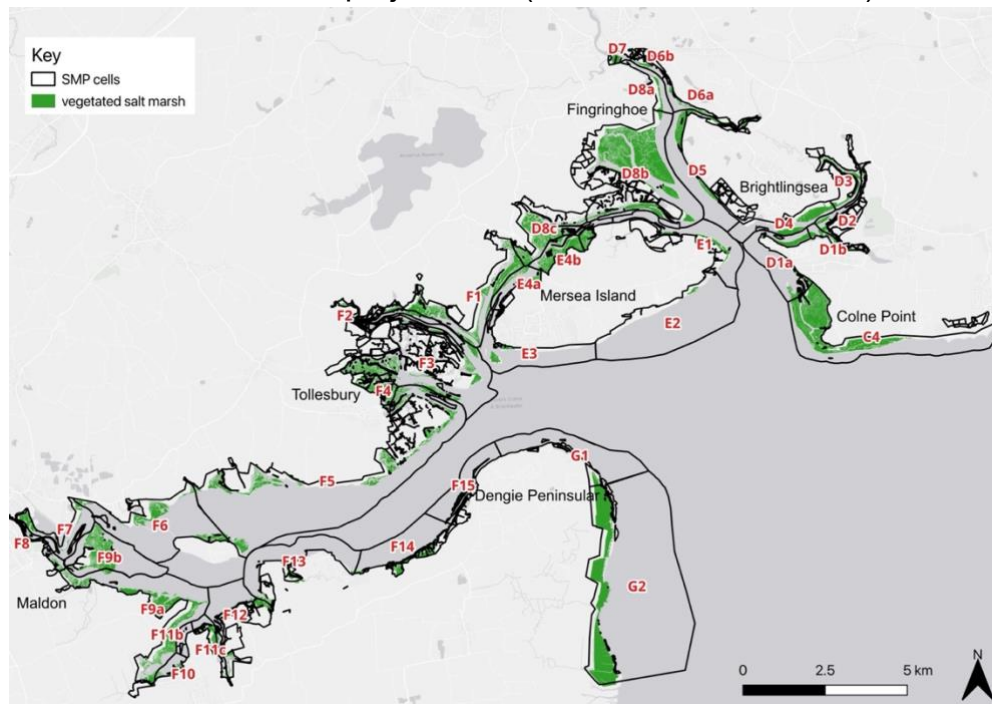


Figure 2.3. Essex and South Suffolk Shoreline Management Plan cell policy units (outlined in black and labelled in red) and the current scenario vegetated salt marsh areas (green) which were supplied by Ladd et al. (2019).

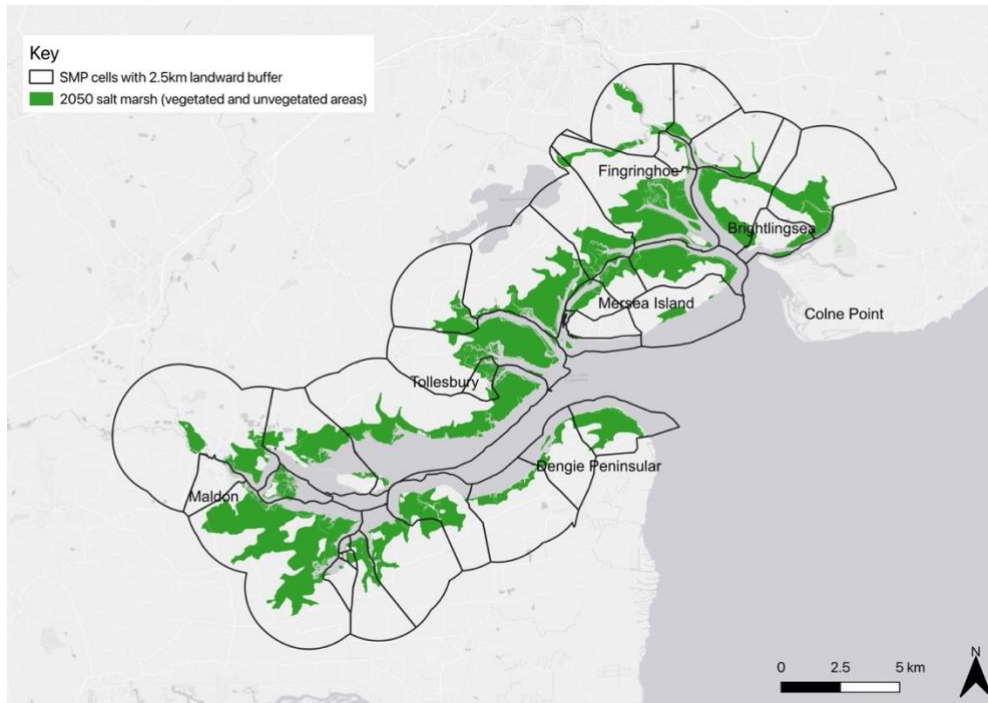


Figure 2.4. Future SMP cell policy units (outlined in black) and the 2055 scenario salt marsh areas (green) (MMO1135 Potential Habitat Creation Sites data) (note: policy unit G2, C4, D1a, D1b and D2 were not included in the future analysis due to unavailable future natural capital predictions).

2.2.3 Salt Marsh Condition: Unvegetated-to-Vegetated Ratio (UVVR)

The condition of salt marsh habitats within the study area was assessed using the unvegetated-to-vegetated ratio (UVVR), following the approach developed by Ganju et al. (2017) and Ladd et al. (2019). UVVR provides a measure of marsh condition by comparing the area of vegetated marsh with the total marsh area, with the latter including unvegetated sections (creeks, saline pools and areas of bare mud). The greater the proportion of unvegetated area a particular marsh complex has, has been found to be related to export of sediment from the marsh (Ganju et al., 2017), ecologically this makes sense as there is less vegetation to stabilise sediment so it is more easily dislodged and washed away. Vegetated marshes are more likely to import sediment (Ladd et al., 2019),

the vegetation not only stabilises sediment but acts as a sediment trap as the tide ebbs. These functions were used to estimate changes in the overall sediment budget of salt marshes within each policy unit; UVVR for all marshes within a policy unit were averaged per policy unit to get one measure for each policy unit.

Spatial datasets from Ladd et al. (2019) representing vegetated marsh and total marsh extent were clipped to the project area using the QGIS intersect tool. Unvegetated areas were calculated by subtracting vegetated marsh from the total marsh extent.

UVVR was calculated as:

$$UVVR = \frac{\text{Unvegetated Area}}{\text{Vegetated Area}}$$

This ratio was then used to estimate net sediment flux using the relationship (Ganju et al., 2017):

$$\text{Net sediment flux} = -0.855(UVVR) + 0.330$$

This relationship links marsh condition to sediment accretion or erosion processes. Marsh condition was interpreted using the Unvegetated–Vegetated Ratio (UVVR), where values below ~0.1 indicate stable, sediment-accreting marshes, values between ~0.1–0.3 represent a transitional resilience threshold, and values above ~0.3 suggest marsh degradation and sediment loss (Ladd et al., 2019). Net sediment flux was estimated using the UVVR based empirical relationship from Ladd et al. (2019), producing a dimensionless index representing the relative balance between sediment accretion and erosion. Positive values indicate net sediment gain, while negative values indicate net sediment loss.

Because the Dengie Peninsula was not included in the Ladd et al. (2019) dataset, estimated UVVR values for this region were calculated using salt marsh extent and zonation data from the Environment Agency. The salt marsh extent and vegetation zonation were obtained from the Environment Agency *Saltmarsh Extent and Zonation* dataset, a national GIS layer derived from aerial imagery (2016–2019) and ground-truth surveys that map salt marsh extent and ecological zonation across England (Environment Agency, 2022). This dataset already has large creek systems removed from the salt marsh area so this was used as salt marsh vegetated area (Figure 2.5). To get the unvegetated areas, the EA salt marsh zonation and extent shapefile was buffered by 75m to fill in gaps in the salt marsh and then dissolved to create one large salt marsh shapefile, and then buffered again by -75m – this provided the salt marsh vegetated and unvegetated areas. The original shapefile was then subtracted from this one to get unvegetated areas. As this approach does not use satellite imagery to directly detect vegetated areas, it was not as accurate as Ladd et al. (2019), this should be considered when interpreting the results for the Dengie peninsula (policy unit G2 and G3).



Figure 2.5. Map of the Dengie Peninsula, showcasing the EA salt marsh extent and zonation data (green) (Environment Agency, 2022) which excludes small creek systems from the shapefile. This data was used to calculate the UVVR for the Dengie peninsula.

2.2.4 Natural Capital Indicators

For the Source 2 Sea Blackwater and Colne Natural Capital project, Natural capital indicators were calculated for five key ecosystem services delivered by estuarine habitats. These ecosystem services were carbon storage, carbon sequestration, nitrogen removal through denitrification, wave attenuation capacity (as a proxy for storm protection), and species richness (as a proxy for biodiversity). These natural capital indicators are used in this study to assess the relationship between connectivity and natural capital for the current scenario analysis. For the salt marsh 2055 future scenario, carbon sequestration, nitrogen removal, and wave attenuation were all predicted for 2055 as per the Underwood et al. (2025) study. A detailed analysis of the natural capital assets can be found in Underwood et al. (2025).

2.2.4.1 Carbon Storage and Sequestration

Carbon stocks in the upper 10 cm of sediments were derived from data collected through the Coastal Biodiversity and Ecosystem Service Sustainability (CBESS) project (Wood et al., 2015), supplemented by peer-reviewed studies, NERC data centres, and University of Essex datasets collected between 2003 and 2025 (Underwood et al., 2025).

From the sediment samples, carbon stocks were calculated using measurements of sediment bulk density, organic carbon content, and sediment depth. These variables were combined to estimate carbon storage per unit area and scaled by habitat area within each SMP policy unit.

Sediment accretion and erosion rates were incorporated using the UVVR-derived sediment flux relationship to estimate changes in carbon storage over time. Carbon fluxes were converted to CO₂ equivalents using the standard conversion factor of 3.67 (IPCC, 2006) (Underwood et al., 2025).

2.2.4.2 Nitrogen Removal through Denitrification

Denitrification rates were estimated using long-term nitrate concentration data obtained from the Environment Agency Water Information Management System (WIMS) and University of Essex monitoring programmes spanning 1981–2024. Both estuaries were divided into seven nutrient zones (Figure 2.6), delineated in QGIS based on salinity gradients and estuarine features. Nutrient zones represent broad hydro-chemical regions and are larger than individual Shoreline Management Plan (SMP) policy units.

Average nitrate concentrations ($\mu\text{mol L}^{-1}$) were calculated for summer–autumn (May–October) and winter–spring (November–April) across all sampling points. In QGIS, nitrate

data points were assigned to nutrient zones using the shortest line function, and values were averaged to produce one seasonal nitrate concentration per nutrient zone. Each SMP policy unit was then assigned the nitrate concentration of the nutrient zone within which it is located. This approach assumes spatial homogeneity of nitrate concentration within each nutrient zone while allowing denitrification to be estimated at the policy unit scale.

The area of salt marsh, intertidal, and subtidal habitats was calculated within each SMP policy unit.

Denitrification rates were estimated using a Michaelis–Menten formulation, parameterised using values reported for estuaries in south-east England. Water-column denitrification (D_w) was calculated as:

$$D_w = \frac{D_{w,\max} \cdot [NO_3^-]}{K_m + [NO_3^-]}$$

where D_w is the denitrification rate ($\mu\text{mol m}^{-2} \text{h}^{-1}$), $D_{w,\max}$ is the maximum denitrification rate, $[NO_3^-]$ is nitrate concentration ($\mu\text{mol L}^{-1}$), and K_m is the half-saturation constant. Values for $D_{w,\max}$ and K_m were obtained from Trimmer et al. (1997) and Dong et al. (2000), averaged, and applied across all nutrient zones.

Denitrification rates were calculated on a seasonal basis for each habitat type. Hourly rates ($\mu\text{mol m}^{-2} \text{h}^{-1}$) were scaled to seasonal fluxes by multiplying by the duration of inundation and the length of each season (182.5 days). Habitat-specific inundation periods were applied as follows: 24 hours for subtidal habitats, 12 hours for intertidal habitats, and 6.79 hours for salt marsh. Resulting values ($\mu\text{mol m}^{-2} \text{season}^{-1}$) were

multiplied by habitat area (m^2) within each SMP policy unit to estimate total nitrogen removal per season.

Sediment-coupled nitrification–denitrification (D_n), representing nitrogen loss supported by nitrate generated within the sediment through the nitrification of ammonium, was estimated following Ogilvie et al. (1997) and Dong et al. (2000), assuming a fixed proportional relationship where $D_n = 0.405 \times D_w$. D_n was scaled over a 24-hour period across all habitat types, reflecting the assumption in this study that coupled nitrification–denitrification was not restricted to periods of tidal inundation. This differs from the habitat-specific inundation periods applied to D_w , which represents denitrification supported by nitrate supplied from the overlying water. Seasonal fluxes were subsequently calculated using the same temporal scaling approach.

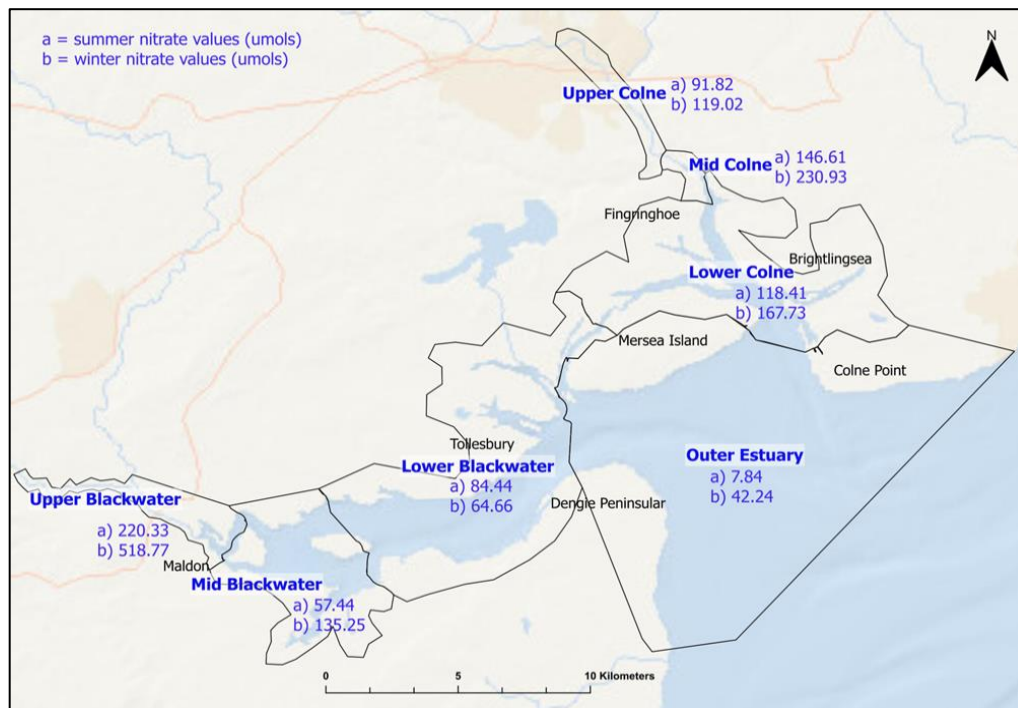


Figure 2.6. Map showing the nutrient zones and the concentration of nitrogen ($\mu\text{mol L}^{-1}$) for summer (a) and winter (b) in the Blackwater and Colne estuaries (Underwood et al., 2025).

2.2.4.3 Wave Attenuation Potential

Wave attenuation potential is defined here as the reduction in potential wave energy reaching the shoreline due to the presence of salt marsh and is used as an indicator of coastal protection. Wave attenuation potential was quantified using fetch-based metrics derived from Gilbertson et al. (2020).

In this context, fetch is defined as the distance over which wind can act on the water surface to generate waves. Gilbertson et al. (2020) calculated fetch from point locations across eight directional bearings (0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°), measuring the distance to the nearest landmass in each direction. Distances were truncated at a maximum of 200 km, and mean fetch was calculated as the average across all directions (Gilbertson et al., 2020).

Effective fetch represents the remaining wave-generating distance after accounting for attenuation by intervening coastal habitats, including salt marsh, along these directional pathways. This was calculated within a defined search radius of up to 5 km (Gilbertson et al., 2020).

Point-based estimates of fetch and effective fetch for the Blackwater and Colne estuaries were obtained directly from Gilbertson et al. (2020) following personal communication with the authors. The dataset included Easting and Northing coordinates alongside corresponding fetch and effective fetch values for locations across Essex. These point-based values were spatially aggregated to the SMP policy unit scale by averaging all observations falling within each unit. To calculate wave attenuation for each SMP policy unit, fetch and effective fetch were used in the equation presented by Gilbertson et al. (2020):

$$z = f - \frac{y \times f}{100}$$

where z is effective wave fetch, f is wave fetch, and y is percent attenuation. As the dataset provided values for both fetch (f) and effective fetch (z), the equation was rearranged to calculate percentage wave attenuation:

$$y = \frac{(f - z)}{f} \times 100$$

The resulting value (y) therefore represents the percentage reduction in fetch associated with the presence of intervening coastal habitat and was used as the indicator of wave attenuation potential for each SMP policy unit.

2.2.5 Connectivity Analysis

Structural connectivity of salt marsh habitat was quantified for each Shoreline Management Plan (SMP) policy unit using landscape metrics calculated in R with the *landscapemetrics* package, an implementation of FRAGSTATS (Hesselbarth et al., 2019) (Figure 2.7). Each SMP policy unit was treated as an independent landscape, within which salt marsh habitat was represented as a binary raster (salt marsh vs non-salt marsh). Connectivity was therefore assessed within policy units rather than across the estuary as a whole.

The following landscape metrics were calculated for salt marsh habitat within each policy unit: total salt marsh area, mean Euclidean nearest neighbour distance, mean contiguity index and landscape shape index (Table 2.1). These metrics were selected to represent key components of habitat configuration: habitat extent, patch isolation, patch cohesion and compactness, and patch geometry, which are known to influence ecological

processes such as species movement, sediment transport, and ecosystem functioning (Turner and Gardner, 2015; Boström et al., 2011).

Total salt marsh area

Total salt marsh area represents the total extent of salt marsh habitat within each SMP policy unit (Figure 2.7). This metric captures the amount of available habitat and is a fundamental determinant of ecological functioning. Larger habitat areas provide greater continuous habitat and are typically associated with increased connectivity potential, supporting processes such as species dispersal, sediment exchange, and biogeochemical cycling.

Mean Euclidean nearest neighbour distance

Mean Euclidean nearest neighbour distance quantifies the average distance between discrete salt marsh patches within each policy unit (Figure 2.7). For each salt marsh patch, Euclidean nearest neighbour distance was calculated as the shortest straight-line distance between the edges of that patch and the nearest neighbouring salt marsh patch; therefore, distances were measured edge-to-edge rather than between patch centres. The mean of these distances was then calculated for the salt marsh patches within each policy unit. This metric measures patch isolation, with larger values indicating greater separation between patches and therefore increased fragmentation. Increased nearest neighbour distance reduces the likelihood of ecological interactions between patches, including species movement and material exchange, and is therefore interpreted as reduced structural connectivity.

Mean contiguity index

The mean contiguity index measures the degree of internal connectedness and compactness of salt marsh patches within each policy unit (Figure 2.7). It is calculated based on the arrangement and adjacency of raster cells within individual habitat patches. Higher contiguity values indicate more compact and cohesive patch structures, whereas lower values indicate less connected, elongated or irregular patch configurations. Unlike mean Euclidean nearest neighbour distance, which measures isolation between separate patches, the contiguity index describes the internal spatial configuration of individual patches. In salt marsh systems, variation in contiguity may reflect geomorphological features such as tidal creek networks, erosion, or habitat fragmentation, which influence patch cohesion and the spatial structure of the marsh landscape.

Landscape Shape Index

The landscape shape index quantifies the complexity of patch geometry relative to a simple, compact shape (Figure 2.7). Higher values indicate more irregular and convoluted patch shapes, often associated with increased edge length. In salt marsh systems, complex patch geometry may arise from geomorphological processes such as tidal creek formation and erosion (Allen, 2000; Temmerman et al., 2013). Patch shape influences ecological processes by altering edge dynamics, exposure to environmental stressors, and interactions between marsh and adjacent habitats. Shape index was selected as a structural connectivity metric because variation in patch geometry reflects patterns of fragmentation and edge configuration within the marsh landscape, both of which influence the spatial structure and functional interactions of connected habitat areas.

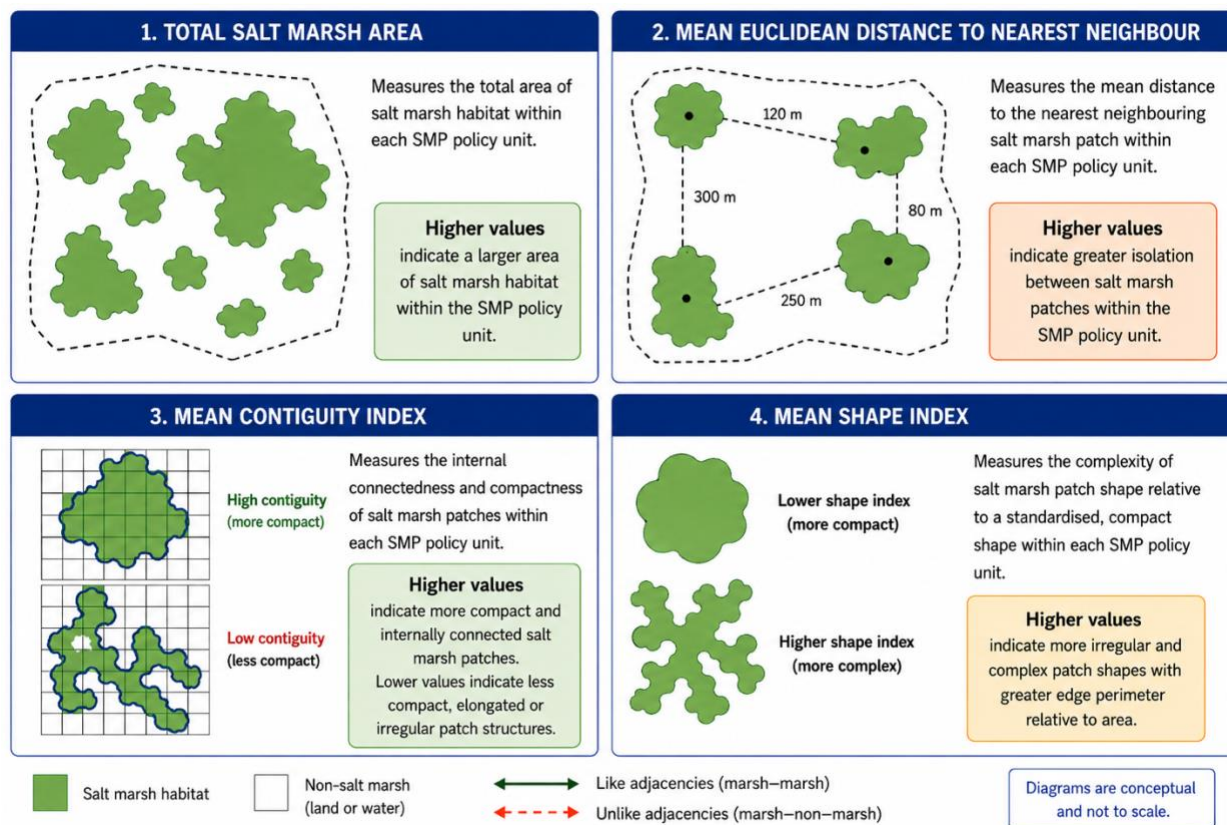


Figure 2.7. The four FragStats connectivity metrics (total area, mean Euclidean distance to nearest neighbour, mean contiguity index and mean shape index) used to measure the structural connectivity of the salt marsh within each SMP policy unit.

Table 2.1. Showing a summary of the landscape structural connectivity metrics which were used to assess structural connectivity within each SMP policy unit.

Metric	What it measures	Expected relationship with ecological function / natural capital	Ecological interpretation
Total salt marsh area	Total area of salt marsh habitat	Positive	Larger habitat area provides a greater capacity for ecosystem service delivery.
Mean Euclidean distance to nearest neighbour	Mean distance between individual salt marsh patches	Negative	Greater distances indicate increased patch isolation and reduced connectivity, which may limit ecological processes such as species movement, sediment exchange, and nutrient cycling.
Mean contiguity index	Degree of internal connectedness and compactness of salt marsh patches	Positive (general expectation)	Higher contiguity values indicate more compact and internally connected salt marsh patches, reflecting greater patch cohesion. Lower values indicate elongated, irregular or less cohesive patch structures,

			which may arise from fragmentation, erosion or complex creek networks.
Mean shape index	Complexity of patch shape relative to a standardised form	Context-dependent (no assumed directional relationship)	Higher values indicate more irregular and complex patch shapes, which may arise from natural creek networks (potentially beneficial) or from fragmentation and erosion (potentially indicative of degradation). Lower values may reflect more compact and cohesive marsh geometries. Interpretation is therefore context-dependent and should be considered alongside other connectivity metrics.

Scale and interpretation of metrics

The selected landscape metrics operate at different spatial levels and therefore capture distinct aspects of habitat configuration. Total salt marsh area is a class-level metric describing the overall extent of salt marsh habitat within a policy unit. Mean Euclidean

nearest neighbour distance, mean contiguity index and mean shape index are derived from individual habitat patches and therefore describe patch-level properties, including patch isolation, internal cohesion and geometric complexity.

Mean Euclidean nearest neighbour distance measures the degree of isolation between separate habitat patches, whereas the mean contiguity index measures the internal connectedness and compactness of individual patches. Mean shape index describes the geometric complexity of patch boundaries relative to a standardised compact shape. Together, these metrics provide complementary information on the spatial structure of salt marsh habitat.

This distinction is important because different metrics capture different dimensions of structural connectivity. For example, two policy units may contain salt marsh patches with similar nearest neighbour distances but differ substantially in patch cohesion or shape complexity. Similarly, landscapes with comparable total salt marsh area may exhibit very different patterns of patch isolation and internal patch structure. Interpreting these metrics collectively therefore provides a more complete understanding of habitat configuration than any individual metric alone.

Scale of analysis

Connectivity metrics were calculated at the scale of SMP policy units, with each policy unit treated as an independent landscape. This reflects the management relevance of SMP policy units, which represent spatially discrete coastal management zones used in shoreline planning. However, this approach constrains the analysis to within-unit structural connectivity, and does not capture connectivity between adjacent policy units.

Furthermore, the metrics used in this study describe structural connectivity only, and do not account for species-specific movement behaviour or hydrodynamic connectivity processes.

Statistical analysis

Relationships between landscape connectivity metrics and natural capital indicators were assessed using Kendall's rank correlation coefficient (τ). A non-parametric approach was selected because of the relatively small sample size and substantial variation between SMP policy units, including potentially influential extreme values, meaning that the assumptions required for parametric correlation could not be reliably established. Kendall's rank correlation coefficient was therefore considered appropriate because it evaluates monotonic relationships based on ranked data without requiring the assumptions of normality and linearity associated with parametric correlation methods. It is also suitable for variables measured on different scales, which was relevant to this study because the natural capital and connectivity metrics were expressed using different units and ranges.

To account for multiple comparisons, p-values were adjusted using the Benjamini–Hochberg procedure to control the false discovery rate, with statistical significance assessed at $p < 0.05$.

Policy unit F11b was excluded from the correlation analyses in all scenarios because it contained negligible or no salt marsh habitat and produced disproportionately high nearest-neighbour distances. For the future scenario, C4, D1a, D1b, D2, G2 and G3 were

additionally excluded from the correlation analyses because corresponding natural capital data were unavailable.

Connectivity scenarios

Three connectivity scenarios were analysed:

1. Current scenario 1 – vegetated salt marsh only
2. Current scenario 2 – full salt marsh extent (combined vegetated and unvegetated areas)
3. Future scenario – salt marsh full 2055

The two current scenarios allowed comparison between connectivity patterns based solely on vegetated salt marsh and those based on the full salt marsh extent. The future scenario incorporated projected habitat creation areas identified within the MMO1135 Potential Habitat Creation dataset. To accommodate these future habitat areas, SMP policy units were extended landwards by 2.5 km prior to raster creation (Figure 2.3).

Structural connectivity metrics were calculated independently for each scenario using the same methodological approach. Comparisons between current and future scenarios therefore provide an indication of how projected habitat creation may alter salt marsh extent, patch isolation, patch cohesion and patch geometry within SMP policy units.

Species richness and carbon stocks were not included in the future scenario analysis. Reliable projection of these variables would require assumptions regarding future vegetation communities, habitat condition, sediment accumulation and carbon sequestration rates that could not be robustly supported by the available data.

Consequently, future scenario analysis focused on structural connectivity metrics and those natural capital indicators for which defensible projections were available.

2.3 Results

2.3.1 Natural Capital

Across SMP policy units, carbon stocks were highly variable in both current scenarios (vegetated salt marsh only compared to full salt marsh) (Figure 2.8). In current scenario 1 (vegetated salt marsh), carbon stocks ranged from 0.38 to 6128.36 tonnes, with a median of 786.93 tonnes (IQR: 229.35–1537.28 tonnes) (Table 2.2). In current scenario 2 (full salt marsh: combined vegetated and unvegetated salt marsh areas), values were very similar, ranging from 0.19 to 6128.36 tonnes, with a median of 782.53 tonnes (IQR: 227.13–1513.18 tonnes) (Figure 2.8). Carbon sequestration also varied substantially, with median values of 24.86 tonnes per year in current scenario 1 and 22.66 tonnes per year in current scenario 2 (Table 2.2 and Figure 2.8). In the future scenario (salt marsh full 2055), median carbon sequestration was slightly higher at 26.91 tonnes per year, although the maximum value increased markedly to 4737.76 tonnes per year, indicating a strongly skewed distribution (Table 2.2).

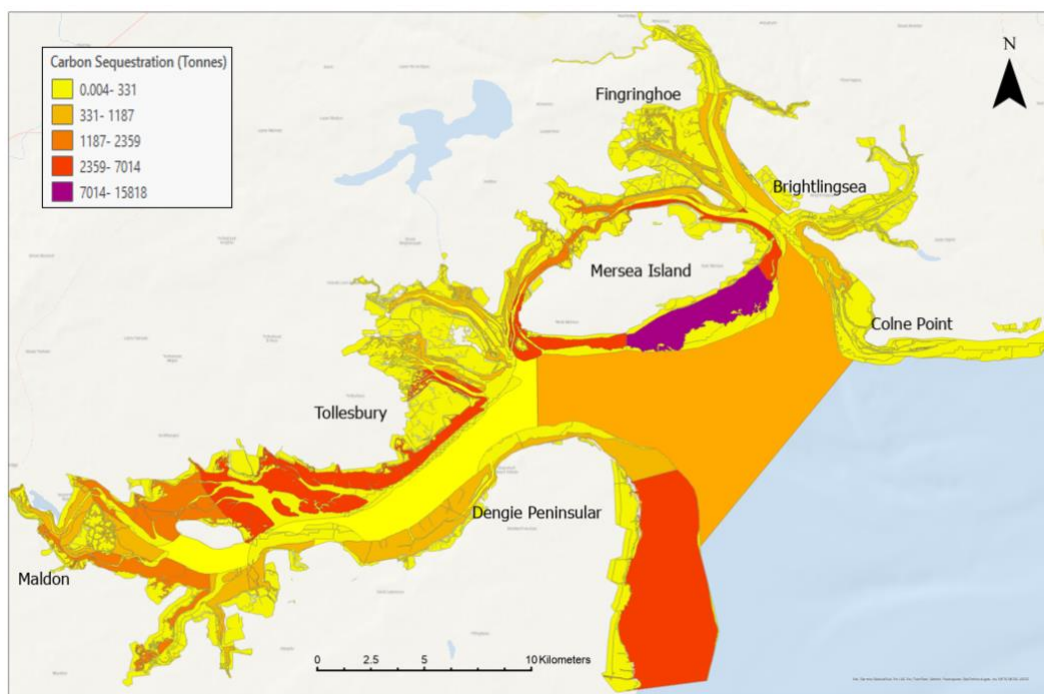


Figure 2.8. Carbon sequestered (tonnes per year) by salt marsh and mudflats under current scenario 1 and 2 across the Blackwater and Colne estuaries (Underwood et al., 2025).

Nitrogen removal showed broadly similar distributions across the three scenarios. Median nitrogen removal was 2.34 tonnes per year in current scenario 1, 2.27 tonnes per year in current scenario 2 (Figure 2.9), and 2.33 tonnes per year in the future scenario, with all scenarios ranging from 0.00 to 20.28 tonnes per year (Table 2.2).

Salt marsh plant species richness was only available for the current scenarios and there was little difference between them, with a median richness value of 3.54.

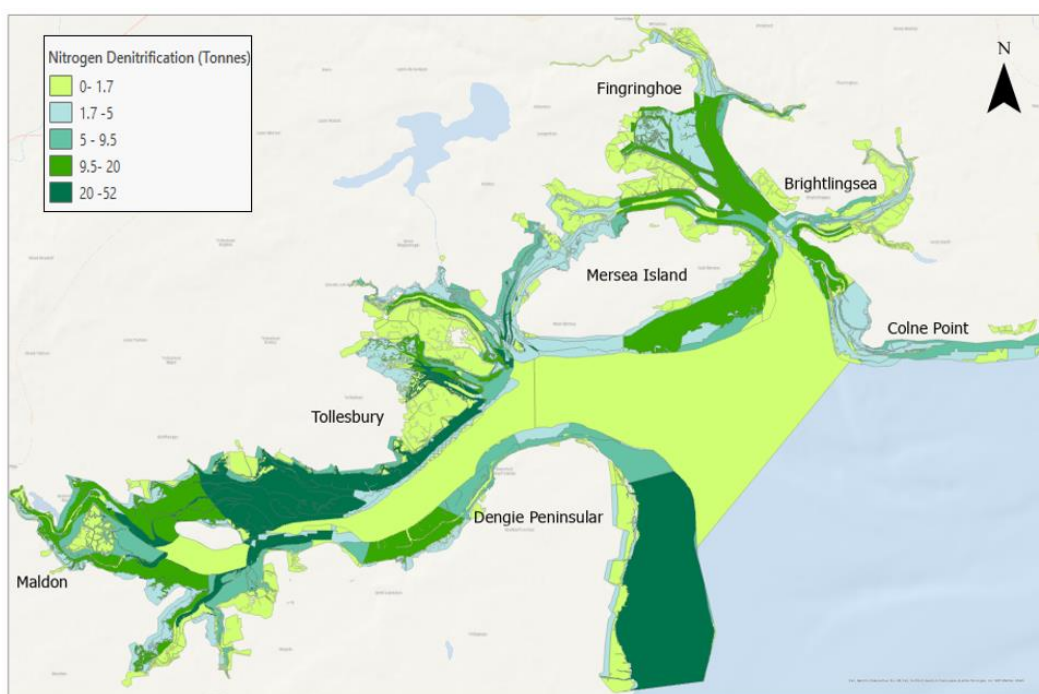


Figure 2.9. Nitrogen denitrification (tonnes per year) by salt marsh and mudflats under current scenario 1 and 2 across the Blackwater and Colne estuaries (Underwood et al., 2025).

Wave attenuation was also identical between the two current scenarios, with a median of 77.50% (IQR: 71.75–81.25%) (Figure 2.10). In contrast, the future scenario showed a higher median wave attenuation value of 82.94% (IQR: 80.19–85.17%), although values ranged from 58.33% to 86.68%.

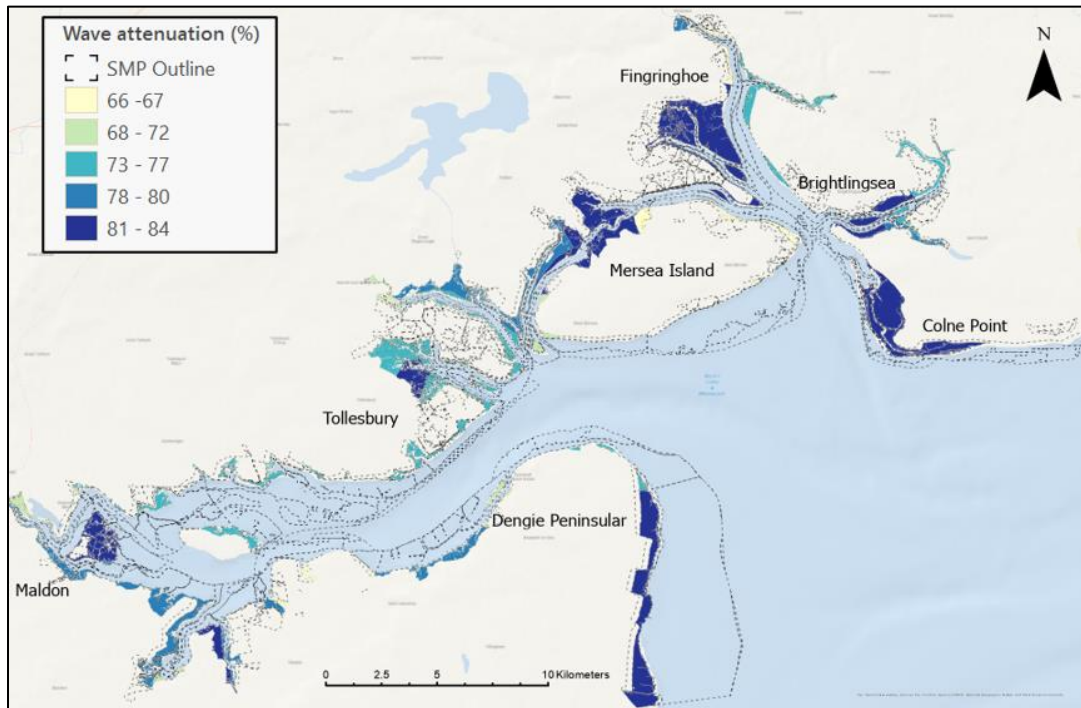


Figure 2.10. Wave attenuation (%) by salt marsh under current scenario 1 and 2 across the Blackwater and Colne estuaries (Underwood et al., 2025).

Table 2.2. Descriptive results of the natural capital metrics; carbon stocks, carbon sequestration, nitrogen removal, species richness and wave attenuation across all three scenarios.

Metric	Current scenario 1: vegetated only	Current scenario 2: full marsh	Future Scenario 2055
Carbon stocks (tonnes)	Median 786.93, IQR 229.35 - 1537.28, range 0.38– 6128.36	Median 782.53, IQR 227.13 - 1513.18, range 0.19 - 6128.36	NA
Carbon sequestration (tonnes per year)	Median 24.86, IQR 8.46 - 50.99, range 0.96 - 251.73	Median 22.66, IQR 7.87 - 50.29, range 0.00 - 251.73	Median 26.91, IQR 8.79 - 45.53, range 0.01 - 4737.76
Nitrogen removal (tonnes per year)	Median 2.34, IQR 0.78 - 4.34, range 0.00 - 20.28	Median 2.27, IQR 0.74 - 4.20, range 0.00 - 20.28	Median 2.33, IQR 0.66 - 4.92, range 0.00–20.28
Species richness	Median 3.54, IQR 1.97 - 4.22, range 0.50 - 7.71	Median 3.55, IQR 2.15 - 4.22, range 0.50 - 7.71	NA
Wave attenuation (%)	Median 77.50, IQR 71.75 - 81.25, range 63.00 - 84.00	Median 77.50, IQR 71.75 - 81.25, range 63.00 - 84.00	Median 82.94, IQR 80.19 - 85.17, range 58.33 - 86.68

2.3.2 Connectivity Metrics

Connectivity metrics varied across SMP policy units and between scenarios. Salt marsh area across SMP policy units in current scenario 1 (vegetated salt marsh) ranged from 0.28 to 231.26 ha, with a median of 26.49 ha (IQR: 9.32–47.30 ha) (Table 2.3 and Figure 2.11). In current scenario 2 (full salt marsh: combined vegetated and unvegetated salt marsh areas), area ranged from 0.01 to 239.00 ha, with a slightly higher median of 28.39 ha (IQR: 11.89–53.16 ha) (Table 2.3 and Figure 2.12). The future scenario (salt marsh full 2055) showed a marked increase in marsh area, ranging from 3.03 to 1184.85 ha, with a median of 90.52 ha (IQR: 35.32–270.78 ha) (Table 2.3 and Figure 2.13).

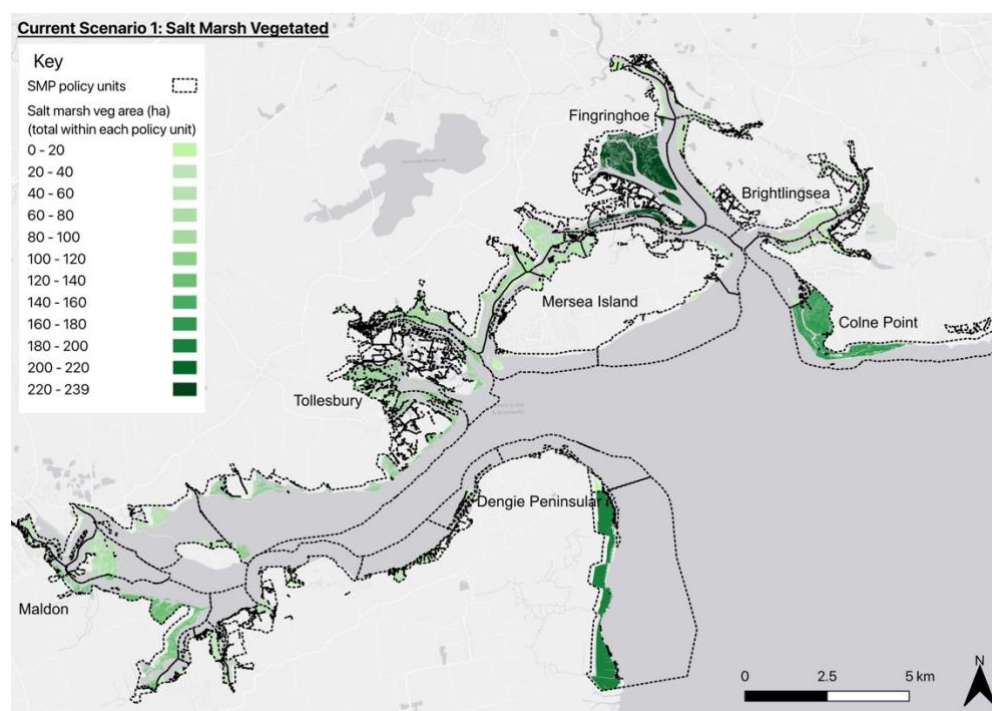


Figure 2.11. Current scenario 1 vegetated salt marsh, colour-coded by total vegetated salt marsh area (ha) within each Shoreline Management Plan policy unit (dotted line).

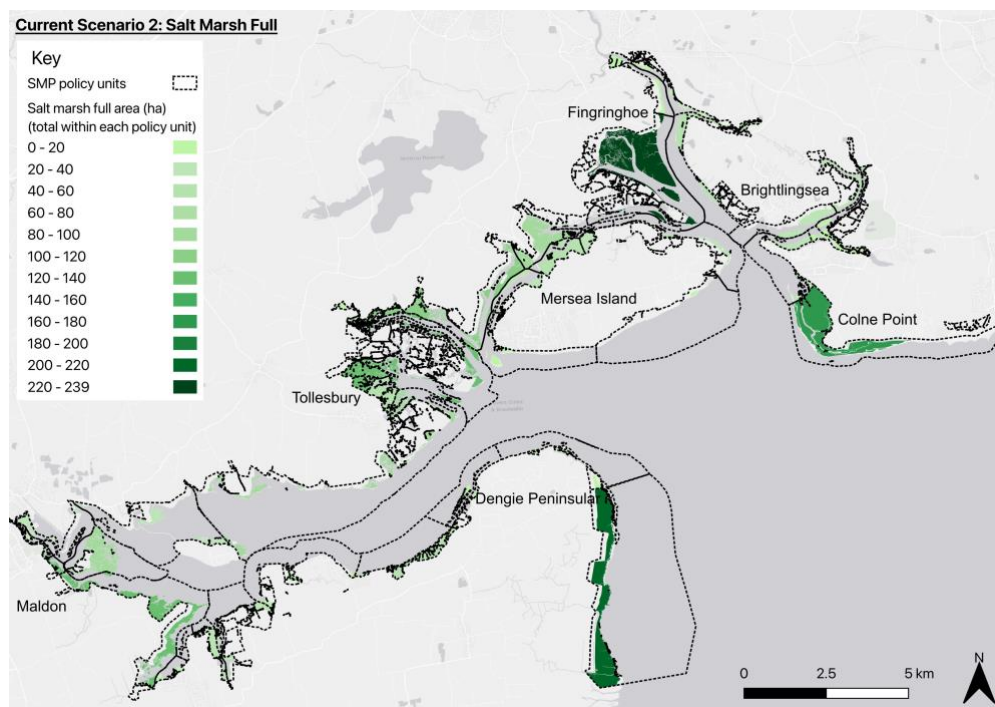


Figure 2.12. Current scenario 2 full salt marsh (vegetated and unvegetated areas combined), colour-coded by total salt marsh area (ha) within each Shoreline Management Plan policy unit (dotted line).

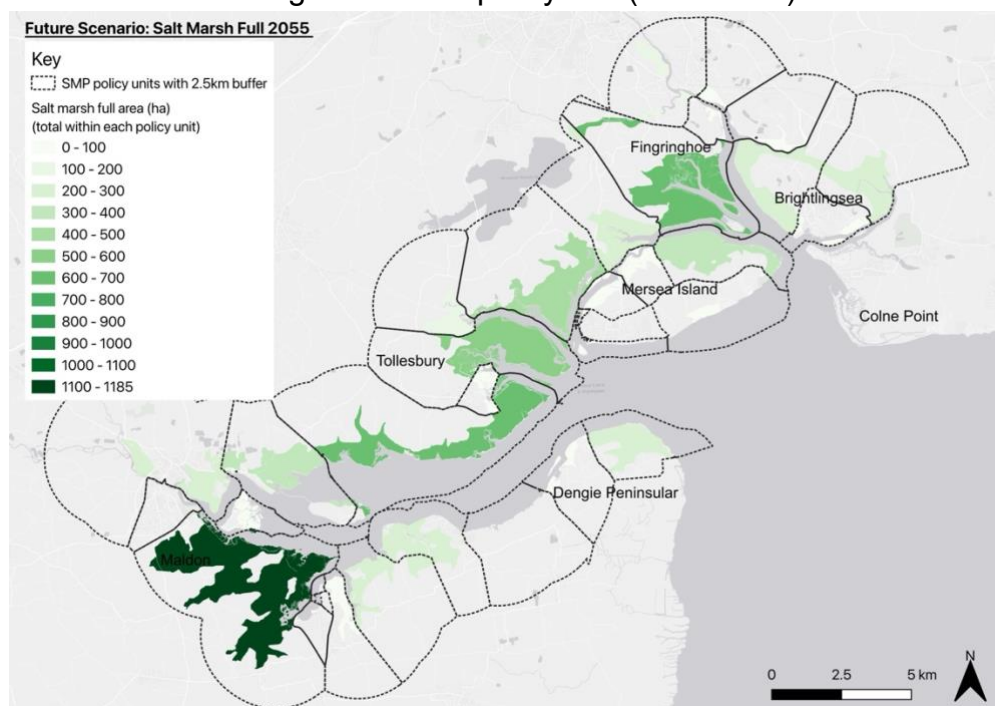


Figure 2.13. Future scenario full salt marsh 2055, colour-coded by total salt marsh area (ha) within each Shoreline Management Plan policy unit (dotted line). Note that the scale differs from the current scenario 1 and 2 area maps.

The median of the policy unit mean distances to nearest neighbour (DTNN) was lowest in current scenario 1, at 5.51 m (IQR: 5.09–7.12 m), indicating relatively close spacing between vegetated marsh patches (Table 2.3 and Figure 2.14). The median increased in current scenario 2 to 10.57 m (IQR: 6.25–16.92 m), suggesting greater separation when the full marsh extent was included (Table 2.3 and Figure 2.15). In the future scenario, the median policy-unit mean distance to nearest neighbour was 9.13 m (IQR: 6.75–21.88 m), with values ranging from 4.20 to 201.54 m (Table 2.3 and Figure 2.16).

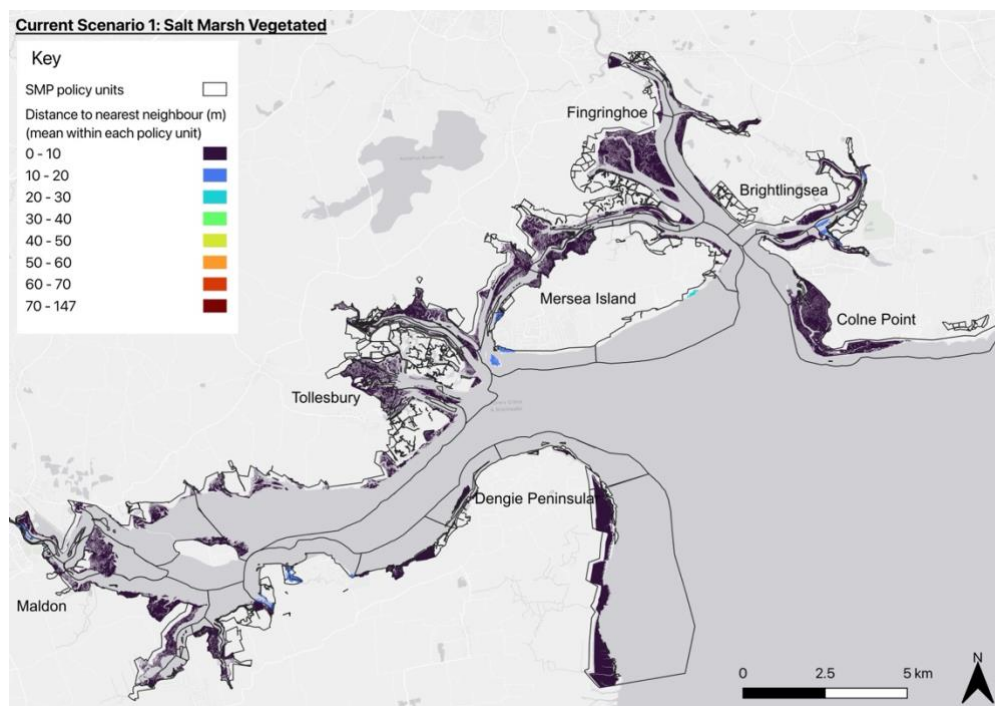


Figure 2.14. Current scenario 1 vegetated salt marsh colour coded by mean distance to nearest neighbour (m) within each Shoreline Management Plan policy unit (dotted line). Note that the scale differs from the current scenario 2 and future scenario DTNN maps.

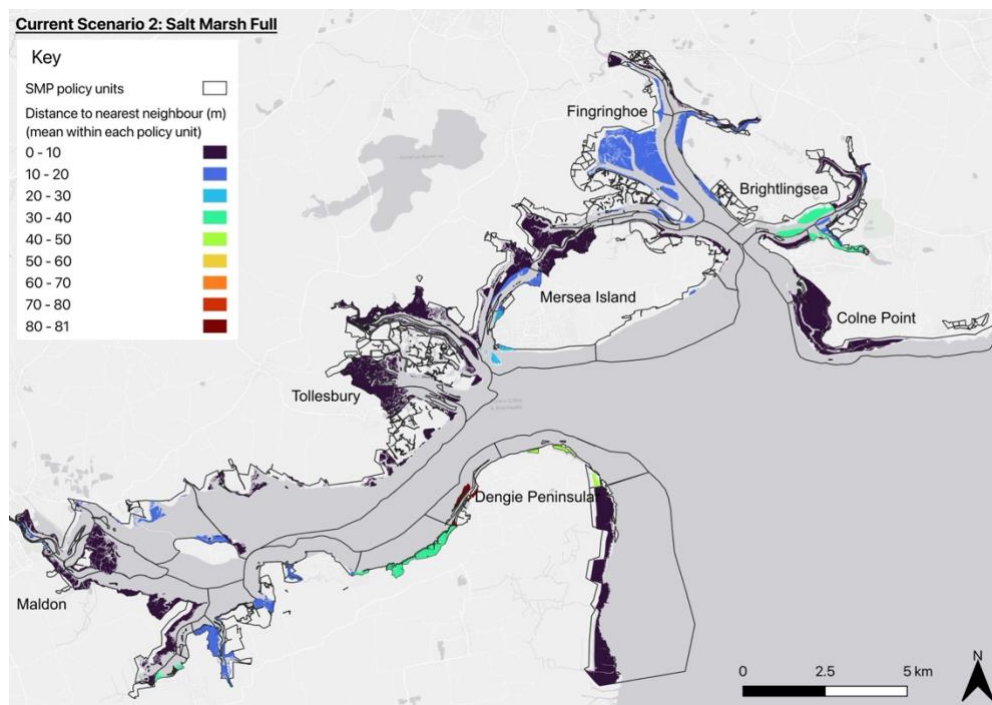


Figure 2.15. Current scenario 2 salt marsh colour coded by mean distance to nearest neighbour (m) within each Shoreline Management Plan policy unit (dotted line). Note that the scale differs from the current scenario 1 and future scenario DTNN maps.

Policy unit F11b is not displayed on this map.

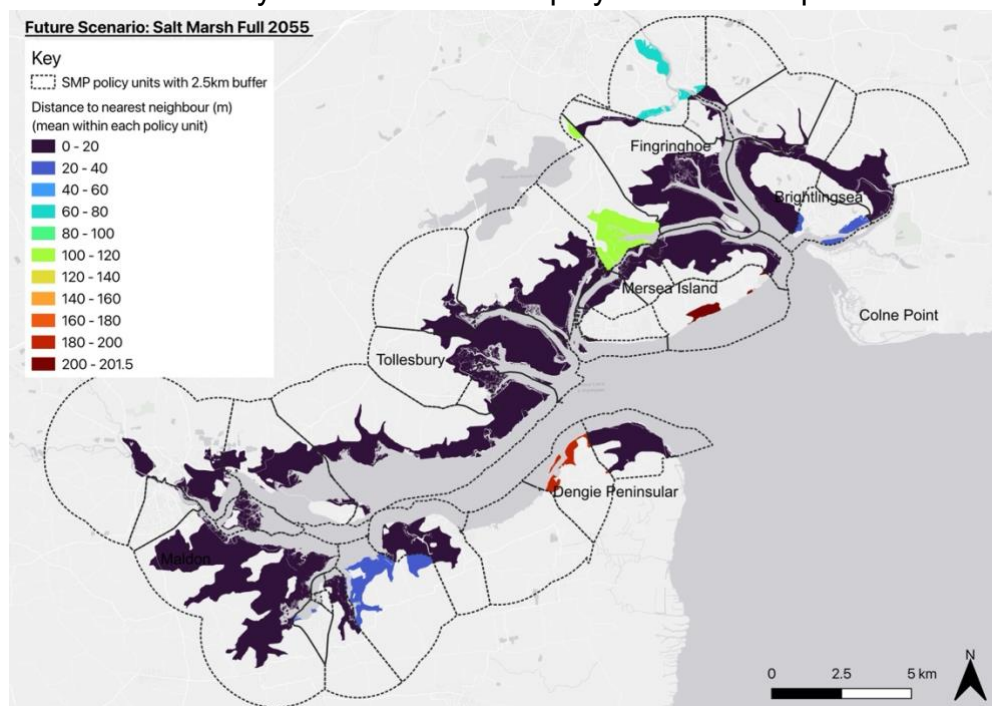


Figure 2.16. Future scenario salt marsh colour coded by mean distance to nearest neighbour (m) within each Shoreline Management Plan policy unit (dotted line). Note that scale differs to the current scenario 1 and 2 DTNN maps.

The median of the policy unit mean contiguity index values increased progressively across scenarios, from 0.31 (IQR: 0.28–0.37) in current scenario 1 (Figure 2.17) to 0.50 (IQR: 0.40–0.61) in current scenario 2 (Figure 2.18) and 0.56 (IQR: 0.50–0.68) in the future scenario (Figure 2.19 and Table 2.3). This suggests that salt marsh patches became increasingly compact and internally cohesive when the full marsh extent and future habitat creation areas were considered. The increase in contiguity indicates a shift towards more continuous patch structures and reduced internal fragmentation of individual marsh patches.

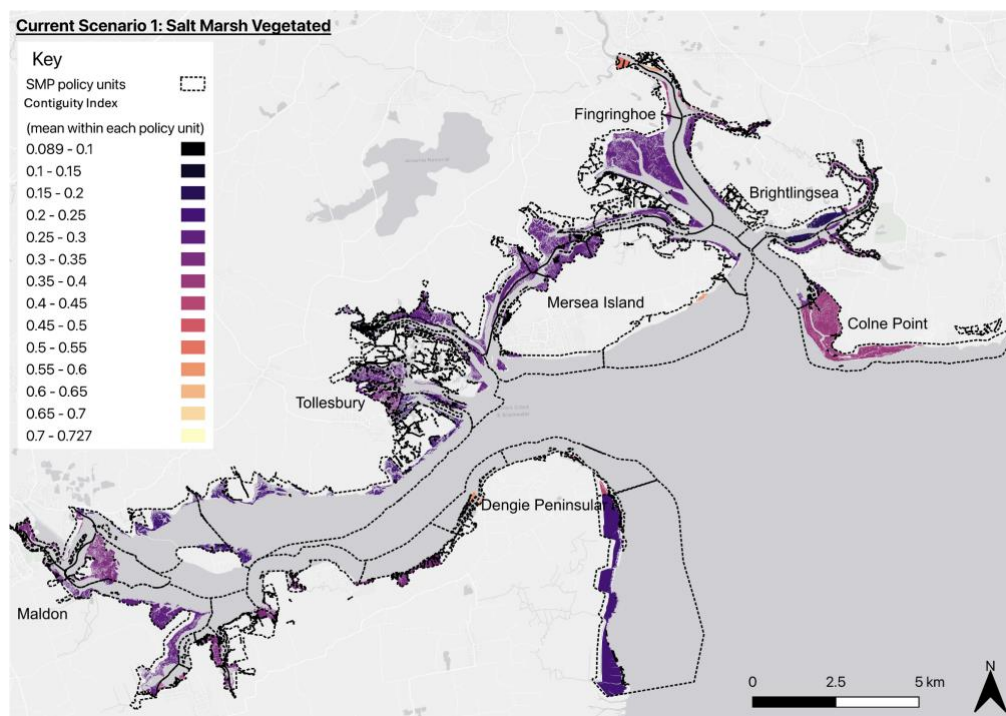


Figure 2.17. Current scenario 1 vegetated salt marsh colour coded by mean contiguity index within each Shoreline Management Plan policy unit (dotted line).

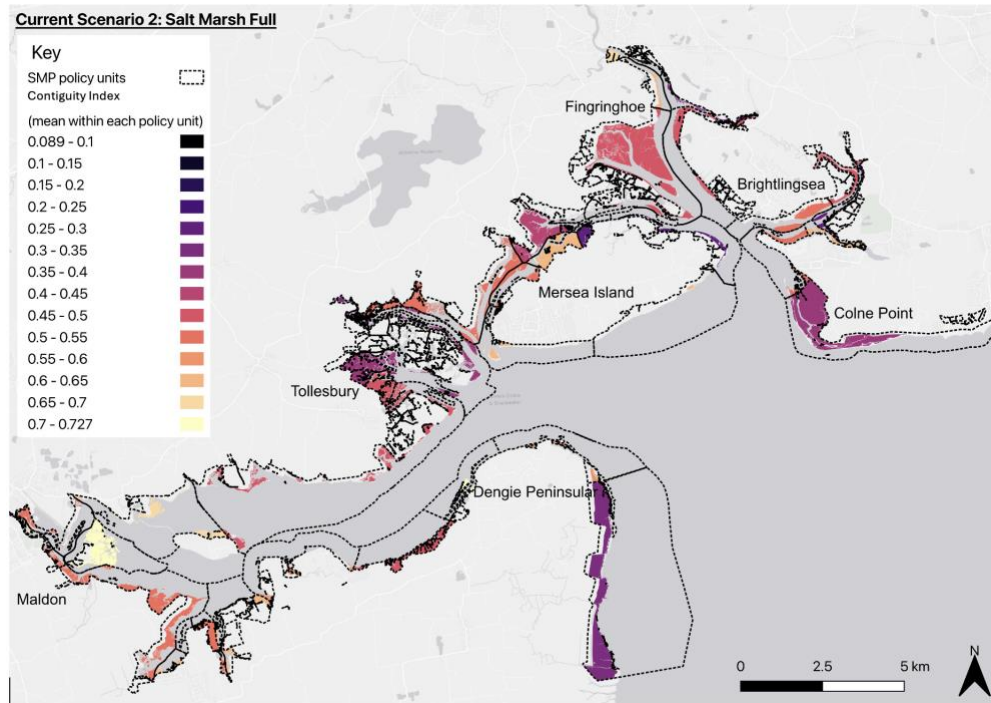


Figure 2.18. Current scenario 2 salt marsh colour coded by mean contiguity index within each Shoreline Management Plan policy unit (dotted line).

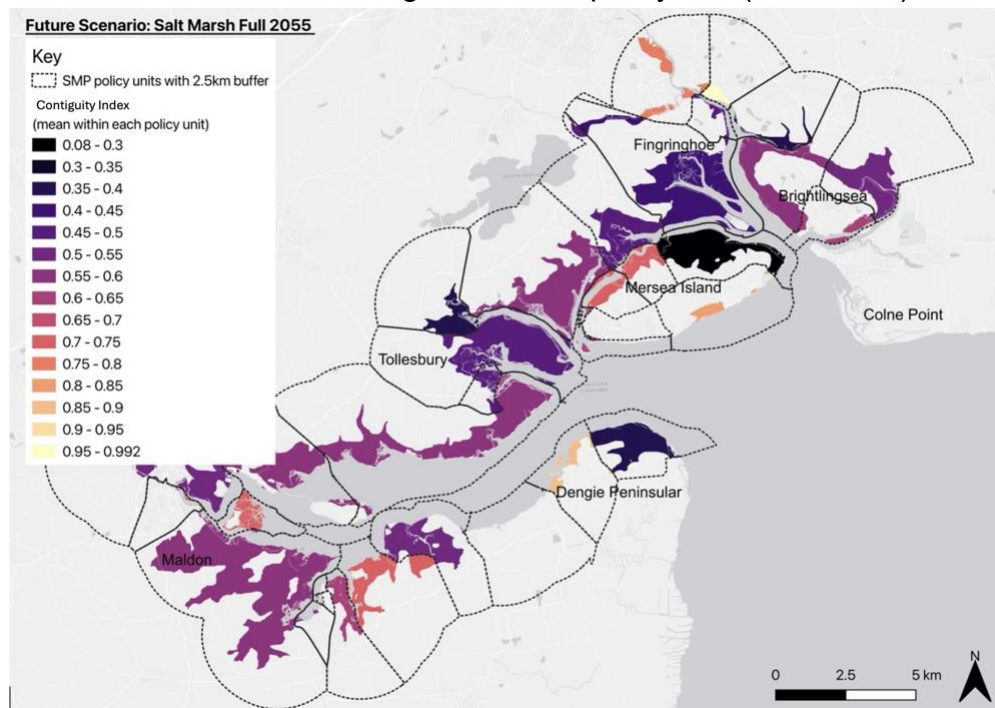


Figure 2.19. Future scenario salt marsh colour-coded by mean contiguity index within each Shoreline Management Plan policy unit (dotted line). Note that the symbology value ranges differ from the current scenario 1 and 2 contiguity index maps.

The median of the policy unit mean shape index values was 1.62 (IQR: 1.53–1.70) in current scenario 1 (Figure 2.20), increasing to 2.08 (IQR: 1.83–2.22) in current scenario 2 (Figure 2.21 and Table 2.3). The future scenario showed a similarly elevated median policy-unit mean shape index of 2.00 (IQR: 1.84–2.20), indicating that larger and more irregular marsh geometries were associated with full marsh inclusion and projected future habitat expansion (Figure 2.22 and Table 2.3).

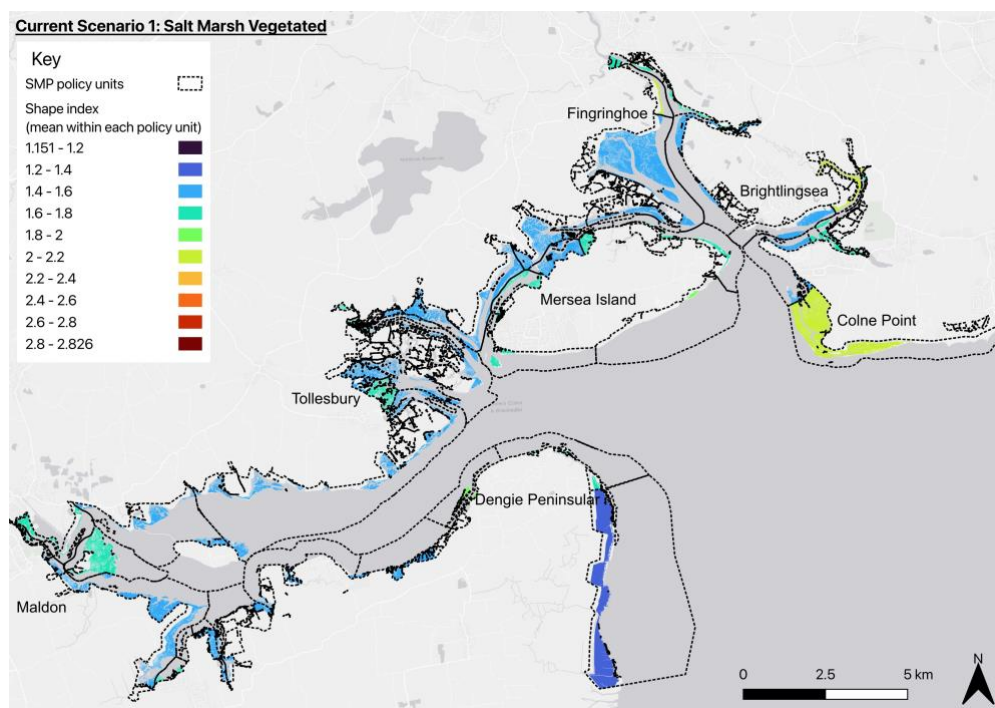


Figure 2.20. Current scenario 1 vegetated salt marsh colour coded by mean shape index within each Shoreline Management Plan policy unit (dotted line).

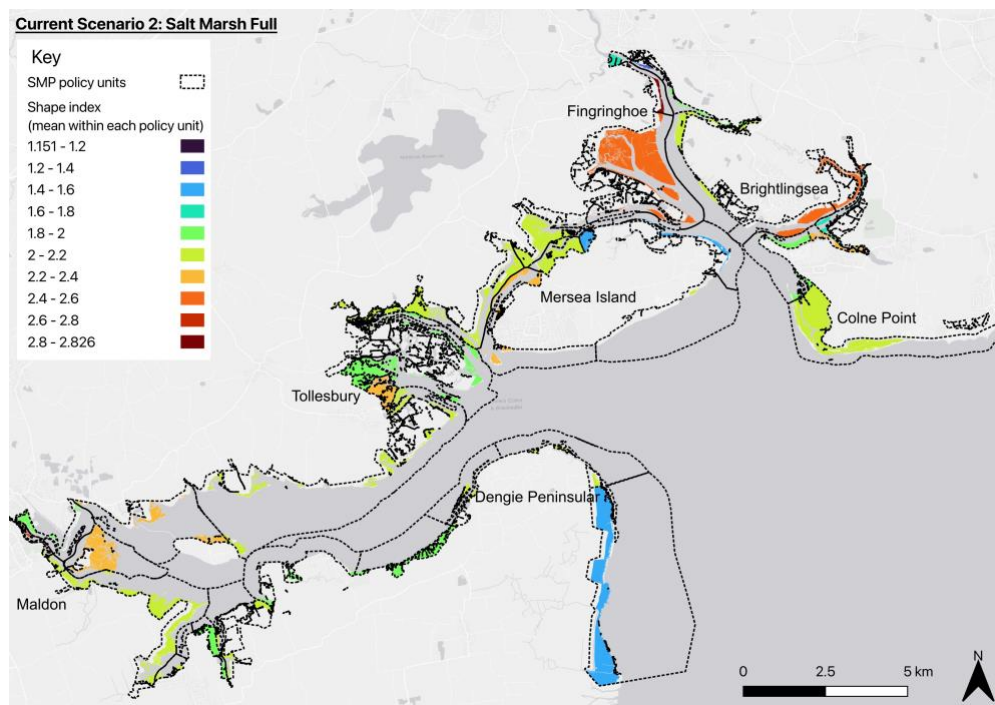


Figure 2.21. Current scenario 2 salt marsh colour coded by mean shape index within each Shoreline Management Plan policy unit (dotted line).

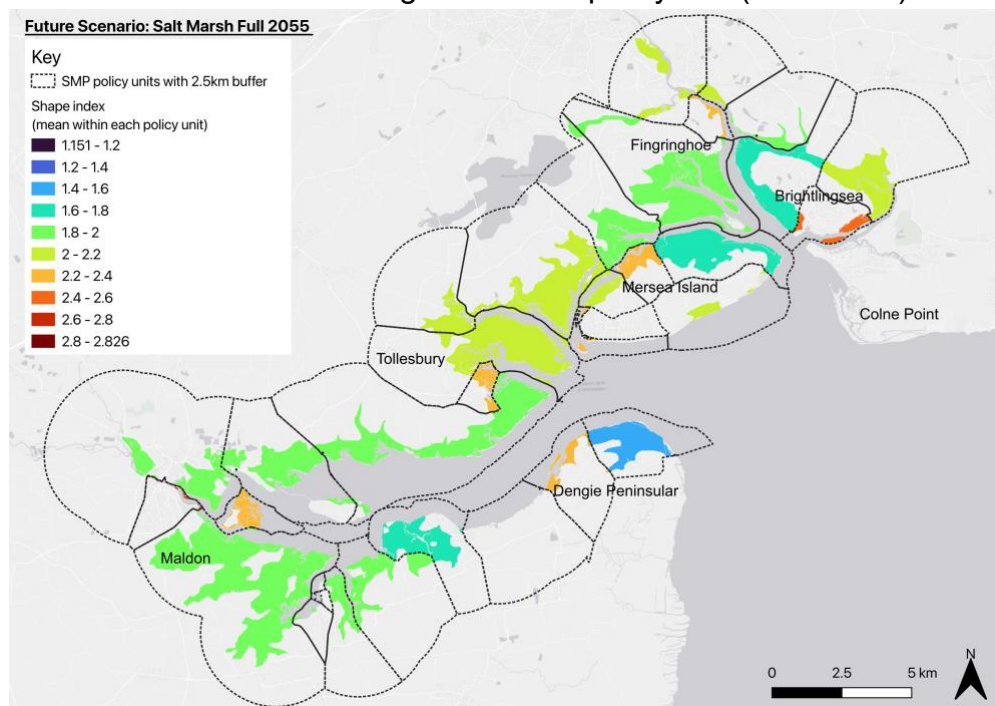


Figure 2.22. Future scenario salt marsh colour coded by mean shape index within each Shoreline Management Plan policy unit (dotted line).

Table 2.3. Descriptive results of the connectivity metrics; salt marsh area, distance to nearest neighbour, contiguity index and shape index across all three scenarios.

Metric	Current scenario 1: vegetated salt marsh only	Current scenario 2: full salt marsh	Future Scenario: salt marsh full 2055
Salt marsh area (ha)	Median 26.49, IQR 9.32 - 47.30, range 0.28 - 231.26	Median 28.39, IQR 11.89 - 53.16, range 0.01 - 239.00	Median 90.52, IQR 35.32 - 270.78, range 3.03 - 1184.85
Distance to nearest neighbour (m)	Median 5.51, IQR 5.09 - 7.12, range 4.90 - 29.97	Median 10.57, IQR 6.25 - 16.92, range 4.90 - 43.39	Median 9.13, IQR 6.75 - 21.88, range 0.00 - 44.35
Contiguity index	Median 0.31, IQR 0.28 - 0.37, range 0.19 - 0.48	Median 0.50, IQR 0.40 - 0.61, range 0.21 - 0.73	Median 0.56, IQR 0.50 - 0.68, range 0.31 - 0.79
Shape index	Median 1.62, IQR 1.53 - 1.70, range 1.35 - 2.02	Median 2.08, IQR 1.83 - 2.22, range 1.46 - 2.74	Median 2.00, IQR 1.84 - 2.20, range 1.42 - 2.92

2.3.3 Correlation between Natural Capital and Connectivity Metrics

2.3.3.1 Current scenario 1: vegetated salt marsh area

In current scenario 1, larger vegetated salt marsh areas were generally associated with higher regulating ecosystem service values, particularly carbon storage, carbon sequestration, nitrogen removal, and wave attenuation. Increasing distance between marsh patches was associated with reductions in these ecosystem service metrics. The mean contiguity index (patch cohesion and compactness) also showed moderate negative relationships with carbon storage, carbon sequestration, and nitrogen removal, indicating that variation in the internal configuration and cohesion of salt marsh patches was associated with differences in regulating ecosystem service provision. Shape index (patch geometry) showed comparatively weaker and less consistent relationships with natural capital metrics than patch area or spacing. Species richness displayed weaker and less consistent relationships with connectivity metrics than the regulating ecosystem service variables.

Vegetated salt marsh area showed strong positive correlations with carbon stocks ($\tau = 0.76$, $p < 0.001$), carbon sequestration ($\tau = 0.91$, $p < 0.001$), nitrogen removal ($\tau = 0.81$, $p < 0.001$), and wave attenuation ($\tau = 0.44$, $p < 0.001$), but a weak negative relationship with species richness ($\tau = -0.21$). Distance to nearest neighbour showed moderate negative correlations with carbon stocks ($\tau = -0.51$, $p < 0.001$), carbon sequestration ($\tau = -0.47$, $p < 0.001$), nitrogen removal ($\tau = -0.44$, $p < 0.001$), and wave attenuation ($\tau = -0.33$, $p < 0.01$), alongside a weak positive relationship with species richness ($\tau = 0.31$, $p < 0.05$). The mean contiguity index demonstrated moderate negative relationships with carbon stocks ($\tau = -0.42$, $p < 0.001$), carbon sequestration ($\tau = -0.46$, $p < 0.001$), and nitrogen

removal ($\tau = -0.44$, $p < 0.001$), but weaker relationships with wave attenuation and species richness. Shape index exhibited weaker negative relationships with carbon stocks ($\tau = -0.34$, $p < 0.01$), carbon sequestration ($\tau = -0.39$, $p < 0.01$), and nitrogen removal ($\tau = -0.31$, $p < 0.01$), while relationships with wave attenuation and species richness were not significant (Figure 2.23).

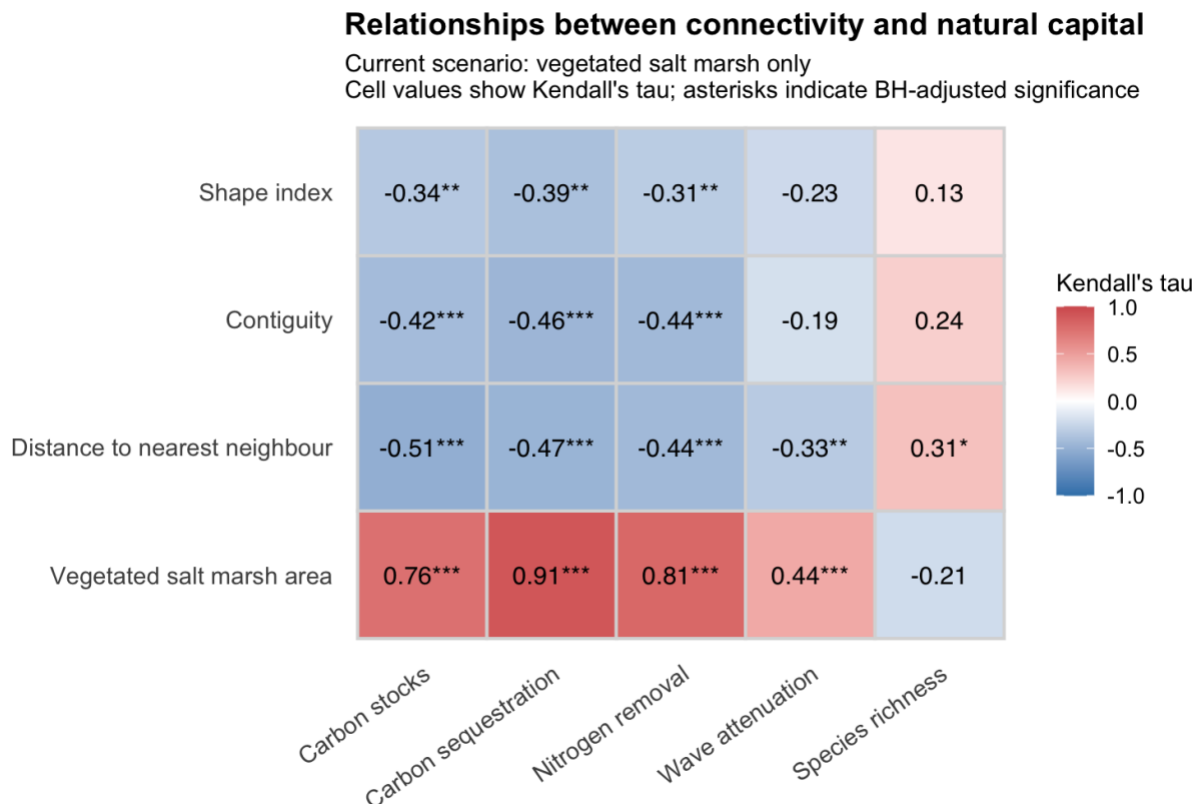


Figure 2.23. Kendall's tau correlation matrix between natural capital metrics and current scenario 1 (vegetated salt marsh) connectivity metrics. Red indicates positive relationships and blue indicates negative relationships, with colour intensity representing the strength of the relationship. Asterisks denote Benjamini–Hochberg-adjusted significance values ($p < 0.05$, $*p < 0.01$, $**p < 0.001$).

The relationships between vegetated salt marsh area and carbon sequestration, carbon stocks, and nitrogen removal were strongly positive, with larger salt marsh areas corresponding to higher regulating ecosystem service values (Figure 2.24, 2.25 and 2.26). However, several SMP policy units deviated from the overall trend in the relationships between vegetated salt marsh area and both carbon stocks and nitrogen removal (Figure 2.25 and 2.26). In particular, G2 (Dengie Peninsula) and C4 (Colne Point) showed notable deviation from the overall linear trend, with C4 exhibiting comparatively high carbon stocks and G2 comparatively low carbon stocks relative to marsh area. D8b (Fingringhoe) also deviated from the trend, exhibiting comparatively lower carbon stocks and higher nitrogen removal values relative to vegetated salt marsh area. F3 (Tollesbury) showed comparatively higher carbon stocks than expected from the overall trend line. Both C4 and G2 also exhibited lower nitrogen removal values than expected from the trend line. These variations suggest that factors beyond marsh area alone may influence carbon storage and nutrient processing capacity within individual SMP policy units.

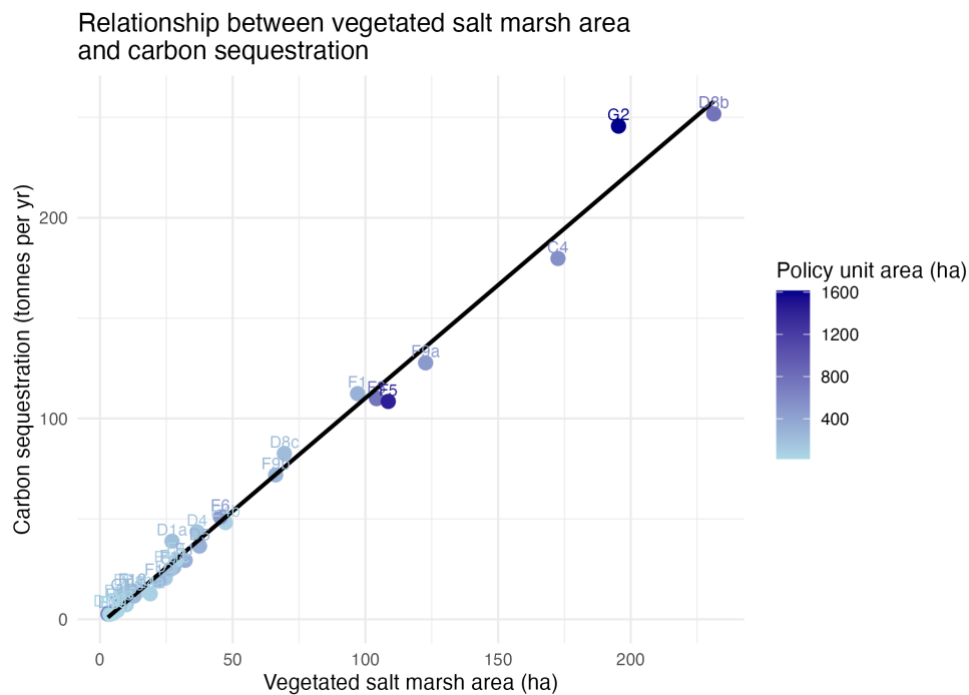


Figure 2.24. The linear relationship between carbon sequestration (tonnes per year) and vegetated salt marsh area (ha).

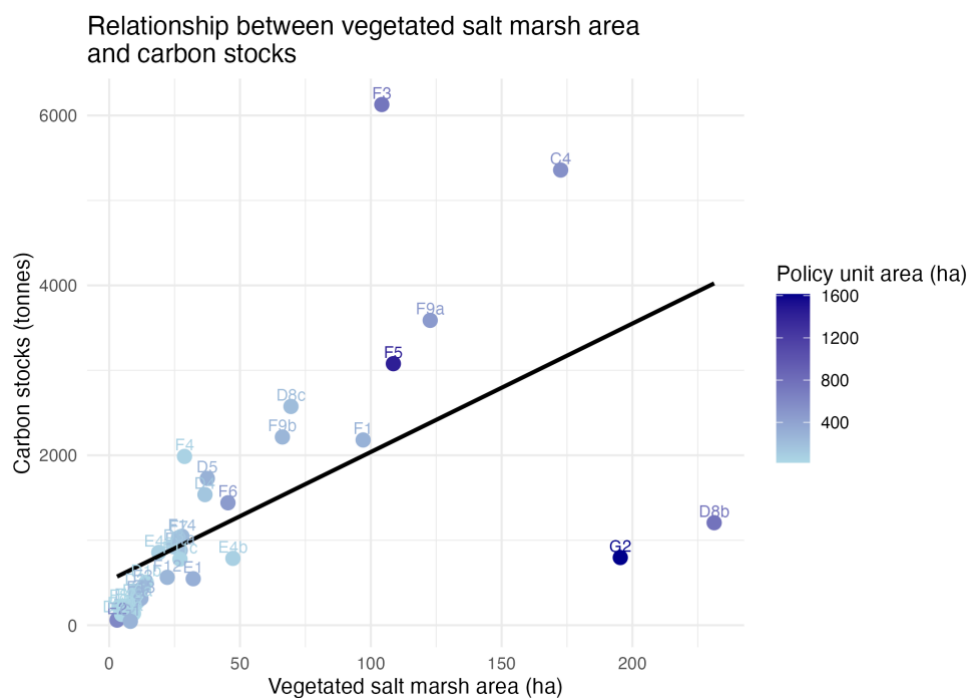


Figure 2.25. The linear relationship between carbon stocks (tonnes) and vegetated salt marsh area (ha).

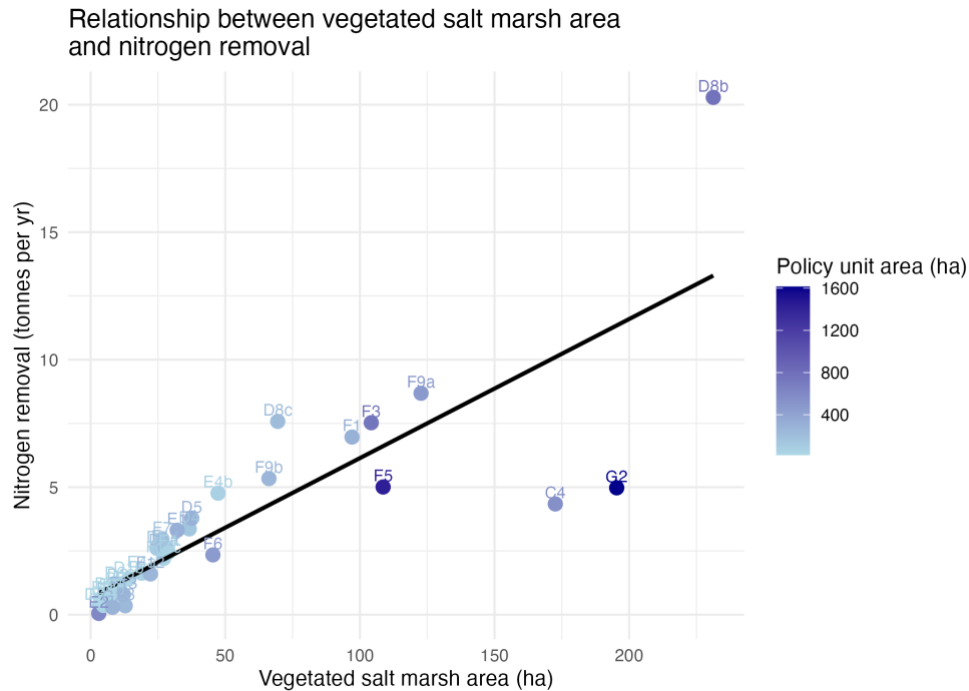
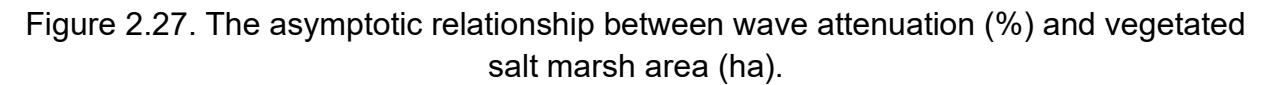


Figure 2.26. The linear relationship between nitrogen removal (tonnes per year) and vegetated salt marsh area (ha).

The relationship between vegetated salt marsh area and wave attenuation appeared asymptotic (Figure 2.27), with wave attenuation increasing rapidly at lower marsh areas before approaching a plateau at larger marsh extents. This suggests diminishing increases in wave attenuation potential beyond a certain marsh size, consistent with previous studies demonstrating non-linear relationships between marsh width and wave energy dissipation (Möller et al., 2014).



In current scenario 2, where the full salt marsh area (combined vegetated and

In current scenario 2, where the full salt marsh area (combined vegetated and unvegetated salt marsh areas) was included, salt marsh area remained strongly positively associated with carbon stocks ($\tau = 0.78$, $p < 0.001$), carbon sequestration ($\tau = 0.87$, $p < 0.001$), nitrogen removal ($\tau = 0.82$, $p < 0.001$), and wave attenuation ($\tau = 0.46$, $p < 0.001$) (Figure 2.28). Again, no significant relationship was observed with species richness. Distance to nearest neighbour retained weak negative correlations with carbon stocks ($\tau = -0.27$, $p < 0.05$), carbon sequestration ($\tau = -0.30$, $p < 0.05$), and nitrogen removal ($\tau = -0.31$, $p < 0.05$), indicating that increasing distance between salt marsh patches was associated with decreasing carbon stocks, carbon sequestration and nitrogen removal.

However, these associations were weaker than those observed in current scenario 1 (Figure 2.28).

In contrast to current scenario 1, neither mean contiguity index nor mean shape index showed significant relationships with any natural capital metric. This suggests that when the full salt marsh extent was considered, variation in patch cohesion, compactness and geometric complexity was less strongly associated with ecosystem service provision than habitat area or patch isolation.

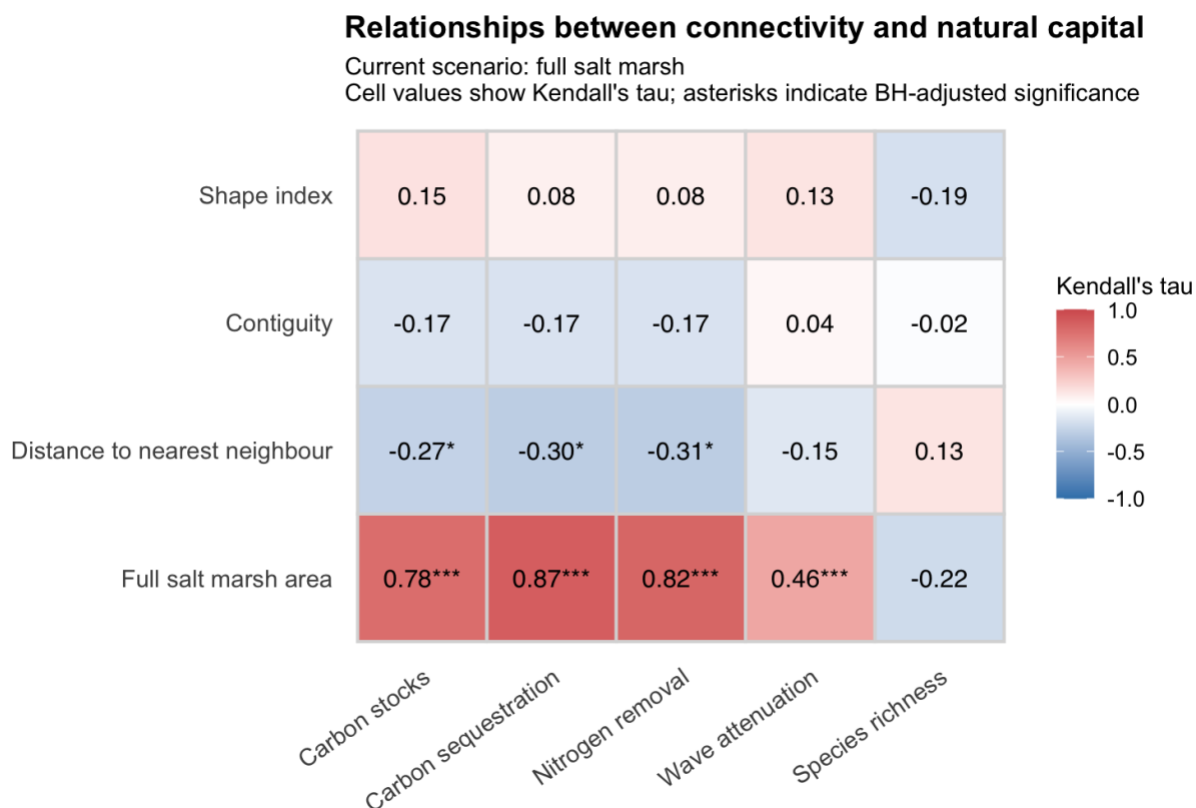


Figure 2.28. Kendall's tau correlation matrix between natural capital metrics and current scenario 2 (full salt marsh) connectivity metrics. Red indicates positive relationships and blue indicates negative relationships, with colour intensity representing the strength of the relationship. Asterisks denote Benjamini–Hochberg-adjusted significance values ($p < 0.05$, $*p < 0.01$, $**p < 0.001$).

2.3.3.3 Future scenario: salt marsh full 2055

In the future scenario, no statistically significant correlations were detected between connectivity metrics and ecosystem service indicators. Kendall's tau coefficients were uniformly weak ($\tau \leq 0.09$), suggesting that projected future ecosystem service values were not strongly associated with variation in salt marsh area, distance to nearest neighbour, mean contiguity index, or mean shape index at the SMP policy unit scale (Figure 2.29).

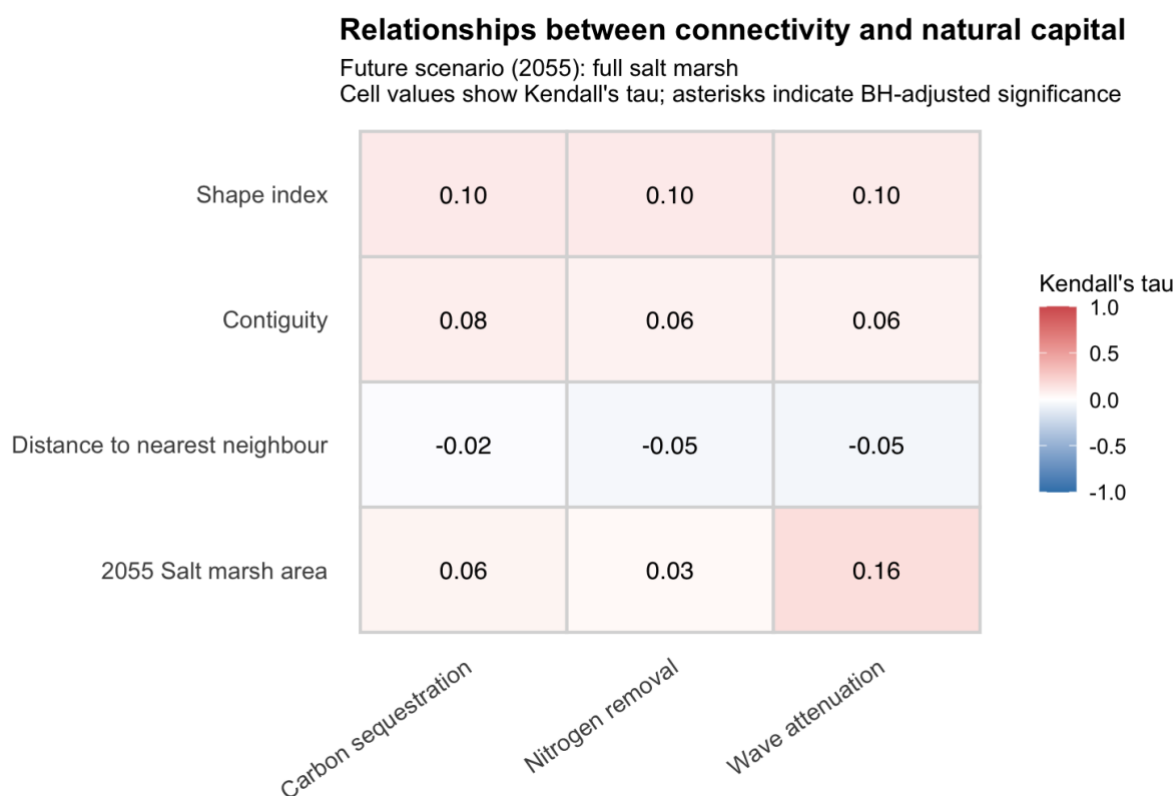


Figure 2.29. Kendall's tau correlation matrix between natural capital metrics and future scenario (salt marsh full 2055) connectivity metrics. Red indicates positive relationships and blue indicates negative relationships, with colour intensity representing the strength of the relationship. Asterisks denote Benjamini–Hochberg-adjusted significance values ($p < 0.05$, $*p < 0.01$, $**p < 0.001$).

2.4 Discussion

This study quantified structural connectivity for salt marsh habitats within the Blackwater and Colne estuaries and examined how structural connectivity metrics relate to natural capital indicators under current and future scenarios. Overall, the findings show that structural connectivity can be effectively characterised using landscape metrics derived from habitat extent, patch isolation, patch cohesion and patch geometry. Metrics such as salt marsh area, distance to nearest neighbour, mean contiguity index and mean shape index captured different dimensions of spatial structure across SMP policy units. However, across the three scenarios investigated (current scenario 1: vegetated salt marsh, current scenario 2: full salt marsh, and future scenario: salt marsh full 2055), the relationships between these metrics and natural capital indicators were uneven. Salt marsh area was the most consistent predictor of ecosystem service values, whereas patch configuration metrics such as mean contiguity index and mean shape index showed weaker and more scenario-dependent relationships. These results suggest that structural connectivity provides useful information for estuarine natural capital assessment, but that habitat extent remains a dominant control on several ecosystem services. The stronger relationships observed in the vegetated salt marsh scenario compared with the full marsh extent scenario further suggest that the spatial arrangement of vegetated marsh habitat may be more closely associated with ecosystem service provision than the spatial configuration of the broader salt marsh complex. This finding highlights the importance of considering which components of the habitat are included when assessing structural connectivity and its relationship with natural capital.

2.4.1 Structural connectivity of salt marsh habitats within the Blackwater and Colne estuaries

The first research question asked how structural connectivity can be quantified for salt marsh habitats within the Blackwater and Colne estuaries. Results demonstrate that structural connectivity can be measured through a combination of spatial metrics describing habitat extent, patch isolation, patch cohesion and patch geometry. Salt marsh area provided a measure of habitat quantity within each SMP policy unit. Distance to nearest neighbour reflected the degree of spatial isolation between salt marsh patches. Mean contiguity index described the internal connectedness and compactness of individual salt marsh patches, while mean shape index quantified patch complexity and deviation from simple geometric forms.

Together, these metrics provide a multidimensional representation of structural connectivity. No single metric fully captures connectivity, but the combination allows interpretation of how marsh habitat is distributed across the estuarine landscape. This aligns with wider landscape ecology literature, where habitat extent, patch isolation, patch cohesion and shape complexity are considered complementary descriptors of habitat structure rather than interchangeable measures of connectivity (Turner et al., 2015).

The use of SMP policy units as analytical boundaries is particularly important. Connectivity studies are often undertaken at ecological scales that do not align easily with governance structures. By quantifying structural connectivity within SMP policy units, this study translates ecological pattern into management-relevant units already used in shoreline planning in England. This increases the practical value of the results for

decision-makers concerned with flood risk management, habitat creation and adaptation planning.

However, the findings also show that structural connectivity metrics are sensitive to how habitat is delineated. Current scenario 1 (vegetated salt marsh), produced lower median salt marsh area and lower mean contiguity values than current scenario 2, which included the full salt marsh, including creeks, salt pans and unvegetated areas. This indicates that connectivity metrics do not simply describe an objective ecological reality; they are partly shaped by classification choices. The same marsh system can appear less cohesive or more fragmented depending on whether only vegetated habitat is mapped or whether the broader geomorphological marsh platform is included. Consequently, the spatial resolution and classification of habitat data can strongly influence the connectivity patterns that are identified.

This is an important methodological consideration. In coastal systems, habitat boundaries are often transitional rather than discrete, particularly where vegetation grades into mudflat, creek margins or pioneer zones. Consequently, connectivity metrics should always be interpreted in relation to habitat definition. Current scenario 1 and current scenario 2 therefore provide complementary but conceptually distinct representations: one emphasises vegetated ecological habitat, while the other captures the salt marsh as an integrated geomorphological unit. The delineation used in current scenario 2 is consistent with how salt marsh is commonly mapped by the Environment Agency and other UK regulatory bodies. These habitat maps are widely used in conservation assessments, habitat accounting and licensing decisions, but they may not fully reflect variation in marsh condition, such as the degree of internal fragmentation or the extent of

unvegetated areas. The differences observed between the two scenarios therefore highlight the importance of using up-to-date habitat data when evaluating connectivity and informing future management decisions.

The future scenario (salt marsh full 2055) further demonstrated how structural connectivity metrics respond to changes in habitat distribution. Median salt marsh area increased substantially relative to the current scenarios, while mean contiguity values also increased. This suggests that projected habitat creation and landward migration may result in larger and more internally cohesive marsh patches. Such patterns are consistent with restoration studies showing that habitat expansion can increase patch cohesion when newly created marshes develop adjacent to existing habitat rather than as isolated patches. However, the future salt marsh dataset developed through the ReMeMaRe initiative represents a potential future distribution and does not account for future variation in habitat condition, erosion rates, creek development or internal marsh structure. Consequently, the projected marshes are represented as relatively homogeneous habitat units, which may reduce the ability of metrics such as nearest neighbour distance and contiguity to capture the full complexity of future marsh landscapes.

Despite these strengths, structural connectivity should be interpreted as potential rather than realised ecological connectivity. Spatial proximity and patch cohesion do not necessarily guarantee movement of organisms, dispersal of propagules or exchange of materials. Hydrodynamic barriers, habitat condition and species-specific behavioural responses may reduce functional connectivity even where structural metrics indicate a connected habitat network. This distinction between structural and functional connectivity

is well established within connectivity theory and remains particularly important in dynamic estuarine environments.

2.4.2 Relationships between structural connectivity and natural capital indicators

The second research question asked how structural connectivity metrics relate to natural capital indicators across the estuarine system. Results showed that salt marsh area was the strongest and most consistent correlate of carbon stocks, carbon sequestration, nitrogen removal and wave attenuation under current scenarios. In contrast, distance to nearest neighbour, mean contiguity index and mean shape index showed weaker or more inconsistent relationships, and all associations disappeared in the future scenario.

These findings suggest that, at the SMP policy unit scale used in this study, habitat extent has a greater influence on several natural capital indicators than more complex aspects of habitat configuration. This is particularly plausible for regulating ecosystem services such as carbon storage and nutrient removal, where larger salt marshes contain greater sediment volume, vegetation biomass and microbial processing area. Greater habitat extent can therefore support a larger overall capacity for ecosystem service provision.

However, caution is needed when interpreting the strength of correlations between salt marsh area and carbon or nitrogen metrics. Some of these variables were calculated using habitat area as part of the underlying methodology, meaning that the relationship is partly influenced by shared mathematical structure. This creates a degree of coupling, whereby larger mapped habitats will inherently generate larger total stock or flow

estimates. As a result, strong positive correlations may overstate the degree to which ecological function independently responds to structural connectivity.

This distinction is particularly important for natural capital accounting. Total ecosystem service values often scale with habitat quantity, but this does not necessarily indicate that per-unit efficiency or ecological condition is higher in larger habitats. Future work could address this by analysing area-normalised metrics, such as carbon stock per square metre or nitrogen removal per square metre, allowing clearer separation of habitat size effects from ecological performance.

The weaker and more variable relationships observed for distance to nearest neighbour, mean contiguity index and mean shape index suggest that patch isolation, patch cohesion and patch geometry may influence ecosystem service provision in more complex and context-dependent ways than habitat extent alone. Furthermore, the stronger relationships observed in current scenario 1 compared with current scenario 2 indicate that the spatial arrangement of vegetated marsh habitat may be more closely associated with ecosystem service provision than the configuration of the broader geomorphological marsh platform.

Features of the salt marsh itself may also be incorporated into future studies to better represent habitat condition within natural capital assessments. For example, species richness, vegetation zonation, habitat heterogeneity and measures of marsh condition could be used alongside structural connectivity metrics to provide a more complete representation of ecological functioning and ecosystem service delivery (Adam, 1990; Barbier et al., 2011).

2.4.2.1 Carbon Stocks and Carbon Sequestration

Strong positive associations between salt marsh area and carbon stocks were expected, given that larger marshes contain greater sediment volumes in which organic carbon can accumulate. Salt marsh sediments are widely recognised as important long-term blue carbon stores (Chmura et al., 2003; Mcleod et al., 2011), and greater habitat area typically supports larger cumulative stocks. However, the relationship between area and carbon stocks should be interpreted in the context of the use of total carbon estimates within each SMP policy unit, as larger areas of salt marsh inherently provide greater potential for total carbon storage. Habitat extent nevertheless remains an important component of carbon-related natural capital, with changes in salt marsh area contributing substantially to changes in total blue carbon stocks (Zheng et al., 2026). Carbon storage can also vary spatially according to sediment and environmental characteristics, with fine-resolution mapping demonstrating variation in soil organic carbon density across tidal marshes (Maxwell et al., 2024). Future analyses could therefore consider carbon metrics on a unit-area basis (e.g., per hectare), allowing variation in carbon storage to be considered independently of the effect of total habitat extent. Similarly, carbon sequestration increased with salt marsh area in current scenarios, suggesting that larger marsh systems may support greater rates of annual carbon burial.

Yet these relationships were absent in the future scenario, despite substantial increases in projected salt marsh area. If area alone controlled carbon processes, correlations might be expected to persist or strengthen. However, future carbon estimates were derived using scaled current-day carbon values rather than spatially resolved future carbon accumulation rates. As a result, variability between SMP policy units may have been

reduced in the future scenario, limiting the range of outcomes available for correlation analysis to detect relationships. The disappearance of significant correlations therefore likely reflects both methodological constraints within the future scenario modelling and the influence of additional factors such as habitat redistribution, geomorphological change, and the uncertain maturity and functioning of newly created marsh habitat.

This interpretation aligns with restoration literature showing that created or restored marshes may take years or decades to develop sediment properties, vegetation communities, and carbon accumulation rates comparable to mature natural marshes (Craft et al., 2002). Therefore, increases in mapped habitat area do not automatically translate into proportional increases in realised carbon function.

2.4.2.2 Nitrogen Removal

Nitrogen removal showed a similar pattern to carbon metrics, with positive relationships with salt marsh area under current scenarios but weak associations in the future scenario. This is ecologically plausible because nitrogen removal processes such as denitrification, plant uptake, and sediment burial require physical habitat area over which biogeochemical processing can occur.

However, nitrogen cycling is also strongly influenced by hydrology, nutrient loading, sediment conditions, and plant community composition (Herbert, 1999). Two marshes of equal area may therefore differ substantially in nitrogen removal performance. For example, C4 (Colne Point) and G2 (Dengie Peninsula) both exhibited relatively low nitrogen removal compared to the overall trend despite differing spatial characteristics and carbon relationships. This likely reflects differences in local environmental conditions and nutrient availability between estuarine zones, rather than habitat area alone. The

weakening of relationships in the future scenario may therefore indicate that area alone is insufficient to capture these process controls once habitat is redistributed or newly created.

This finding is useful for management because it suggests that simply increasing salt marsh area may not maximise nutrient remediation benefits unless hydrological design and ecological condition are also considered.

2.4.2.3 Wave Attenuation

Wave attenuation showed a weaker but still significant positive relationship with salt marsh area under current scenarios. This relationship likely reflects the tendency for larger marshes to also contain greater cross-shore width, allowing more wave energy to be dissipated before reaching the landward boundary. However, wave attenuation is primarily governed by marsh width, vegetation structure, elevation, and local wave exposure conditions rather than total marsh area alone (Möller et al., 2014). In particular, fetch and effective fetch influence the magnitude of incoming wave energy reaching marsh surfaces, affecting the degree to which vegetation can attenuate waves (Gilbertson et al., 2020). Salt marsh area combines both cross-shore width and alongshore length, making it only a proxy for the mechanisms directly controlling wave dissipation. This likely explains why relationships between area and wave attenuation were weaker than those observed for carbon metrics. Consequently, marshes with similar total area may differ substantially in attenuation potential depending on their orientation, width, and exposure to open-water fetch.

The apparent non-linear pattern observed in the results, where attenuation increased rapidly at low salt marsh area before approaching a plateau, is consistent with process-

based studies showing diminishing returns in wave attenuation with increasing marsh width (Möller et al., 2014). Much wave energy is dissipated across the seaward portion of a marsh, after which additional width provides progressively smaller incremental reductions in wave energy. This has practical implications for coastal management, suggesting that the strategic placement and sufficient cross-shore width of restored marsh may be more important for coastal protection than maximising total marsh area alone.

2.4.2.4 Species Richness

Species richness showed weak and largely non-significant relationships with most structural connectivity metrics. This contrasts with some terrestrial and marine studies where connectivity can strongly influence biodiversity through colonisation and dispersal processes. Several explanations are possible. First, species richness within salt marsh systems may respond more strongly to habitat quality, hydroperiod, salinity gradients, disturbance regimes, and vegetation composition than to broad structural metrics measured at the SMP policy unit scale (Adam, 1990). Second, richness alone is a relatively coarse biodiversity metric that does not capture species identity, rarity, abundance, or functional diversity. Third, the taxonomic groups represented in the richness metric may depend on habitat heterogeneity operating at finer spatial scales than those analysed here.

In addition, the relatively weak richness relationships may reflect the limited variability present within the dataset itself. Many marshes within the Blackwater and Colne estuaries are dominated by similar mid–low salt marsh vegetation communities, resulting in a comparatively narrow species richness gradient across SMP policy units. Highly diverse

marshes containing a full range of salt marsh zones and associated plant communities are relatively uncommon within the study area. Consequently, the restricted range of richness values may reduce the ability of correlation analysis to detect strong ecological relationships. More spatially heterogeneous marsh systems, or assessments incorporating vegetation zonation and community composition, may reveal stronger links between biodiversity, connectivity, and natural capital function.

2.4.2.5 Role of Distance to Nearest Neighbour

Distance to nearest neighbour showed negative associations with several natural capital metrics in current scenarios, indicating that SMP policy units with more isolated salt marsh patches tended to have lower carbon, nitrogen, and wave attenuation values. This likely reflects the tendency for larger, more continuous marsh complexes to contain patches that are spatially closer together while also supporting greater ecosystem service capacity.

Distance to nearest neighbour may therefore partly function as an indicator of fragmentation. Where marshes are highly fragmented and isolated, total habitat area may be lower and ecological functioning may be reduced. However, these associations weakened in the future scenario, potentially reflecting both ecological and methodological influences. In the future scenario, SMP policy unit landscapes were expanded landward to incorporate projected habitat creation areas, altering the overall spatial extent within which patch isolation was calculated. As a result, future distance to nearest neighbour values reflect broader landscape-scale configuration changes in addition to patch-level isolation processes.

The weakening of these relationships highlights the distinction between structural spatial pattern and ecological process. Reduced spacing between patches may improve opportunities for dispersal, hydrological exchange, or sediment transfer, but ecosystem service delivery remains dependent on additional controls such as habitat maturity, geomorphological setting, vegetation structure, and ecological condition.

2.4.2.6 Role of Contiguity and Shape Index

Mean contiguity index and mean shape index showed the weakest and least consistent relationships with natural capital indicators. In current scenario 1, moderate negative associations were observed between mean contiguity index and several regulating ecosystem services, including carbon stocks, carbon sequestration and nitrogen removal. However, these relationships disappeared when the full salt marsh extent was considered and were absent in the future scenario.

These findings suggest that patch cohesion and geometric complexity may be highly sensitive to habitat classification and may not directly control the ecosystem services examined here. Instead, these metrics appear to describe aspects of habitat structure that are not captured by habitat area alone. While habitat extent was strongly associated with cumulative ecosystem service values, variation in patch cohesion and shape complexity showed weaker and more context-dependent relationships.

The negative relationships observed between mean contiguity index and regulating ecosystem services in current scenario 1 are particularly noteworthy. Higher contiguity values indicate more compact and internally cohesive marsh patches, whereas lower values indicate increasingly irregular or dissected patch structures. The observed negative correlations therefore suggest that larger carbon stocks, carbon sequestration

rates and nitrogen removal values were often associated with less compact marsh configurations. One possible explanation is that larger marsh systems frequently contain extensive creek networks and complex internal structure, which reduce contiguity values while simultaneously supporting greater overall ecosystem service capacity due to their larger extent.

Shape index exhibited similarly weak and inconsistent relationships with natural capital indicators. This is perhaps unsurprising given that patch geometry can reflect multiple and potentially contrasting ecological conditions. More complex marsh perimeters may indicate extensive creek networks, greater edge habitat and increased environmental heterogeneity, all of which can support ecological functioning and biodiversity. Conversely, high shape complexity may also result from fragmentation and erosion, where irregular marsh edges develop through creek enlargement, edge retreat or marsh breakdown. Consequently, similar shape index values may represent very different ecological states depending on local geomorphological context.

This complexity was evident within the study area. For example, D8b (Fingringhoe) exhibited relatively high shape index values despite containing a large marsh area, potentially reflecting the influence of extensive creek systems and internal marsh complexity. In contrast, other SMP policy units with irregular marsh boundaries may represent more fragmented or eroding marsh structures. The relatively uniform shape index values observed within the future scenario likely reflect the simplified geometries of projected habitat creation areas, which may not yet capture the geomorphological complexity characteristic of mature natural marshes.

These findings reinforce the distinction between management-scale structural metrics and ecological process-based measures. Landscape metrics provide useful indicators of habitat extent, patch isolation, cohesion and geometry at the SMP policy unit scale, but they may not fully capture the finer-scale geomorphological, hydrological and ecological processes that regulate ecosystem functioning within estuarine marsh systems. Consequently, metrics such as mean contiguity index and mean shape index may be more useful for describing spatial pattern than for predicting cumulative ecosystem service provision directly.

2.4.3 Future Scenario

One of the most notable findings was the near absence of significant correlations in the future scenario. Several explanations are plausible. First, future habitat creation may redistribute ecosystem service potential more evenly across SMP policy units, reducing the spatial contrasts that generate strong statistical relationships. Second, future habitats were modelled using scaled current-day ecosystem service values rather than spatially resolved future process rates, meaning that projected service estimates may have become comparatively homogenised between policy units. This reduction in variability may limit the ability of correlation analyses to detect strong relationships. Third, the future scenario inevitably contained modelling assumptions and uncertainties associated with habitat creation, geomorphological development, and long-term ecological functioning. Importantly, these findings suggest that increases in habitat area alone do not necessarily preserve present-day structure–function relationships. Restoration planning should therefore consider not only the quantity of habitat created, but also its spatial

configuration, geomorphological setting, exposure regime, and capacity to develop functional ecological characteristics through time. Achieving functional maturity may be particularly important for regulating ecosystem services such as carbon sequestration, nitrogen removal, and wave attenuation, which depend on vegetation development, sediment processes, and hydrodynamic interactions.

2.4.4 Implications for Natural Capital Assessment and Management

These findings have important implications for natural capital accounting and coastal management. First, salt marsh area remains a useful and interpretable predictor of several regulating ecosystem services, particularly where total ecosystem service quantity is the primary management objective. However, reliance on area-based habitat targets alone may oversimplify ecological functioning and restoration success. Policy frameworks such as the Water Framework Directive may classify habitats as salt marsh under relatively low vegetation cover thresholds, despite substantial variation in ecological maturity, vegetation zonation, and functional capacity.

Second, structural connectivity metrics can provide additional insight into fragmentation and spatial organisation, but they should not be assumed to predict ecosystem service delivery consistently. For practitioners, this suggests that habitat creation targets based solely on total hectares restored may be insufficient. Spatial arrangement, cross-shore geometry, habitat condition, and long-term geomorphological development also influence ecosystem service performance. For example, some SMP policy units within this study exhibited relatively high natural capital values despite weaker relationships with total marsh area, indicating that local environmental characteristics and marsh configuration

may influence ecological functioning alongside habitat quantity. Similarly, wave attenuation relationships suggested diminishing returns with increasing marsh area, highlighting the importance of marsh width and exposure rather than area alone.

At a policy level, integrating connectivity and spatial configuration into SMP planning could help identify where restoration may contribute to cohesive marsh networks rather than isolated habitat fragments. This is particularly relevant under climate adaptation strategies involving managed realignment and coastal realignment, where restoration success may depend not only on habitat extent but also on the capacity of restored marshes to develop mature ecological and geomorphological functioning through time.

2.4.5 Limitations and Future Research

Several limitations should be acknowledged. First, this study assessed structural rather than functional connectivity. The analysis quantified spatial configuration of salt marsh habitat but did not directly measure ecological flows such as species movement, propagule dispersal, sediment transport, or hydrodynamic exchange. As a result, the connectivity metrics used here represent potential structural pathways rather than realised ecological connectivity.

Second, some ecosystem service metrics were partly area-derived, which may inflate correlations with salt marsh area through shared mathematical structure. Although these relationships remain ecologically meaningful from a natural capital accounting perspective, they should not necessarily be interpreted as evidence of increased per-unit ecosystem functioning.

Third, the future scenario represents a modelled projection rather than an observed ecosystem. Future ecosystem service values were generated using scaled current-day estimates rather than spatially resolved future process rates, potentially reducing variability between SMP policy units and influencing the strength of statistical relationships. In addition, projected habitat creation areas are unlikely to immediately replicate the geomorphological complexity, vegetation zonation, and sediment characteristics of mature natural marshes.

Fourth, analysis at the SMP policy unit scale may obscure finer-scale ecological processes operating at patch, creek-network, or tidal-channel scales. The choice of habitat definition may also influence interpretation, as vegetated marsh-only and full-marsh classifications produced different connectivity patterns across several metrics.

Future research should integrate structural metrics with functional approaches such as hydrodynamic modelling, sediment transport analysis, propagule dispersal modelling, or species movement data. Incorporating habitat condition indicators, vegetation zonation, creek density, and area-normalised ecosystem service metrics would also strengthen ecological interpretation. Multi-scale analysis could further reveal whether connectivity–ecosystem service relationships emerge more strongly at patch, creek-network, estuary, or regional scales, helping to better link management-scale spatial planning with ecological functioning.

Chapter 3

The Influence of Spatial Classification Framework on Salt Marsh Structural Connectivity Metrics

3.1 Introduction

The spatial arrangement of habitats influences ecological processes operating within landscapes and seascapes. Consequently, understanding habitat connectivity has become an important component of conservation planning, restoration design and natural capital assessment. As discussed in Chapter 1, connectivity represents the degree to which a landscape facilitates or impedes the movement of organisms, materials and ecological processes between habitat patches. In coastal systems, connectivity influences processes including species dispersal, sediment transport, nutrient cycling and ecosystem resilience (Boström et al., 2011; Carr et al., 2017; Preston et al., 2025).

Structural connectivity is commonly quantified using landscape metrics that describe habitat amount, patch isolation, patch cohesion and spatial configuration. These metrics have been widely applied within terrestrial landscape ecology to investigate habitat fragmentation and its ecological consequences (McGarigal and Marks, 1995; Turner et al., 2001). Increasingly, similar approaches have been applied within marine and coastal environments, where habitat mosaics and ecological processes operate across complex seascapes (Boström et al., 2011; Pittman et al., 2021). However, a longstanding principle of landscape ecology is that landscape pattern is inherently scale-dependent (Turner et al., 1989; Wiens, 1989; Wu, 2004). The same habitat mosaic may exhibit markedly different spatial properties depending on the spatial extent or resolution used for analysis. Consequently, structural connectivity metrics are not purely intrinsic properties of ecological systems, but are also influenced by how the landscape itself is defined.

Scale dependence represents one of the central challenges within landscape ecology. Ecological processes frequently operate across multiple spatial scales, with different

patterns becoming evident at different extents and resolutions (Wiens, 1989; Levin, 1992). Broad-scale analyses may obscure local heterogeneity through spatial averaging, whereas fine-scale analyses may reveal fragmentation patterns that are not apparent at larger extents. Landscape metrics are particularly sensitive to the definition of analytical boundaries, with habitat area, patch isolation and configuration metrics often varying substantially as landscape extent changes (Wu et al., 2002; Cushman et al., 2008). As a result, comparisons between studies or management units can become difficult when different spatial frameworks are used.

This issue is particularly relevant within estuarine environments. Estuaries are characterised by nested ecological processes operating across multiple spatial scales, from individual vegetation patches and tidal creek networks to whole-estuary sediment dynamics and hydrodynamic processes (Boström et al., 2011; Levin, 1992). At the same time, coastal management operates through a variety of administrative and ecological frameworks that differ substantially in both scale and purpose. Water Framework Directive (WFD) water bodies represent hydrographic management units (European Parliament and Council, 2000), nutrient zones reflect broad biogeochemical gradients, and Shoreline Management Plan (SMP) policy units define coastal management boundaries associated with flood and erosion risk (Environment Agency, 2006). Each of these frameworks provides a legitimate means of subdividing the estuarine landscape, yet each imposes different analytical boundaries on the same ecological system.

Chapter 2 quantified structural connectivity within SMP policy units and examined relationships between salt marsh connectivity and natural capital indicators in the Blackwater and Colne Estuaries, Essex, UK. The results demonstrated that structural

connectivity metrics can provide useful information regarding habitat extent, patch isolation, cohesion and geometric complexity, and that these characteristics may influence patterns of ecosystem service provision. However, it remains unclear whether these connectivity patterns are robust when alternative methods of defining the landscape are applied. If connectivity metrics vary substantially between spatial frameworks, interpretations of fragmentation, habitat condition and connectivity may depend as much on analytical scale as on underlying ecological processes. This would need to be taken into account when management decisions are being considered.

Although the influence of scale on landscape metrics has been widely demonstrated in terrestrial systems (Turner et al., 1989; Wu et al., 2002; Wu, 2004; Cushman et al., 2008), estuarine research has largely focused on understanding scale-dependent ecological and geomorphological processes, with comparatively less attention given to how alternative spatial classification frameworks influence the calculation of structural connectivity metrics (van de Koppel et al., 2012; Mason et al., 2023; Stoorvogel et al., 2024; Cornacchia et al., 2024). Consequently, relatively little attention has been given to how the choice of analytical spatial framework influences the calculation and interpretation of structural connectivity metrics within estuarine landscapes.

This chapter investigates how structural connectivity metrics change when salt marsh habitats are analysed using four alternative spatial classification frameworks (from largest to smallest): whole-estuary landscape, Water Framework Directive water bodies, nutrient zones and Shoreline Management Plan policy units. By comparing connectivity metrics across multiple spatial extents, this chapter examines the sensitivity of structural

connectivity to analytical scale and considers the implications of scale dependency for estuarine habitat assessment.

Research question

How sensitive are structural connectivity metrics to the spatial classification framework used to define the landscape?

Objectives

1. Quantify salt marsh structural connectivity across four spatial frameworks.
2. Compare connectivity metric values between scales.
3. Identify which connectivity metrics are most sensitive to analytical extent.
4. Consider the implications of scale dependency for estuarine connectivity assessment, natural capital evaluation and coastal management.

3.2 Method

3.2.1 Spatial frameworks

Structural connectivity was quantified for salt marsh habitat using four alternative spatial frameworks representing different ecological and management scales within the Blackwater and Colne estuaries:

- Whole-estuary landscape (Figure 3.1).
- Water Framework Directive (WFD) water bodies (Figure 3.2).
- Nutrient zones (Figure 3.3).
- Shoreline Management Plan (SMP) policy units (Figure 3.4).

The whole-estuary landscape represented the broadest spatial extent and treated the entire estuarine system as a single landscape. WFD water bodies represent hydrological management units defined under the Water Framework Directive. Nutrient zones represent broad biogeochemical regions previously developed for nitrogen removal analysis (Chapter 2), while SMP policy units represent coastal management units used within shoreline planning. These frameworks differ substantially in their spatial extent and management purpose, allowing the influence of analytical scale on connectivity metrics to be examined.

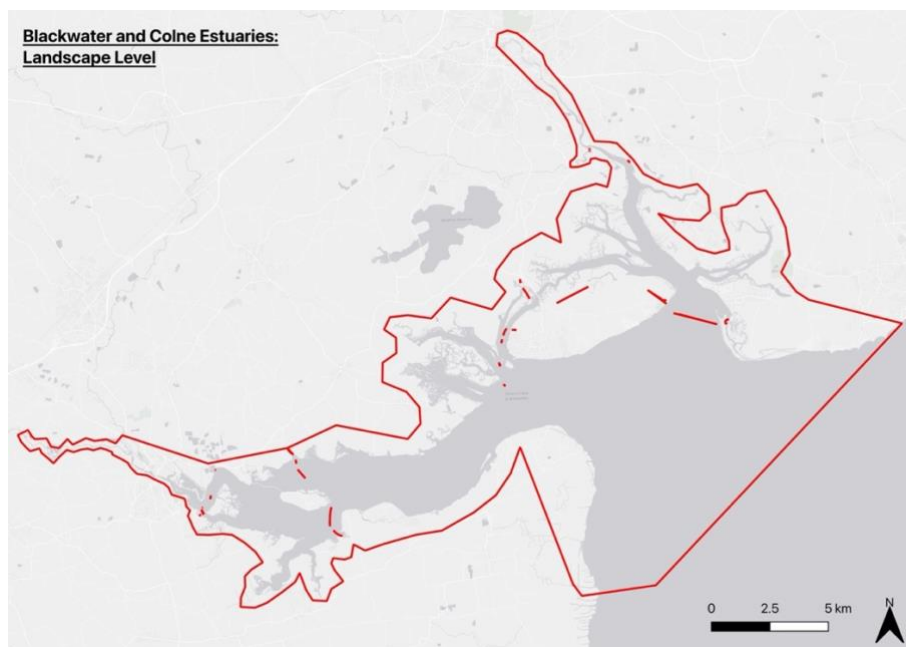


Figure 3.1. The Blackwater and Colne estuaries boundary used for the landscape level assessment outlined in red. The boundary is the same boundary used for the nutrient zones, the red lines within the boundary are a byproduct of mapping and should be disregarded).

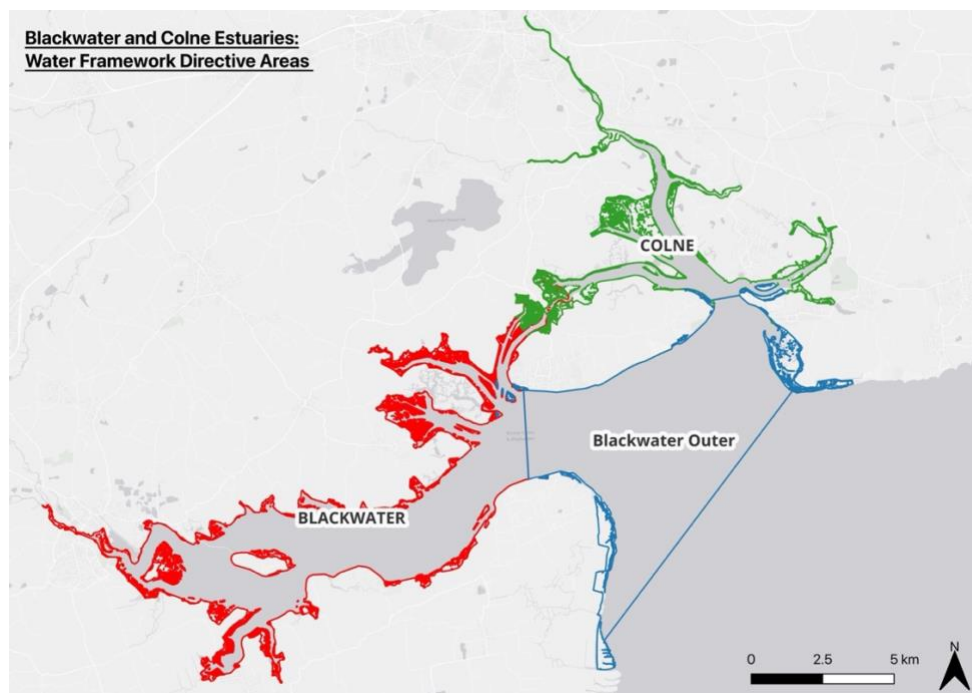


Figure 3.2. The Blackwater and Colne estuaries boundaries used for the Water Framework Directive level assessment; Colne outlined in green, Blackwater Outer outlined in blue, Blackwater outlined in red.

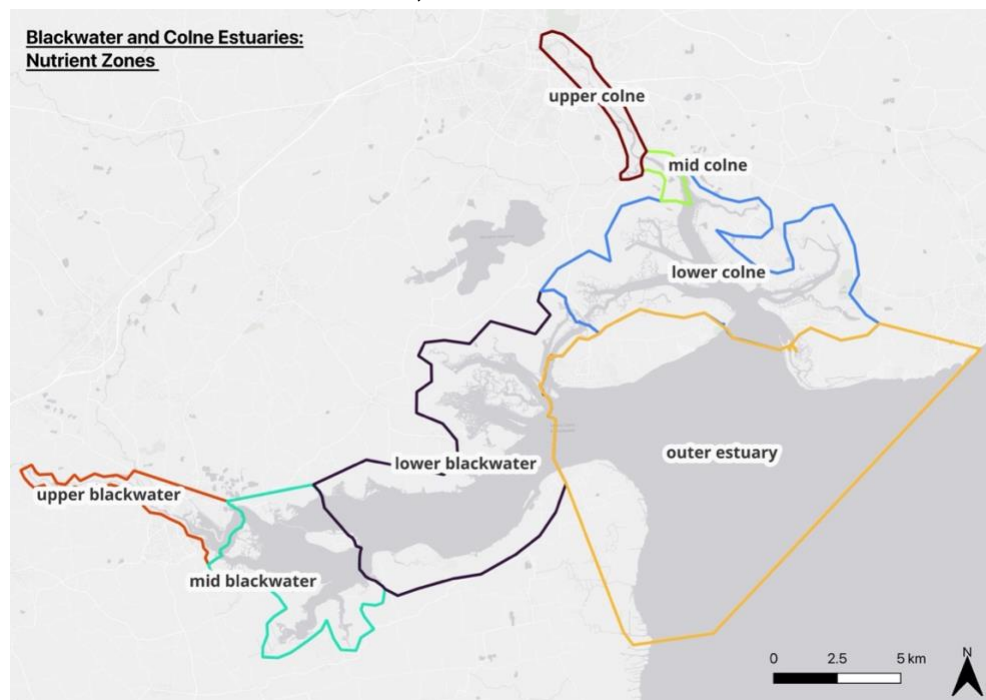


Figure 3.3. The Blackwater and Colne estuary boundaries used for the nutrient zone-level assessment. Different colours represent the individual nutrient zones, as labelled on the map. The same nutrient zones were used in Chapter 2.

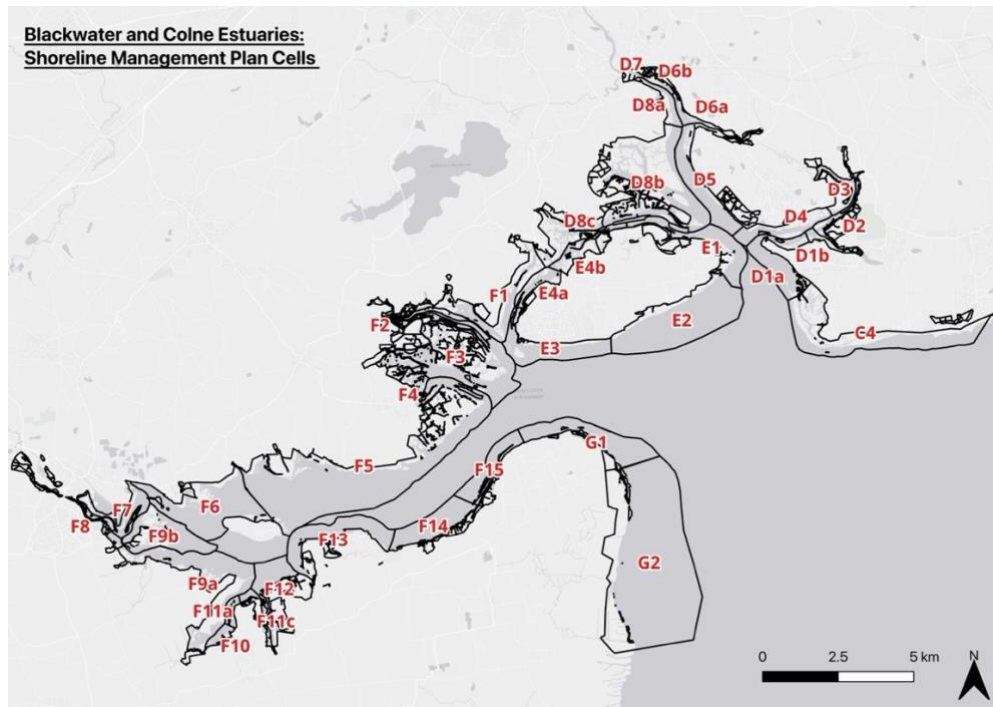


Figure 3.4. The Blackwater and Colne estuaries boundaries used for the Shoreline Management Plan cells assessment level. The same SMP areas used in Chapter 2.

3.2.2 Salt marsh habitat data

Salt marsh extent was derived from the Environment Agency salt marsh zonation and extent dataset used throughout this thesis (see Chapter 2 pp 58 - 60); this includes vegetated and unvegetated areas of salt marsh. Only the current salt marsh extent was considered in this chapter to allow direct comparison of structural connectivity between spatial frameworks while minimising the influence of differences in habitat classification. The salt marsh dataset was dissolved, removing the different salt marsh zones, to create a single habitat layer representing the complete extent of mapped salt marsh within the study area. Salt marsh habitat cells were assigned a value of 1, while the surrounding landscape within each analytical unit was assigned a value of 2. This process produced binary rasters representing salt marsh and non-salt marsh areas.

3.2.3 Raster preparation

Spatial processing was undertaken in QGIS version 3.44.5. Separate binary raster datasets were created for each spatial framework.

For nutrient zones, salt marsh habitat was clipped to each nutrient zone boundary and combined with the remaining non-marsh area within each zone. For WFD water bodies, water body boundaries were buffered by 1 km prior to intersection with the salt marsh dataset to ensure complete inclusion of adjacent marsh habitat. The resulting habitat layers were merged with the remaining landscape area within each WFD unit.

All datasets were rasterised using a cell size of 2 m × 2 m with output resolution specified in georeferenced units. Salt marsh cells were assigned a value of 1, non-marsh cells a value of 2, and areas outside the analytical units were assigned a value of 0 (no data). Individual raster layers for each nutrient zone, WFD water body and SMP policy unit were subsequently generated using the QGIS Easy Raster Splitter tool.

The whole-estuary landscape was represented as a single raster covering the complete study area. To reduce computational requirements, the landscape raster was aggregated from 2 m resolution to 10 m resolution using a majority rule approach, whereby the dominant cell value within each 5 × 5 cell block was assigned to the aggregated raster.

3.2.4 Connectivity metrics

Structural connectivity metrics were calculated in R (version 4.5.0) using the packages *terra* and *landscapemetrics*, an implementation of FRAGSTATS within R (Hesselbarth et al., 2019).

For each raster, four connectivity metrics were calculated:

- Total salt marsh area.
- Mean Euclidean distance to nearest neighbour.
- Mean contiguity index.
- Mean shape index.

Total salt marsh area quantified habitat extent within each spatial unit. Mean Euclidean distance to nearest neighbour measured the degree of isolation between salt marsh patches. Mean contiguity index quantified the internal connectedness and compactness of individual habitat patches, while mean shape index described patch geometry and perimeter complexity (see Chapter 2, pp 71 for more detail on these metrics).

Connectivity metrics were calculated at the class level for the salt marsh habitat class only. The non-marsh class was retained during raster creation to provide landscape context but was excluded from subsequent analysis.

3.2.5 Statistical comparison between spatial frameworks

Connectivity metrics from the four spatial frameworks were combined into a single dataset for comparative analysis. Summary statistics, including mean values and standard errors, were calculated for each metric at each spatial scale. Boxplots and bar plots were produced to examine differences in both the magnitude and variability of connectivity metrics between spatial frameworks. Comparisons focused on identifying whether connectivity metrics exhibited systematic changes with analytical extent and whether finer spatial frameworks revealed additional variation in habitat configuration that was obscured at broader scales.

3.3 Results

3.3.1 Overall patterns across spatial scales

Structural connectivity metrics varied substantially among the four spatial frameworks used to define the landscape (Figures 3.5 and 3.6). Both the magnitude and variability of the metrics changed with analytical extent, indicating that estimates of structural connectivity depend on the spatial classification framework adopted for analysis.

Broad spatial scales generally produced greater habitat areas and reduced variability in connectivity metrics, whereas finer spatial scales revealed greater heterogeneity in habitat configuration. The whole-estuary landscape produced a single aggregated value for each metric and therefore masked much of the spatial variation evident at smaller scales. In contrast, SMP policy units exhibited the greatest variability for all metrics, reflecting the greater spatial heterogeneity captured when connectivity metrics were calculated using finer analytical units.

These results demonstrate that estimates of structural connectivity are influenced not only by the spatial arrangement of salt marsh habitat, but also by the analytical boundaries used to define the landscape. The observed differences do not indicate that one spatial framework is inherently more representative than another, but rather that each emphasises different components of landscape structure.

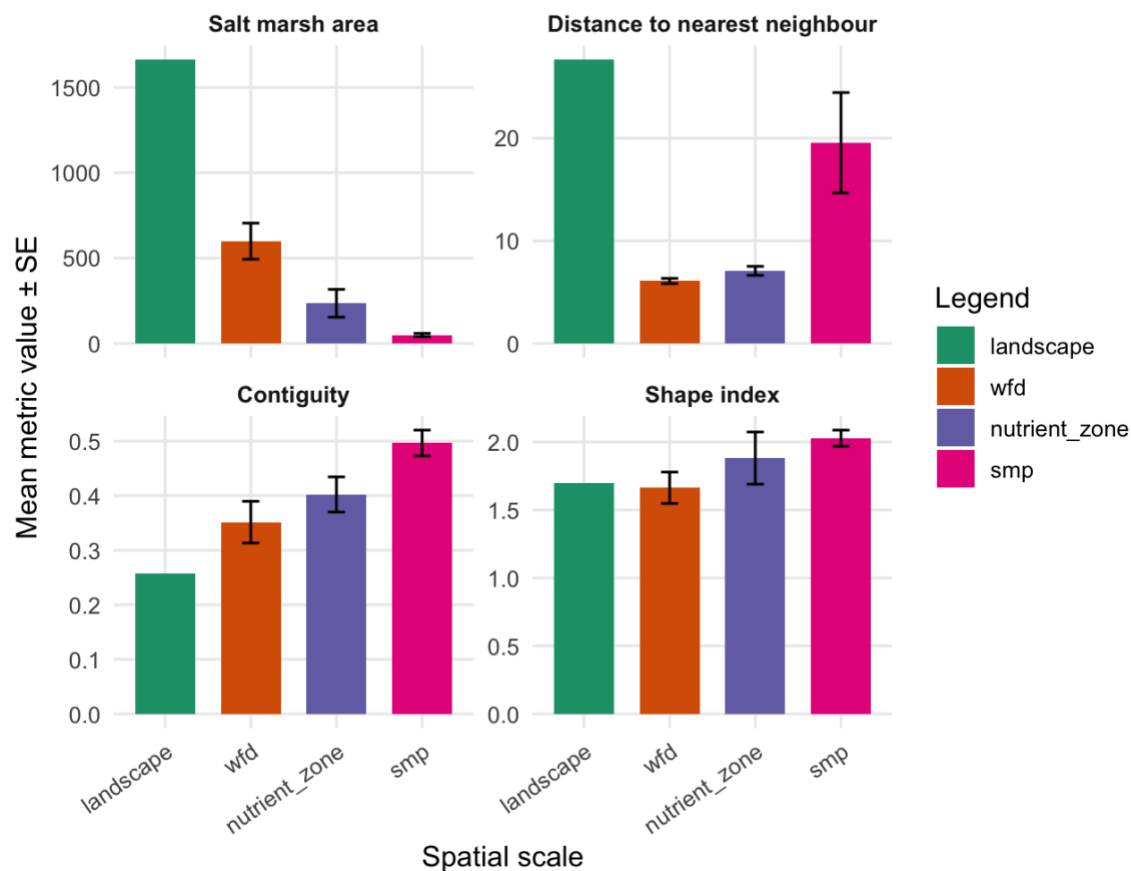


Figure 3.5. Mean values ($\pm$ standard error, where applicable) of the four structural connectivity metrics (total salt marsh area, mean Euclidean distance to nearest neighbour, mean contiguity index and mean shape index) across four spatial frameworks: whole-estuary landscape ($n = 1$; no standard error), Water Framework Directive (WFD) water bodies ($n = 3$), nutrient zones ($n = 7$), and Shoreline Management Plan (SMP) policy units ($n = 38$).

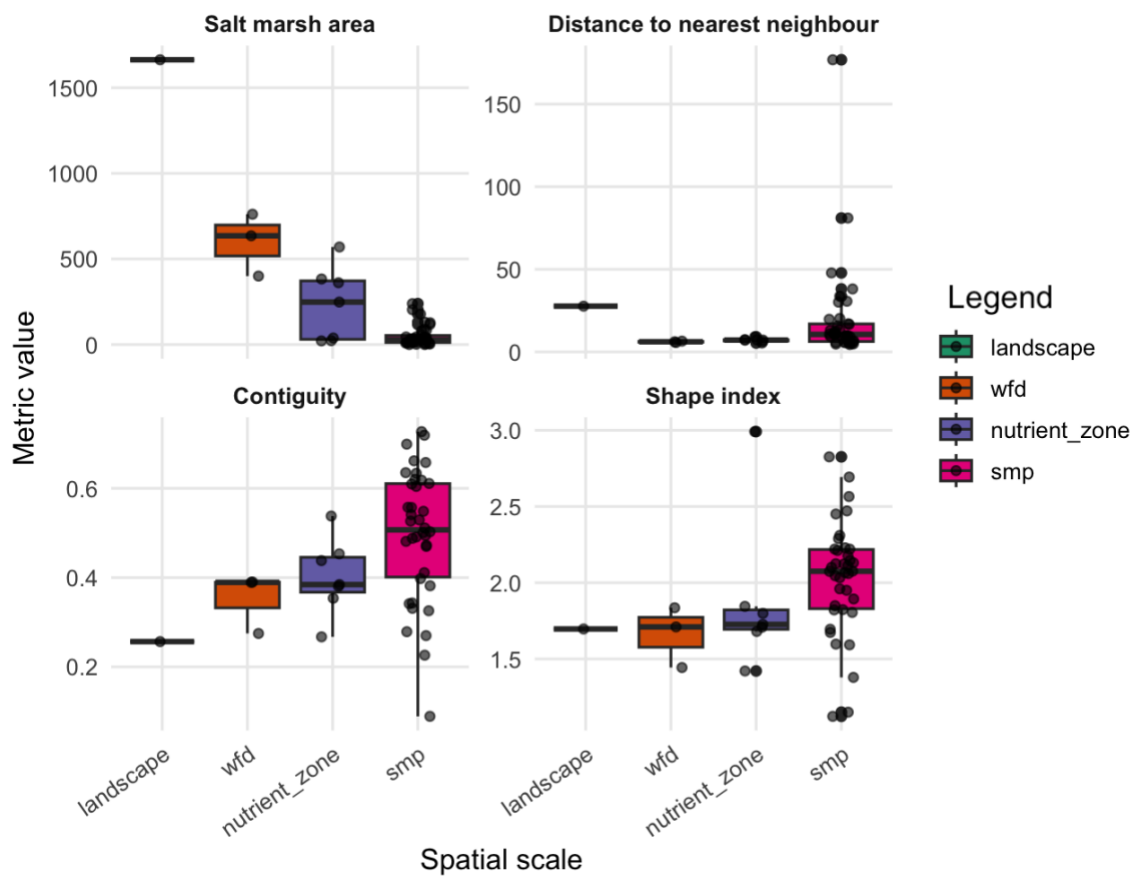


Figure 3.6. Distribution of structural connectivity metrics across four spatial frameworks: whole-estuary landscape ($n = 1$), Water Framework Directive (WFD) water bodies ($n = 3$), nutrient zones ($n = 7$), and Shoreline Management Plan (SMP) policy units ($n = 38$). Boxplots show the median, interquartile range and outliers.

3.3.2 Salt marsh area

Salt marsh area decreased progressively as the spatial extent of the analytical units became smaller (Figure 3.5). The whole-estuary landscape contained the largest habitat area because it represented the entire estuarine system as a single landscape. WFD water bodies exhibited intermediate values, while nutrient zones generally contained smaller areas of salt marsh.

SMP policy units showed the smallest median salt marsh area and the greatest variability among observations (Figure 3.6). Several policy units contained relatively little salt marsh habitat, whereas others supported substantially larger areas. This increased variability reflects the heterogeneous distribution of salt marsh habitat throughout the estuary and demonstrates that broad-scale analyses can obscure local differences in habitat extent. The reduction in salt marsh area with decreasing spatial extent illustrates the strong scale dependency of area-based metrics and highlights the influence of landscape definition on habitat quantity estimates.

3.3.3 Mean Euclidean distance to nearest neighbour

Mean Euclidean distance to nearest neighbour exhibited the greatest variation among the four spatial frameworks (Figures 3.5 and 3.6). The whole-estuary landscape had the highest mean Euclidean distance to nearest neighbour values because all salt marsh patches within the estuary were treated as part of a single landscape, allowing distances to be measured between patches separated by large expanses of open water.

Distances to the nearest neighbour decreased markedly from the whole-estuary landscape to both the WFD water body and nutrient zone frameworks (Figures 3.5 and 3.6). Mean nearest neighbour distances were similar between the WFD and nutrient zone frameworks, which had comparable mean landscape areas (39.16 km² and 41.03 km², respectively). In contrast, SMP policy units exhibited substantially higher and more variable nearest neighbour distances than the broader spatial frameworks.

Several SMP policy units exhibited substantially larger mean Euclidean nearest neighbour distances than the broader spatial frameworks. For example, F15 had a mean nearest neighbour distance of 81 m, reflecting considerable variation in patch spacing among individual management units (as discussed in Chapter 2). These larger values were not apparent at the broader spatial scales, where aggregation of habitat into larger analytical units reduced the influence of local variation in patch spacing. Consequently, variability in nearest neighbour distance became increasingly evident as the analytical extent decreased.

Overall, mean Euclidean distance to nearest neighbour exhibited greater variation among spatial frameworks than the other connectivity metrics, indicating that estimates of patch isolation were strongly influenced by the spatial framework used for analysis.

3.3.4 Mean contiguity index

Mean contiguity values increased progressively from the landscape scale to the SMP scale (Figures 3.5 and 3.6). The whole-estuary landscape exhibited the lowest mean contiguity values, whereas SMP policy units generally exhibited the highest mean contiguity values.

WFD water bodies and nutrient zones showed intermediate values with comparatively limited variability. In contrast, SMP policy units exhibited greater variation between individual units, indicating that patch cohesion and compactness vary considerably throughout the estuary.

The increase in contiguity at finer scales suggests that smaller analytical units contain more internally cohesive and compact salt marsh patches. Conversely, the lower values observed at broader scales reflect the inclusion of a wider range of habitat configurations and more heterogeneous landscape conditions.

These results indicate that estimates of patch cohesion vary according to the spatial framework used to define the landscape.

3.3.5 Mean shape index

Mean shape index showed changes between spatial frameworks compared with the other connectivity metrics (Figures 3.5 and 3.6). Landscape and WFD scales exhibited similar values, whereas nutrient zones and SMP policy units generally displayed slightly higher shape index values.

Variability in mean shape index also increased towards finer spatial scales, with several SMP policy units exhibiting particularly high shape index values. These elevated values indicate the presence of highly irregular patch geometries within some areas of the estuary.

The increased variability observed at the SMP scale suggests that finer spatial frameworks are more capable of capturing local differences in marsh geometry and

perimeter complexity. In contrast, broader analytical units tend to average these differences across larger areas.

Overall, shape index appeared less sensitive to changes in analytical scale than distance to nearest neighbour, although finer spatial units revealed greater heterogeneity in patch geometry.

3.4 Discussion

This chapter investigated how structural connectivity metrics respond to alternative methods of delineating the landscape. The results demonstrate that structural connectivity is strongly influenced by analytical scale, with both the magnitude and variability of connectivity metrics changing substantially between spatial frameworks. The whole-estuary landscape, WFD water bodies, nutrient zones and SMP policy units each produced different representations of the same salt marsh system, indicating that structural connectivity is not solely an intrinsic property of habitat distribution but is also influenced by the spatial framework used for analysis.

The greatest variation across spatial frameworks was observed for mean Euclidean distance to nearest neighbour, whereas shape index showed comparatively limited changes across spatial frameworks. SMP policy units consistently exhibited the greatest variability in connectivity metrics, revealing local fragmentation patterns that were obscured at broader scales. These findings highlight the importance of scale when interpreting connectivity metrics and demonstrate that the choice of spatial framework can substantially influence how habitat fragmentation and structural connectivity are quantified and interpreted.

3.4.1 Scale dependence of structural connectivity metrics

The influence of scale on landscape metrics has long been recognised within landscape ecology. Turner et al. (1989) and Wiens (1989) argued that ecological patterns and processes are inherently scale dependent, while Levin (1992) described scale as one of the fundamental problems in ecology. Landscape metrics frequently change with spatial extent because the boundaries used to define landscapes alter the spatial relationships between habitat patches (Wu et al., 2002; Wu, 2004).

The present study demonstrates this effect within estuarine salt marsh systems. Habitat area decreased progressively as spatial units became smaller, while variability increased substantially at finer scales. Broad analytical units integrate multiple habitat patches and environmental conditions into a single landscape, thereby reducing apparent heterogeneity. Conversely, smaller analytical units reveal local variation in habitat configuration that becomes averaged at broader scales.

The whole-estuary landscape produced a single connectivity value for each metric and therefore masked much of the spatial variation present within the estuary. Similar effects have been observed in terrestrial systems, where large analytical extents frequently reduce observed fragmentation through spatial averaging (Cushman et al., 2008). The present results suggest that this principle also applies to temperate estuarine landscapes.

3.4.2 Scale sensitivity of distance to nearest neighbour

Mean Euclidean distance to nearest neighbour was the connectivity metric most strongly influenced by the choice of spatial framework. Similar mean nearest neighbour distances

were observed for the WFD and nutrient zone frameworks, despite representing different management frameworks. Given that these frameworks had comparable mean landscape areas (39.16 and 41.03 km², respectively), this finding suggests that estimates of Euclidean nearest neighbour distance may be relatively insensitive to the choice of spatial framework when analytical units are of a similar spatial extent. This indicates that the size of the analytical unit may exert a greater influence on estimates of patch isolation than the specific management framework used to define it, provided the analytical units are of comparable size. In contrast, the substantially greater variability observed among SMP policy units demonstrates that finer analytical units capture greater local variation in patch spacing than broader landscape definitions.

Distance to nearest neighbour quantifies the isolation between habitat patches and is widely used as an indicator of structural connectivity and the potential for movement between habitat patches (McGarigal and Marks, 1995). The large SMP outliers identified in Chapter 2 demonstrate that local variation in patch isolation can be masked when connectivity is assessed using broader analytical frameworks such as the whole estuary, WFD water bodies or nutrient zones. This suggests that analyses undertaken at broader spatial scales may overlook areas where habitat patches are relatively isolated within the landscape.

However, the greater variability observed at the SMP scale should also be interpreted with caution. Unlike the broader frameworks, SMP policy unit boundaries frequently intersect continuous salt marsh complexes, artificially subdividing habitat that is ecologically connected. Consequently, high nearest neighbour distances calculated within individual SMP policy units may not always represent genuine ecological

fragmentation, but instead reflect the truncation of continuous habitat at administrative boundaries. This demonstrates that finer analytical units can both reveal local variation in habitat configuration and introduce artefacts associated with the way the landscape is partitioned.

These findings have important implications for the application of connectivity metrics in conservation planning and natural capital assessment. In Chapter 2, greater nearest neighbour distances were associated with lower carbon stocks, carbon sequestration and wave attenuation under current salt marsh conditions, suggesting that patch isolation is linked to reductions in several regulating ecosystem services. However, where elevated nearest neighbour distances arise primarily from the subdivision of continuous marshes by administrative boundaries, these relationships should be interpreted carefully. Rather than identifying restoration priorities directly, high nearest neighbour distances at the SMP scale may be most useful as a screening tool to identify locations where further ecological assessment is warranted. Management decisions should therefore consider whether apparent isolation reflects genuine fragmentation of the salt marsh landscape or whether habitat connectivity extends across neighbouring management units.

Overall, these findings highlight that the interpretation of nearest neighbour distance depends not only on the ecological characteristics of the landscape but also on the analytical framework used to define it. The most appropriate spatial framework will therefore depend on the management objective: broader frameworks may be more appropriate for understanding estuary-wide patterns of connectivity, whereas finer frameworks can provide greater insight into local spatial heterogeneity, provided their limitations and the influence of administrative boundaries are recognised.

3.4.3 Patch cohesion and geometric complexity

Mean contiguity index and mean shape index exhibited more moderate responses to analytical scale than distance to nearest neighbour. Contiguity generally increased towards finer spatial scales, suggesting that the analytical units contained patches with greater internal cohesion and compactness. Shape index showed comparatively limited changes in mean values, although variability increased substantially within SMP policy units.

The relatively small differences in shape index observed across the four spatial frameworks suggest that patch geometry was less influenced by the choice of analytical extent than the other connectivity metrics. This may reflect the fact that patch geometry is primarily determined by geomorphological processes rather than by the spatial framework used to define the landscape. Tidal creek development, sediment deposition and erosion all contribute to patch complexity and may operate independently of the administrative boundaries used to define landscapes (Allen, 2000; Temmerman et al., 2013).

Similarly, patch cohesion may reflect local habitat organisation rather than broad-scale landscape structure. The increased variability observed within SMP policy units indicates that local marsh characteristics become increasingly important at finer scales. Because contiguity values varied across the four spatial frameworks, the relationship between patch cohesion and ecosystem service provision may also depend on the analytical framework used. In Chapter 2, contiguity was significantly associated with several natural capital indicators, suggesting that the influence of patch cohesion on ecosystem service provision may be interpreted differently depending on the spatial framework adopted.

Although ecosystem service models were not recalculated for the alternative spatial frameworks in this study, the observed scale-dependent variation in contiguity indicates that different conclusions regarding the role of connectivity in supporting natural capital could emerge if analyses were undertaken at different spatial scales. This supports previous work suggesting that multiple connectivity metrics are required to capture different aspects of habitat configuration (Turner et al., 2001).

3.4.4 Implications for estuarine management

The use of multiple spatial frameworks highlights an important challenge for coastal management. Ecological processes frequently operate across spatial scales that do not correspond to administrative boundaries. WFD water bodies, nutrient zones and SMP policy units each represent legitimate management units, yet they produce different interpretations of structural connectivity.

SMP policy units revealed the greatest variability in connectivity metrics and therefore captured local variation in habitat configuration that was not evident at broader scales. Because SMPs are already used to inform shoreline planning and climate adaptation decisions, they provide a practical framework within which structural connectivity could be incorporated into coastal management. However, their relatively small extent and the fact that they frequently intersect continuous salt marsh complexes mean that they may also exaggerate fragmentation by imposing artificial analytical boundaries. Rather than interpreting connectivity solely within individual SMP policy units, assessments could incorporate information from adjacent policy units where continuous marshes extend

across administrative boundaries. This would enable management decisions to remain aligned with the SMP framework while better reflecting the ecological continuity of the salt marsh landscape.

Conversely, whole-estuary and WFD-scale analyses provide a broader understanding of landscape structure but may overlook local variation that is relevant for site-specific management interventions. For example, an estuary-wide assessment may indicate that connectivity across the Blackwater and Colne estuaries is generally high, whereas analysis at the SMP scale can identify individual management units where patch spacing differs substantially from surrounding areas. Interpreting these local patterns alongside information from neighbouring SMP policy units would allow managers to distinguish between genuinely fragmented marshes and cases where apparent fragmentation simply reflects an administrative boundary intersecting a larger, continuous marsh system. This would help ensure that restoration or managed realignment is directed towards areas where connectivity is genuinely limited, rather than artefacts of the analytical framework. These findings suggest that no single spatial framework is universally appropriate and that the choice of analytical scale should depend on the ecological process or management objective being considered. This conclusion is consistent with hierarchical approaches to landscape ecology, which recognise that ecological processes operate simultaneously across multiple scales (Wiens, 1989; Levin, 1992). Consequently, connectivity assessments are likely to benefit from multi-scale approaches that combine broad-scale assessments of estuary-wide connectivity with finer-scale analyses to identify local variation relevant to management and restoration planning.

3.4.5 Implications for natural capital assessment

The results of Chapter 2 demonstrated that relationships between structural connectivity and natural capital varied among connectivity metrics, with habitat area and nearest neighbour distance showing the strongest and most consistent associations with ecosystem service provision. The findings of the present chapter indicate that these connectivity metrics are themselves influenced by the spatial framework used to define the landscape. Consequently, interpretations of the relationship between structural connectivity and natural capital may also vary depending on the analytical scale adopted. Although natural capital assessments were not repeated across the alternative spatial frameworks in this study, the observed scale-dependent variation in connectivity metrics suggests that different conclusions regarding the role of connectivity in supporting ecosystem service provision could be reached if analyses were undertaken at different spatial scales.

Because habitat area, patch isolation and patch cohesion varied between analytical scales, estimates of fragmentation and connectivity are likely to depend on the management units used within natural capital assessments. This is particularly relevant given the increasing incorporation of connectivity into ecosystem service assessments, habitat accounting frameworks and nature-based restoration planning. If connectivity metrics are sensitive to analytical scale, comparisons between studies or management areas may be misleading unless the spatial framework used to calculate those metrics is explicitly considered.

The results suggest that broad-scale assessments may underestimate local fragmentation, whereas fine-scale analyses may identify spatial variation that is directly

relevant to management. However, finer analytical units may also introduce artificial fragmentation where administrative boundaries intersect continuous marsh systems. Consequently, the selection of an appropriate spatial framework should be guided by the ecological process or management objective being considered. Incorporating connectivity into natural capital assessments may therefore benefit from a multi-scale approach that combines broad-scale assessments of landscape structure with finer-scale analyses capable of identifying local variation while recognising the influence of analytical boundaries on connectivity estimates.

3.4.6 Limitations and future research

Several limitations should be acknowledged. First, this study considered structural rather than functional connectivity and therefore did not directly assess movement of organisms, sediment or propagules between habitat patches. Second, the analysis focused solely on current salt marsh extent and did not examine how scale effects may change under future habitat scenarios. Third, connectivity was assessed using administrative and management frameworks rather than ecological process-based boundaries (except from nutrient zones).

Future research could integrate structural and functional connectivity approaches by incorporating hydrodynamic modelling, species movement data or sediment transport processes. Multi-scale analyses that combine management units with ecological boundaries may also provide further insight into the relationship between landscape structure and estuarine functioning.

Overall, the results demonstrate that structural connectivity metrics are strongly influenced by the spatial framework used to define the landscape. Connectivity is therefore not simply a property of habitat distribution, but also a consequence of analytical scale. Recognising this scale dependency is essential if connectivity metrics are to be applied reliably within estuarine management, habitat restoration and natural capital assessment.

Chapter 4

Discussion

4.1 Pattern, Process and Natural Capital

Temperate estuaries are dynamic transitional environments in which terrestrial, freshwater and marine processes interact to create highly heterogeneous landscapes. Within these systems, the spatial arrangement of habitats influences ecological processes that underpin biodiversity, carbon cycling, nutrient regulation and coastal protection, all of which contribute to the natural capital provided by estuarine ecosystems (Barbier et al., 2011; Boström et al., 2011; Ziegler et al., 2021). As pressures associated with climate change, sea-level rise and coastal development continue to alter estuarine landscapes, understanding how habitat structure influences ecosystem functioning has become increasingly important for informing conservation, restoration and natural capital assessment.

This research aimed to quantify the structural connectivity of salt marsh habitats and investigate how structural connectivity and analytical scale influence natural capital assessment within temperate estuarine ecosystems. Using the Blackwater and Colne estuaries as a case study, the research quantified structural connectivity using landscape metrics, examined relationships between connectivity metrics and spatially explicit natural capital indicators, and evaluated how estimates of structural connectivity varied across alternative spatial frameworks relevant to coastal management. Collectively, these analyses provide a more integrated understanding of how landscape ecological principles can inform the assessment and management of estuarine natural capital.

Three principal findings emerge from this research. First, habitat extent consistently exhibited the strongest relationships with regulating ecosystem services, reinforcing the fundamental importance of salt marsh area in supporting natural capital. Second,

structural connectivity metrics provided complementary information by describing different aspects of habitat configuration, although their ecological relevance varied according to the metric and ecosystem service considered. Third, estimates of structural connectivity were strongly influenced by the spatial framework used to define the landscape, demonstrating that assessments of habitat fragmentation and connectivity are dependent not only on ecological pattern but also on the scale at which that pattern is analysed.

Collectively, these findings reinforce a central principle of landscape ecology: ecological pattern and ecological process cannot be interpreted independently of spatial scale (Wiens, 1989; Levin, 1992; Turner, 2005). More importantly, they demonstrate that structural connectivity should not be viewed as a replacement for conventional measures of habitat extent within natural capital assessment, but as a complementary descriptor of habitat structure that provides additional spatial context for understanding ecological assets. Incorporating habitat configuration alongside habitat extent therefore offers a more comprehensive framework for evaluating estuarine natural capital and provides a stronger evidence base for restoration planning and coastal management.

The following sections examine these findings in greater detail. First, the relationship between habitat configuration and natural capital is considered, before exploring the influence of analytical scale on structural connectivity and discussing the implications of these findings for estuarine restoration, natural capital assessment and future coastal management.

4.2 Habitat Configuration and Natural Capital

Natural capital assessments have traditionally focused on the quantity and condition of habitats as the primary determinants of ecosystem service provision (Costanza et al., 1997; Natural Capital Committee, 2015). While these characteristics remain fundamental, landscape and seascape ecology recognise that the spatial arrangement of habitats also influences ecological functioning by affecting the movement of organisms, materials and energy across ecosystems (Boström et al., 2011; Pittman et al., 2021; Wedding et al., 2025). The present study demonstrates that these perspectives are complementary rather than competing. Habitat extent provides the fundamental capacity for ecosystem service provision, while habitat configuration offers additional insight into how ecological assets are organised within the landscape.

The strongest relationships observed in this study were between salt marsh area and regulating ecosystem services, particularly carbon stocks, carbon sequestration, nitrogen removal and wave attenuation. These findings are consistent with previous research demonstrating that larger areas of salt marsh generally support greater ecosystem service provision because they contain a greater volume of vegetated habitat capable of storing carbon, cycling nutrients and dissipating wave energy (Barbier et al., 2011; Möller et al., 2014; Watson et al., 2020). Habitat area therefore remains the most informative single indicator of regulating ecosystem service capacity within temperate estuarine salt marshes.

However, habitat extent did not explain all observed variation in natural capital indicators. Distance to nearest neighbour exhibited consistent relationships with several regulating ecosystem services, suggesting that landscape fragmentation may influence ecosystem

functioning independently of habitat quantity. Although structural connectivity does not directly measure ecological processes, greater patch isolation may reflect reduced opportunities for sediment exchange, hydrological connectivity and other landscape-scale interactions that contribute to ecosystem functioning. These findings are therefore consistent with broader seascape ecological theory, which proposes that habitat configuration influences ecological processes operating across coastal landscapes (Boström et al., 2011; Carr et al., 2017). Recent evidence also demonstrates the ecological relevance of habitat configuration in coastal wetlands, with habitat structure and connectivity shown to contribute to patterns of terrestrial fauna occurrence beyond the influence of habitat extent alone (Willis et al., 2026).

By comparison, metrics describing patch cohesion and geometric complexity showed comparatively weak relationships with natural capital indicators. This suggests that different structural connectivity metrics capture different dimensions of habitat pattern and should not be interpreted interchangeably (Tischendorf and Fahrig, 2000). In Chapter 2, regulating ecosystem services appeared to be influenced primarily by habitat quantity and fragmentation, whereas internal patch cohesion and shape contributed relatively little additional explanatory power. This does not imply that these metrics lack ecological significance, but rather that their importance is likely to depend upon the ecological process being considered.

These findings reinforce the multidimensional nature of structural connectivity. No single metric adequately characterises all aspects of landscape structure, and different measures are likely to be relevant for different ecological functions. Consequently, structural connectivity should not be regarded as a replacement for habitat extent within

natural capital assessment. Instead, connectivity metrics provide complementary information that can improve understanding of how ecological assets are distributed within the landscape and where fragmentation may influence ecosystem functioning. Integrating habitat configuration alongside conventional measures of habitat extent therefore offers a more complete representation of estuarine natural capital than either approach in isolation. For practitioners, this suggests that restoration planning should consider not only increasing the quantity of salt marsh habitat, but also how newly created habitat is spatially arranged relative to existing marshes.

4.3 Scale Shapes Connectivity

One of the most important contributions of this research is demonstrating that estimates of structural connectivity are strongly influenced by the spatial framework used to define the landscape. Although scale dependence has long been recognised as a fundamental principle of landscape ecology (Wiens, 1989; Levin, 1992; Turner, 2005; Wu, 2004), relatively few studies have examined how alternative coastal management frameworks influence estimates of structural connectivity within temperate estuarine habitats. The findings presented here demonstrate that the same salt marsh landscape can appear more or less fragmented depending on whether connectivity is assessed at the scale of the whole estuary, Water Framework Directive (WFD) water bodies, nutrient management zones or Shoreline Management Plan (SMP) policy units.

This finding has important implications for the interpretation of structural connectivity metrics. Connectivity is often treated as an intrinsic property of landscapes; however, the present study demonstrates that connectivity estimates are also shaped by the analytical

framework through which habitat patterns are measured. Consequently, differences in reported connectivity between studies may not necessarily reflect ecological change, but may instead arise from differences in landscape definition, spatial extent or management boundaries. Connectivity should therefore be interpreted as a scale-dependent representation of habitat structure rather than as a single fixed characteristic of an ecosystem.

Among the metrics examined, distance to nearest neighbour exhibited the greatest sensitivity to analytical scale, reflecting its dependence on the spatial extent over which patch relationships are calculated. Broader analytical frameworks tended to integrate a greater number of habitat patches within individual landscapes, whereas smaller management units revealed local variation in fragmentation that was obscured at coarser scales. These findings are consistent with the Modifiable Areal Unit Problem (MAUP), whereby spatial statistics vary according to the size and configuration of analytical units rather than changes in the underlying ecological system (Openshaw, 1984; Jelinski and Wu, 1996). Although MAUP is well established within geographical analysis, its implications for quantifying structural connectivity within estuarine landscapes have received little attention.

The observed scale dependence also has practical implications for coastal management. Different spatial frameworks emphasise different aspects of landscape structure and therefore support different management objectives. Broad-scale analyses are well suited to strategic planning by identifying regional habitat networks and overall patterns of fragmentation across estuaries. In contrast, finer-scale frameworks, such as SMP policy units, provide greater resolution for identifying local fragmentation, evaluating restoration

opportunities and supporting site-based management decisions. Rather than identifying a single optimal scale for connectivity assessment, these findings suggest that the choice of analytical framework should be guided by the ecological process or management objective under consideration.

More broadly, this study demonstrates that scale should be regarded as an integral component of structural connectivity assessment rather than a methodological consideration. Incorporating multiple spatial frameworks provides a more comprehensive understanding of landscape structure than analyses conducted at a single scale and enables connectivity to be interpreted within the context most relevant to ecological function and management. This represents an important step towards integrating landscape ecological principles into natural capital assessment and evidence-based coastal planning.

4.4 From Connectivity to Coastal Management

The findings of this study demonstrate that structural connectivity has practical value beyond describing landscape pattern; it provides information that can support more spatially informed approaches to habitat restoration, natural capital assessment and coastal management. While habitat extent remained the strongest determinant of regulating ecosystem service capacity, structural connectivity provided complementary information regarding habitat fragmentation and spatial organisation. Together, these measures offer a more complete understanding of estuarine landscapes than either habitat area or connectivity alone.

For restoration practitioners, these findings suggest that increasing habitat area should remain a primary objective where the aim is to enhance ecosystem service provision. This is consistent with recent evidence from large-scale marine restoration initiatives demonstrating that increases in restored coastal habitat extent can be associated with broader ecological benefits and ecosystem recovery (Chen et al., 2026). Within the present study, greater salt marsh area was particularly associated with increased carbon storage, carbon sequestration, nitrogen removal and wave attenuation. However, the spatial arrangement of restored habitat should also be considered.

Chapter 3 demonstrates that the choice of analytical framework influences how structural connectivity is interpreted. This has important implications for coastal management because the spatial units used for decision-making frequently differ according to legislative or administrative requirements. Broad analytical frameworks are well suited to strategic planning by identifying regional habitat networks and overall patterns of fragmentation, whereas smaller management units, such as Shoreline Management Plan (SMP) policy units, provide greater resolution for identifying local restoration priorities and evaluating changes in habitat structure. Consequently, no single spatial framework is universally appropriate. Instead, the selection of analytical scale should reflect the ecological process or management objective under consideration.

These findings are also relevant to the continued development of natural capital assessment. Existing frameworks typically quantify habitat extent and condition but rarely incorporate explicit measures of habitat configuration. The results presented here suggest that structural connectivity metrics can provide valuable additional information by describing the spatial arrangement of ecological assets and identifying areas where

fragmentation may influence ecosystem functioning. Incorporating structural connectivity alongside conventional measures of habitat extent therefore has the potential to strengthen natural capital assessments by providing greater spatial context for interpreting ecosystem service capacity.

More broadly, this research demonstrates how landscape ecological principles can be integrated into coastal decision-making using management frameworks that are already widely applied within the UK. Because the analyses were undertaken using Shoreline Management Plan policy units, Water Framework Directive water bodies and nutrient management zones, the methods developed here could be readily incorporated into existing planning and monitoring frameworks. Rather than requiring entirely new assessment approaches, structural connectivity metrics could complement current habitat-based assessments by providing an additional layer of spatial information to support evidence-based conservation, restoration and adaptive management.

Ultimately, the greatest contribution of this work is not identifying a single optimum measure of connectivity, but in demonstrating that the interpretation of structural connectivity depends on both the metric selected and the spatial framework within which it is measured. Recognising this enables managers to select connectivity metrics that are appropriate for their management objectives and supports more robust, transparent and ecologically informed decision-making within temperate estuarine ecosystems.

4.5 Limitations and Future Directions

Although this study provides new insights into the relationship between structural connectivity, natural capital and analytical scale within temperate estuarine salt marshes, several limitations should be considered when interpreting the findings.

First, the study focused exclusively on structural connectivity, which describes the physical arrangement of habitat patches rather than the realised movement of organisms, sediments, nutrients or water between them. Structural connectivity provides an objective and reproducible measure of landscape pattern and is well suited to habitat mapping and natural capital assessment. However, it cannot directly determine whether ecological processes occur between habitat patches. Consequently, the mechanisms proposed to explain relationships between connectivity metrics and ecosystem service provision remain inferential and require validation through functional studies (Taylor et al., 1993; Tischendorf and Fahrig, 2000).

Second, several natural capital indicators examined in this study were intrinsically related to habitat extent. Carbon storage, carbon sequestration and nitrogen removal all increase with the amount of vegetated salt marsh present, which may have strengthened the observed relationships between habitat area and regulating ecosystem services. Future studies could build upon this work by incorporating area-normalised ecosystem service indicators, habitat condition metrics or process-based measurements to better distinguish the influence of habitat quantity from habitat configuration.

Third, the future habitat scenario represented projected habitat creation rather than realised ecosystem development. While this provided valuable insight into how structural connectivity may change under future restoration scenarios, newly created salt marshes

are unlikely to immediately exhibit the vegetation structure, sediment characteristics or ecological functioning of mature marsh systems. Consequently, the future analyses should be interpreted as estimates of potential changes in habitat configuration rather than predictions of future ecosystem service delivery.

Finally, this study was undertaken within the Blackwater and Colne estuaries, which provide an excellent case study because of their extensive salt marshes and well-established management frameworks. Nevertheless, estuarine geomorphology, tidal regimes and habitat distributions vary considerably between regions. Applying the analytical framework developed here to a wider range of estuarine systems would help determine the generality of the observed relationships and identify whether similar scale-dependent patterns occur elsewhere.

These limitations identify several priorities for future research. Integrating structural connectivity metrics with functional approaches, including hydrodynamic modelling, sediment transport analyses, propagule dispersal, species movement studies and environmental DNA (eDNA), would improve understanding of the mechanisms linking habitat pattern to ecosystem functioning. Future research should also examine whether connectivity plays a greater role in ecosystem services that depend more directly on ecological interactions, such as biodiversity conservation, fisheries support and ecological resilience. Finally, applying this framework across multiple estuaries and restoration projects would help establish whether structural connectivity metrics can be routinely incorporated into natural capital assessments and used to evaluate the long-term outcomes of habitat restoration.

4.6 Conclusions

This research investigated how structural connectivity and analytical scale influence natural capital assessment within temperate estuarine salt marshes using the Blackwater and Colne estuaries as a case study. By integrating landscape ecological metrics with spatially explicit natural capital indicators, the study examined the relationships between habitat configuration and regulating ecosystem services and evaluated how estimates of structural connectivity vary across alternative spatial frameworks relevant to coastal management.

Three principal conclusions emerge from this research. First, habitat extent was consistently the strongest predictor of regulating ecosystem service capacity, confirming that the quantity of salt marsh remains fundamental to the provision of ecosystem services such as carbon storage, carbon sequestration, nitrogen removal and wave attenuation. Second, structural connectivity metrics provided complementary information by characterising habitat fragmentation and spatial organisation, although their relationships with natural capital varied according to the metric considered. Structural connectivity should therefore be regarded as an additional descriptor of landscape structure rather than a replacement for conventional measures of habitat extent. Third, estimates of structural connectivity were strongly influenced by the spatial framework used to define the landscape, demonstrating that connectivity is not a fixed property of estuarine ecosystems but a scale-dependent representation of habitat pattern.

Collectively, these findings demonstrate that incorporating structural connectivity alongside habitat extent can provide a more comprehensive understanding of estuarine natural capital. However, they also highlight that connectivity metrics cannot be

interpreted independently of analytical scale. The ecological insights obtained from structural connectivity therefore depend not only on the metric selected but also on the spatial framework within which it is applied. This has important implications for the comparison of connectivity studies and for the application of landscape ecological metrics within conservation planning, habitat restoration and natural capital assessment.

Ultimately, this research contributes to the growing integration of landscape ecology and natural capital science by demonstrating that habitat quantity, habitat configuration and analytical scale should be considered together when assessing estuarine ecosystems. By showing how structural connectivity metrics can complement traditional habitat-based assessments while acknowledging their scale dependence, the study provides a framework for more spatially informed natural capital assessment and supports evidence-based approaches to coastal restoration and management.

References

Adams, C.A., Andrews, J.E. and Jickells, T. (2012) Nitrous oxide and methane fluxes vs. carbon, nitrogen and phosphorous burial in new intertidal and saltmarsh sediments. *Science of The Total Environment*, 434, pp.240-251. <https://doi.org/10.1016/j.scitotenv.2011.11.058>.

Adam, P. (1990) *Saltmarsh Ecology*. Cambridge: Cambridge University Press.

Agiadi, K., Caswell, B.A., Almeida, R., Becheker, A., Blanco, A., Brito, C., León-Cobo, M.J., Cook, E.-M.E., Costantini, F., Karakuş, M., Leprieur, F., López, C., López-López, L., O'Dea, A., Pallacks, S., Rabanal, I., Schultz, L., Tanner, S.E., Theodoropoulou, T. and Thurstan, R.H. (2024) Geohistorical insights into marine functional connectivity. *ICES Journal of Marine Science*, [online] 81(10). <https://doi.org/10.1093/icesjms/fsae117>.

Allen, J.R.L. (2000) Morpho-dynamics of Holocene salt marshes: a review sketch from the Atlantic and southern North Sea coasts of Europe. *Quaternary Science Reviews*, 19(12), pp.1155–1231.

Alvera-Azcárate, A., Van der Zande, D., Barth, A., Dille, A., Massant, J. and Beckers, J.-M. (2025) Generation of super-resolution gap-free ocean colour satellite products using data-interpolating empirical orthogonal functions (DINEOF). *Ocean Science*, [online] 21(2), pp.787–805. <https://doi.org/10.5194/os-21-787-2025>.

Balbar, A.C. and Metaxas, A. (2019) The current application of ecological connectivity in the design of marine protected areas. *Global Ecology and Conservation*. <https://doi.org/10.1016/j.gecco.2019.e00569>.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. and Silliman, B.R. (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs*, 81(2), pp.169–193. <https://doi.org/10.1890/10-1510.1>.

Barbier, E. (2013) Valuing Ecosystem Services for Coastal Wetland Protection and Restoration: Progress and Challenges. *Resources*, 2(3), pp.213–230. <https://doi.org/10.3390/resources2030213>.

Bateman, I.J. and Mace, G.M. (2020) The natural capital framework for sustainably efficient and equitable decision making. *Nature Sustainability*, 3(10), pp.776–783. <https://doi.org/10.1038/s41893-020-0552-3>.

Battisti, C., Gallitelli, L., Scalici, M. and Angelici, F.M. (2022) Habitat Fragmentation, Connectivity Conservation and Related Key-Concepts: Temporal Trends in Their Recurrences on Web of Science (1960–2020). *Land*, [online] 11(2), p.230. <https://doi.org/10.3390/land11020230>.

Briers, R. (n.d.). Habitat networks - reviewing the evidence base: Final Report. [online] NatureScot. Available at: <https://www.nature.scot/doc/habitat-networks-reviewing-evidence-base-final-report#Executive+summary> [Accessed 28 Apr. 2025].

Brown, C., Alexander, P., Arneth, A., Holman, I. and Rounsevell, M. (2019) Achievement of Paris climate goals unlikely due to time lags in the land system, *Nature Climate Change*, 9(3), pp. 203–208.

Blondel, J. (2006) The “design” of Mediterranean landscapes: A millennial story of humans and ecological systems, *Human Ecology*, 34(5), pp. 713–729.

Boström, C., Pittman, S.J., Simenstad, C. and Kneib, R.T. (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Marine Ecology Progress Series*, [online] 427, pp.191–217. <https://doi.org/10.3354/meps09051>.

Carr, M.H., Robinson, S.P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacker, E.J. and Williams, M. (2017) The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. *Aquatic Conservation: Marine and Freshwater Ecosystems*, [online] 27(1), pp.6–29. <https://doi.org/10.1002/aqc.2800>.

Chen, X., Wang, N., Bao, X., Wu, W., Chen, X., Dong, P., Williams, S., Yu, J., Zhou, L., Ding, Y. and Song, D., 2026. National restoration initiatives promote China's marine ecosystem recovery. *Communications Earth & Environment*.

Chmura, G.L., Anisfeld, S.C., Cahoon, D.R. and Lynch, J.C., (2003) Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles*, 17(4), 1111.

Christie, M.R., Meirmans, P.G., Gaggiotti, O.E., Toonen, R.J. and White, C. (2017) Disentangling the relative merits and disadvantages of parentage analysis and assignment tests for inferring population connectivity. *ICES Journal of Marine Science*, [online] 74(6), pp.1749–1762. <https://doi.org/10.1093/icesjms/fsx044>.

Chu N, Liu G, Xu J, Yao P, Du Y, Liu Z and Cai Z (2022) Hydrodynamical transport structure and lagrangian connectivity of circulations in the Pearl River Estuary. *Frontiers in Marine Science*. <https://doi.org/10.3389/fmars.2022.996551>.

Convention on Biological Diversity (CBD) (2022) Kunming–Montreal Global Biodiversity Framework. [online] Available at: <https://www.cbd.int/gbf>.

Cooke, G.M., Schlub, T.E., Sherwin, W.B. and Ord, T.J. (2016) Understanding the Spatial Scale of Genetic Connectivity at Sea: Unique Insights from a Land Fish and a Meta-Analysis. *PLOS ONE*. <https://doi.org/10.1371/journal.pone.0150991>.

Cornacchia, L., van de Vijssel, R.C., van der Wal, D., Ysebaert, T., Sun, J., van Prooijen, B., de Vet, P.L.M., Liu, Q.-X. and van de Koppel, J., (2024) Vegetation traits and biogeomorphic complexity shape the resilience of salt marshes to sea-level rise. *Communications Earth and Environment*, 17, pp.562–569. <https://doi.org/10.1038/s43247-024-01829-2>.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. and van den Belt, M. (1997) The value of the world's ecosystem services and natural capital. *Ecological Economics*, [online] pp.253–260. Available at: https://www.researchgate.net/publication/309563023_The_value_of_the_world's_ecosystem_services_and_natural_capital.

Craft, C., Broome, S. and Campbell, C. (2002) Fifteen years of vegetation and soil development after brackish-water marsh creation, *Restoration Ecology*, 10(2), pp. 248–258.

Cushman, S.A., McGarigal, K. and Neel, M.C., (2008) Parsimony in landscape metrics: strength, universality and consistency. *Ecological Indicators*, 8(5), pp.691–703.

Davies, J., Baxter, J., Bradley, M., Connor, D.W., Khan, J., Murray, E., Sanderson, W.G., Turnbull, C.G. and Vincent, M.A. (2001) *Marine Monitoring Handbook*. Peterborough: Joint Nature Conservation Committee.

DEFRA, (2013) Blackwater, Crouch, Roach and Colne Estuaries Marine Conservation Zone: designation order. London: Department for Environment, Food and Rural Affairs.

de Groot, R.S., Alkemade, R., Braat, L., Hein, L. and Willemen, L. (2010) Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making, *Ecological Complexity*, 7(3), pp. 260–272.

Dou, P., Chen, Y., Wang, F., Lin, Q., Zhang, S., and Fang, Y. (2014) Dynamics and integrity of wetland network in estuary, *Ecological Engineering*, 72, pp. 77–88.

ECSA (2026) Restoring Meadow, Marsh and Reef (ReMeMaRe), *Estuarine and Coastal Sciences Association*. [online] Restoring Meadow, Marsh and Reef (ReMeMaRe). Available at: <https://ecsa.international/rememare/restoring-meadow-marsh-and-reef-rememare> [Accessed 6 Apr. 2026].

Endangered Landscapes and Seascapes Programme, (2024) Restoring Our Seascapes. [pdf] Available at: <https://www.endangeredlandscapes.org/wp-content/uploads/2024/11/Restoring-our-seascapes-1.pdf> [Accessed 28 July 2025].

Engelhard, S.L., Huijbers, C.M., Stewart-Koster, B., Olds, A.D., Schlacher, T.A. and Connolly, R.M. (2017) Prioritising seascape connectivity in conservation using network

analysis, *Journal of Applied Ecology*, 54(4), pp. 1130–1141. <https://doi.org/10.1111/1365-2664.12824>.

Environment Agency (2022) The extent and zonation of saltmarsh in England: 2016–2019. Bristol: Environment Agency.

Environment Agency, (2006) Shoreline Management Plan Guidance. Volume 1: Aims and Requirements. Bristol: Environment Agency.

Elliott, M. and Quintino, V. (2007) The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas, *Marine Pollution Bulletin*, 54(6), pp. 640–645.

European Parliament and Council of the European Union, (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Communities*, L327, pp.1–73.

European Environment Agency (2020) Natural capital and ecosystem services. [online] Available at: <https://www.eea.europa.eu/soer/2015/europe/natural-capital-and-ecosystem-services> [Accessed 3 Jul. 2025].

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity, *Annual Review of Ecology, Evolution, and Systematics*, 34, pp. 487–515.

Fairbrass, A., Fradera, K., Shucksmith, R., Greenhill, L., Acott, T. and Ekins, P. (2025) Revealing gaps in marine evidence with a natural capital lens. *Philosophical Transactions of the Royal Society Biological Sciences*, [online] 380(1917). <https://doi.org/10.1098/rstb.2023.0214>.

Ferraro, K.M., Ferraro, A.L., Lundgren, E. and Sommer, N.R. (2025) The use and abuse of ecosystem service concepts and terms. *Biological Conservation*, [online] 308, p.111218. <https://doi.org/10.1016/j.biocon.2025.111218>.

Foster, N.L., Wilding, T.A., Bohn, K., Howlett, R.M., Lunda, J.J. and Attrill, M.J. (2014) Mapping the extent and intertidal zonation of seagrass habitats using aerial photographic interpretation and bathymetric LiDAR. *Estuarine, Coastal and Shelf Science*, 137, pp. 27–37.

FragStats, n.d. FRAGSTATS v4: Spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst. Available at: <https://www.fragstats.org>

Ganju, N.K., Defne, Z., Kirwan, M.L., Fagherazzi, S., D’Alpaos, A. and Carniello, L., (2017) Spatially integrative metrics reveal hidden vulnerability of microtidal salt marshes. *Nature Communications*.

Gilbertson, N.M., Adams, T.P. and Burrows, M.T. (2020) From marshes to coastlines: A metric for local and national scale identification of high-value habitat for coastal protection. *Estuarine, Coastal and Shelf Science*. <https://doi.org/10.1016/j.ecss.2020.107022>.

Green, B., Smith, D. and Underwood, G. (2012) Habitat connectivity and spatial complexity differentially affect mangrove and salt marsh fish assemblages. *Marine Ecology Progress Series*, 466, pp.177–192. <https://doi.org/10.3354/meps09791>.

Harrison, J.B., Sunday, J.M. and Rogers, S.M. (2019) Predicting the fate of eDNA in the environment and implications for studying biodiversity, *Proceedings of the Royal Society B: Biological Sciences*.

Haines-Young, R. and Potschin, M., (2009) Common International Classification of Ecosystem Services (CICES) V1. [online]. Available at: <https://cices.eu/> (Accessed: 15 January 2026).

Hilty, J.A., Worboys, G.L., Keeley, A.T.H., Woodley, S., Lausche, B.J., Locke, H., Carr, M., Pulsford, I. and Tabor, G.M. (2020) Guidelines for conserving connectivity through ecological networks and corridors. Gland, Switzerland: IUCN.

Herbert, R.A. (1999) Nitrogen cycling in coastal marine ecosystems. *FEMS Microbiology Reviews*, 23(5), pp. 563–590.

Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K. and Nowosad, J., (2019) landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography*, 42(10), pp.1648–1657.

Howard, J., Hoyt, S., Isensee, K., Pidgeon, E., Telszewski, M. (eds.) (2014) Coastal Blue Carbon: Methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrass meadows. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature.

Ignatyeva, M., Yurak, V. and Dushin, A. (2022) Valuating Natural Resources and Ecosystem Services: Systematic Review of Methods in Use. *Sustainability*, 14(3), p.1901. <https://doi.org/10.3390/su14031901>.

IPBES (2019) Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Bonn, Germany: IPBES Secretariat.

IPCC, (2006) 2006 IPCC Guidelines for National Greenhouse Gas Inventories. Hayama, Japan: Institute for Global Environmental Strategies.

Jelinski, D.E. and Wu, J. (1996) The modifiable areal unit problem and implications for landscape ecology, *Landscape Ecology*, 11(3), pp. 129–140.

Kindlmann, P. and Burel, F., (2005) Connectivity measures in spatial ecology. *Environmental and Ecological Statistics*, 12(4), pp.445-467.

Koch, E.W., Barbier, E.B., Silliman, B.R., Reed, D.J., Perillo, G.M., Hacker, S.D., Granek, E.F., Primavera, J.H., Muthiga, N., Polasky, S., Halpern, B.S., Kennedy, C.J., Kappel, C.V. and Wolanski, E. (2009) Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment*, 7(1), pp.29–37. <https://doi.org/10.1890/080126>.

Ladd, C., Duggan-Edwards, M.F., Bouma, T.J., Pagès, J.F. and Skov, M. (2019) Sediment Supply Explains Long-Term and Large-Scale Patterns in Salt Marsh Lateral Expansion and Erosion. *Geophysical Research Letters*, 46(20), pp.11178–11187. <https://doi.org/10.1029/2019gl083315>.

Ladd, C.J.T., Smeaton, C., Skov, M.W. and Austin, W.E.N. (2022) Best practice for upscaling soil organic carbon stocks in salt marshes. *Geoderma*, 428, p.116188. <https://doi.org/10.1016/j.geoderma.2022.116188>.

Legge, O., Johnson, M., Hicks, N., Jickells, T., Diesing, M., Aldridge, J., Andrews, J., Artioli, Y., Bakker, D.C.E., Burrows, M.T., Carr, N., Cripps, G., Felgate, S.L., Fernand, L., Greenwood, N., Hartman, S., Kröger, S., Lessin, G., Mahaffey, C., Mayor, D.J., Parker, R., Queirós, A.M., Shutler, J.D., Silva, T., Stahl, H., Tinker, J., Underwood, G.J.C., Van

Der Molen, J., Wakelin, S., Weston, K. and Williamson, P. (2020) 'Carbon on the Northwest European Shelf: Contemporary Budget and Future Influences', *Frontiers in Marine Science*, 7, p. 143. Available at: <https://doi.org/10.3389/fmars.2020.00143>

Lester, S.E., Dubel, A.K., Hernán, G., McHenry, J. and Rassweiler, A. (2020) Spatial Planning Principles for Marine Ecosystem Restoration. *Frontiers in Marine Science*, 7. <https://doi.org/10.3389/fmars.2020.00328>.

Levin, S.A., (1992) The problem of pattern and scale in ecology. *Ecology*, 73(6), pp.1943–1967.

Lippi, S., Piroddi, C., Graziano, M. and Di Franco, A. (2024) Highlighting the gap on spatial regulatory data in the official MPAs databases. *Frontiers in Marine Science*. [online]. <https://doi.org/10.3389/fmars.2024.1369447>.

MacArthur, R.H. and Wilson, E.O., (1967) The Theory of Island Biogeography. *Princeton*, N.J.: Princeton University Press.

Mace, G.M., Hails, R.S., Cryle, P., Harlow, J. and Clarke, S.J. (2015) REVIEW: Towards a risk register for natural capital. *Journal of Applied Ecology*, 52(3), pp.641–653. <https://doi.org/10.1111/1365-2664.12431>.

Mason, C., Jackson, E.L. and Griffiths, C.A. (2018) Acoustic mapping to inform seagrass bed conservation: A case study in south-west England. *Estuarine, Coastal and Shelf Science*, 200, pp. 341–350.

Mason, V.G., Willemsen, P.W.J.M., Adams, R.O., Borsje, B.W., Fivash, G.S., van de Koppel, J., Stoorvogel, M.M. and Bouma, T.J., (2025) Emerging trade-offs in saltmarsh ecosystem services under sea-level rise. *Estuarine, Coastal and Shelf Science*. <https://doi.org/10.1016/j.ecss.2025.109319>.

Maxwell, T.L., Spalding, M.D., Friess, D.A., Murray, N.J., Rogers, K., Rovai, A.S., Smart, L.S., Weilguny, L., Adame, M.F., Adams, J.B., Austin, W.E.N., Copertino, M.S., Cott, G.M., Costa, M.D.P., Holmquist, J.R., Ladd, C.J.T., Lovelock, C.E., Ludwig, M., Moritsch, M.M., Navarro, A., Raw, J.L., Ruiz-Fernández, A.C., Serrano, O., Smeaton, C., Van de Broek, M., Windham-Myers, L., Landis, E. and Worthington, T.A. (2024) 'Soil carbon in the world's tidal marshes', *Nature Communications*, 15, 10265. Available at: <https://doi.org/10.1038/s41467-024-54572-9>

Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H. and Silliman, B.R. (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9(10), pp. 552–560.

McGarigal, K., Cushman, S.A. and Ene, E. (2023) *FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical Maps*. Computer software program produced by the authors. Available at: [FRAGSTATS](#) [Accessed 23 September 2026].

McGarigal, K. and Marks, B.J., (1995) *FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure*. Portland, Oregon: USDA Forest Service, Pacific Northwest Research Station. General Technical Report PNW-GTR-351.

McRae, B.H., Hall, S.A., Beier, P. and Theobald, D.M. (2012) Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. *PLOS ONE*, 7(12), e52604.

McRae, B.H., Dickson, B.G., Keitt, T.H. and Shah, V.B. (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, 89(10), pp. 2712–2724.

Mehvar, S., Filatova, T., Dastgheib, A., de Ruyter van Steveninck, E. and Ranasinghe, R. (2018) Quantifying Economic Value of Coastal Ecosystem Services: A Review. *Journal of Marine Science and Engineering*, 6(1), p.5. <https://doi.org/10.3390/jmse6010005>.

Merriam, G., (1984) Connectivity: a fundamental ecological characteristic of landscape pattern. In: Brandt, J. and Agger, P. (eds.) *Proceedings of the First International Seminar*

on Methodology in Landscape Ecological Research and Planning. Roskilde University Centre, pp. 5-15.

Messié, M., Sherlock, R.E., Huffard, C.L., J. Timothy Pennington, C. Anela Choy, Michisaki, R.P., Gomes, K., Chavez, F.P., Robison, B.H. and Smith, K.L. (2023) Coastal upwelling drives ecosystem temporal variability from the surface to the abyssal seafloor. *Proceedings of the National Academy of Sciences*, [online] 120(13). <https://doi.org/10.1073/pnas.2214567120>.

Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., van Wesenbeeck, B.K., Wolters, G., Jensen, K., Bouma, T.J., Miranda-Lange, M. and Schimmels, S. (2014) Wave attenuation over coastal salt marshes under storm surge conditions. *Nature Geoscience*, 7(10), pp.727–731. <https://doi.org/10.1038/ngeo2251>.

Natural Capital Committee (2015) The State of Natural Capital: Protecting and Improving Natural Capital for Prosperity. London: Natural Capital Committee.

Natural England (2012) Ecosystem services from Environmental Stewardship that benefit agricultural production - NECR102. [online] Natural England - Access to Evidence. Available at: <https://publications.naturalengland.org.uk/publication/2322452>.

NatureScot (2023) Habitat network parts and connections. [online] NatureScot. Available at: <https://www.nature.scot/professional-advice/land-and-sea-management/managing-land/habitat-networks/habitat-network-parts-and-connections>.

Nedwell, D.B., Underwood, G.J.C., McGenity, T.J., Whitby, C. and Dumbrell, A.J. (2016) Chapter Five - The Colne Estuary: A Long-Term Microbial Ecology Observatory. *Advances in Ecological Research*, pp.227–281. <https://doi.org/10.1016/bs.aecr.2016.08.004>.

Neill, A.M., O'Donoghue, C. and Stout, J.C., (2020) A Natural Capital Lens for a Sustainable Bioeconomy: Determining the Unrealised and Unrecognised Services from Nature. *Sustainability*, 12(19), p.8033.

Olds, A.D., Connolly, R.M., Pitt, K.A., Pittman, S.J., Maxwell, P.S., Huijbers, C.M., Moore, B.R., Albert, S., Rissik, D., Babcock, R.C. and Schlacher, T.A., (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. *Global Ecology and Biogeography*, 25(1), pp.3–15

Openshaw, S. (1984) The Modifiable Areal Unit Problem. Norwich: Geo Books.

Pacifico, A.M., Mulazzani, L. and Malorgio, G. (2025) Are the economic valuations of marine and coastal ecosystem services supporting policymakers? A systematic review

and remaining gaps and challenges. *Frontiers in Marine Science*, 11. <https://doi.org/10.3389/fmars.2024.1501812>.

Parliamentary Office of Science and Technology (2007) Postnote: Ecosystem Services. [online] Parliament Global Assets. Available at: <https://www.parliament.uk/globalassets/documents/post/postpn281.pdf> [Accessed 27 Mar. 2025].

Paterson, D.M., Defew, E.C. and Jabour, J. (2012) Ecosystem function and co-evolution of terminology in marine science and management, in Solan, M., Aspden, R.J. and Paterson, D.M. (eds.) *Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and Integration*. Oxford: Oxford University Press, pp. 24–33. <https://doi.org/10.1093/acprof:oso/9780199642250.003.0003>

Pittman, S.J., Kneib, R.T. and Simenstad, C.A., (2021) Practising coastal seascape ecology. *Marine Ecology Progress Series*, 670, pp.1–12.

Pittman, S.J., Wedding, L.M., Yates, K.L., Bonaldo, R.M., Fulton, C.J., Bennett, S., Hosack, G.R., Williams, I.D., Brown, C.J. and Saunders, M.I. (2021) Seascape ecology: identifying research priorities for an emerging ocean sustainability science, *Marine Ecology Progress Series*, 663, pp. 1–29.

Preston, J., Debney, A., Gamble, C., Hardy, M.J., Underwood, G.J.C., Garbutt, A., Harley, J., Baker, R., Dunk, R.M., Grigg, M., Hancock, B.T., Hendy, I.W., La, C., Murray, J., Pettoirelli, N., Pittman, S.J., Reeves, S.E., Robertson, M., Sturrock, A.M. and Thurstan, R.H. (2025) Seascape connectivity: evidence, knowledge gaps and implications for temperate coastal ecosystem restoration practice and policy. *Ocean Sustainability*. <https://doi.org/10.1038/s44183-025-00128-3>.

Posit team, (2026) *RStudio: Integrated Development Environment for R*. Boston, MA: Posit Software, PBC. Available at: <http://www.posit.co/> (Accessed: 03.04.2026).

Quigley, C.N., Roughan, M., Chaput, R., Jeffs, A.G. and Gardner, J.P.A. (2022) Combined biophysical and genetic modelling approaches reveal new insights into population connectivity of New Zealand green-lipped mussels. *Frontiers in Marine Science*. <https://doi.org/10.3389/fmars.2022.971209>.

Rogers, M. and Möller, I. (2019) Wave protection provided by salt marshes: A GIS and remote sensing basic analysis approach. Suffolk Marine Pioneer, Coast and Heaths Area of Outstanding Natural Beauty.

Saura, S. and Pascual-Hortal, L. (2007) A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landscape and Urban Planning*, 83(2–3), pp. 91–103.

Saura, S. and Rubio, L. (2010) A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography*, 33(3), pp. 523–537.

Seitzinger, S., Harrison, J.A., Böhlke, J.K., Bouwman, A.F., Lowrance, R., Peterson, B., Tobias, C. and Van Drecht, G., (2006) Denitrification across landscapes and waterscapes: a synthesis. *Ecological Applications*, 16(6), pp.2064–2090.

Selivanov, E. and Hlaváčková, P. (2021) Methods for monetary valuation of ecosystem services: A scoping review. *Journal of Forest Science*. <https://doi.org/10.17221/96/2021-jfs>.

Selkoe, K.A., D'Aloia, C.C., Crandall, E.D., Iacchei, M., Liggins, L., Puritz, J.B., Von der Heyden, S. and Toonen, R.J. (2016) A decade of seascape genetics: contributions to basic and applied marine connectivity. *Marine Ecology Progress Series*, 554, pp. 1–19. <https://doi.org/10.3354/meps11818>.

Smeaton, C., Burden, A., Ruranska, P., Ladd, C.J.T., Garbutt, A., Jones, L., McMahon, L., Miller, L.C., Skov, M.W. and Austin, W.E.N. (2022) Using citizen science to estimate surficial soil Blue Carbon stocks in Great British saltmarshes. *Frontiers in Marine Science*, 9. <https://doi.org/10.3389/fmars.2022.959459>.

Stoorvogel, M.M., Temmerman, S., Oosterlee, L., Schoutens, K., Maris, T., van de Koppel, J., Meire, P. and Bouma, T.J., (2024) *Nature-based shoreline protection in newly formed tidal marshes is controlled by tidal inundation and sedimentation rate*. Communications Earth and Environment. <https://doi.org/10.1038/s43247-024-01200-9>.

Stuart, C., Wedding, L., Pittman, S., Serafy, J., Moura, A., Bruckner, A. and Green, S. (2023) Seascape connectivity modelling predicts hotspots of fish-derived nutrient provisioning to restored coral reefs. Marine Ecology Progress Series, MFC. <https://doi.org/10.3354/meps14321>.

Suykerbuyk, W., Govers, L.L., Bouma, T.J., Giesen, W.B.J.T. and van Katwijk, M.M. (2016) Unpacking the ecosystem services of intertidal seagrass meadows: More than just a nursery for fish. *Marine Ecology Progress Series*, 558, pp. 55–66.

Tanner, S., Sturrock, A., Öztürk, R., Smoliński, S., Terzi, Y., Reis-Santos, P., Barboza, F., Blanco, A., Borsa, P., Castilho, R., Costantini, F., Feyzioğlu, A., Guizien, K., Guy-Haim, T., Kaplan, D., Kotta, J., Lett, C., Martinho, F., Nanninga, G. and Pérez-Ruzafa, Á. (2025) A systematic review of the current state of marine functional connectivity research. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps14888>.

Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G., (1993) Connectivity is a vital element of landscape structure. *Oikos*, 68(3), pp.571-573.

Temmerman, S., Meire, P., Bouma, T.J., Herman, P.M.J., Ysebaert, T. and De Vriend, H.J., (2013) Ecosystem-based coastal defence in the face of global change. *Nature*, 504, pp.79–83.

Thompson, P.L. and Fronhofer, E.A. (2019) The conflict between adaptation and dispersal for maintaining biodiversity in changing environments. *Proceedings of the National Academy of Sciences*, [online] 116(42), pp.21061–21067. <https://doi.org/10.1073/pnas.1911796116>.

Tischendorf, L. and Fahrig, L. (2000) On the usage and measurement of landscape connectivity, *Oikos*, 90(1), pp. 7–19.

Townsend, M., Davies, K., Hanley, N., Hewitt, J.E., Lundquist, C.J. and Lohrer, A.M. (2018) The Challenge of Implementing the Marine Ecosystem Service Concept. *Frontiers in Marine Science*, 5. <https://doi.org/10.3389/fmars.2018.00359>.

Turner, M.G., Gardner, R.H. and O'Neill, R.V., (2001) *Landscape Ecology in Theory and Practice: Pattern and Process*. New York: Springer.

Turner, M.G. (2005) Landscape ecology: what is the state of the science? *Annual Review of Ecology, Evolution, and Systematics*, 36, pp. 319–344.

Turner, M.G. and Gardner, R.H., (2015) *Landscape Ecology in Theory and Practice: Pattern and Process*. 2nd ed. New York: Springer.

Turner, M.G., O'Neill, R.V., Gardner, R.H. and Milne, B.T., (1989) Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology*, 3(3–4), pp.153–162.

Underwood, G. J. C., Slee, N. J. D., Cameron, T., Worrall, C., Kesner, S., and Watson, S.C.L (2025) Blackwater Colne Estuaries Natural Capital Assessment. University of Essex and Plymouth Marine Laboratory. Funded by the Department for Environment, Food and Rural Affairs (Defra) and the Environment Agency. Project ID NC74.

van den Belt, M., Forgie, V. and Farley, J. (2011) Valuation of Coastal Ecosystem Services. *Treatise on Estuarine and Coastal Science*, [online] pp.35–54. <https://doi.org/10.1016/b978-0-12-374711-2.01203-1>.

van de Koppel, J., Bouma, T.J. and Herman, P.M.J., (2012) The influence of local- and landscape-scale processes on spatial self-organization in estuarine ecosystems. *The Journal of Experimental Biology*, 215(6), pp.962–967. <https://doi.org/10.1242/jeb.060467>.

Virtanen, E.A., Moilanen, A. and Viitasalo, M., (2020) Marine connectivity in spatial conservation planning: analogues from the terrestrial realm. *Landscape Ecology*, 35(5), pp.1021–1034. <https://doi.org/10.1007/s10980-020-00995-4>.

Water Framework Directive UK (2012) Practitioners Guide to the Saltmarsh Tool
 Practitioners Guide to the Saltmarsh Tool Water Framework Directive: Transitional and
 Coastal Waters. [online] Available at:
<https://www.wfduk.org/sites/default/files/Media/Environmental%20standards/Annex%2017%20Transitional%20and%20coastal%20waters%20Angiosperms%20Saltmarsh%20Index.pdf> [Accessed 11 Apr. 2025].

Watson, E.B., Raposa, K.B., Carey, J.C., Wigand, C. and Warren, R.S. (2020) Anthropocene survival of southern New England's salt marshes. *Estuaries and Coasts*, 43(1), pp. 19–36.

Watson, E.B., Oczkowski, A.J., Wigand, C., Hanson, A.R., Davey, E.W., Crosby, S.C., Johnson, R.L. and Andrews, H.M., (2016) Nutrient enrichment and precipitation changes do not enhance resiliency of salt marshes to sea-level rise in the northeastern United States. *Climatic Change*, 134, pp.501–513.

Watson, J.E.M., Jones, K.R., Fuller, R.A., Marco, M.D., Segan, D.B. and Butchart, S.H.M. (2018) Protect the last of the wild. *Nature*, 563(7729), pp. 27–30.

Watson, S.C., Paterson, D.M., Queirós, A.M., Rees, A.P., Stephens, N., Widdicombe, S. and Beaumont, N.J., (2016) A conceptual framework for assessing the ecosystem service of waste remediation: In the marine environment. *Ecosystem services*, 20, pp.69-81.

Watson, S.C.L., Preston, J., Beaumont, N.J. and Watson, G.J. (2020) Assessing the natural capital value of water quality and climate regulation in temperate marine systems using a EUNIS biotope classification approach. *Science of The Total Environment*, p.140688. <https://doi.org/10.1016/j.scitotenv.2020.140688>.

Watson, S.C.L., Watson, G.J., Beaumont, N.J. and Preston, J. (2022) Inclusion of condition in natural capital assessments is critical to the implementation of marine nature-based solutions. *Science of The Total Environment*, [online] 838, p.156026. <https://doi.org/10.1016/j.scitotenv.2022.156026>.

Wedding, L.M., Stuart, C.E., Govers, L.L., Lilley, R.J., Olds, A., Preston, J., Tavasi, L.E. and Pittman, S.J. (2025) Five ways seascape ecology can help to achieve marine restoration goals. *Landscape Ecology*. <https://doi.org/10.1007/s10980-025-02099-9>.

Weeks, R. (2017) Incorporating seascape connectivity in conservation prioritisation. *PLOS ONE*. <https://doi.org/10.1371/journal.pone.0182396>.

Wiens, J.A., (1989) Spatial scaling in ecology. *Functional Ecology*, 3(4), pp.385–397.

Willis, C.S., Wills, E.K. and Gilby, B.L., 2026. Habitat structure and connectivity underpin bright spots for terrestrial fauna in urban coastal wetlands. *Urban Ecosystems*, 29(2), p.61.

Windham-Myers, L., Crooks, S. and Troxler, T.G. (eds.) (2018) A Blue Carbon Primer: The State of Coastal Wetland Carbon Science, Practice and Policy. Boca Raton: CRC Press.

Wood, C.M., Pinn, E.H. and Widdicombe, S., (2015) Coastal Biodiversity and Ecosystem Service Sustainability (CBESS): linking ecosystem science and policy. *Marine Pollution Bulletin*, 96(1–2), pp.1–3.

Wu, J., Shen, W., Sun, W. and Tueller, P.T., (2002) Empirical patterns of the effects of changing scale on landscape metrics. *Landscape Ecology*, 17(8), pp.761–782.

Wu, J., (2004) Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology*, 19(2), pp.125–138.

Zheng, Y., Jiang, Q., He, Q., Xiao, X., Macreadie, P.I., Xu, X., Nie, M., Wu, J., Ye, G., Wu, J., Gu, J., Cui, L., Wang, X. and Li, B. (2026) 'Global blue carbon losses from salt marshes exceed restoration gains', *Nature Communications*, 17, 3744. Available at: <https://doi.org/10.1038/s41467-026-70158-z>

Ziegler, S.L., Able, K.W., Fodrie, F.J. and Martin, C.W. (2021) Geographic variation in salt marsh structure and function for nekton: a guide to finding commonality across multiple scales. *Estuaries and Coasts*, 44, pp. 1497–1507.

Appendices

1. Chapter 2: Current scenario 1: vegetated salt marsh natural capital and connectivity metrics per SMP policy unit.

SMP policy unit	Salt marsh area (ha)	Distance to nearest neighbour (m)	Contiguity Index (mean)	Shape Index (mean)	CO2 Stocks (tonnes)	CO2 sequestered (tonnes per year)	Species richness	Nitrogen removal (tonnes per year)	Wave attenuation (%)
C4	172.58	4.56	0.37	2.04	5357.56	179.72	3.52	4.34	82
D1a	27.17	5.61	0.29	1.57	881.90	38.87	0.75	2.49	82
D1b	14.16	8.37	0.31	1.66	506.42	13.79	7.71	1.40	80
D2	9.92	11.07	0.30	1.61	400.97	7.28	7.71	1.13	74
D3	24.61	6.93	0.34	2.02	923.88	20.47	7.71	2.60	77
D4	36.61	4.67	0.16	1.45	1537.28	43.58	3.54	3.36	81
D5	37.52	5.25	0.29	1.56	1727.69	36.46	3.54	3.78	74
D6a	10.81	5.24	0.39	1.68	277.59	13.98	3.82	1.20	74
D6b	3.28	5.20	0.55	1.71	82.68	3.42	3.82	0.36	65
D7	9.32	8.27	0.53	1.73	137.96	7.67	3.82	0.99	79
D8a	7.21	7.12	0.35	2.06	103.95	8.46	3.82	0.78	67
D8b	231.26	5.01	0.28	1.57	1206.68	251.73	3.61	20.28	82
D8c	69.47	5.17	0.29	1.53	2575.03	82.60	1.54	7.58	82
E1	32.13	6.44	0.28	1.67	547.36	29.38	4.22	3.31	67
E2	3.01	21.16	0.58	1.84	60.27	2.63	4.22	0.05	63
E3	12.84	12.22	0.28	1.67	445.13	11.62	2.68	0.35	70
E4a	18.96	4.97	0.29	1.70	857.22	12.70	2.68	1.63	82
E4b	47.30	5.17	0.30	1.58	786.93	48.17	4.22	4.76	84

F1	97.07	4.94	0.26	1.52	2180.53	112.41	1.97	6.96	78
F10	4.77	6.97	0.38	1.63	127.65	2.85	4.52	0.36	72
F11b	0.28	146.47	0.56	1.63	0.38	0.96	4.52	0.00	NA
F11c	27.07	5.61	0.31	1.51	778.14	25.25	4.52	2.21	81
F12	22.21	5.61	0.31	1.51	563.63	19.12	4.52	1.60	80
F13	12.16	14.99	0.31	1.57	315.87	14.16	4.32	0.79	66
F14	27.82	5.16	0.30	1.50	1046.94	25.93	3.57	2.63	78
F15	7.43	9.88	0.55	1.87	226.39	6.62	3.57	0.57	70
F2	6.54	4.96	0.27	1.61	229.35	4.38	1.97	0.73	71
F3	104.20	5.09	0.26	1.47	6128.36	109.91	0.93	7.53	76
F4	28.79	4.80	0.32	1.64	1986.67	29.54	0.93	2.44	82
F5	108.62	5.06	0.25	1.51	3078.54	108.50	0.50	5.01	75
F6	45.40	5.13	0.23	1.48	1440.89	50.99	0.50	2.34	77
F7	26.49	5.33	0.33	1.75	1029.92	24.86	0.50	2.96	70
F8	3.75	15.93	0.40	1.72	217.61	2.47	0.50	0.63	80
F9a	122.70	5.51	0.29	1.54	3588.42	127.73	2.83	8.68	79
F9b	66.21	4.65	0.31	1.68	2215.58	71.91	2.83	5.34	82
G1	8.11	6.15	0.42	1.62	46.35	11.64	3.52	0.29	75
G2	195.38	6.63	0.23	1.29	797.01	245.64	3.52	4.97	83

2. Chapter 2: Current scenario 2: salt marsh full natural capital and connectivity metrics per SMP policy unit.

SMP policy unit	Salt marsh area (ha)	Distance to nearest neighbour (m)	Contiguity index (mean)	Shape index (mean)	CO2 Stocks (tonnes)	CO2 sequestered (tonnes per year)	Species richness	Nitrogen removal (tonnes per year)	Wave attenuation (%)
C4	177.92	6.08	0.40	2.12	5357.56	179.72	3.52	4.34	82
D1a	29.22	7.90	0.53	1.82	881.90	38.87	0.75	2.49	82
D1b	16.50	30.10	0.62	2.29	506.42	13.79	7.71	1.40	80
D2	13.23	13.09	0.28	1.67	400.97	7.28	7.71	1.13	74
D3	30.57	5.23	0.49	2.57	923.88	20.47	7.71	2.60	77
D4	39.65	30.63	0.55	2.47	1537.28	43.58	3.54	3.36	81
D5	44.47	10.77	0.48	2.07	1727.69	36.46	3.54	3.78	74
D6a	12.52	5.08	0.33	1.80	277.59	13.98	3.82	1.20	74
D6b	3.74	4.81	0.09	1.38	82.68	3.42	3.82	0.36	65
D7	10.30	9.41	0.70	1.69	137.96	7.67	3.82	0.99	79
D8a	9.20	19.72	0.64	2.83	103.95	8.46	3.82	0.78	67
D8b	239.00	11.02	0.49	2.45	1206.68	251.73	3.61	20.28	82
D8c	89.15	9.74	0.41	2.11	2575.03	82.60	1.54	7.58	82
E1	38.85	5.95	0.27	1.59	547.36	29.38	4.22	3.31	67
E2	2.00	13.47	0.63	2.03	60.27	2.63	4.22	0.05	63
E3	14.32	20.23	0.60	2.31	445.13	11.62	2.68	0.35	70
E4a	27.56	11.00	0.54	2.22	857.22	12.70	2.68	1.63	82
E4b	56.05	9.30	0.62	2.07	786.93	48.17	4.22	4.76	84
F1	117.84	6.14	0.50	2.13	2180.53	112.41	1.97	6.96	78
F10	5.43	38.10	0.61	2.08	127.65	2.85	4.52	0.36	72

F11a	0.01	17.00	0.23	1.15	0.19	0.00	4.52	0.00	NA
F11b	0.01	176.83	0.34	1.12	0.38	0.96	4.52	0.00	NA
F11c	33.04	11.08	0.53	1.82	778.14	25.25	4.52	2.21	81
F12	23.93	12.46	0.61	2.05	563.63	19.12	4.52	1.60	80
F13	13.37	10.37	0.56	1.85	315.87	14.16	4.32	0.79	66
F14	44.48	33.73	0.49	1.96	1046.94	25.93	3.57	2.63	78
F15	9.62	81.01	0.72	2.18	226.39	6.62	3.57	0.57	70
F2	12.20	5.59	0.34	2.12	229.35	4.38	1.97	0.73	71
F3	127.39	6.69	0.38	1.89	6128.36	109.91	0.93	7.53	76
F4	41.32	4.41	0.47	2.22	1986.67	29.54	0.93	2.44	82
F5	84.85	9.21	0.47	2.15	3078.54	108.50	0.50	5.01	75
F6	35.23	15.79	0.66	2.21	1440.89	50.99	0.50	2.34	77
F7	25.15	9.82	0.50	1.95	1029.92	24.86	0.50	2.96	70
F8	5.28	16.67	0.66	2.69	217.61	2.47	0.50	0.63	80
F9a	130.52	6.57	0.51	2.06	3588.42	127.73	2.83	8.68	79
F9b	80.54	5.50	0.73	2.23	2215.58	71.91	2.83	5.34	82
G1	11.79	47.80	0.56	2.10	46.35	11.64	3.52	0.29	75
G2	203.70	4.69	0.33	1.60	797.01	245.64	3.52	4.97	83

3. Chapter 2: Future scenario: salt marsh full 2055 natural capital and connectivity metrics per SMP policy unit.

SMP policy unit	Salt marsh area (ha)	Distance to nearest neighbour (m)	Contiguity index (mean)	Shape index (mean)	CO2 sequestered (tonnes per year)	Nitrogen removal (tonnes per year)	Wave attenuation (%)
D1a	29.32	8.11	0.53	1.83	2.66	0.05	82.94
D1b	16.54	38.94	0.69	2.43	11.96	0.35	58.33
D2	13.28	14.81	0.29	1.84	2.98	0.36	66.81
D3	273.24	4.74	0.54	2.10	78.83	6.96	86.05
D4	58.55	31.91	0.63	2.49	30.34	1.63	85.08
D5	298.55	17.98	0.58	1.78	45.93	4.76	83.28
D6a	58.28	5.17	0.38	1.97	226.66	4.97	82.23
D6b	32.69	NA	0.99	2.18	213.94	5.71	NA
D7	104.31	66.18	0.80	2.16	6.85	0.78	72.65
D8a	24.18	4.26	0.50	2.36	0.01	0.00	NA
D8b	628.20	8.71	0.42	1.83	0.02	0.00	NA
D8c	263.40	111.73	0.47	1.92	41.21	3.78	85.38
E1	359.23	4.96	0.27	1.70	24.99	2.21	80.05
E2	43.20	201.54	0.84	2.02	31.60	1.60	78.77
E3	14.36	13.35	0.64	2.30	3.03	0.36	82.92
E4a	71.71	5.46	0.71	2.07	6.20	0.79	83.68
E4b	84.16	9.80	0.71	2.22	38.34	2.63	83.55
F1	487.09	6.95	0.59	2.13	9.19	0.57	79.07
F10	5.78	21.88	0.54	1.84	8.66	1.40	77.22
F11b	3.03	24.94	0.46	1.39	4737.76	5.34	86.68

F11c	96.87	13.19	0.61	1.93	67.90	7.58	84.13
F12	212.00	26.35	0.72	1.88	9.39	0.29	85.54
F13	262.36	8.42	0.55	1.75	13.21	1.20	80.34
F15	60.38	188.56	0.85	2.21	17.32	2.96	82.40
F2	131.84	5.98	0.38	2.11	13.98	3.36	78.90
F3	554.04	6.75	0.50	2.03	10.70	0.73	80.45
F4	66.30	10.10	0.50	2.21	170.40	20.28	86.25
F5	629.00	9.13	0.58	1.96	163.13	7.53	86.07
F6	304.27	7.27	0.56	1.89	44.33	2.60	85.26
F7	241.71	8.87	0.54	1.89	40.79	2.44	81.29
F8	5.36	12.72	0.67	2.61	39.39	5.01	85.56
F9a	1184.85	7.11	0.56	1.84	5.21	0.63	84.59
F9b	80.57	5.54	0.72	2.23	116.97	8.68	83.18
G1	246.60	4.20	0.35	1.56	28.84	2.49	80.92

4. Chapter 3: Blackwater and Colne estuaries salt marsh connectivity metrics per SMP policy unit.

SMP policy unit	Salt marsh area (ha)	Distance to nearest neighbour (m)	Contiguity index (mean)	Shape index (mean)	Total SMP cell area (ha)
C4	177.92	6.08	0.4	2.12	550.69
D1a	29.22	7.9	0.53	1.82	199.25
D1b	16.5	30.1	0.62	2.29	35.96
D2	13.23	13.09	0.28	1.67	104.08
D3	30.57	5.23	0.49	2.57	117.09
D4	39.65	30.63	0.55	2.47	151.31
D5	44.47	10.77	0.48	2.07	299.36
D6a	12.52	5.08	0.33	1.8	53.31
D6b	3.74	4.81	0.09	1.38	41.33
D7	10.3	9.41	0.7	1.69	23.77
D8a	9.2	19.72	0.64	2.83	65.35
D8b	239	11.02	0.49	2.45	770.02
D8c	89.15	9.74	0.41	2.11	213.23
E1	38.85	5.95	0.27	1.59	316.27
E2	2	13.47	0.63	2.03	605.82
E3	14.32	20.23	0.6	2.31	244.41
E4a	27.56	11	0.54	2.22	77.1
E4b	56.05	9.3	0.62	2.07	79.24
F1	117.84	6.14	0.5	2.13	298.03
F10	5.43	38.1	0.61	2.08	34.44
F11a	0.01	17	0.23	1.15	9.66
F11b	0.01	176.83	0.34	1.12	20.21

F11c	33.04	11.08	0.53	1.82	53.53
F12	23.93	12.46	0.61	2.05	263.57
F13	13.37	10.37	0.56	1.85	276.23
F14	44.48	33.73	0.49	1.96	246.41
F15	9.62	81.01	0.72	2.18	167.31
F2	12.2	5.59	0.34	2.12	39.05
F3	127.39	6.69	0.38	1.89	751.08
F4	41.32	4.41	0.47	2.22	58.88
F5	84.85	9.21	0.47	2.15	1424.5
F6	35.23	15.79	0.66	2.21	464.78
F7	25.15	9.82	0.5	1.95	168.6
F8	5.28	16.67	0.66	2.69	18.8
F9a	130.52	6.57	0.51	2.06	473.45
F9b	80.54	5.5	0.73	2.23	265.47
G1	11.79	47.8	0.56	2.1	289.01
G2	203.7	4.69	0.33	1.6	1613.95

5. Chapter 3: Blackwater and Colne estuaries salt marsh connectivity metrics per Nutrient Zones.

Nutrient Zones	Salt marsh area (ha)	Distance to nearest neighbour (m)	Contiguity index (mean)	Shape index (mean)	Total SMP cell area (ha)
Lower Blackwater	361.17	5.37	0.38	1.71	6214.25
Lower Colne	569.98	7.14	0.38	1.8	4981.62
Mid Blackwater	248.25	6.15	0.45	1.73	2621.21
Mid Colne	21.47	7.39	0.44	1.84	220.59
Outer Estuary	383.03	7.08	0.27	1.42	13216.18
Upper Blackwater	38.43	7.24	0.35	1.68	904.64
Upper Colne	22.71	9.11	0.54	2.99	570.93

6. Chapter 3: Blackwater and Colne estuaries salt marsh connectivity metrics per Water Framework Directive Areas.

Water Framework Directive	Salt marsh area (ha)	Distance to nearest neighbour (m)	Contiguity index (mean)	Shape index (mean)	Total SMP cell area (ha)
Blackwater Outer	400.08	6.5	0.28	1.44	5238.72
Blackwater	761.15	5.62	0.39	1.71	4987.93
Colne	635.4	6.12	0.39	1.84	1522.41

7. Chapter 3: Blackwater and Colne estuaries salt marsh connectivity metrics for the whole Blackwater and Colne estuaries (landscape scale).

Scale	Salt marsh area (ha)	Distance to nearest neighbour (m)	Contiguity index (mean)	Shape index (mean)	Total SMP cell area (ha)
Landscape	1663.44	27.67	0.26	1.7	28805.02