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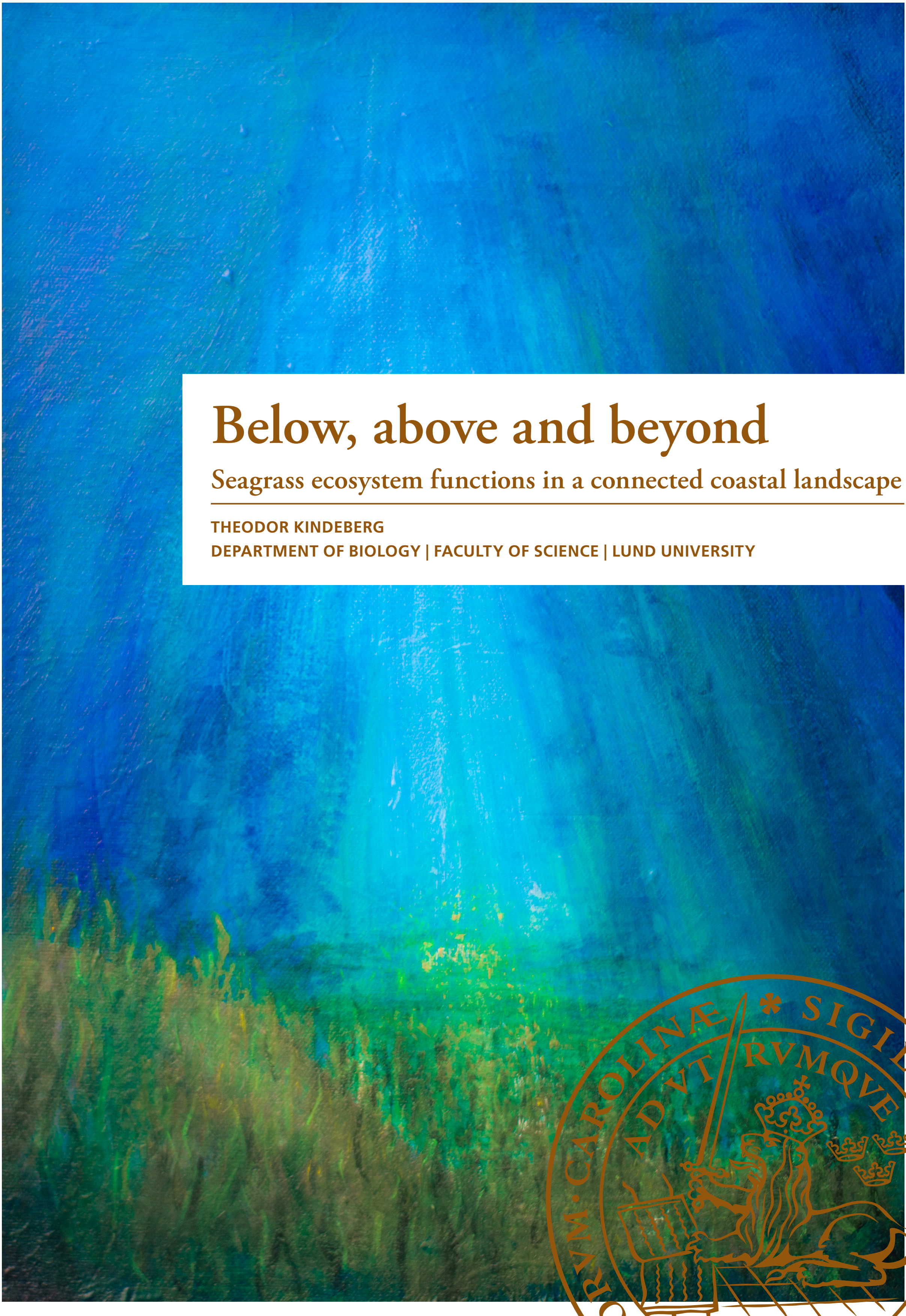

Below, above and beyond

Seagrass ecosystem functions in a connected coastal landscape

THEODOR KINDEBERG

DEPARTMENT OF BIOLOGY | FACULTY OF SCIENCE | LUND UNIVERSITY

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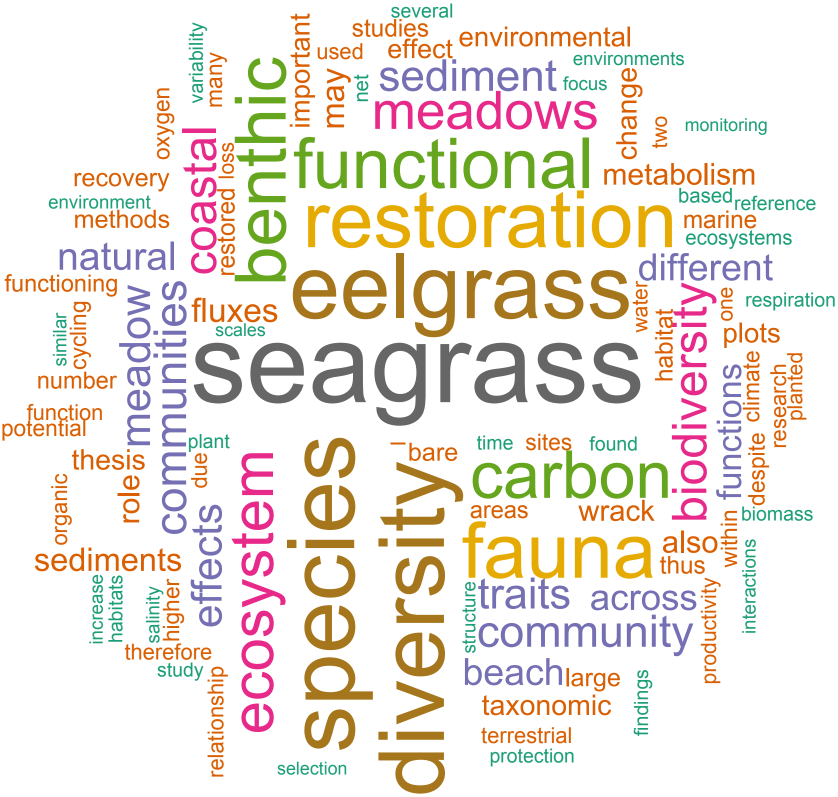

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Department of Biology

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Below, above and beyond

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Theodor Kindeberg

DOCTORAL DISSERTATION

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Title and subtitle: Below, above and beyond – seagrass ecosystem functions in a connected coastal landscape

Abstract: Seagrass meadows constitute important habitat for a plethora of organisms, rendering them important habitats for conserving biodiversity. Seagrass meadows also modify the environment by attenuating wave and current energy. As a result of this, seagrass meadows trap organic matter and in addition to their high productivity, are able to sequester carbon that is stored in their underlying sediments. Due to these ecosystem functions, seagrass meadows are proposed as potential nature-based solutions (NbS) for climate change adaptation and mitigation that concomitantly strengthens local biodiversity. However, the magnitude and relative importance of these ecosystem functions are context-dependent, and it is therefore crucial to understand how and why they differ in space and time. Moreover, it is imperative to apply a broad perspective as these functions can affect and are affected by adjacent ecosystems beyond the seagrass meadow itself.

In this thesis, I focus on eelgrass (*Zostera marina*) and its role in coastal biodiversity and carbon cycling across both natural and restored meadows as well as eelgrass exported onto land. I follow a restoration project in an exposed and a sheltered environment and leverage these field trials to try to understand the timescales of biodiversity effects following seagrass restoration. I focus on fauna diversity and investigate colonization patterns. I relate these features to ecosystem functioning by measuring community metabolism and carbon cycling across restored and natural eelgrass meadows.

My findings reveal that benthic fauna rapidly recovers following restoration and attains diversity levels comparable to natural reference meadows. Initial colonization seems to be driven by a few, opportunistic species that occur in large densities during early stages. As these species are generalists, their elevated abundance can increase the functional redundancy and resilience of fauna communities during early restoration stages.

I show that eelgrass habitat provisioning is important in both natural and restored eelgrass and across land-sea boundaries. Exported eelgrass biomass that ends up on beaches supports a high abundance of terrestrial fauna. However, vascular plant diversity may instead benefit from removal of eelgrass wrack and it is therefore important to apply a differentiated management approach to sandy beaches that considers different communities and interests.

While eelgrass restoration is unequivocally beneficial for benthic diversity, net effects on carbon fluxes vary. I found a positive relationship between benthic diversity and fluxes of dissolved inorganic carbon going out of the meadow, highlighting potential tradeoffs between biodiversity and climate change mitigation.

Collectively, the findings in this thesis contribute to a better understanding of how seagrass fauna diversity varies in space and time and what can be expected from restoring seagrass meadows. It reveals novel insights into the balance between diversity and community metabolism and shows how exported eelgrass can have dichotomous effects depending on the community of interest. This knowledge can inform coastal managers on relevant aspects to consider when implementing coastal adaptation measures and how eelgrass can be utilized below and above the waterline.

Key words: *Zostera marina*, eelgrass, carbon cycling, infauna, seagrass restoration, nature-based solution, metabolism, eddy covariance, biodiversity, functional traits, coastal adaptation, beach wrack

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“Where there is an ocean, a marine biologist is never on holiday”

- James Bond

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Summary

Seagrass meadows constitute important habitat for a plethora of organisms, rendering them important habitats for conserving biodiversity. Seagrass meadows also modify the environment by attenuating wave and current energy. As a result of this, seagrass meadows trap organic matter and in addition to their high productivity, are able to sequester carbon that is stored in their underlying sediments. Due to these ecosystem functions, seagrass meadows are proposed as potential nature-based solutions (NbS) for climate change adaptation and mitigation that concomitantly strengthens local biodiversity. However, the magnitude and relative importance of these ecosystem functions are context-dependent, and it is therefore crucial to understand how and why they differ in space and time. Moreover, it is imperative to apply a broad perspective as these functions can affect and are affected by adjacent ecosystems beyond the seagrass meadow itself.

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Populärvetenskaplig sammanfattning

Sjögräs är en blommande växt som kan bilda stora undervattensängar längs våra kuster. I sjögräsängen myllrar det ofta av liv då olika djurarter söker föda och skydd både bland bladen och nere bland rötterna i sedimentet. När det stormar rycks en del av sjögräset loss och sköljs upp på stränder där de utgör tillfällig levnadsmiljö och födokälla för en rad organismer.

Ålgräs (*Zostera marina*) är den dominerande sjögräsarten på nordliga breddgrader och även om den lokalt växer och frodas har det skett en omfattande tillbakagång det senaste århundradet. Som ett svar på denna tillbakagång har metoder för att återställa försvunna ålgräsängar utvecklats, något som sammanfattas med begreppet ålgräsrestaurering.

I min forskning visar jag att en mångfald av arter snabbt koloniserar en restaurerad ålgräsäng och att antal individer och arter i planterade ålgräsängar ofta är lika många som i naturliga referensängar. Samtidigt kan det ta längre tid för dessa djursamhällens funktionella egenskaper att etablera sig, vilket delvis beror på att de arter som först koloniserar nyplanterat ålgräs till stor del är generalister och att kolonisering av specialister dröjer längre.

Förutom att återställa viktiga levnadsmiljöer har ålgräsrestaurering de senaste åren kommit att föreslås som en möjlig så kallad naturbaserad lösning för att minska kusterosion. Anledningen till detta är bland annat att vågor förlorar kraft när de rullar över en ålgräsäng, och våghöjden minskar således innan de når stranden. Tanken är att ålgräset ska fungera som ett naturbaserat kustskydd istället för – eller kanske som ett tillägg till – konventionella lösningar som vågbrytare eller stenskoningar. Detta skulle då utgöra ett multifunktionellt kustskydd som bidrar med fler funktioner än bara kustskyddet i sig.

I mitt avhandlingsarbete har jag följt och deltagit i två olika projekt där ålgräs restaurerats med olika bakomliggande syften och i olika miljöer. Inom EU-projektet LIFE Coast Adapt har olika naturbaserade lösningar mot kusterosion testats vid exponerade sandstränder i Skåne. I det andra projektet har syftet framför allt varit att återetablera förlorat ålgräs i skyddade vikar i Bohuslän.

Liksom träd på land kan sjögräs omsätta stora mängder koldioxid, varav en del binds in och lagras i sedimentet, och har därför en roll att spela i att dämpa den globala uppvärmningen. I denna avhandling visar jag att ålgräsängar över tid ackumulerar stora lösdrivande fleråriga alger som fångas upp av ålgräset. Dessa alger ses ofta som ett hot mot ålgräs då de bland annat konkurrerar om solljus och kan röra upp sediment. Samtidigt bidrar de till att öka den strukturella komplexiteten i ängen vilket kan leda till ett totalt sett mer effektivt utnyttjande av solljus för fotosyntes. Således är äldre ålgrässamhällen med fler algarter mer effektiva att ta upp koldioxid under dagens ljusa timmar jämfört med yngre, restaurerade ängar. Det omvända gäller dock nattetid, då den högre respirationen från alger och djur kan leda till att äldre ängar är större nettoutsläppare av koldioxid i vattnet jämfört med yngre ängar eller bar botten. Detta fynd visar på att tänkbara motsatsförhållanden kan uppstå mellan å ena sidan biologisk mångfald och å andra sidan nettoupptag av koldioxid.

När det blåser mycket kan ålgräs och tång (s.k. makroalger) transporteras ända upp på land, något de flesta som besökt en badstrand säkert känner igen. Utöver att konkurrera om plats med badhandduken visar jag att denna struktur fyller en viktig funktion som levnadsmiljö för ryggradslösa djur på stranden. Dessa är i sin tur viktiga födokällor för bland annat vadarfåglar. Tvärtemot vad tidigare forskning visat har jag uppmätt avsevärt högre individantal och artrikedom av dessa djur i uppspolat ålgräs jämfört med makroalger. Detta trots att makroalger är betydligt mer näringsrika och lättsmälta än ålgräs. I förlängningen innebär detta att ålgräsrestaurering kan ha positiva effekter på biologisk mångfald bortom själva restaureringsplatsen och visar på vikten av att ha ett brett perspektiv när dylika åtgärder införs i kustzonen.

Den hittills begränsade forskningen om ålgräsrestaurering som kustskydd, tyder på att det sannolikt inte fungerar som ett effektivt skydd i de områden längs Skånes kust där kusterosion är ett problem. Detta beror till viss del på att ålgräs på dessa platser endast kan växa på så pass djupt vatten att dess vågdämpande effekt blir förhållandevis liten. På våra nordliga breddgrader släpper ålgräs dessutom mycket av sin biomassa på höst och vinter (tänk ålgräset på stranden) vilket gör att den vågdämpande effekten blir som minst när den behövs som mest, det vill säga när höst- och vinterstormarna drar in. För att skydda kusten mot erosion finns andra naturbaserade kustskydd, exempelvis strandfodring som innebär att man tillför stora mängder sand till stranden. Det kan finnas möjligheter att kombinera ålgräsplantering med strandfodring för att uppnå positiva effekter på både kustskydd och biologisk mångfald.

Sammantaget kan fynden i denna avhandling bidra till att bättre utforma uppföljningar av ålgräsrestaurering samt ge en djupare förståelse för samspelet mellan biologisk mångfald och produktivitet i både naturliga och restaurerade ålgräsängar.

List of Papers

This thesis is submitted with the support of the following papers, which are referred to by their numerals in the body of text:

I. Kindeberg, T., Severinson, J., Carlsson, P. (2022) Eelgrass meadows harbor more macrofaunal species but bare sediments can be as functionally diverse. Journal of Experimental Marine Biology and Ecology 554, 151777

II. Kindeberg, T., Attard, K. M., Hüller, J., Müller, J., Quintana, C. O., Infantes, E. (2023) Structural complexity and benthic metabolism: resolving the links between carbon cycling and biodiversity in restored seagrass meadows. *Manuscript submitted to Biogeosciences*

III. Kindeberg, T., Carlsson, P., Hollander, J. (2024). Benthic fauna recovery dynamics following large-scale seagrass restoration in an exposed environment. *Manuscript*

IV. Kindeberg, T., Hollander, J., Olsson, PA. (2024). Mixed effects of beach wrack removal on flora and fauna across the land-sea interface – with positive effects of eelgrass. *Manuscript submitted to Ecosystems*

V. Kindeberg, T., Almström, B., Skoog, M., Olsson, PA., Hollander, J. (2023) Toward a multifunctional nature-based coastal defense: a review of the interaction between beach nourishment and ecological restoration. Nordic Journal of Botany 2023(1), e03751

Author's contribution to the papers

Paper I

TK conceived and designed the study with input from PC. TK and JS conducted the field work and analyzed samples. TK and JS analyzed data and TK wrote the first draft of the manuscript. All authors commented on and approved the final version of the manuscript.

Paper II

TK conceived the study with input from KMA, COQ and EI. TK, KMA, CQ and EI designed the field study. TK, KMA, JHü, JM and EI conducted field work. TK and KMA analyzed data. TK wrote the first draft of the manuscript. All authors commented on and approved the final version of the manuscript.

Paper III

TK, PC, JH conceptualized the study. TK designed the field study with input from JH and PC. TK and PC carried out field work. TK performed laboratory and data analyses. TK wrote the manuscript. All authors contributed to revision of the manuscript and approved the final version.

Paper IV

TK, JH, and PAO conceptualized the study. TK designed the field study with input from PAO and JH. TK carried out field work and performed all laboratory and data analyses. TK drafted the manuscript with input from JH and PAO. All authors contributed to revision of the manuscript and approved the final version.

Paper V

JH, PAO and TK conceived the study. TK performed the literature review. TK wrote the first draft with input from BA, MS and PAO. All authors contributed to revision and approved the final version.

Authors: Theodor Kindeberg (TK), Björn Almström (BA), Cintia O. Quintana (COQ), Eduardo Infantes (EI), Jana Hüller (JHü), Julia Müller (JM), Johan Hollander (JH), Johan Severinson (JS), Karl M. Attard (KMA), Mona Skoog (MS), Per Carlsson (PC), Pål Axel Olsson (PAO).

Abbreviations

AFDW	Ash-free dry weight
BC	Benthic chamber
BEF	Biodiversity – ecosystem functioning
CR	Community respiration
DCA	Detrended correspondence analysis
DIC	Dissolved inorganic carbon
DOC	Dissolved organic carbon
DW	Dry weight
EC	Eddy covariance
FD_{eff}	Effective functional diversity
GPP	Gross primary productivity
H_{eff}	Effective taxonomic diversity
LOI	Loss on ignition
LUE	Light-use efficiency
NbS	Nature-based solution
NCP	Net community productivity
NMDS	Non-metric multidimensional scaling
OM	Organic matter
PAR	Photosynthetic active radiation
PCA	Principal components analysis
PIC	Particulate inorganic carbon
POC	Particulate organic carbon
RDA	Redundancy analysis
ROL	Radial oxygen release
TA	Total alkalinity
TC	Total carbon
TN	Total nitrogen
Tris	2-amino-2-hydroxymethyl-1,3-propanediol

Introduction

Setting the stage

The impending climate crisis and rapid biodiversity loss have tangible effects across all levels of society and biological organization (UNFCCC 2015; CBD 2020). The coastal zone faces a multitude of anthropogenic stressors that threaten ecosystems and local communities (Cardinale et al. 2012). The coastal zone is not only a disproportionally biologically active zone, but also home for about 60% of the global population (Vitousek et al. 1997), of which an estimated 680 million people live in low-lying coastal areas directly affected by sea-level rise (IPCC 2019). On land, sea-level rise and a resulting 'coastal squeeze' has ramifications for habitats and species, as well as for highly valuable ecosystem services such as flood protection and recreation (Schlacher et al. 2007; Chávez et al. 2021). In the marine realm, ecosystems are threatened by an additional set of stressors related to global (e.g. increasing seawater temperature and decreasing pH), regional (e.g. eutrophication, overfishing) and local (e.g. land-use changes and exploitation) change (Worm et al. 2006; IPCC 2019). Many of these stressors may interact synergistically and thus exacerbate ecological consequences (Hewitt et al. 2016).

Conservation and restoration efforts are therefore initiated to alleviate these threats and stimulate the recovery of degraded ecosystems (Aronson et al. 2006; Hobbs et al. 2011). The United Nations has declared the years 2021-2030 the 'United Nations Decade on Ecosystem Restoration' and the 'Decade of Ocean Science for Sustainable Development' (UNESCO 2018; United Nations 2019). Moreover, there is an increased awareness about 'coastal resilience' and several so-called nature-based solutions (NbS) are being implemented in coastal communities worldwide (Sutton-Grier et al. 2015; Waryszak et al. 2021).

One proposed NbS is establishing a marine macrophyte, seagrass, on shallow bottoms. Seagrasses can form dense meadows with potential to reduce wave energy and limit coastal erosion in local areas (Paul 2018). Additionally, seagrass meadows can efficiently sequester atmospheric carbon dioxide and thus constitute important carbon sinks (Duarte et al. 2010; Fourqurean et al. 2012). Perhaps most significantly, however, is the fact that they constitute habitat for a wide range of organisms and often comprise high diversity of flora and fauna (Duffy 2006). Thus, conserving and replanting seagrass meadows could ideally be used as a tool both for climate change mitigation and adaptation while at the same time counteracting biodiversity loss (Duarte et al. 2013a; Unsworth et al. 2022).

This new type of use occurs against a backdrop of massive historic and ongoing losses of seagrass, and efforts to restore these habitats and the ecosystem functions and services they sustain have been carried out for decades (Orth et al. 2006; Waycott et al. 2009). However, despite the fact that restoration methods are constantly improving, it is still very difficult to plant under water and most attempts fail (Fonseca et al. 1998; van Katwijk et al. 2016). Nevertheless, there are several examples for success where degraded ecosystems have been converted back to dense meadows, and ecosystem services returned (e.g. Orth et al. 2020). Inarguably, transforming the benthic environment this way profoundly alters the ecosystem structure and ostensibly its function, but many open questions remain.

Several NbS, including seagrass restoration, are implemented and evaluated in the regional EU-funded project LIFE Coast Adapt (Region Skåne 2023), around which this thesis centers many of its research questions. Throughout this work, I use a multidisciplinary approach to try to understand the effect seagrass restoration has on ecosystem structure and function. I focus on benthic fauna communities within seagrass meadows, and how traditional taxonomic diversity descriptors relate to ecosystem functioning and resilience. I investigate the cycling of carbon in restored seagrass and relate diversity to function across stages of seagrass development. Finally, I explore whether seagrass influences biodiversity beyond the meadow itself, through an ecological and management perspective on coastal land ecosystems.

I will begin this introduction with a theoretical background of the concepts and research topics relevant for the thesis. I will then discuss the current state of knowledge and the scientific rationale behind my research before moving into specifying the aims and overall scope of this thesis.

The seagrass ecosystem

Seagrasses are pervasive marine macrophytes growing on shallow soft bottoms in all continents except Antarctica. They are flowering plants – angiosperms – that are able to reproduce both sexually, with flowers and seeds, and asexually, through lateral rhizome extension. Seagrasses are referred to as 'coastal canaries' due to their sensitivity and rapid response to environmental perturbations such as pollution and deteriorating light climate (Orth et al. 2006). For the same reason, seagrasses are listed as bioindicators for water clarity and eutrophication under the European Water Framework Directive (WFD: 2000/60/EC) and Marine Strategy Framework Directive (MSFD: 2008/56/EC), respectively (Krause-Jensen et al. 2005).

There are more than 70 species described to date, which belong to four families and 13 genera. Estimates of their global distribution have ranged between 177 000 and 600 000 km^2 (Waycott et al. 2009), with the latest high-confidence estimate being 160 000 km^2 (McKenzie et al. 2020). For comparison, the estimated area where seagrasses *could* occur based on light availability and their light requirements is about 26 times larger, or 4.3 million km^2 (Gattuso et al. 2006). One of the most widely distributed seagrass species is eelgrass (*Zostera marina*). Eelgrass is found across the entire Northern hemisphere where it forms meadows on low to moderately exposed shallow soft bottoms. Since eelgrass is the dominating species in Sweden and the focus of my thesis work, this introduction will henceforth primarily focus on this species.

Biodiversity of the seagrass habitat

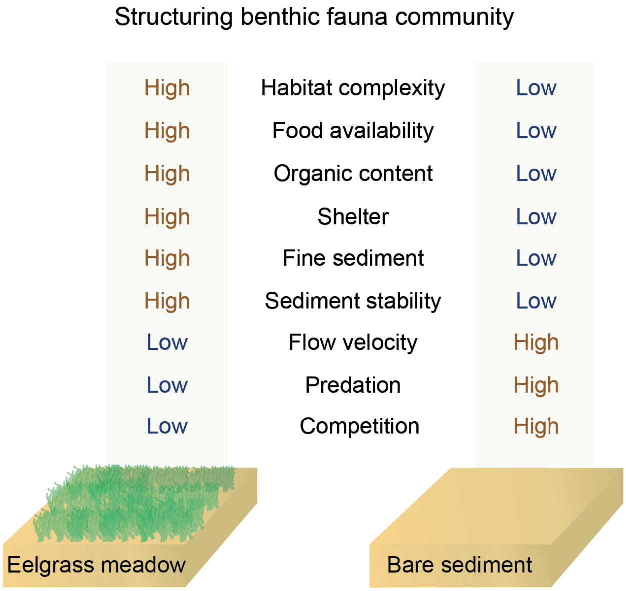
As habitat-forming plants, seagrasses can create vast meadows transforming otherwise apparently feature-less bare sediments into complex environments. Perhaps most notably, seagrasses act as an ecosystem engineer that alters its surrounding environment by affecting hydrodynamic energy, modifying sediment properties and providing a three-dimensional structure that constitutes shelter, nursing ground, feeding ground, spawning ground, substrate and food for other species (Polte and Asmus 2006; Gilby et al. 2018).

Benthic fauna

The seagrass habitat comprises organisms across all trophic levels. A large part consists of benthic macroinvertebrates (Duffy 2006), here referred to as 'benthic fauna'. Benthic fauna communities in seagrass meadows include taxa such as polychaetes, mollusks, crustaceans and echinoderms, and comprise both sessile and mobile species, ranging from bryozoans and barnacles to fast-swimming mysids and burrowing bivalves.

Despite the evidence of seagrass meadows as hotspots of benthic diversity, less is known regarding what properties of the meadow, or other abiotic factors of the environment, that are central in structuring benthic fauna communities. There is evidence of both features and configuration of the seagrass meadow itself (Eggleston et al. 1998; Webster et al. 1998; Mattila et al. 1999; Lee et al. 2001) and abiotic factors such as sediment properties or hydrodynamic setting (Frost et al. 1999; Turner et al. 1999; Bowden et al. 2001; Boström et al. 2006). Although benthic fauna communities are most likely structured by a combination of biotic and abiotic factors (Figure 1), the relative importance of these drivers is largely unknown. It is, however, important information for predicting restoration effects, especially in the light of climate change and marine biodiversity loss. For example, the effect of warming can lead to reduction or loss of certain species, which in turn alters interspecific interactions within and between meadows with consequences for the whole community structure and function (Whippo et al. 2018). Moreover, seagrass meadows and their associated fauna communities are heterogeneous and fauna diversity can vary over small spatial scales. Understanding what is driving this heterogeneity is key for predicting consequences of structural change on ecosystem functioning. Such knowledge is also important for informing coastal management interventions such as restoration, which relies on strategically selecting areas where both effective recolonization, improved ecosystem functioning and resilience can be attained. Indeed, knowledge on abiotic and biotic interactions in seagrass biodiversity is integral in the context of successful restoration (van Katwijk et al. 2009; van der Heide et al. 2011; Bekkby et al. 2020; Meysick et al. 2020), as recently illustrated by the finding that *a priori* characterization of benthic fauna diversity can be a useful tool for restoration site selection (Gräfnings et al. 2023).

Furthermore, fauna diversity and colonization patterns are known to vary across several temporal scales ranging from annual to diel timescales (Greening and Livingston 1982; Edgar 1992; Gagnon et al. 2023; García-Trasviña et al. 2023). Unless characterized and accounted for, this natural variability can confound assessments of restoration outcomes with respect to the recovery of biodiversity. Moreover, because of this temporal component in community dynamics, it is imperative to consider the timing and frequency of sampling when designing monitoring programs following restoration.


Structuring benthic fauna community

High	Habitat complexity	Low
High	Food availability	Low
High	Organic content	Low
High	Shelter	Low
High	Fine sediment	Low
High	Sediment stability	Low
Low	Flow velocity	High
Low	Predation	High
Low	Competition	High

Figure 1 Schematic illustration of abiotic and biotic factors structuring benthic fauna communities in eelgrass and bare sediments. Based on generalized model by Boström and Bonsdorff (1997).

The functional aspect of diversity

The term ‘function’, or any derivatives of the word such as ‘functional’ or ‘functioning’, is an ambiguous concept and its definition and use has been widely debated in the scientific literature (see e.g. Jax 2005; Dawson et al. 2021). Put frankly, it concerns what something *does* rather than what it *is*. To avoid confusion, I have clarified the interpretations I use herein and summarized in Table 1. Unless otherwise stated, I discuss ‘function’ in the context of ecosystem functions sustained by communities as opposed to the function of, or performance by, an individual organism. For instance, measuring the oxygen fluxes going in and out of an eelgrass meadow integrates the contribution of all the individual organisms within that eelgrass meadow that contribute to the uptake or release of oxygen.

Table 1 Definition of terms of functional ecology. Many of these terms are ambiguous and used interchangably throughout the literature. I here define the way I use them together with the literature those interpretations are based on. An example of each term from the seagrass ecosystem is provided.

TERM	DEFINITION	EXAMPLE
Biological trait	Any measureble morphological, physiological, phenological, behavioral or life history feature of an organism[a]	Body weight of a herbivorous mud snail
Functional trait	Any biological trait that strongly influences the performance of the organism or its ecosystem[b]	Bioturbation mode by infaunal annelids, affecting oxygen fluxes across the sediment-water interface
Functional diversity	The number, type and distribution of functional traits within a community. Ultimately the diversity of functions performed by organisms within an ecosystem[c,d]	The relative abundance of fauna species with different functional traits
Functional redundancy	When multiple species in a system perform the same function, e.g. 'insurance effect'. Based on the relationship between taxonomic and functional diversity[e,f,g]	Multiple species of burrow-dwelling polychaetes with the same bioturbation mode occupying the same niche
Ecosystem function	Process that maintains and determines an ecosystem[h]	Primary productivity by seagrass leaves and associated epiphytes
Ecosystem functioning	Descriptive term often relating to the sum of ecosystem functions sustaining the system[i,j]	Net community productivity = balance between gross primary productivity and total respiration
Ecosystem service	An ecosystem function rendering goods or services to humans[k]	CO_2 sequestration due to positive net ecosystem productivity and subsequent burial of organic carbon in seagrass meadows

[a]McGill et al. (2006) [b]Violle et al. (2007); [c]Díaz and Cabido (2001) [d]Petchey and Gaston (2006) [e]Walker (1992) [f]Naeem and Li (1997) [g]Micheli and Halpern (2005) [h]Walker (1995) [i]Hooper et al. (2005) [j]Jax (2005) [k]Costanza (2008)

Functional traits can describe the organisms' feeding strategy, the way they reproduce, move or their morphology and functional traits can thus serve as a link between ecosystem composition and ecosystem function. A functional trait perspective also provides insight into disturbance-recovery dynamics and reveal information of a community's resilience to stress. An integral component of biodiversity is the diversity of functional traits, hereafter "functional diversity" (Table 1). Functional diversity has gained increasing attention during the last decades both in the context of quantifying ecosystem functions and services and to better predict ecosystem-level responses to environmental disturbance (Díaz and Cabido 2001). Ultimately, the number and diversity of functional traits in a community can be used as a proxy for ecosystem functions (Braeckman et al. 2010; Kristensen et al. 2014) and provide insight into how the community interacts with its ecosystem (Petchey and Gaston 2006).

Functional redundancy as a measure of resilience

Knowledge of what traits are present in a community can assist in predictions of future environmental change as it is often one or more traits of a species that is sensitive to change rather than the species itself. In this context of resilience, 'functional redundancy' (Table 1) and changes thereof can be useful in identifying sensitive systems that warrant action to conserve or protect.

The concept of functional redundancy is coupled to the relationship between taxonomic and functional diversity (Ricotta et al. 2016). A strong positive relationship between the two suggests that the diversity of functional traits is sensitive to species loss and is thereby less functionally redundant (Micheli and Halpern 2005). It is thus a measure that may be useful as an early warning sign of environmental degradation since functional diversity, and possibly ecosystem function, will rapidly decrease when species are lost (Naeem and Li 1997; Micheli and Halpern 2005). Intuitively, more species should render a larger number of functional traits. However, since different species can exhibit similar functional traits, the relationship between the two is rarely 1:1 and may be nonlinear. A schematic model of potential scenarios proposed by Micheli and Halpern (2005) is shown in Figure 2.

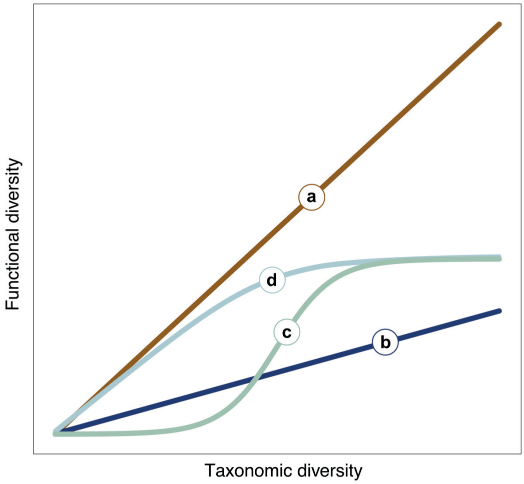


Figure 2 Schematic model of different relationships between taxonomic (i.e. species) diversity and functional diversity. A slope of 1 (a) implies that each species in a community exhibits a unique set of functional traits, but a linear slope lower than 1 (b) means that several species share similar traits. Line (c) illustrates a scenario where functional diversity quickly increases at intermediate species diversity until reaching a plateau at high species diversity. Line (d) shows a scenario in which the rate of increase in functional diversity is slower with increased species diversity and reaches an asymptote. Figure modified from Micheli and Halpern (2005).

A linear relationship with a slope of 1 implies that each species in a community exhibits a unique set of functional traits (Figure 2, line a), which is highly unlikely in nature. A slope lower than 1, however, is more probable as this means that several species share similar traits (Figure 2, line b). If new species enter a community with few species, functional diversity can rapidly increase if the new species exhibits traits that are not already present in the community (Figure 2, line c). Contrarily, if a disturbance removes the majority of species and only a few species sharing a small number of functional traits persist, then the arrival of new species with unique traits will rapidly increase the slope which reaches an asymptote (Figure 2, line d) (Petchey and Gaston 2002; Micheli and Halpern 2005). When assessing these relationships, it is important to keep in mind that the probability of including functionally distinct species – and thus increase the functional diversity – increases with the number of species, through the 'sampling effect' (Huston 1997). However, whether this is to be considered an artefact or inherent feature has been heavily debated (Hooper et al. 2005; Cardinale et al. 2006).

In the context of seagrass conservation and restoration, quantifying taxonomic and functional diversity concomitantly is both valuable to gain insight into ecosystem functioning but also to identify key species and vulnerable seagrass systems (Henseler et al. 2019). Importantly, however, the relationship between taxonomic and functional diversity is sensitive to the number of traits included. It is therefore important to carefully consider the traits included and limit the number of general, descriptive traits to those that are relevant for the functions or drivers of interest (Naeem and Wright 2003).

The link between structure and function

Biodiversity-ecosystem functioning (BEF) is an active research field that ultimately aims to disentangle the role of species diversity in the functions sustained by an ecosystem (Naeem et al. 2009). The structural characteristics (e.g. species diversity) of an ecosystem determine what functional traits are present and together with the environmental setting govern ecosystem functions (Figure 3). These functions in turn sustain ecosystem services, although these are extrinsically determined based on societal needs and depend on what is beneficial for human well-being (Lamarque et al. 2011).

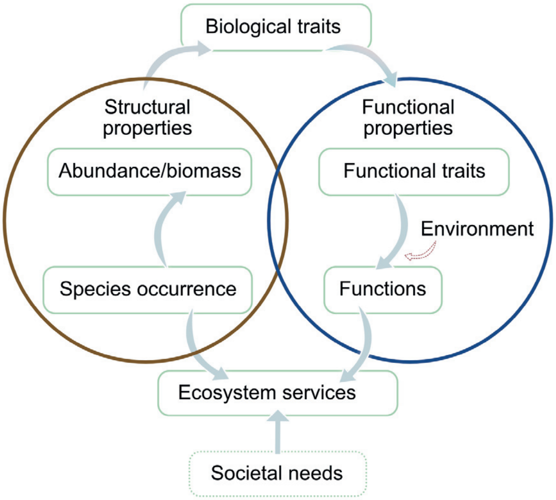


Figure 3 Conceptual diagram illustrating the links between ecosystem structure, function and services.

There is a broad scientific consensus that biodiversity positively affects ecosystem functions such as productivity and nutrient cycling (Cardinale et al. 2012; Tilman et al. 2014; Gamfeldt et al. 2015; Lefcheck et al. 2015) and the seagrass ecosystem is no exception (Duffy 2006). The theoretical underpinning is based on two ecological mechanisms referred to as the ‘selection effect’ and the ‘complementarity effect’ (Loreau and Hector 2001). The selection effect refers to that communities comprising higher diversity has a higher probability of containing highly productive and efficient species and the community thereby outcompetes communities with lower diversity, thus increasing ecosystem functioning. As such, species with a certain set of traits can have a disproportionately high influence on ecosystem functioning, and selection for these traits will lead to dominance by species exhibiting those traits (Loreau 2000). The complementarity effect suggests that complementary functional traits may occur in more diverse communities whereby resource use is more efficiently partitioned among species due to released competition, thereby enhancing collective performance and thus ecosystem functioning (Loreau and Hector 2001; Hooper et al. 2005).

The theoretical basis notwithstanding, there is insufficient knowledge regarding what biotic and abiotic factors affect the BEF relationship and how it varies on different spatial and temporal scales (Cardinale et al. 2000; Alsterberg et al. 2017; Ruesink et al. 2017; Hagan et al. 2021). Yet, studies that have managed to separate the role of environmental factors substantiate the positive effects of biodiversity on ecosystem productivity (Duffy et al. 2017 and references therein).

Observational and experimental field studies concomitantly measuring biodiversity and ecosystem functions in eelgrass meadows have supported the general BEF relationships (e.g. Gustafsson and Boström 2011; Ruesink et al. 2017; Gammal et al. 2022), but relationships are often governed by environmental setting and influential species or traits (Norkko et al. 2013; Gammal et al. 2018; Gammal et al. 2022; Mäkelin et al. 2024). Rodil et al. (2022) explored the *in situ* relationship between benthic fauna diversity and ecosystem productivity in the Baltic sea. The authors found a positive exponential relationship between benthic fauna diversity and ecosystem secondary production in eelgrass meadows, indicating both complementarity and selection effects. Notably, the benthic fauna community was estimated to contribute almost 40% of the total community respiration (Rodil et al. 2022). Indeed, complementarity and selection effects can operate in parallel to modulate ecosystem functioning (Mouillot et al. 2011; Wong and Dowd 2021).

However, while there is ample evidence of the correlation between taxonomic diversity and ecosystem functioning, it is important to note that correlation does not equate causation and the relationship is often bi-directional (Emmerson and Huxham 2002; Naeem 2002). Generally, it is difficult to infer causality of BEF because resource availability ultimately affects both productivity and species richness concomitantly. When resources increase in abundance (e.g. light, nutrients), carrying capacity increases and the system can hold more species. Therefore, experimental manipulations are often required where available resources (i.e. abiotic conditions) can be held constant while taxonomic diversity is manipulated. Nevertheless, field studies in natural environments across spatiotemporal scales are necessary to test hypotheses from experiments (Gamfeldt et al. 2015) and to incorporate realistic species interactions and environmental complexity. Measuring *in situ* community metabolism of whole communities offers useful insight into the functioning of seagrass ecosystems and can provide quantitative measures of carbon cycling (Duarte et al. 2010).

Seagrass ecosystem functions for climate change mitigation and adaptation

The ecosystem functions sustained by seagrass meadows have gained substantial attention in the last decades, largely due to the highly valued ecosystem services they underpin (Ruiz-Frau et al. 2017). Besides their central role in supporting biodiversity, the substantial influence on coastal carbon cycling together with potential effects on coastal protection have rendered seagrass meadows potentially important players in both climate change mitigation and adaptation. A selection of seagrass ecosystem functions relevant for biodiversity provisioning, climate change mitigation and adaptation are illustrated in Figure 4.

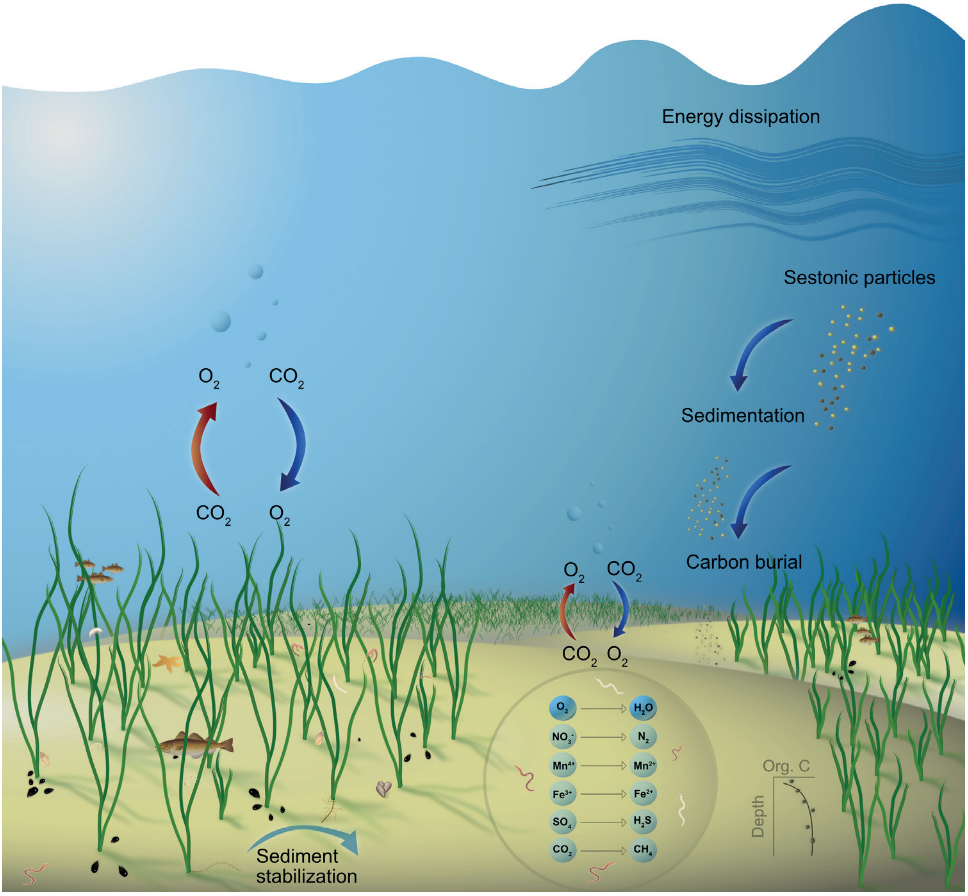


Figure 4 Illustration of various structures and functions in a seagrass ecosystem. The left hand side of the figure illustrates benthic communities inhabiting a meadow, fluxes of O_2 and CO_2 from the whole meadow (large arrows) and across the sediment-water interface (smaller arrows). The circle in the sediment shows sediment redox processes that influence fluxes. On the right hand side, the process of particle trapping through dissipation of wave and current energy is illustrated, and a typical sediment depth profile of organic carbon is depicted with an example profile from **Paper II**. Fauna symbols courtesy of University of Maryland (https://ian.umces.edu).

Carbon cycling

The shallow coastal ocean plays a disproportionately large role in marine carbon cycling considering it only covers about 7% of the ocean floor (Gattuso et al. 1998). This is largely due to high rates of primary productivity by marine angiosperms such as seagrass meadows which, despite only covering about 0.04% of the seafloor, contribute roughly 4% to total marine primary productivity (Duarte and Cebrian 1996; Gattuso et al. 1998; McKenzie et al. 2020). The estimated net primary productivity of seagrass meadows range between 0.06-1.94 Pg C yr^{-1} on a global scale, with large variation between species and areas (Duarte 2017).

A seagrass meadow is comprised of a myriad of autotrophic and heterotrophic primary and secondary producers, all contributing to benthic metabolism and playing a role in seagrass community carbon cycling. High rates of photosynthesis and respiration are carried out not only by the seagrass itself, but also by macro- and microalgae growing on the seagrass leaves and sediment surface. Benthic fauna ingest, process and respire carbon and can stimulate remineralization of sediment organic carbon both directly and indirectly through bioturbation (Lohrer et al. 2004; Snelgrove et al. 2018). The integrated metabolism by all these components can be assessed through benthic community metabolism which is comprised of gross primary productivity (GPP) and community respiration (CR), which is the sum of all autotrophic and heterotrophic respiration. The balance between GPP and CR provides the net community productivity (NCP = GPP – |CR|) of the community, where brackets around CR implies the absolute value. The magnitude and direction of GPP, CR and NCP determine all subsequent carbon flows and are thus integral components of the role of seagrass meadows in coastal carbon cycling (Duarte and Krause-Jensen 2017). For instance, a positive NCP implies that the organic carbon synthesized within the seagrass meadow is in excess, relative to the ecosystem requirements. This excess carbon can either be buried in the underlying sediments or exported out of the system where it can fuel secondary production by fauna, be remineralized by microorganisms or become buried in sediments elsewhere (Duarte and Cebrian 1996). By contrast, a negative NCP implies that that the community is respiring more than it is producing and relies on allochthonous or stored sources of organic matter to maintain metabolism. Although a seagrass meadow can shift between positive (net autotrophy) and negative (net heterotrophy) NCP on a daily and seasonal basis, reviews collating seagrass NCP globally report they are most often net autotrophic (positive NCP) on annual timescales (Duarte et al. 2010; Ward et al. 2022).

The fraction of carbon fixed through NCP that is buried in seagrass sediments can be stored for millennia due to its often refractory nature together with anoxic conditions and slow decomposition rates in the sediment. As the meadow traps more sediment over time, the carbon can become effectually buried and withdrawn from the ocean-atmosphere carbon pool (Figure 4). Albeit slow, this has been shown to be an important sequestration pathway for atmospheric CO_2 and has rendered seagrass meadows important players in the oceanic carbon sink, known as *Blue carbon* (Nellemann et al. 2009; Fourqurean et al. 2012). An additional pathway of CO_2 sequestration is the import of organic carbon from other ecosystems (including terrestrial) by particle trapping and subsequent burial (Figure 4; Oreska et al. 2017). This allochthonous carbon can sometimes supersede the autochthonous carbon in seagrass carbon stocks (Kennedy et al. 2010). For example, a recent study by Dahl et al. (2023) reported a high proportion of macroalgal sources comprising between 41-64% of the organic carbon stored in Swedish eelgrass sediments.

The seagrass and its associated fauna mediate biogeochemical processes in the sediment and contribute to solute fluxes across the sediment-water interface. Seagrass roots have been shown to release oxygen during times of photosynthesis, known as radial oxygen loss (ROL; Jensen et al. 2005; Borum et al. 2007), which creates oxic microenvironments in the sediment protecting the roots from phytotoxic sulfide (Brodersen et al. 2015). As a result, aerobic remineralization can occur which can fuel inorganic carbon fluxes out of the sediment (Burdige et al. 2008). In addition to their own metabolic processes, consuming organic particles and respiring inorganic carbon, burrowing fauna also modulates carbon fluxes in and out of the sediment indirectly through bioturbation. Bioturbation includes the ventilation, irrigation and mixing of the sediment for foraging, maintaining burrows or oxygenating otherwise anoxic sediments (Kristensen et al. 2012). Bioturbation activity can therefore have a substantial effect on oxygen and carbon fluxes between the sediment and overlying water column (Glud 2008; Braeckman et al. 2010; Kristensen et al. 2012; Kristensen et al. 2014) with ramifications for GPP, CR and thus NCP. In fact, bioturbating fauna can stimulate significant losses of seagrass carbon stocks (Thomson et al. 2019) and is a largely underappreciated component of seagrass carbon cycling (Rodil et al. 2022). However, the rates and magnitudes of bioturbation are both species-specific and density-dependent (Kristensen et al. 2011) as well as context-dependent (Braeckman et al. 2010; Needham et al. 2011). Therefore, it is important to characterize benthic fauna communities when assessing benthic carbon cycling, especially in relation to ROL in seagrass meadows.

Hydrodynamic interactions

In addition to mediating carbon fluxes in the coastal ocean, a seagrass meadow has a mechanical influence on local hydrodynamics (Figure 4). Through their canopy structure, seagrass meadows increase the height of the benthic boundary layer and increase the bottom roughness which induces a drag on wave and current energy (Fonseca et al. 1982b; Fonseca and Cahalan 1992). This leads to dissipated energy and thus attenuation of waves and currents (Fonseca et al. 1982a; De Boer 2007; Infantes et al. 2012) which could contribute to coastal protection (Ondiviela et al. 2014; Paul 2018). Furthermore, the energy attenuating effect of the canopy leads to an increased particle deposition and decreased sediment resuspension (Potouroglou et al. 2017). In combination with the seagrass rhizomes and roots that stabilize the sediment, this further reduces resuspension (Figure 4; De Boer 2007; Hansen and Reidenbach 2012) and may counteract localized seabed erosion (Infantes et al. 2022). Through these mechanisms combined, seagrass meadows can facilitate seabed elevation locally (Potouroglou et al. 2017; Paul 2018) but if the effects extend to alleviating – or even exacerbating – coastal erosion in temperate environments remains to be established.

Partly because of these above functions, seagrass restoration is proposed as a NbS that can contribute to both climate change mitigation through its carbon sink function and to climate change adaptation through its wave attenuation function while simultaneously promoting biodiversity (Duarte et al. 2013a; Duarte et al. 2013b; Paul 2018; Duarte et al. 2020; Unsworth et al. 2022).

Seagrass restoration

Seagrass loss and incentives for restoration

Seagrass meadows are globally threatened and suffer ongoing losses, although there are promising examples of trend reversal (Tomasko et al. 2018; de los Santos et al. 2019). Eelgrass suffered substantial mass mortalities in Europe and North America in the 1930's, due to an outbreak of a slime mold (*Labyrinthula zosterae*) termed the 'eelgrass wasting disease' (Muehlstein et al. 1991). As a response to these losses, efforts to restore the species commenced in the 1940's, pioneered by Addy (1947). Following major additional losses during the second half of the century, due primarily to eutrophication and overfishing, the field propelled with methodological development and large-scale restoration projects (Phillips 1960; Fonseca et al. 1998; Fonseca 2011). Further research and even more and larger trials have since been carried out during the past two decades (e.g. Leschen et al. 2010; McGlathery et al. 2012; Orth et al. 2020; Tan et al. 2020; Ward and Beheshti 2023) resulting in restoration guidelines for different areas (e.g. van Katwijk et al. 2009; Gamble et al. 2021; Moksnes et al. 2021a). A guideline developed for Sweden was first published in 2016, and included lessons learned from previous projects together with extensive restoration trials carried out on the northwest coast of Sweden (Moksnes et al. 2016). However, eelgrass grows mainly in sheltered environments on fine sediments in this archipelagic area. The recommended restoration methods may thus not be fully transferrable to exposed, higher-energy areas such as in Southern Sweden, which are often characterized by coarser sediments and different hydrodynamic, light and salinity regimes. Despite its challenges (Van Katwijk and Hermus 2000; Paling et al. 2003), seagrass has been planted in high-energy environments, for example in Australia (Wear et al. 2010), Portugal (Paulo et al. 2019), United Kingdom (Unsworth et al. 2019) and Tanzania (Wegoro et al. 2022), with varying methodologies and results illustrating how restoration success is context-dependent and highly site-specific (van Katwijk et al. 2016). Therefore, the experience obtained from projects elsewhere is not always applicable to other locations.

However, a number of generalizable keys to success have emerged as the field has developed. Before starting a restoration at any given location, it is critical to know that seagrass has existed (i.e. it can grow there), the cause of disappearance (e.g. deteriorated water quality), and finally it is imperative to know that the cause no longer exists (e.g. water quality has improved). While the most applicable method to use is best evaluated through small-scale test planting, studies have identified a few general assumptions. For instance, bigger is better, meaning that the restoration plot(s) need to be sufficiently large scale to facilitate self-reinforcing mechanisms and/or over a sufficiently large area to spread risks (van der Heide et al. 2007; van Katwijk et al. 2016), although contrasting findings exist (Matheson et al. 2022; Mourato et al. 2023). Further, the potential for success may benefit from incorporating known biotic and abiotic interactions in the restoration methodology. For instance, utilizing facilitative interactions between seagrass and bivalves show promising results (Meysick et al. 2020; Gagnon et al. 2021) and the successful use of artificial structures to temporarily stabilize sediments and increase transplant survival can be the key to success in exposed environments (Temmink et al. 2020).

Using seagrass restoration as a nature-based solution

While the habitat restoration described above is characterized by a long tradition of methodological development, using it as a NbS to obtain an ecosystem service (e.g. coastal protection, carbon uptake) is a novel field. Since the main incentive may no longer be to restore something that has been lost, but rather use it at as tool to achieve a service, using restoration as a NbS may violate several of the above assumptions and keys to success. For instance, it is reasonable to believe that a location in need of coastal protection may not be the best location based on site-selection. This potential dichotomy entails additional challenges to seagrass restoration which may require innovative approaches. Contrarily, expected positive effects on biodiversity through facilitation may be higher in stressful (e.g. exposed) compared to sheltered locations (Bruno et al. 2003). For instance, Meysick et al. (2019) showed that the positive effects of eelgrass on fauna abundance increased along a hydrodynamic stress gradient, implying higher relative facilitation of eelgrass at more exposed sites. As such, restoring seagrass where environmental conditions are challenging (e.g. exposed) may thus enhance the positive ecological outcomes of the restoration compared to restoring in quiescent, more suitable environments.

Within the coastal adaptation project LIFE Coast Adapt, seagrass restoration is tested as a NbS in a hydrodynamically challenging environment to explore the feasibility to use it for coastal protection and biodiversity support.

Connectivity between land and sea

The connectivity in a coastal landscape entails the transboundary flows of material, fauna and energy across the supralittoral (land) and littoral zone (water). While largely understudied, this connectivity is crucial to sustain ecosystems. Within the context of this thesis, I focus on the role of eelgrass, mainly in the form as detached deposits on beaches known as 'beach wrack' (Figure 5).

Figure 5 Seagrass (*Zostera marina*) beach wrack deposited on a beach in Höganäs, Sweden 2023. Here, its transient role as a wave breaker and habitat is illustrated.

Biotic interactions at the land-sea interface

The functional role of the seagrass ecosystem extends beyond the meadow and traverses the land-sea boundary. Due to the high abundance and species richness within a seagrass meadow, it could aid in recovery of degraded adjacent ecosystems by acting as an important propagule source in the event of environmental degradation (Bishop et al. 2017). In temperate environments, seagrass meadows shed a large proportion of their aboveground biomass, especially during fall and winter (Mateo et al. 2006). The accumulation of detached seagrass material, commonly referred to as ‘beach wrack’ or ‘beach cast’, represents allochthonous material that supports food webs and biogeochemical processes in beach ecosystems (Kirkman and Kendrick 1997; Malm et al. 2004; Coupland et al. 2007; Ince et al. 2007; Heck et al. 2008; Defeo et al. 2009; MacMillan and Quijón 2012). Sandy beaches are dependent on trophic subsidies by adjacent habitats, such as seagrass meadows or macroalgal beds, to sustain production (Liebowitz et al. 2016). Macroinvertebrates which both feed on, and find refuge in, beach wrack are important secondary producers and are a source of food for species at higher trophic levels (Heck et al. 2008; Schlacher et al. 2008; Defeo et al. 2009).

Nevertheless, the presence of beach wrack can be perceived as a nuisance to beach visitors and coastal managers therefore often remove beach wrack on beaches designated for recreation. Recurring removal, known as ‘beach grooming’, can substantially alter sandy beach habitats and food webs (Defeo et al. 2009). Moreover, changes in adjacent aquatic habitats may affect sandy beach ecosystems and studying the effects of management interventions such as beach grooming and seagrass restoration can therefore provide insights into the elusive link between land and water.

Thesis aims

The overarching goal of this thesis is to better understand the functional role of seagrass meadows, and if and how its ecosystem functions can be utilized to aid in eelgrass change adaptation and mitigation while at the same time strengthening coastal biodiversity. To achieve this, I participated in and monitored ongoing eelgrass restoration projects while also assessing the natural variability in reference meadows across areas. The main novelty of this research is the broad and transdisciplinary focus where ecological concepts meet biogeochemistry and coastal engineering with the ultimate objective to better understand the multifunctionality of eelgrass meadows across marine and terrestrial realms. I hope this thesis provides some answers as to what we can expect from restoring eelgrass and a deeper understanding of the role of seagrass across ecosystem boundaries.

The specific aims of this thesis are to:

- Understand the spatiotemporal variability of fauna diversity (taxonomic and functional) in natural and restored eelgrass meadows in Southern Sweden (**Paper I-III**)
- Discern the timescales of benthic community recovery following eelgrass restoration (**Paper II-III**)
- Explore the link between biodiversity and carbon fluxes in restored meadows (**Paper II**)
- Assess the connectivity between eelgrass meadows and terrestrial biodiversity via the influence of eelgrass export on beach communities (**Paper IV**)
- Evaluate the feasibility of seagrass restoration as a nature-based solution for coastal protection in Southern Sweden and what effects on marine biodiversity can be expected (**Paper III & V**)
- Explore the potential interactions between different NbS for coastal protection with a focus on ecological restoration (**Paper V**)

Scope and outline

Throughout this thesis, I explore coastal biodiversity and functioning from different perspectives. Importantly, however, I remain within a narrow range of biological organization, on the order of communities, focusing primarily on the intersect between species and ecosystem diversity. I use the term ‘community’ repeatedly throughout this thesis, and I adhere to the definition by Mills (1971) that a community is *“a group of organisms occurring in a particular environment,* *presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups"* (p. 1427).

This thesis assumes a broad perspective, trying to bridge multiple disciplines and research areas rather than digging deeply into one. A large focus is on benthic fauna communities, while overlooking microbial communities despite their major importance for ecosystem functioning. I also limit the work to a few functions, focusing primarily on habitat provisioning and the cycling of carbon.

In **Paper I**, I address the spatial variability in eelgrass benthic fauna diversity across a salinity gradient in Southern Sweden and compare bare sediments to sediments underlying natural eelgrass meadows. I further assess the relationship between taxonomic and functional diversity to infer functional redundancy and resilience and explore how environmental setting affects this.

In **Paper II**, I delve into two of the major ecosystem functions seagrass meadows are recognized for, namely carbon cycling and habitat provisioning. This is investigated in restored eelgrass meadows of different ages which are used to assess the role of structural complexity in benthic carbon cycling across aging seagrass. The study encompasses the overarching research objective concerning the relationship between biodiversity and ecosystem functioning.

In **Paper III**, I follow a seagrass restoration project for over three years to assess the effects on benthic fauna diversity. This is accompanied by monitoring of natural variability in a reference meadow which provides information on the timescales of disturbance-recovery dynamics in eelgrass meadows and spatiotemporal variability in community parameters.

In **Paper IV**, I traverse the waterline and investigate the effects of exported eelgrass on beach and dune diversity. The study embraces a broad perspective by including plants and animals on both land and in the water and explores the connectivity between the marine and terrestrial realm.

In **Paper V**, I leave my wetsuit behind and resort to the office to review the scientific literature on beach nourishment and seagrass restoration. I evaluate the potential of combining these two seemingly dichotomous methods for improved coastal resilience. I propose a conceptual framework of potential feedbacks between these methods and how they can be utilized for coastal multifunctionality.

Methods

Study sites

The sites studied in this thesis spans from the NW coast of Sweden in the Skagerrak to the SE coast in the Baltic Sea (Figure 6). Yet, the largest focus has been in the Öresund strait (**Papers I**, **III**, **IV**) which is a dynamic area that constitutes one of the main conduits of water exchange between the brackish Baltic Sea and the saline North Sea. Consequently, the species inhabiting coastal areas in Öresund are adapted to large fluctuations in salinity, which can range between less than 10 to above 30 on a day-to-day basis (Stigebrandt and Gustafsson 2003; Feistel et al. 2010). Moreover, bottom trawling has been prohibited for nearly a century, allowing for diverse benthic communities (Petersen et al. 2018).

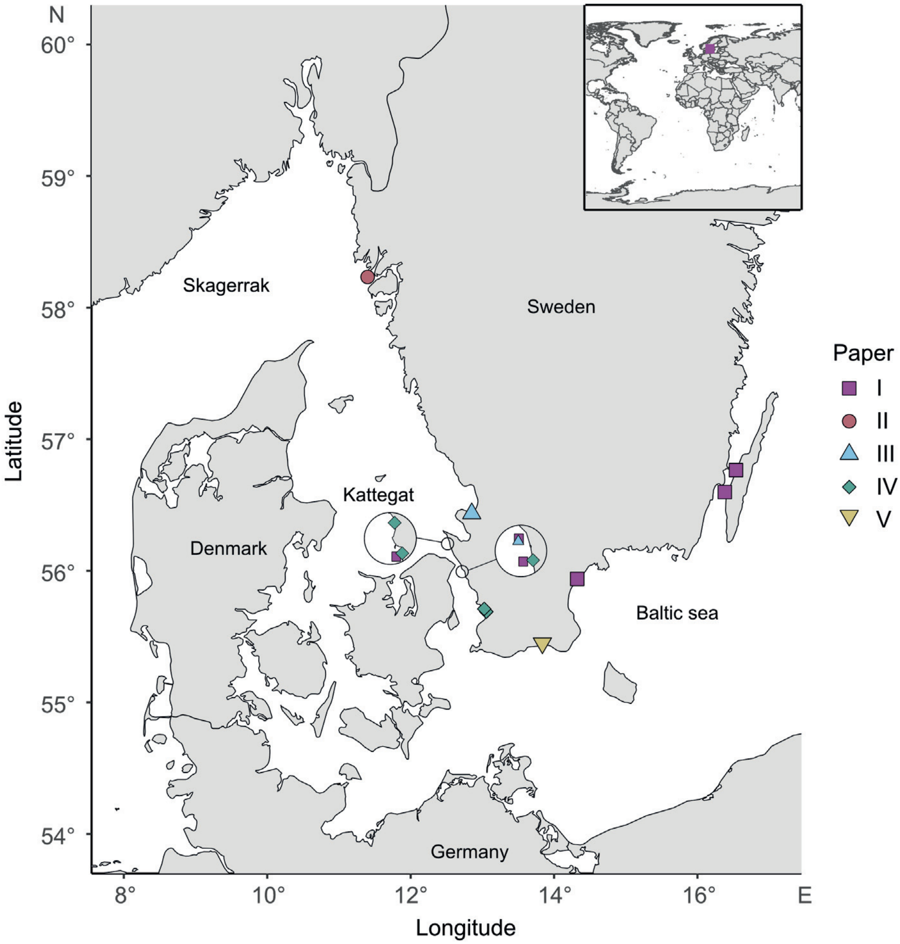


Figure 6 Map of study sites. Paper V did not involve any field work but is included because it concerned a case study on beach nourishments in Ystad.

In **Paper II** and **Paper III**, I explore two different restoration projects located in contrasting areas (Figure 7). The environmental settings of the restoration sites – Båstad and Gåsö – are vastly different. For instance, whereas the site in **Paper II** is located within a sheltered embayment with a fetch length of around 300 meters, the exposed site in **Paper III** is exposed to the Kattegat, and the estimated fetch length is orders of magnitude larger (Figure 6). Accordingly, the contrasting preconditions for restoring biodiversity allow for the comparison of shared features that influence the structure and function of benthic communities.

Whereas early effects on benthic fauna diversity were monitored over time in **Paper III**, **Paper II** employed a space-for-time substitution or 'chronosequence' of four stages of eelgrass development. The chronosequence encompassed bare sediments, two eelgrass plots planted three and seven years prior and a natural meadow representing a mature state (Figure 7). Thereby, the longer-term development could be assessed within the time frame of a PhD.

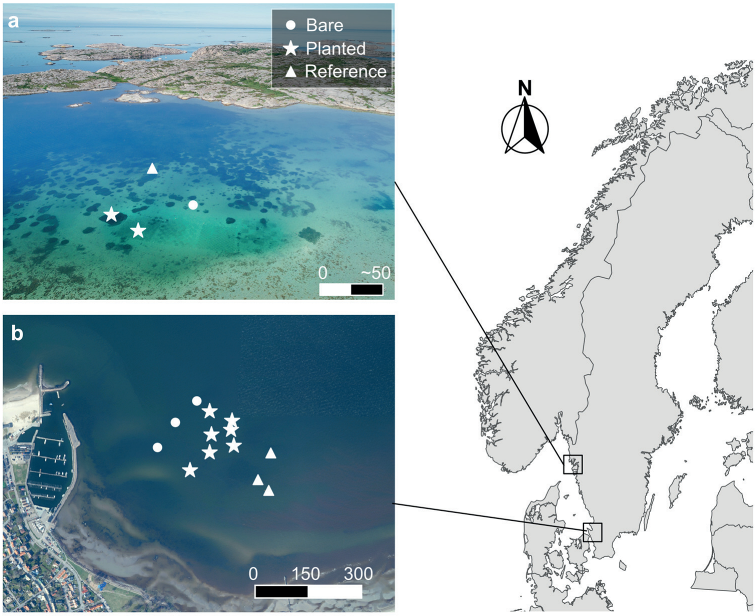


Figure 7 Map of restoration sites. a) shows the bay in Gåsö studied in **Paper II.** Drone image ©Eduardo Infantes. b) shows the eelgrass restoration area in Båstad in **Paper III**. Orthophoto ©Lantmäteriet.

Data collection

Fauna

Benthic fauna

In **Paper I-IV**, I assessed benthic fauna by collecting replicate sediment cores via free diving (Figure 8). The number of cores varied between studies depending on either *a priori* power analyses, research questions or logistical constraints. Fauna was identified to lowest taxonomic level possible, usually species, and counted using a stereo microscope. Species names were aligned with accepted nomenclature according to the World Register of Marine Species (WORMS; www.marinespecies.org). Many studies discriminate between infauna and epifauna, where the former refers to species living in the sediment and the latter to those living above the sediment surface or among the seagrass leaves. For practical reasons, the distinction is often based on sampling methodology (e.g. Baden and Boström 2001) where sediment cores, grabs, dredges or suction samples are considered samples of infauna whereas different kinds of nets, handled manually or by boat are targeting epifauna (Raz-Guzman and Grizzle 2001). However, this is a crude division due to large overlaps. Moreover, many species can move between epifaunal and infaunal positions depending on life history strategies (e.g. larval/adult stage), environmental conditions or biotic interactions. Using sediment cores as herein predominantly targets bottom-dwelling, sessile and slow-moving fauna and will be referred to as 'benthic fauna' hereafter. When discrimination between infauna and epifauna is of interest, an evaluation based on the species' functional traits is applied. However, in **Paper II**, I was specifically interested in epifauna and epiphytic algae, and here I supplemented sediment cores with a mesh net that was submerged over the canopy. Any vertebrates (i.e. fish) were released back to the water when possible and always excluded from further analyses.

Figure 8 Examples of sediment coring in the field. a) shows the author getting ready to hold his breath, b) shows the author inserting a core liner into the eelgrass sediment, c) shows MSc student Julia Müller inspecting a recently collected core in Båstad and d) illustrates slicing of a core for subsequent sediment analyses.

While the sediment coring technique provides a straightforward and reproducible way of sampling benthic fauna it is associated with a number of caveats and potential pitfalls, especially when performed via free diving. For instance, the time it takes from inserting the cylinder into the sediment and extracting a full core is directly dependent on the ability of the diver to hold their breath. This aspect introduces the risk of both systematic and random error whereby the diver improves both their technique and their fitness as more cores are collected, but may also depend on daily variation in performance. It is reasonable to believe that I have become better over the course of this dissertation work (> 200 cores) and that there is a risk of a temporal trend in, for example, the number of species as my ability to collect cores has improved. This source of uncertainty is difficult to account for but should not influence the relative comparison between samples within each study.

A similar aspect is associated with the identification of taxa. The ability to correctly assign a specimen to a taxonomic unit is directly dependent on the experience of the analyst, as a trained eye is necessary despite access to detailed identification keys. As this is a very time-consuming part of sample analysis, several people have been involved in the process. Consequently, reproducibility and repeatability are crucial aspects to consider. Every specimen is photographed under the microscope and stored for easy cross-checking and every fixed sampled is stored in the laboratory and can be reviewed at any time. In the long-term dataset in **Paper III**, microscope images from all years were revisited at the end of the study and any early misidentifications could be corrected. Somewhat reassuringly, there was no apparent trend of increasing species richness or any diversity index over time. The uncertainties associated with species identification is nonetheless a major caveat of taxonomic studies and illustrates the need for novel methods such as environmental DNA (eDNA, Pawlowski et al. 2022) which can be used to reduce human-bias in taxonomy.

Nevertheless, as seen in **Paper I** and **III**, benthic fauna varies naturally in both space (meters) and time (seasons, years) and can even vary substantially on diel timescales (e.g. García-Trasviña et al. 2023). Taken together, this variability is probably much larger than the uncertainty in sampling and identification described above.

Functional traits and diversity

Assessing functional diversity entails the selection of a set of functional traits, and the selection is ultimately dependent on the research question. If the question concerns the role of benthic fauna in modulating benthic fluxes, it is important to include traits that are known to affect these fluxes in one way or another. For instance, in **Paper II** I chose to include bioturbation traits due to their importance in affecting sediment biogeochemical processes and fluxes across the sediment water-interface (Snelgrove et al. 2018). Similarly, feeding mode was an important trait to account for the transfer of carbon across trophic levels. However, neutral traits, that have no direct link to the function in question, can be valuable to get a broad measure of the functional diversity in the studied community. Yet, if functional redundancy is to be assessed, these should be kept to a minimum as to not impose contrived relationships between taxonomic and functional diversity (Naeem and Wright 2003). Due to these considerations, the choice of traits often differs between studies which inevitably will affect the interpretation of functional diversity (and other functional metrics) as well as the comparison between studies.

It is thus important to keep in mind that "high" or "low" functional diversity ultimately depends on a, sometimes arbitrary, *a priori* selection of traits and modalities.

Terrestrial diversity

In **Paper IV**, I targeted three distinctly different communities that each required their separate sampling methods. For terrestrial vascular plants, I used an experienced botanist to survey plant cover and species in quadrats *in situ*. For terrestrial fauna, I used pitfall traps which are buried and left overnight. For benthic fauna, I used sediment cores as described above. These three methods differ both in their specificity and the spatial scales they cover. This is important to keep in mind and precludes direct comparison of diversity metrics between the different communities.

Sediment properties

The sediment is a major key in understanding the physical setting in any coastal environment, as its structure to a large extent depends on the hydrodynamic conditions. But the sediment also constitutes the substrate that both eelgrass and infauna depend on and its properties influence, and is influenced by, both. Information on the sediment structure and composition can therefore provide insights into processes relevant for the functioning of the eelgrass ecosystem. For instance, the distribution of different particle sizes is a proxy for the level of exposure to waves and currents but is also affected by the presence of eelgrass as the energy dissipation provided by eelgrass is conducive to sedimentation of finer particles. This in turn affects fauna communities as different species prefer different grain sizes. Finer sediment composition also has ramifications for solute fluxes across the sediment-water interface resulting in slower, diffusive fluxes rather than advective fluxes present in coarser, permeable sediments. Consequently, the work in this thesis has put a large emphasis on collecting and analyzing sediment samples, albeit for disparate purposes. In **Paper I**, **III** and **IV**, the grain size distribution was assessed to provide information on the physical setting but also as an explanatory variable for variability in fauna communities. In **Paper III**, sediment grain size was evaluated to ensure similarity between donor meadow sediment and restoration sites. These studies were conducted in relatively exposed areas with sandy sediments. With sandy sediments of low organic content, dry sieving is an easy and straightforward method to analyze grain size distribution whereby homogenized sediment samples are sieved through a stack of sieves with different apertures (0.063 – 2 mm). The grain size distribution is calculated from the relative mass of the different size fractions, and properties such as the mean grain size and degree of sorting can be estimated (Folk and Ward 1957; Blott and Pye 2001). The study site in **Paper II** is in a sheltered bay with much finer sediment which is not suitable for dry sieving. Here, grain size analyzed with laser diffraction was obtained from another study (M. Dahl, pers. comm.).

In addition to the inorganic particles, sediment is comprised of organic matter (OM) which can stem from anything from seagrass roots to dead plankton and tree trunks. OM content is assessed through loss on ignition (LOI) where homogenized, dried sediment samples are combusted in a muffle furnace and the weight of the sample is compared to the initial weight. Because temperature and exposure time can have a large influence on the estimated OM content (Heiri et al. 2001), LOI has been performed at 520°C for four hours throughout **Papers I-IV**. Particulate organic carbon (POC), total carbon (TC) and total nitrogen (TN) were analyzed using elemental analyzers for a subset of OM samples (**Paper II** and **IV**).

Metabolic fluxes and seawater chemistry

There are several different approaches to assess diel benthic community metabolism, most having in common that they measure solute fluxes going in and out of the benthic environment. The majority of metabolic fluxes in coastal benthic environments derive from metabolic processes of primary production and heterotrophic and autotrophic respiration. As such, these fluxes integrate metabolism stemming from everything ranging from large macrophytes such as seagrasses to the decomposition of organic matter by microorganisms. All flux estimation methods have their inherent assumptions, limitations and differ in their spatial and temporal resolution. Methods range from discrete water samples above the benthos over a diel cycle compared with offshore water in the so called ‘open water’ method pioneered by (Odum 1956), to laboratory core incubations with artificial light cycles. However, a methodology (see below) adopted from atmospheric science has pushed the frontier on benthic metabolism studies due to its high temporal resolution and its non-invasiveness that allow for natural conditions to be measured (Berg et al. 2003).

Aquatic eddy covariance

Aquatic eddy covariance (EC) is a non-invasive, high-resolution method to measure benthic oxygen fluxes (Berg et al. 2003). The EC system consists of an acoustic doppler velocimeter (ADV) coupled to a high-speed oxygen microsensor capable of measuring the vertical velocity and oxygen concentration with very high temporal resolution (e.g. 8-64 Hz). In addition to being completely autonomous, its main advantage over other benthic flux methods is that it captures the natural hydrodynamic conditions and integrates fluxes over a larger footprint area, thus partly accounting for small-scale heterogeneity. Other benthic flux methods such as core incubations or benthic chambers alter natural water flow and exchange with the water column and typically measure over a much smaller area (Berg et al. 2022). In **Paper II**, the EC system was equipped with two photosynthetic active radiation

(PAR) sensors, an oxygen optode measuring ambient dissolved oxygen and temperature, a turbidity sensor and a salinity sensor (Figure 9). This allowed us to simultaneously record the benthic oxygen flux and its potential drivers (e.g. light, flow, temperature) for multiple days in a row. For instance, by mounting one PAR sensor facing upwards to measure the incident radiation and one facing downwards measuring the reflected PAR, the absorbed light by each habitat could be calculated. Together with the simultaneous oxygen flux recordings, it was possible to assess the light-use efficiency (LUE), which denotes how efficiently a photosynthesizing community uses light (photons) to produce oxygen (Attard and Glud 2020).

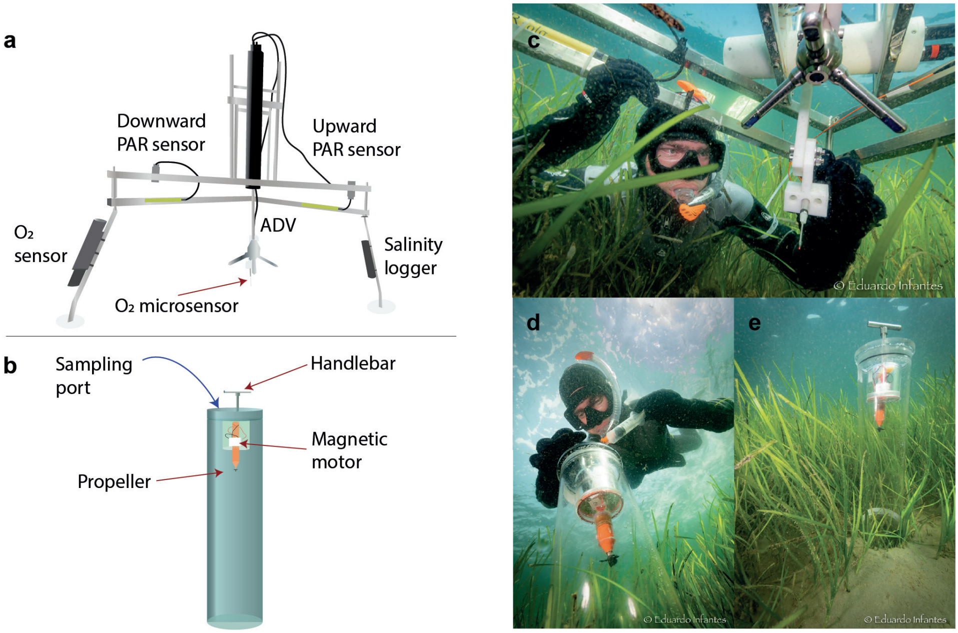


Figure 9 Schematic Illustration of the eddy covariance system (a) and the benthic incubation chambers (b) used to measure fluxes of dissolved oxygen and dissolved inorganic carbon. The turbidity sensor and two additional irradiance loggers are not shown. c) shows the author adjusting the oxygen microsensor on the eddy covariance system, d) shows the author taking a discrete water sample from inside a benthic chamber using a syringe and e) shows a benthic chamber deployed at the edge of an eelgrass meadow. Photographs in panels c, d and e by E. Infantes.

Benthic chambers

Despite its many advantages, aquatic EC does not yet have the ability to measure fluxes of dissolved inorganic carbon (DIC). Instead, oxygen fluxes are used as proxy for carbon fluxes and converted based on an assumed 1:1 ratio between O_2 production and DIC consumption. However, multiple studies have found this ratio to deviate substantially from 1:1 in the field, which can be due to different processes including anaerobic respiration, photorespiration, nitrate assimilation or calcification and $CaCO_3$ dissolution (Barron et al. 2006; Ouisse et al. 2014; Turk et al. 2015; Trentman et al. 2023). I therefore complemented the EC measurements with benthic chamber incubations (Figure 9) from which O_2 and DIC fluxes could be analyzed concomitantly and the *in situ* ratio between the two solutes could be calculated. This empirical ratio could then be applied to EC oxygen fluxes to estimate DIC fluxes under natural conditions. Another advantage with using benthic chambers was that I could simultaneously draw water samples for inorganic nutrients (NO_3^-, NH_4^+ and PO_4^{3-}), dissolved organic carbon (DOC) and characterize the full marine carbonate system through pH, total alkalinity, salinity, temperature and pressure (Zeebe and Wolf-Gladrow 2001). This allowed me to characterize ambient seawater chemistry and explore covariates of metabolism.

Seagrass restoration

Planting and monitoring

Planting eelgrass in exposed locations was one of the objectives of the LIFE Coast Adapt project (Region Skåne 2023). This process consisted of three main parts and was carried out by a contracted consultant agency. First, different planting methods, including anchoring techniques, were tested at six different locations around the coast of Skåne. Following this, the single-shoot method, which is also recommended by the Swedish guideline on eelgrass restoration (Moksnes et al. 2021a), was chosen for larger-scale planting in Båstad (Figure 7). In two restoration trials over two consecutive years, a total of seven plots were planted between 2-3.3 m depth. Plots were either planted in a chessboard pattern where every other square meter was left empty or in a continuous pattern, together totaling a gross area of nearly 3400 m^2 (**Paper III**). Eelgrass shoot density was assessed by scuba divers in October each year to evaluate survival rate.

To follow the early colonization and succession of benthic fauna communities, a monitoring scheme comprising benthic fauna sampling and underwater video surveys was designed. Monitoring followed approximately 1, 3, 12 and 24 months after restoration and covered the planted plots, adjacent bare sediments and natural reference patches of eelgrass. Concurrent monitoring was carried out at a reference meadow. At each field visit, I collected sediment cores as per above resulting in a total of 134 fauna samples (**Paper III**).

In **Paper II**, a single-shoot eelgrass restoration was conducted in Gåsö, on Sweden's northwest coast (Figure 7), within the ZORRO research program at Gothenburg university (www.gu.se/en/research/zorro). The plots studied were planted in 2015 and 2019, with a shoot density of 16 shoots m^{-2} in a 20 x 20 m continuous pattern (E. Infantes, pers. comm). As such, these plots resembled those planted during the second restoration trial in Båstad (**Paper III**). Assessments of benthic fauna have been conducted by Gagnon et al. (2023) and in **Paper II**.

Measuring the role of eelgrass in terrestrial biodiversity

To study the role of eelgrass in structuring biodiversity beyond the eelgrass meadow itself, I assessed beaches with a large influx of exported eelgrass and macroalgal beach wrack (**Paper IV**). The supply of beach wrack is known to function as a trophic subsidy to sandy beaches and constitutes a major connectivity pathway across the marine-terrestrial interface. However, most studies focus on terrestrial fauna, often overlooking other aspects of coastal biodiversity such as beach and dune vegetation. To test the effect of eelgrass wrack on beach and dune diversity, I selected five sites of similar geomorphology and oceanographic conditions. The sites had delineated sections of the beach designated as swimming areas where beach wrack was recurrently removed through beach grooming. Right next to these segments were natural, ungroomed parts of the beach where any accumulated wrack was left intact. This thus provided a study design of control-impact across a gradient of beach wrack deposition and composition. In the southern sites, eelgrass completely dominated beach wrack whereas the relative proportion of macroalgae became progressively higher toward the northern sites (Figure 6).

By means of transects running perpendicular to the coastline and extending from the dunes out into the water, it was possible to sample both terrestrial plant and fauna communities as well as marine benthic fauna and macrophytes. From this, habitat-specific effects from wrack and grooming could be evaluated. Beach wrack was expected to influence fauna and flora communities differently, acting primarily as a food source and habitat for fauna while potentially having a fertilization effect on flora through decomposition and remineralization of organic matter. Therefore, sediment OM, TC and TN were assessed every five meters along the transects.

To further assess the relative contribution of eelgrass and macroalgae, an accompanying colonization experiment was set up where plots of either eelgrass, macroalgae or bare sand was left on the beach plane four consecutive days. Terrestrial fauna was sampled at the onset and termination of the experiment and provided succession patterns of the different functional groups colonizing the different plots.

Data analyses

Biodiversity indices

Taxonomic diversity

In **Paper I-IV**, I used a selection of univariate and multivariate indices to assess the diversity of the communities sampled. Indeed, reducing complex data to an index has its apparent limitations and should not be used for comparison between studies using different sampling gear or different sample sizes (Pearson and Rosenberg 1978). In this thesis, indices are primarily used to monitor differences within and between communities across different scales and as such, the complexity reduction can facilitate interpretation of change. The Shannon-Wiener index (H'), or Shannon entropy, is a commonly used metric of taxonomic diversity that considers the relative abundance of species in relation to the total number of species as:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \tag{1}$$

where p_i is the proportion of community comprised of species i. Throughout this thesis, the effective number, or linear form, of H' is used (H_{eff} = exp(H'); Jost, 2006). The effective form has the advantage that a doubling of H_{eff} represents a doubling in diversity (Hill 1973) which makes it useful when relating it to other diversity parameters (see below). Moreover, the maximum number of H_{eff} equals the maximum number of species (S) in the community such that H_{eff} = S implies that all species are equally abundant.

Functional diversity

I have put a large focus on functional traits of benthic communities, as these underpin many of the processes and functions sustained by eelgrass meadows. There are many different methods to quantify functional diversity, all with their strengths and weaknesses (Pla et al. 2012). I have primarily relied on an index of functional diversity, based on Rao's quadratic entropy (FD_Q; Rao (1982)). While having many of the same properties as taxonomic indices, FD_Q is based on the functional traits of species rather than species identity. It is one of the most applied indices for functional diversity and expresses functional differences in a multivariate trait space, considering both the abundance and the pair-wise functional trait differences of species (Botta-Dukát 2005; de Bello et al. 2007):

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_j \qquad (2)$$

where S is a community of species with the vector p comprising relative abundances and d_{ij} is the Gower distance between species i and j (Gower 1966). To allow for correlation analysis and comparison with taxonomic diversity (H_{eff}) described above, Rao's FD_Q was also transformed to effective number following Jost (2006):

$$FD_{eff} = \frac{1}{1 - FD_Q} \qquad (3)$$

Similar to H_{eff}, the maximum value is S, whereby FD_{eff} = S implies that all species are equally functionally distinct. Functional dispersion (FDis) is an increasingly common metric of functional diversity (Laliberté and Legendre 2010) and was, due to its emerging popularity, also computed in this thesis to allow for comparison with recent studies. It is tightly coupled to the untransformed FD_Q values in this thesis, which is positively linearly correlated with FDis (slope=0.125±0.002; R^2=0.94; $p<0.001$), implying that the interpretational ability is very similar. However, regardless of which index is used, reducing diversity to a single number inevitably overlooks components of diversity that may provide a more detailed interpretation of the mechanistic links between biodiversity and ecosystem functioning (Mason et al. 2005; Villéger et al. 2008). Therefore, measures of functional richness, evenness and divergence (Mason et al. 2005) together with the community-weighted means of trait values were also assessed when relevant.

Functional redundancy was inferred from the relationship between H_{eff} and FD_{eff}, both through their ratio (i.e. FD_{eff}/H_{eff}) and by exploring best fit slopes of their linear or non-linear relationship (see Figure 2).

Statistical models

The univariate statistical models and parametric tests employed in this thesis have focused on a limited number of powerful and straightforward methods. I have relied heavily on linear and linear-mixed effects models (Bates et al. 2015), in conjunction with model selection (**Paper I-IV**). One of the main strengths of linear mixed effects models is that both fixed and random effects can be defined in the model. For instance, in **Paper I**, I studied sites located along a salinity gradient. Since I was interested in fauna diversity variation along this gradient, I wanted to include salinity as a fixed effect in my models. However, since the different sites were selected based on their differing salinity but still differed in many other, unknown ways, site could be included as a random effect. As such, the influence of site on the response variable was accounted for when estimating the effects of other predictors (e.g. salinity, habitat, sediment), while not explicitly considering its effect. In the recurring monitoring of restored eelgrass in **Paper III**, the sampled plots were instead used as a random effect. This allowed for a repeated measures approach, where the fact that the same plots were sampled repeatedly is accounted for. The same approach was employed during the colonization experiment in **Paper IV**, where experimental plots of beach wrack were repeatedly sampled.

Analysis of variance (ANOVA) has been the main parametric statistical method used to infer statistical significance of models and Tukey's Honest Significant Difference (HSD) test has been applied as a post hoc test of univariate predictor variables. Where assumptions of normality or homoscedasticity have been violated, appropriate data transformation or Welch's correction (Welch 1951), respectively, has been applied. Linear regression analyses have been employed to assess relationships between individual continuous variables.

Multivariate methods can provide a more nuanced picture of community composition and the drivers or changes thereof. I have employed both unconstrained ordination methods such as principal components analysis (PCA) and non-metric multidimensional scaling (NMDS) for visualizing patterns and clusters but also constrained methods such as redundancy analysis (RDA). Non-parametric permutational analysis of variance (PERMANOVA) has been applied for multivariate hypothesis testing. All calculations, statistical tests and figures have been carried out using the programming software R (RCoreTeam 2023).

Structural and functional diversity in natural and restored seagrass

An overarching theme of this thesis relates to the biodiversity of eelgrass meadows at different spatiotemporal scales. Although this topic has been studied for decades, the context-dependence makes many of the answers site-specific. As such, a careful characterization of local environmental conditions and biodiversity is needed to evaluate the effects of eelgrass restoration. This first part therefore summarizes the findings relevant for this and continues with the findings related to the functioning of eelgrass meadows.

What drives spatiotemporal differences in eelgrass fauna diversity?

Despite a large body of literature covering the drivers of benthic fauna diversity in eelgrass meadows (e.g. Eggleston et al. 1998; Webster et al. 1998; Frost et al. 1999; Mattila et al. 1999; Turner et al. 1999; Bowden et al. 2001; Lee et al. 2001; Boström et al. 2006) the conclusions remain equivocal. Based on the findings in **Paper I**, no single environmental variable could explain variation in diversity, with habitat completely overshadowing the effect of the environmental variables measured. Abundance and fauna biomass were partly a function of salinity, as these variables decreased with decreasing salinity. we found an interaction between habitat and salinity, suggesting that the presence of eelgrass became increasingly important at lower salinities. Nevertheless, the overwhelming influence of the mere presence of eelgrass rather than any specific attribute highlights the importance of eelgrass meadows in structuring benthic fauna communities. Ultimately, this implies that restoration effects are likely to be similar regardless of where restoration takes place, at least within the range of sites explored in this thesis. It is, however, possible that a relatively larger increase in abundance and biomass of fauna can be expected when planting eelgrass in brackish environments compared to higher salinity environments.

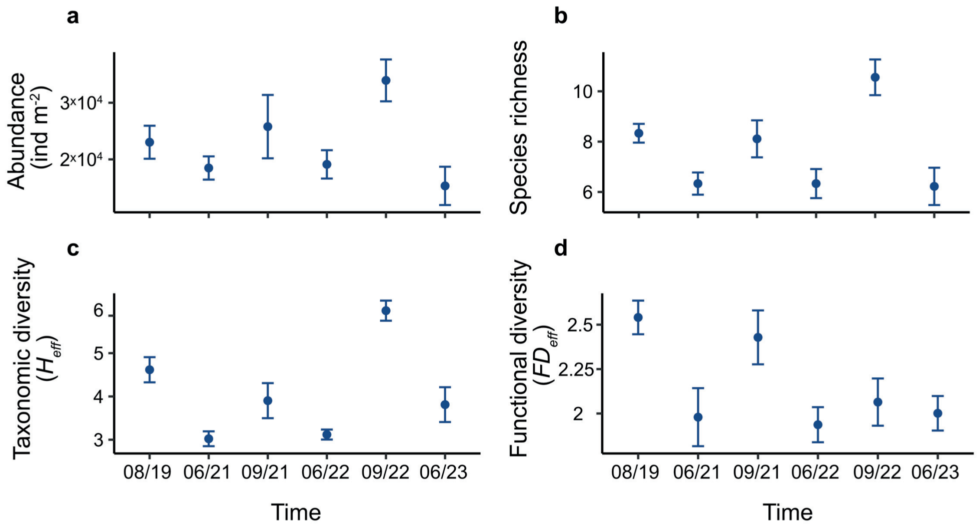


Figure 10 Temporal variability of benthic fauna metrics. Multiple components of biodiversity including a) abundance; b) species richness; c) Shannon diversity (H_{eff}) and d) functional diversity (FD_{eff}) in a natural eelgrass meadow in Råå sampled in early summer and early fall over four years and illustrates seasonal and annual variation. Time represents sampling period (mm/yy). Figure based on data from **Paper III**.

In addition to the spatial heterogeneity in eelgrass fauna communities, temporal variability is important and seasonal variation may even exceed differences between bare and vegetated habitats. From our reference meadow dataset in **Paper III**, which was sampled biannually in early summer and fall between 2019 and 2023, we observed a doubling in species richness and taxonomic diversity along with abundance increases on the order of ten thousand individuals between seasons (Figure 10). Seasonal cycles in reproduction and timing of recruitment among benthic fauna and their food sources as well as the seasonal variation in eelgrass biomass are all likely contributing to the observed differences. Some species may also migrate in- and offshore depending on season (Persson 1983). Species composition can also vary on very short timescales in response to disturbance events which can confound spatial habitat differences (Boström et al. 2011). Regardless of the drivers of temporal variability, these findings highlight the natural variation in eelgrass benthic fauna diversity. Thus, it is evident that inference based on a snapshot evaluation on a small spatial scale has limited practical application and should be interpreted with caution.

Rapid recovery of benthic fauna communities following eelgrass restoration

Whereas the findings in **Paper I** illustrated the important role of natural eelgrass across spatial scales, the spatiotemporal aspect of fauna diversity in restored eelgrass across different environmental settings remains largely understudied. **Paper II** and **Paper III** therefore explored the timescales of fauna colonization following eelgrass restoration in two contrasting environments (Figure 6). Granted that the restored eelgrass survives – which is often not the case – the findings in this thesis points to rapid recovery of benthic fauna communities. The sheltered restoration plots investigated in **Paper II** were on par with the nearby natural meadow within seven years, and a recent study by Gagnon et al. (2023) found recovery rates at the same site to occur on the order of 1-2 years. In **Paper III**, we showed that several diversity metrics such as benthic fauna species richness, H_{eff} and FD_{eff} were indistinguishable between planted plots of 2-4 months of age and natural eelgrass reference patches. These findings add to a growing body of evidence showing rapid recovery of benthic diversity following eelgrass restoration, and results are largely consistent across environments, seagrass species and restoration methods (Fonseca et al. 1996; McSkimming et al. 2016; Lefcheck et al. 2017; Orth et al. 2020; Tanner et al. 2020; Steinfurth et al. 2022; Gagnon et al. 2023; Gräfnings et al. 2024). This is especially noteworthy as most restoration projects in general fail to meet reference levels of biodiversity (Benayas et al. 2009).

Importantly, the restoration sites in **Paper II** and **III**, along with several of the abovementioned studies, were located in the direct vicinity of natural eelgrass (e.g. tens to hundreds of meters). Indeed, these short distances allow for a higher connectivity which is known to govern recovery trajectories (Duarte et al. 2015) and natural reference meadows can function as propagule sources to newly restored plots. In **Paper III,** the rapid colonization was to a certain extent driven by mobile species. It is reasonable to infer that if there is eelgrass adjacent to restoration plots, colonization is primarily facilitated by species with motility traits that can actively select habitats (Stoner 1980a). Thereby, colonization does not have to rely on larval dispersal, which is mostly governed by hydrodynamics (Boström et al. 2010; Robins et al. 2013). Along those same lines, results from the sheltered Gåsö bay suggested that infauna diversity recovered later than epifauna. A recent study by Gagnon et al. (2023), which covered the first and second year after restoration in the same site, observed similar indications of a faster recovery among epifauna compared to infauna. As such, the authors suggested that infaunal communities may require a longer time to transition from bare sediments to vegetated sediments (Gagnon et al. 2023). Indeed, the emergence of roots and rhizomes alter the sediment environment in profound ways and can impede burrowing activity by hard-bodied species (Stoner 1980b).

Consistent across both studies in **Paper II-III** is a tendency toward an overrepresentation of opportunistic species in early stages of colonization, when comparing to natural reference eelgrass. For instance, the opportunistic polychaete *Capitella capitata* was nearly twice as abundant in one-year old planted plots relative to reference patches, albeit displaying large within-site variability (**Paper III**). Even more strikingly, the complete dominance of *C. capitata* in the youngest restored plot (three-years-old) in Gåsö rendered the highest total infauna abundance and lowest evenness of all sites (**Paper II**). In the seven-year-old plot however, *C. capitata* was back at reference levels and taxonomic diversity and evenness was fully recovered, as inferred from being near-identical to the natural reference meadow. Similarly, Gagnon et al. (2023) reported rapid colonization of opportunistic gastropods (rissoids) within the same year as plots were planted. This agrees with our findings from the restored plots in Båstad where rissoids were 2-3 times more abundant in planted plots compared to reference eelgrass within four months after restoration (**Paper III**). As such, it seems that these two sites exhibit similar recovery trajectories of pioneering species despite their contrasting environmental settings.

Diverging relationships between taxonomic and functional diversity

Taxonomic and functional diversity is often highly correlated, but the shape of the relationship can provide useful information of the level of functional redundancy (Micheli and Halpern 2005). In **Paper I**, we found that functional redundancy could be as high or even higher in bare relative to vegetated sediments and tended to increase with decreasing salinity. This illustrates the implications of having many, but highly specialized species in marine eelgrass habitats compared to fewer, mostly generalist, species in brackish, bare sediments. Having multiple species comprising the same trait modalities – and performing the same functions – thus makes the system more resilient to disturbance and species loss (Walker 1992). Nevertheless, recovery trajectories differ between taxonomic and functional components of diversity. Therefore, monitoring the recovery of functional traits rather than species can be more informative both with respect to recovery of ecosystem functions and for understanding response to disturbance.

Looking at a larger spatial scale and across nearly all benthic fauna samples collected within this thesis (**Paper I-III),** the differences between bare and vegetated habitats become more pronounced, despite large between-site differences. Species richness and H_{eff} are consistently higher in natural and planted eelgrass habitats relative to bare sediments (Figure 11). Conversely, bare sediments and planted eelgrass display a lower functional diversity compared to natural eelgrass ($F_{2,192}$=28.2; p<0.001; Figure 11). Functional redundancy, as inferred from the FD_{eff} to H_{eff} ratio, is marginally higher (i.e. lower ratio) in planted compared to natural eelgrass and bare sediments ($F_{2,192}$=3.8; p=0.02).

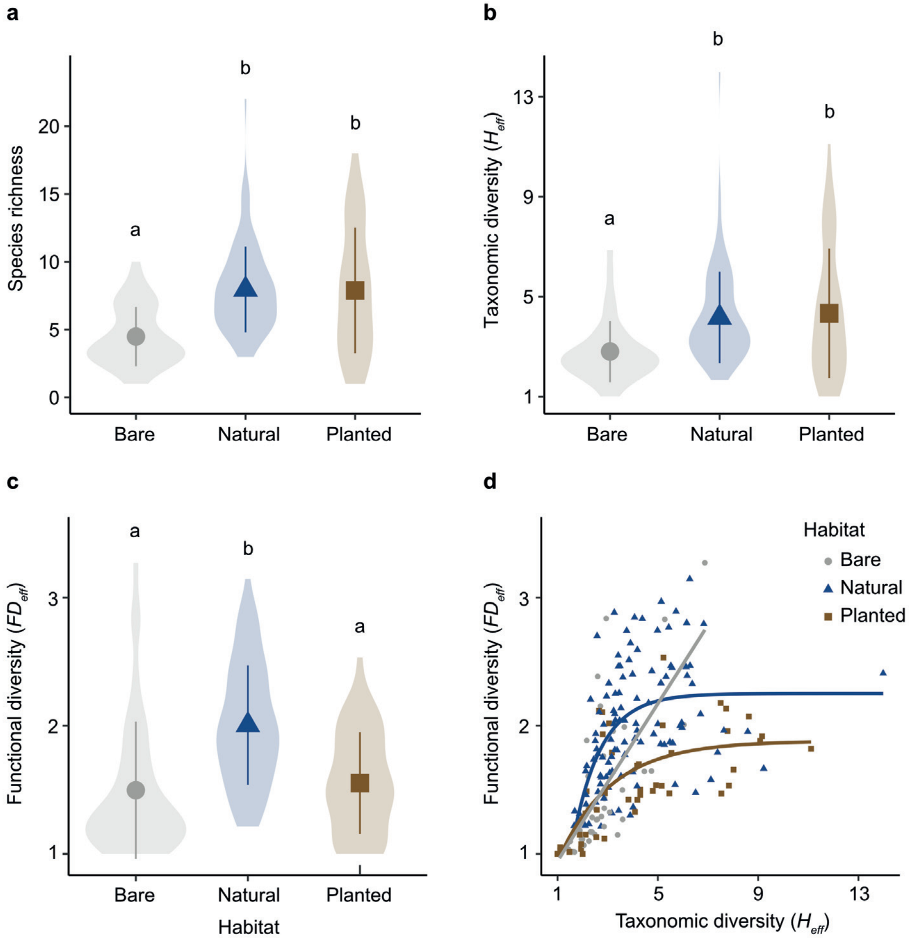


Figure 11 Violin plots of a) species richness; b) taxonomic diversity (H_{eff}) and; c) functional diversity (FD_{eff}) of benthic fauna communities in the habitat types bare sediments, natural eelgrass and planted eelgrass based on data from **Paper I-III**. Points and error bars in a-c show mean±SD and different letters indicate significant difference ($p<0.05$) following Games-Howell post hoc test. d) Regression analysis of the relationship between H_{eff} and FD_{eff} across the three habitat types with fitted slopes for each habitat type. Best fit lines show linear relationship for bare sediments and asymptotic relationship for natural and planted eelgrass. To facilitate comparisons between studies, FD_{eff} was scaled by its maximum values in each separate study and based on unstandardized traits, which is why the numbers may deviate from those reported in the individual studies. Samples are from 195 sediment cores of which n=43 bare, n=107 for natural and n=45 for planted.

However, the relationship between taxonomic and functional diversity varies depending on when and where diversity is measured and different best fit slopes between H_{eff} and FD_{eff} emerge in the different habitats (Figure 11). Specifically, it seems that bare sediments in general exhibit a linear relationship with a relatively moderate slope whereas natural and planted meadows are best explained by asymptotic regression curves (Figure 11). Planted sites display a more homogenous response with a better fit whereas natural sites are more variable. Furthermore, the initial slope in planted eelgrass is significantly lower and plateaus earlier compared to natural systems. This can indicate a stronger environmental filtering that only allows a limited number of traits in newly planted eelgrass (Hooper et al. 2005). Because restored plots are mostly in their early stages of development, it is possible that this reflects how a less developed canopy, for instance, with lower shoot density limits the occurrence of species that require a certain density or habitat complexity. Thereby, functional diversity will not increase regardless of how much species diversity increases until the restored meadow reaches the density or complexity levels that allow for other functional groups. Colonization by new species will thus only contribute to a more crowded niche space which will be divided into smaller parts, rather than elevating functional diversity (Díaz and Cabido 2001; Hooper et al. 2005). As a consequence of this, planted plots are more functionally redundant and the functions sustained during early stages – albeit fewer – may be more resilient to stress and species loss (Gamfeldt et al. 2008).

The deviating relationships observed between areas and habitats also further underscore the uncertainty in estimating functional diversity – and ultimately ecosystem functions – solely from taxonomic diversity. They illustrate how functional diversity can shift rapidly if a species with multiple functional trait modalities colonize a habitat, as is exemplified by the generalists that dominate early stages of meadow development following restoration (**Paper II-III**). As such, taxonomic diversity can be a poor proxy for functional diversity in certain situations, as seen in previous studies (e.g. Paganelli et al. 2012; Wong and Dowd 2015).

Newly planted eelgrass habitats do not always comprise the same levels functional diversity as their natural counterparts (Figure 11), despite attaining a similar community structure. Conversely, functional diversity can remain high even in less speciose communities, as illustrated for instance by bare and brackish environments in **Paper I**. This demonstrates how the set of functional traits among an assemblage of species can remain more or less intact despite different community composition, if highly specialized species with a narrow set of trait modalities are replaced by generalist species that can occupy a broader niche. In addition, functional traits are not always static. Instead, many species exhibit a certain plasticity in their functional traits which can vary depending on environmental conditions, species interactions and life history strategies (Törnroos et al. 2015). Odum (1985) suggested that ecosystem functions such as primary production can be maintained despite severe alterations in community structure following stress exposure. As such, ecosystem functions display homeostasis to a larger extent than ecosystem structure (Odum 1985; Duarte et al. 2015). Along those lines, it is possible that functional traits can be restored more rapidly following restoration despite not attaining the same species composition. This demonstrates the importance of monitoring functional parameters in addition to taxonomic when evaluating restoration effects.

Carbon cycling and biodiversity

While the above findings suggest rapid recovery of fauna diversity, the question remains how this translates into ecosystem functions. Benthic metabolism is in some respects a cardinal function as it is inherently linked to energy transfer and relates to valued ecosystem services such as carbon sequestration and nutrient cycling. Planting eelgrass fundamentally reshapes the benthic environment and, together with its associated communities, presumably greatly affects benthic metabolism.

Increasing metabolism as the meadow grows

In **Paper II**, we found that daily metabolic fluxes of dissolved oxygen and inorganic carbon increased as the benthic environment transitioned from bare sediments into eelgrass following restoration (Figure 12). Restored eelgrass plots displayed progressively higher gross primary productivity (GPP) and community respiration (CR) as a function of age. Contrary to our hypothesis, this did not seem to be a result of higher eelgrass biomass or shoot density, as both these parameters were similar across restored and natural eelgrass. Rather, the presence and relative proportion of red and brown macroalgae such as *Furcellaria lumbricalis* and *Fucus* species likely contributed to a higher GPP of the whole community. At the same time, several organic carbon pools including fauna biomass also increased with meadow age, possibly driving even larger increases in community respiration (CR) which exceeded GPP on diel timescales (Figure 12). Consequently, all sites were net heterotrophic (NCP < 0) with increasing net heterotrophy with meadow age (Figure 12).

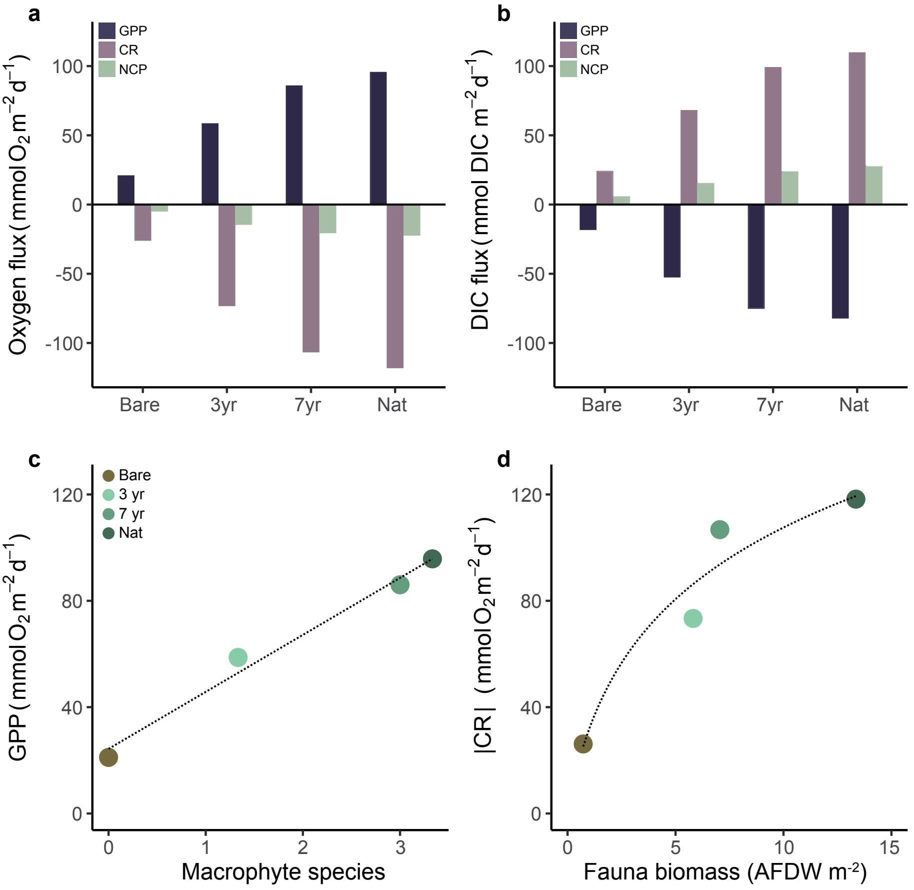


Figure 12 Community metabolism and its drivers. a) Daily oxygen fluxes as gross primary productivity (GPP), community respiration (CR) and net community productivity (NCP) based on oxygen fluxes (a) and dissolved inorganic carbon fluxes (b). c) Linear regression of GPP as a function of the mean macrophyte species richness, dashed line indicates best fit slope linear slope; d) Absolute CR as a function of benthic fauna biomass as ash-free dry weight (AFDW) m^{-2} where dashed line is best fit slope (y~ln(x+1)). Figure modified from **Paper II**.

Light-use efficiency and niche complementarity

We propose different mechanisms for the increasing GPP and |CR| with meadow age. The efficiency by which the autotrophic communities utilized incident irradiance for photosynthesis increased as function of meadow age. Light-use efficiency (LUE) was 0.001, 0.004, 0.005 and 0.007 O_2 photon^{-1} in the bare, 3 yr, 7 yr and the natural site, respectively, resulting in higher GPP (Figure 12). As eelgrass morphometrics were similar, LUE appeared to be a function of diversity of macrophytes and the associated structural complexity rather than the eelgrass itself. We hypothesized that this was related to complementarity mechanisms such as photosynthetic pigment complementarity, differing affinities for forms of inorganic nutrients and carbon as well as self-shading. Complementarity effects in macroalgal assemblages have previously been shown in experimental studies revealing that the productivity of multi-specific communities is larger than the sum of its parts (Tait and Schiel 2011; Tait et al. 2014). However, Angove et al. (2020) found no evidence of complementarity effects in macrophyte communities but rather selection effects for highly productive macrophyte traits, such as canopy height (Gustafsson and Norkko 2019). Although macroalgal traits were not assessed in this study, we did not observe any correlation between eelgrass morphology (including canopy height) and GPP.

Heterotrophic biomass fueling respiration

Fauna diversity generally did not differ significantly between restored and natural eelgrass, but total fauna biomass did. Total ash-free dry weight (AFDW) exhibited an eightfold increase between bare sediments and the youngest restored plot, an additional 20% increase in the oldest restored plot and a further near-doubling in the natural meadow. Moreover, certain functional traits related to bioturbation were more prevalent in older and natural eelgrass. We therefore postulate that benthic fauna, in conjunction with more labile macroalgal biomass, contributed to the increasing CR with meadow age. Thus, we see indications of a positive BEF relationship with respect to macrophytes but due to the concurrent effects of heterotrophic biomass on community respiration, the net effect on community productivity is negative. The observed net heterotrophy implies that the system relies on either historic production of autochthonous carbon or on trophic subsidies to sustain metabolism. As such, we infer that in sheltered, semi-enclosed bays such as the one studied in **Paper II**, eelgrass meadows may act as effective bioreactors of stored and imported carbon which is a direct effect of the rich autotrophic and heterotrophic diversity it comprises. Despite covering only a month during summer, potential tradeoffs between biodiversity and carbon sequestration emerge that warrant further scrutiny.

The accumulation and fluxes of carbon following restoration

One of the main advantages of the study design in **Paper II** is the concurrent assessment of oxygen and carbon fluxes with two independent methods running simultaneously (Figure 9). This allowed for an estimation of dissolved inorganic carbon (DIC) fluxes based on empirically-derived O_2:DIC ratios together with high-resolution flux measurements under natural conditions. By assessing the major benthic particulate organic carbon (POC) pools in sediment, fauna, macrophyte and microalgal biomass, we were able to construct a carbon budget for the four stages of eelgrass development (Figure 13). The fluxes of DIC going in and out of the eelgrass system increased as the meadow developed from bare sediments to a mature meadow. The organic carbon pools of benthic fauna and macroalgae followed this trend with consistent increases of biomass C, but other POC pools showed variable trends. For instance, sediment POC was highest in the natural meadow (74±28 mol C m^{-2}), followed by the three-year-old plot (54±12 mol C m^{-2}), the seven-year-old plot (41±3 mol C m^{-2}) and was lowest in bare sediments (29±8 mol C m^{-2}) (Figure 13). Assuming a similar import of allochthonous POC to the four sites, these results show that sediment carbon stocks may start to build up shortly after restoration, but further increases can be slowed or reversed by biodiversity colonization and increased metabolism. Importantly, seasonal variation in metabolism together with lateral import and export fluxes need to be constrained to be able to close the carbon budget.

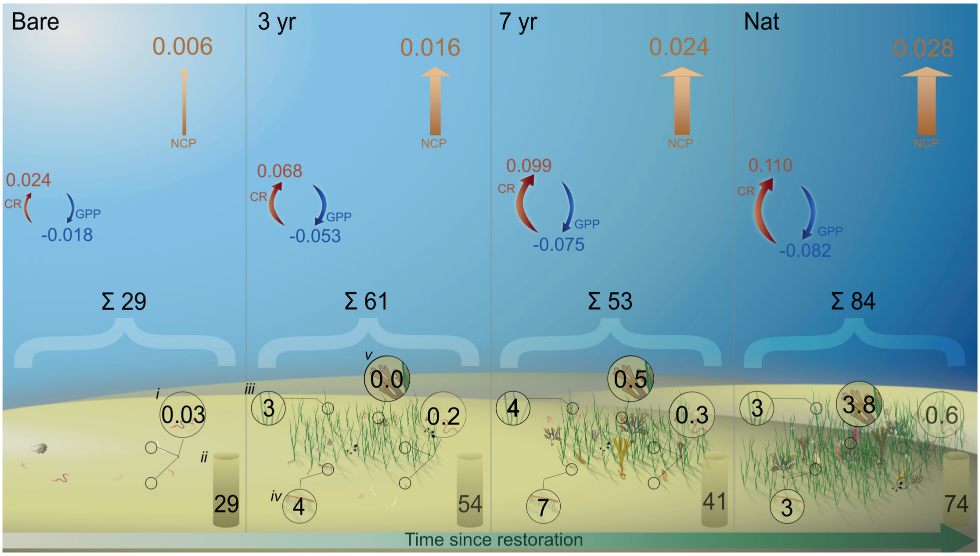


Figure 13 Carbon budget or different stages in eelgrass development since restoration, going from bare sediments to a mature natural meadow. Arrows indicate fluxes of dissolved inorganic carbon from gross primary productivity (GPP, blue arrow), community respiration (CR, red arrow) and net community productivity (NCP, orange arrow). Pools of particulate organic carbon include *i)* fauna, *ii)* sediment, *iii)* eelgrass aboveground biomass, *iv)* eelgrass belowground biomass, and *v)* macroalgae and summation sign indicates the total benthic carbon stock. Fluxes are in mol m^{-2} day^{-1} and pools in mol m^{-2}. Fauna and algae symbols courtesy of University of Maryland (https://ian.umces.edu). Figure modified from **Paper II**.

Seagrass ecosystem functions beyond the meadow

Ecological connectivity and beach wrack

Having established the important role of eelgrass meadows in benthic diversity (**Paper I-III**), its effect beyond the meadow itself is less well known, especially with regards to plant species.

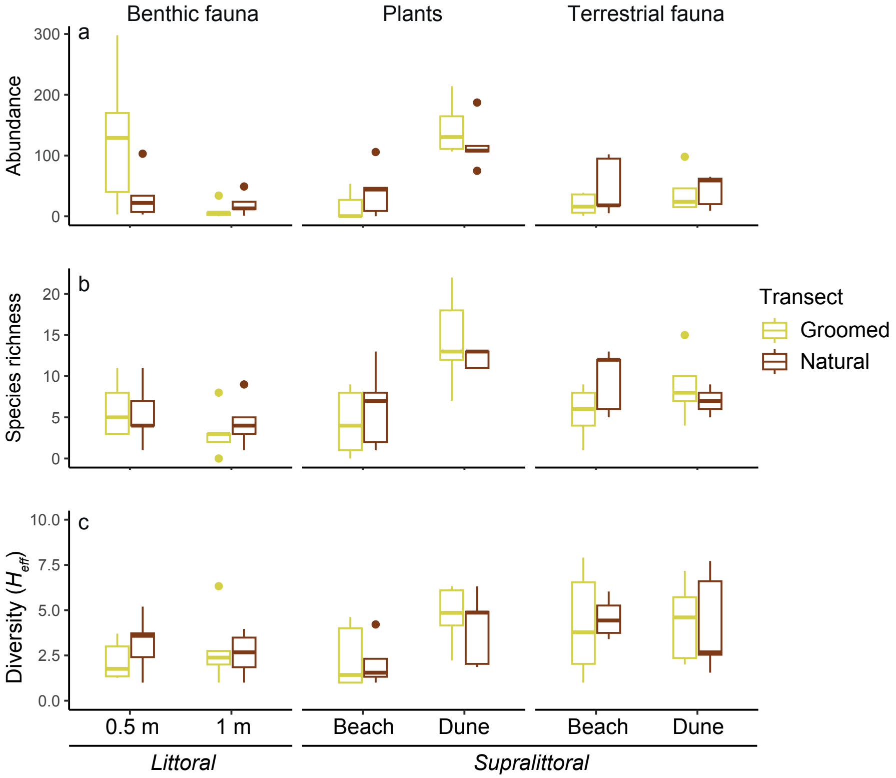


Figure 14 Abundance (a), species richness (b) and taxonomic diversity (c) of benthic fauna, terrestrial plants and terrestrial fauna in groomed and natural beach segments. 0.5 m and 1 m represent the water depth in meters. Figure from **Paper IV**.

We found mixed effects on biodiversity where beach wrack tended to stimulate mainly terrestrial fauna abundance but had variable effects on terrestrial plants (**Paper IV**). Effects were also highly variable between dunes, beach plane and the shallow littoral environment (Figure 14). For instance, we observed positive effects of beach wrack on terrestrial fauna on the beach plane (Figure 15) whereas removal of beach wrack through grooming had a positive, albeit weak, effect on benthic fauna abundance. Unexpectedly, eelgrass wrack attracted a richer and more abundant fauna compared to macroalgal wrack. This finding is surprising and counter-intuitive based on the lower nutritional content in eelgrass compared to macroalgae (MacMillan and Quijón 2012; Quintanilla-Ahumada et al. 2023). However, several of the species that favored eelgrass are commonly found further inland and those that do not feed directly on wrack may use it to forage for prey, to hide from predators or to lay their eggs (Colombini et al. 2003; Rodil et al. 2008; Davis and Keppel 2021). This illustrates how eelgrass wrack can function as a habitat despite its lower nutritional value compared to macroalgae and warrants further research into the multifunctional role of eelgrass wrack.

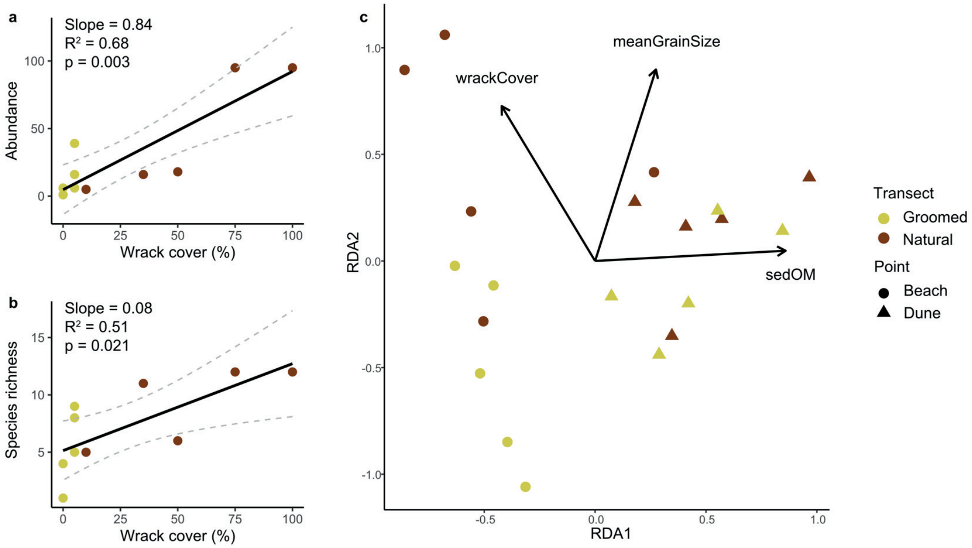


Figure 15 Terrestrial fauna diversity as a function of wrack cover. Linear regression of abundance (a) and species richness (b) as a function of wrack cover. c) shows redundancy analysis of terrestrial fauna communities with the dominant predictor variables outlined as arrows. sedOM is the sediment organic matter content as % dry weight. Figure modified from **Paper IV**.

As opposed to fauna, terrestrial plant diversity seemed to benefit from grooming, potentially due to lower cover of encroaching invasive species to favor stress-tolerant species. It is also possible that the higher abundance of beach visitors together with repeated grooming represents an intermediary disturbance regime (sensu Connell 1978) that promotes plant diversity. Additionally, we hypothesized that influx of wrack may constitute a nutrient supply that stimulates plant growth. However, while plant cover was indeed positively related to soil nitrogen content, our results do not suggest a significant nitrogen supply from beach wrack. Here, future research could employ analyses using tracers and stable isotopes (^{13}C and ^{15}N) to track the sources of mineral nutrients in dune landscapes and explore links to plant diversity.

Seagrass restoration as a nature-based solution for coastal protection

One of the central themes leading up to this thesis was the potential of using seagrass restoration as a nature-based method to protect shorelines against erosion, flooding and storms. While not being explicitly evaluated in the field, a review of the scientific literature gave little evidence of the feasibility of seagrass restoration for such purposes in temperate areas. One of the reasons for this is the apparent temporal mismatch where the highest intensity and frequency of storms coincide with seagrass senescence, and a substantial amount of the leaves is shed (Paul and Amos 2011; Hansen and Reidenbach 2013). In Southern Sweden, this is during late fall and winter. Furthermore, in an ongoing study not included herein, preliminary findings suggest that the wave attenuation capacity of a large continuous eelgrass meadow in Öresund is low (< 5%). Importantly, the wave attenuation capacity quickly diminishes at depths above three meters, and the net effect on coastal erosion appears to be negligible (Almström et al. unpublished). Combined with the findings from **Paper III**, which indicated that seagrass restoration may not be feasible at depths shallower than three meters, it is reasonable to believe that seagrass restoration is not a viable NbS for coastal protection in these areas. However, while active restoration alone may not be a feasible solution to rely on for coastal protection in exposed, temperate areas, it could be used as a component in a suite of NbS where synergistic effects may arise (**Paper V**; Chen et al. 2022).

Using seagrass restoration in combination with other NbS

Based on the literature review in **Paper V**, we propose a multi-methodological approach combining restoration of vegetation (e.g. seagrass) and beach nourishment to yield a viable coastal defense utilizing potential self-reinforcing mechanisms. We identified both additive and antagonistic effects between seagrass restoration and beach nourishment that influenced both technical and ecological aspects. For instance, beach nourishment is an increasingly popular intervention in areas with severe coastal erosion and risks to local infrastructure. However, detrimental effects on fauna communities have been reported and while these may be difficult to avoid, complementary restoration of vegetation could improve recovery trajectories by providing refugia for mobile species and acting as a propagule source during recovery (**Paper V**). Importantly, no studies were found that had explicitly evaluated these interactions in the field, warranting future field studies that specifically address the effects on coastal multifunctionality.

Collectively, my findings have shown that the mere presence of eelgrass, rather than any specific attribute, constitutes important habitat for benthic fauna across environments (**Paper I-III**). Restoration rapidly improves benthic diversity although ecosystem functioning may be affected in variable ways (**Paper II-III**). Exported eelgrass can indirectly play a vital role in structuring beach diversity but excess beach wrack deposits could impair rare plant species (**Paper IV**). Where no direct coastal protection effects are obtained, it may alleviate the negative impacts on biodiversity associated with other coastal adaptation strategies such as beach nourishment (**Paper V**).

Conclusions

The main conclusions from this thesis are as follows:

i. Planting eelgrass rapidly restores benthic fauna communities and ecological integrity, thereby elevating taxonomic diversity across environmental gradients. However, functional diversity may lag as environmental filtering can impede colonization of rare and functionally distinct species.

ii. Benthic metabolism increases as a seabed transitions from bare sediments to an eelgrass meadow, resulting in oxygen and carbon fluxes that scales with meadow age.

iii. Eelgrass meadows can be highly net heterotrophic. Relationships between benthic diversity and metabolism imply that colonization of macroalgae and fauna can fuel community respiration that exceeds carbon uptake on diel timescales.

iv. Eelgrass habitat provisioning extends beyond meadow boundaries and facilitates terrestrial fauna diversity across sandy beaches. Beach wrack comprised of eelgrass is preferred over macroalgae, despite its lower nutritional content, highlighting other functions than a direct food source.

v. Eelgrass and dune vegetation could be utilized in conjunction with other NbS such as beach nourishment to amplify positive effects on coastal diversity and resilience.

Outlook and future direction

The seagrass habitat plays a vital role in marine benthic diversity, structuring faunal communities through biotic and abiotic interactions. Preventing further loss and assisting in the recovery of these habitats are low-regret management options to deter biodiversity loss. Importantly, active restoration interventions should be preceded by careful site selection based on comprehensive test trials. With successful restoration, a growing body of evidence points to possibilities of rapid increases in fauna diversity, and recovery trajectories should be closely monitored after restoration. The findings in this thesis suggest that functional redundancy can be higher in bare sediments and at initial stages of restoration because species with unique traits have not colonized yet. Due to a dominance of several generalist species among these early colonizers, a higher resilience to disturbance could be expected. This is a largely overlooked aspect in seagrass restoration research, and the implications for the recovery of ecosystem functions is an interesting avenue to explore.

Importantly, the marked seasonality in fauna dynamics calls for carefully designed monitoring schemes, that ideally characterize the natural temporal variation in reference meadows prior to initiating restoration. However, it can be argued that there is now sufficient empirical evidence pointing to the near immediate positive effects on biodiversity across environments such that they can be assumed, provided sufficient survival of the restored seagrass (Fonseca et al. 1998). Accordingly, efforts and funds should be allocated primarily towards monitoring of seagrass development rather than its associated communities. Recent developments in remote sensing (e.g. by drones, airplanes and satellites) can enable cost-effective monitoring of areal coverage and survival rates of restored plots (Hossain et al. 2015; Hedley et al. 2017), especially if boosted by artificial intelligence (e.g. Yang et al. 2023).

Seagrass meadows sustain many ecosystem functions, some of which have been deemed relevant for climate mitigation and adaptation solutions. In the face of global change, nature-based alternatives to ameliorate negative impacts are being promoted and implemented in coastal areas. Albeit covering only a month during summer, the findings presented herein point to potential tradeoffs between biodiversity and net carbon uptake. Future research should therefore focus on establishing annual rates and assessing the lateral import and export of carbon to close the carbon budget for restoration projects. Otherwise, there is a tangible risk of overestimating the role of seagrass restoration in combatting climate change and its effects, and more research is therefore urgently needed.

The specific role of macroalgal diversity within otherwise monospecific seagrass meadows is a largely unexplored topic in seagrass carbon cycling. Indeed, seagrass meadows are often mixed either due to interspersion of different bottom substrates or, as seen here, drifting macroalgae are captured by the seagrass meadow and becomes an integral part of the species composition in the meadow (**Paper II**). Future research should address the net effect on carbon cycling from multi-specific macrophyte habitats. There are opportunities to explore fundamental concepts of biodiversity-ecosystem functioning, such as niche complementarity, in the field, that can advance our abilities to predict restoration effects on local carbon budgets.

The export of seagrass material provides a habitat and trophic subsidy to terrestrial fauna which can extend far inland. However, the role in fertilizing dune plant communities against a backdrop of encroaching invasive species warrants further investigation. This is especially relevant for frequently visited beaches where management practices often involve repeated removal of beach wrack. Ideally, managers should consider how management practices can be structured to obtain positive effects on biodiversity where sandy beaches are kept free from overgrowth of invasive species while at the same time sufficient wrack biomass is left to sustain faunal diversity and secondary production on the beach. As benthic fauna diversity may also respond to beach grooming activities, ensuring healthy macrophyte habitats is key in conservation of marine biodiversity. Moreover, the possibility to utilize beach wrack for armoring coastal dunes should be studied further, as this could truly extend the multifunctionality aspect of a nature-based coastal protection measure. As restoration projects scale up, efforts should embrace a seascape perspective that includes multiple habitats and considers the connectivity within and between heterogenous benthic landscapes. Such a seascape approach to restoration can pave the way for healthy and resilient coastal ecosystems that sustain multiple functions.

For coastal adaptation, there is a pressing need to conduct more field studies that investigate *in situ* wave attenuation in seagrass meadows across seasons, particularly in temperate areas with large seasonal variation in weather patterns and seagrass phenology. The effects of seagrass on sediment transport processes and coastal erosion in temperate areas are knowledge gaps that should also be addressed in future research. Restoring seagrass as a nature-based solution to limit coastal erosion is still in an exploratory phase with no definite answers, albeit with preliminary results pointing to negligible effects. Promisingly however, with NbS and habitat restoration in general gaining traction, there are ample opportunities to assess interactions between methods in the field, both in terms of ecological and coastal protection effects. The potential synergies if several actions are implemented simultaneously is an appealing topic to further examine. Moreover, restoration projects that involve local communities and leverage municipal or regional partners in monitoring programs can ensure cost-effective, long-term monitoring not only of restoration success but also the effects on biodiversity and ecosystem services.

The present decade has been declared the decade of restoration (United Nations 2019), and the European Union has provisionally pledged to restore 20% of degraded habitats by 2030 (European Council 2023). Coincidentally, it is also proclaimed as the ocean decade (UNESCO 2018). Undoubtedly, this should positively influence marine restoration efforts such as seagrass restoration. The increased awareness of the role of the ocean in future solutions (Gattuso et al. 2018; Hoegh-Guldberg et al. 2019) is encouraging, and the focus on restoration hopefully opens up prospects to undo historical damages. However, while disseminating the severity of marine biodiversity loss to broader audiences is essential, it is imperative that the focus is still primarily on limiting further loss by conserving what we have and minimizing the negative anthropogenic effects exerted on existing ecosystems. By succeeding to do so, recovery of degraded ecosystems and threatened species can follow. Equally important, burning of fossil fuels must be phased out before we can seize the potential of any climate change mitigation strategy (Ho 2023). Because carbon sequestration is a very slow process, preserving existing seagrass is a much more efficient way of mitigating climate change compared to planting new (Johannessen 2022; Unsworth et al. 2022; Johannessen and Christian 2023). Indeed, many seagrass ecosystems hold large carbon stocks that can turn into non-trivial sources of CO_2 if a meadow is lost (Arias-Ortiz et al. 2017; Moksnes et al. 2021b).

From a broader perspective, there are conceivable intrinsic problems with the concept of restoration, largely related to our anthropocentric view on nature. One of the cardinal rules for restoration should arguably be that it ought to re-create lost habitat, rather than creating a new. Yet, using it as a tool intended to supply an ecosystem service to society – whether it is coastal protection or carbon sequestration – entails a sense of commodification of nature (e.g. McCauley 2006). Moreover, it invokes the view of unvegetated sediments as biological deserts. However, bare sediments may play an important role in the coastal system as a whole, despite not being as species-rich as seagrass meadows (Boudouresque et al. 2021). Finally, considering the economic costs associated with seagrass restoration, which are roughly a hundred thousand US dollars per hectare in general (Bayraktarov et al. 2016), it is worth weighing these against the costs of limiting habitat destruction through policy change such as instatement of marine protection areas, fishing restrictions, eutrophication control et cetera.

As climate change and biodiversity loss continue to unfold, we need a holistic perspective on mitigation and adaptation strategies. The coastal zone requires a multitude of solutions that consider context-dependent interactions. This thesis hopefully provides some clarity on what role eelgrass meadows can play – below, above and beyond.

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