Plant and invertebrate diversity and management in wetlands

The salt marsh and reed beds of De Østlige Vejler, Denmark

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PLANT AND INVERTEBRATE DIVERSITY AND MANAGEMENT INWETLANDS

THE SALT MARSH AND REED BEDS OF DE ØSTLIGE VEJLER, DENMARK

BY
LINE HOLM ANDERSEN

DISSERTATION SUBMITTED 2020

AALBORG UNIVERSITY
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Back cover photo: A wooden pathway leading visitors into the reed bed in De Østlige Vejler by Line Holm Andersen
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PREFACE

This thesis represent the final product of three years of Ph.D. study at the Department of Chemistry and Bioscience, Aalborg University, Denmark. The study was funded by Aage V. Jensens Nature Fond and all fieldwork presented within the thesis were conducted within their scientific reserve *De Østlige Vejler*. The thesis is dived into two parts. First, an introduction to the area of investigation: the wetland habitats salt marsh and reed beds, and their diversity and management. This part serve to give a broader overview of the general field of wetland ecology and management while placing the work conducted during this Ph.D. in perspective. The second part is a collection of four articles and manuscripts written during my time as a Ph.D. student. The four manuscripts are the main products of my Ph.D.

Line Holm Andersen, May 2020

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First, I would like to thank my main supervisor Dan Bruhn, who reintroduced me to the world of botany. Throughout my time as a Ph.D. student, you have always welcomed academic meetings and discussions, and been ready with plenty of academic career advice. You have challenged me and made me strive for perfection. I would also like to thank my co-supervisors, Cino Pertoldi and Simon Bahrndorff. Cino, thank you for believing in me ever since we started working together during my bachelor project. Simon, thank you for great talks on invertebrates and for helping me aim towards journals with higher impacts. I hope to have continued cooperation's with all of you in the future.

Thanks all my colleagues at the biology department at Aalborg University. Thank you for lunchtime chats, fun summer parties and Christmas lunches. Thanks to fellow Ph.D. students Natasja and Julie for talks on Ph.D. life. I would also like to thank all the project and master students that decided to work with me in Vejlerne for all their assistance in the field. Further, I would like to thank our lab-technician Helle for helping me in the lab with my many, many samples. I would also like to thank lab-interns Lotte, Rasmus and Sofie for helping me with different and very time-consuming laboratory tasks. Thank you Susan for always making sure my invertebrate traps were clean and ready to take to the field.

Next, I would like to thank Petri Nummi for welcoming me at his lab at Helsinki University, Finland. I felt welcome and at home from day one, and really appreciate you including me in both academic discussions and social engagements. I would also like to thank my office-mates in Finland, Maijo, Somayeh, Elina, Stella and Mia, as well as Wenfei (though technically not an office-mate), for many wonderful conversations, both academic and personal, and talks about life as a Ph.D. student.

I would like to thank Aage V. Jensen Naturfond for funding my project and giving me the chance to work in beautiful Vejlerne. Without their financial support, this project would not have been possible. I would also like to thank Niels Dahlin for introducing me to Vejlerne. I am grateful for having been allowed to stay at *det lille gule hus*, as living within Vejlerne during my fieldwork saved time and energy.

Finally, I would like to thank my family and friends for support and understanding during the past three years where most of my time have been spend on research rather than social engagements. Your encouragements have been greatly valued!

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PAPER IV	**Andersen, LH**, Nummi, P, Rafn, J, Frederiksen, CMS, Kristjansen, MP, Pertoldi, C, Trøjelsgaard, K, Bruhn, D and Bahrndorff, S. Time since last harvest affect both biomass and diversity of invertebrates. In preparation.

ENGLISH SUMMARY

The recurring theme in this thesis is the diversity and management of coastal wetland habitats with focus on plant and invertebrates. The common denominator for the papers presented in this thesis is that all results build on fieldwork conducted within the scientific reserve *De Østlige Vejler*, Denmark. *De Østlige Vejler* is owned and managed by Aage V. Jensens Nature Fond and contain salt marshes, reed beds and lakes. The area is home to an abundance of birds, which have been studied extensively, whereas the plant and invertebrate communities have received little attention prior to this thesis.

PAPERS I-II, I focused on the salt marsh habitat of *De Østlige Vejler*. The salt marsh is facing a number of threats including land reclamation, human infrastructure and climate change.

In **PAPER I**, I investigated the vegetation and environmental conditions of a salt marsh entrapped behind a dike, thereby shielded from tidal floods. Dikes are problematic as they limit natural hydrology patterns. I found that the salt marsh had a low soil salinity level and that the vegetation was significantly different from that of Danish salt marshes not found behind dikes. The vegetation, however, did not resemble that of a fresh meadow either. High species richness and diversity levels correlated positively with ammonia availability and were negatively correlated with soil salinity.

In **PAPER II**, I took advantage of interannual weather fluctuations experienced during the fieldwork of 2017, where the summer was wet and cold, and 2018, which experience record-breaking heat and a low precipitation. Species richness decreased during the warm and dry conditions, and I found a large turnover in species composition between years. The plant community contained a significantly higher proportion of salt marsh specific species (halophytes) during dry conditions than wet. One explanation for the change in the plant community could be the corresponding change in the physical environment where soil moisture levels decreased and soil salinity levels and the amount of available nutrient increased during the warm, dry year.

Ungrazed salt marsh vegetation on low salinity soils often develop into reed beds dominated by perennial grass *Phragmites australis*. In **PAPERS III-IV**, I looked at the effect of reed bed management and time since last management (reed bed age) on reed bed vegetation and invertebrate community. I included reed beds aged 0, 3 and 25 years, and management methods cutting and harvest. In **PAPER III**, I compare the effects of reed bed harvest (stems removed) to reed bed cutting (stems left behind) and found that when reed stems were removed, significantly more light-lowing plants were found compared to when the stems were left behind. In **PAPER III,** I also looked

at the effect of time since last management and found that it significantly impacted species richness and habitat heterogeneity. Unique species were found in each reed bed age and treatment indicating that overall reed bed species richness would decline should any of the treatments be terminated.

In **PAPER IV**, I still looked at the effect of time since last reed bed harvest, but shifted focus from plants to invertebrates. Multiple studies have looked at the effect of reed management on invertebrates but have not reached a consensus on the effects of harvest, and next to no studies have included the effects of time since last management. I saw a clear positive effect of management as well as a negative effect of time since last management on the biomass of both ground-dwelling and flying invertebrates. Time since last harvest had a significant effect on the invertebrate community and distinct communities were found in recently harvested areas and areas that had last been harvested 3 or 25 years ago. The differences between reed bed communities were already clear from data at the Order level, but increased if using data at the family level (Coleoptera), whereas little extra information was gained by increasing the taxonomic scale to genus or species. The response to reed bed age was both Order and family specific. This indicate that reed bed managers surveying invertebrates can gain useful information on the effects of management by surveying coarser taxonomic levels. In order to retain a diverse habitat benefitting most invertebrate Orders ad Coleoptera families, while also retaining a high invertebrate biomass, small scale harevest that create a reed bed mosaic containing different reed bed ages is recommended.

DANSK RESUME

Det gennemgående tema i denne ph.d. afhandling er kystnære vådområder med fokus på planter og invertebrater. Fællesnævneren for de artikler, der præsenteres i afhandlingen, er, at de alle bygger på feltarbejde foretaget i det videnskabelige reservat De Østlige Vejler, Danmark. De Østlige Vejler ejes og forvaltes af Aage V. Jensens Naturfond og indeholder strandenge, rørskove og søer. Området er hjemsted for et væld af fugle, der er blevet studeret indgående, mens plante- og invertebratsamfundet kun har være genstand for en begrænset mængde forskning forud for denne afhandling.

ARTIKLERNE I-II fokuserer på strandengen i De Østlige Vejler. Strandenge står over for et væld af trusler inklusiv landindvinding, infrastruktur og klimaforandringer.

I **ARTIKEL I** undersøger jeg både vegetationen og de miljømæssige forhold på en strandeng, indelukket bag et dige, der skærmer den fra tidevandspåvirkning. Diger er problematiske, idet de begrænser den naturlige hydrologi. Jeg erfarede, at jorden på strandengen havde en lav salinitet og at vegetationen adskilte sig signifikant fra vegetationen på danske strandenge, der ikke befinder sig bag diger. Vegetationen lignede dog heller ikke den man finder på tidvis våde enge. En høj artsrigdom og diversitet korrelerede positivt med ammonium tilgængelighed og korrelerede negativt med jordens saltholdighed.

I **ARTIKEL II** udnyttede jeg de klimamæssige udsving, der fandt sted under feltarbejdet i 2017, hvor sommeren var kold og våd, og 2018, hvor sommeren var rekordvarm og med en lille mængde nedbør. Artsrigdommen faldt under de varme og tørre betingelser, og der var et stort turnover i artssammensætningen mellem de to år. Plantesamfundet indeholdt en signifikant større andel af strandengsplanter (halofytter) under de varme end under de våde forhold. En mulig forklaring på ændringen i plantesamfundet var de ændringer der skete i det fysiske miljø mellem de to år, idet jorden fugtighed faldt, hvorimod saliniteten og mængden af tilgængelige næringsstoffer steg under de tørre, varme betingelser.

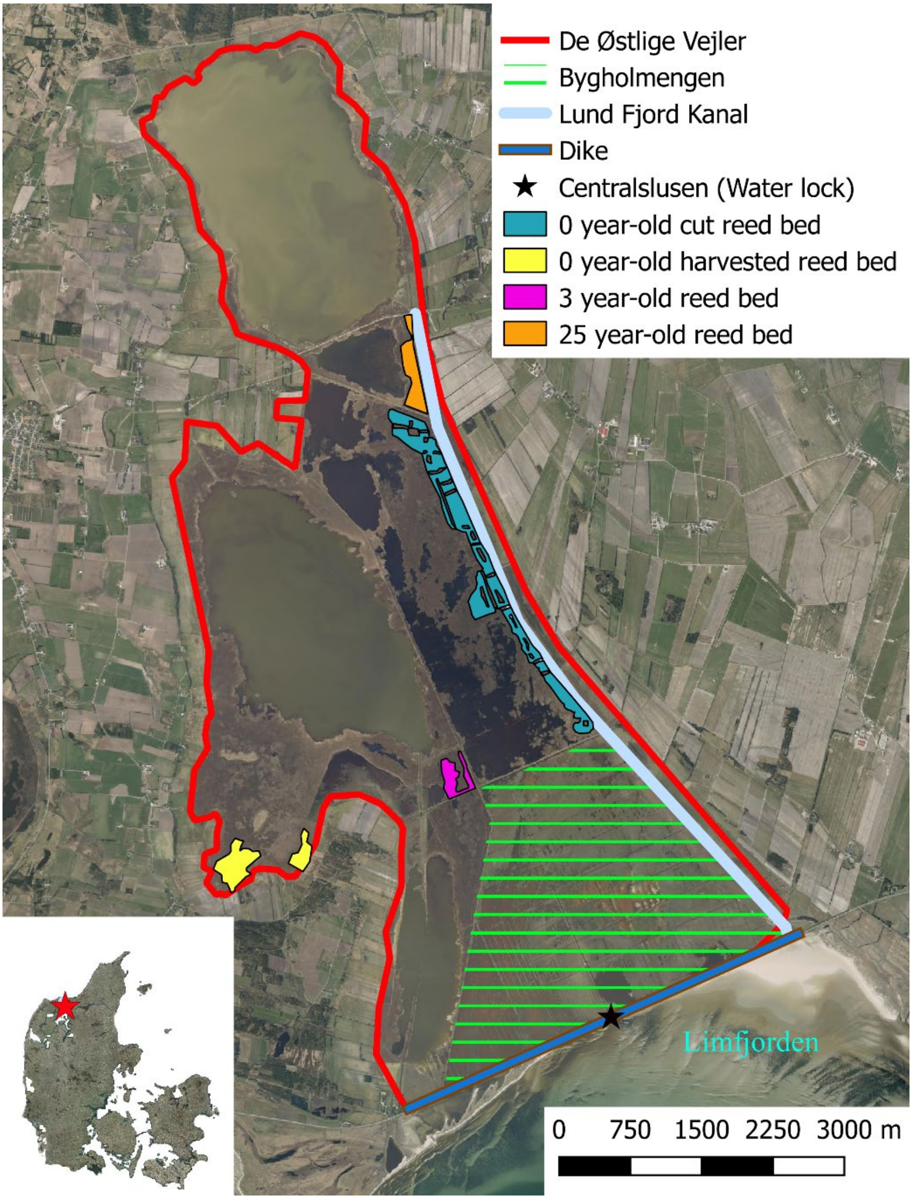
Strandengsvegetationer, der ikke afgræsses, og hvor jorden har et lavt saltindhold, udvikler sig ofte til rørskove domineret af den flerårige græs *Phragmites australis*. I **ARTIKLERNE III-IV** så jeg på effekten af rørskovsforvaltning og tid siden sidste forvaltning (rørskovs alder) på rørskovens vegetation og invertebratsamfund. Jeg sammenholdet aldrene 0, 3 og 25 år, samt forvaltningsmetoderne høst og rørslåning. I **ARTIKEL III** sammenholdt jeg rørhøst (tagrør fjernes) og rørslåning (tagrør efterlades) og opdagede at når man høstede og fjernede tagrørene, spirede der signifikant flere planter op, der trives ved højere lysintensitet, i forhold til, når tagrørene blev efterladt. I **ARTIKEL III** så jeg også på, hvilken effekt det har, hvor længe en rørskov har stået uforvaltet (rørskovens alder), og fandt, at det både

påvirkede artssammensætningen og habitatets heterogenitet. Der var unikke arter i hvert af de undersøgte områder, såvel som i de forskellige rørskovaldre, hvilket viser, at man vil miste arter, hvis man ikke opretholder alle behandlingsmuligheder og aldre.

I **ARTIKEL IV** så jeg stadig på, hvilken effekt rørskovsalder har, men ændrede fokus fra planter til invertebrater. Flere studier har undersøgt, hvordan rørskovsforvaltning påvirker invertebratsamfund uden at nå til en konsensus om, hvilken effekt rørhøst har, og kun meget få studier har inkluderet rørskovsalderen i deres analyser. Jeg fandt, at invertebratbiomassen af både flyvende og overfladelevende invertebrater reagerede positivt på rørhøst og negativt på øget rørskovsalder. Rørskovens alder havde også en signifikant effekt på invertebratsamfundet, idet forskellige invertebratsamfundet blev fundet i det nyhøstede område, den 3-årige rørskov og den 25-årige rørskov. Det var allerede muligt at se forskellen, når man så på invertebraterne på det grove taxonomiske niveau Orden, og mens forskellen blev mere tydelig af at se på data på et familie niveau (Coleoptera), vandt man mindre ved at øge det taxonomiske niveau til genus eller art. Det betyder, at rørskovsforvaltere kan opnå nyttig information om effekten af forvaltning allerede ved at undersøge grovere taxonomiske niveauer. Vi anbefaler rørhøst på et mindre skala, hvor en rørskovsmosaik af rørskove i forskellige aldre opretholdes, hvilket både vil sikre en høj invertebratbiomasse samt gavne de fleste invertebrat Ordner og Coleoptera familier.

MAP OF DE ØSTLIGE VEJLER

Reference map of *De Østlige Vejler*, Denmark with location names. I will refer to these areas repeatedly throughout this thesis.



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INTRODUCTION

1.1. DIVERSITY IN A WORLD MANAGED BY MAN

The world is currently facing a biodiversity crisis caused by human reproduction, consumption and an increasingly effective exploitation of the environment (Small 2011). Just 5% of Earth's terrestrial surface (excluding Antarctica) remain untouched by man and the remaining 95% is impacted to a varying degree (Kennedy et al. 2019). Europe is one of the most intensively used continents on the globe with up to 80% land used for settlement, agriculture, forestry and infrastructure (European Environment Agency 2008). Coastal wetlands are especially vulnerable to human use, primarily due to agricultural drainage, and experience an annual estimated habitat loss of 1% worldwide (Zedler, Joy B. & Kercher 2005). The diversity in Europe is also under threat as 42% of terrestrial plants and animals have declined within Europe and Central Asia during the last decade (Fischer et al. 2018). Luckily, protecting nature is considered increasingly important and by 2017, almost 26% of the land and inland waters of Europe were designated protected areas (European Environment Agency 2018).

Even though mismatches between protected areas and biodiversity hotspots exist (Jenkins et al. 2015), protected areas overall hold a significantly higher biodiversity than non-protected areas (Gray et al. 2016). Most protected land is under some form of human management (Primack 2010). As humans have modified the majority of protected land to some extent, the best way of obtaining or maintaining high levels of biodiversity is through active management rather than leaving nature to itself (Primack 2010). If unmanaged or managed to an extent where efforts are insufficient to halt habitat degradation, protected areas might become so-called 'paper-parks', areas that are protected on paper but in reality has a decreasing conservation value (Joppa et al. 2008; Primack 2010). For example, traditional agricultural landscapes shaped by humans through centuries contain a high species diversity, which is in risk of disappearing due to agricultural intensification, but would equally risk a decline in an unmanaged scenario where succession gradually turn open landscapes into woodlands (Fuller 2000; Luoto et al. 2003; Paracchini et al. 2007; Schmitt & Rákosy 2007; Shephard et al. 2013; Andersen, L. H. et al. 2017). A different example is the wetland habitat, which due to human exploitation during the last century has declined dramatically with up to 50% of the world's wetlands having disappeared; hence, active management including limiting drainage for agriculture, reinstatement of grazing in overgrown wetlands and removal of dams are required to protect remaining wetlands (Silva et al. 2007). Sometimes, an abandonment of management is suitable for the diversity of some organisms, even it if decreases the diversity of others, as is the case of the abandonment of forest management which decrease plant richness but increase crane fly richness (Schmidt, Wolfgang 2005; Byriel et al. 2020). Yet other times, management is present but is targeted human needs rather than biodiversity conservation, e.g. by eliminating top predators in order to increase deer populations for hunting or by not allowing natural wildfires in fire dependent habitats (Primack 2010). In wetlands, stakeholders might argue for contrasting management goals including flood risk mitigation, biodiversity conservation and recreational activities (Herath 2004; Birol et al. 2009). A cessation of wetland drainage, for instance, might please conservationists but be problematic for neighbouring farmers whose lands now risk being flooded (Jakobsen & Sørensen 1993). Other times, creating or restoring wetlands benefit multiple stakeholders. Created wetlands have recreational value in addition to a positive effect on hunting and act as a buffer for water that would otherwise have been retained on nearby, low-laying agricultural fields, while retaining nutrients from agricultural drainage water thereby protecting near-by streams (Johnson & Linder 1986; Pease et al. 1997; Zedler, Joy & Leach 1998; Woltemade 2000).

With this large variety of management options, it is important that managers set management targets and use the available knowledge to meet their goals. This means that there is a need for knowledge useful to managers – First, knowledge on the diversity present and second knowledge on how diversity respond to management.

1.2. WETLANDS

The term 'wetland' is defined in many ways in the literature with definitions ranging from broad to more narrow. Wetlands are areas where water is the primary factor controlling the environment as well as its plant and animal life (Zedler, Joy B. & Kercher 2005). According to the Ramsar Convention, wetlands include areas with static or flowing water at a maximum depth of six meter, and the water can be fresh, brackish or marine (Ramsar Convention Secretariat 2013). Wetlands have also been defined as the transitional area in between terrestrial and aquatic habitats, and is the broad term for a large number of habitats including marsh, swamp, fens and bog (Cowardin et al. 1979). When salinity levels are below 0.5 ppt, the wetland is fresh while salinity levels above indicate brackish or saline conditions (Odum 1988).

Wetland ecosystems cover less than 9% of earth's land area (Zedler & Kercher 2005) and is currently in decline (Vadász et al. 2008; Čížková et al. 2013). Wetlands are important habitats that pose value to humans via food provisioning, water supply, recreation, electricity generation, raw materials and in nutrient retention (Wilson & Carpenter 1999; Hansson et al. 2005; Ramsar Convention Secretariat 2013). Wetlands are also important to a large number of flora and fauna (Holland et al. 1990; Costanza et al. 1997) due to its high biodiversity value (Hansson et al. 2005; Ramsar Convention Secretariat 2013). Countless species of plants and invertebrates depend on its water and high primary production (Junk et al. 2006; Flinn et al. 2008; Ramsar Convention Secretariat 2013; Epele & Miserendino 2016). A high number of both aquatic and terrestrial invertebrates inhabit wetlands with more than 130 invertebrate families observed with ephemeral wetlands alone (Batzer & Boix 2016). Obligate wetland

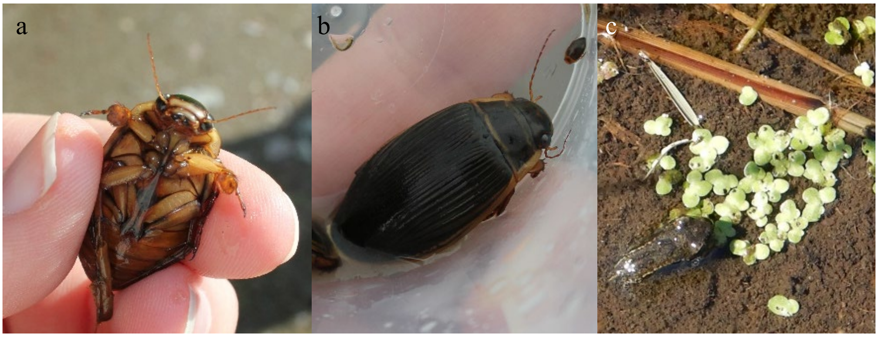


Figure 1 *Obligate wetland species Coleoptera: Dytiscidae sp. from a Finnish wetland and duckweed from a Danish wetland. Male dytiscidae (a) with tarsi modified into suckers used to hold on to females during mating and female (b) with a grooved elytra making it difficult for males to hold on during mating. Duckweed (Lemna minor) (c) is an obligate wetland plant.*

invertebrates, referring to species occurring in >99% of wetlands and only rarely outside wetlands, include Coleoptera: Dytiscidae (Fig. 1), Diptera: Culicidae and Chironomidae, Hemiptera: Notonectidae and Odonata: Coenagrionidae (Batzer & Boix 2016). A high number of plants species also depend on the wetland habitat with more than 6700 macrophytes listed as wetland obligates in the United States including families Lemneae (Fig. 1) and Typhaceae (Kadlec & Wallace 2008).

Luckily, human needs for ecosystems services sometimes go hand-in-hand with biodiversity conservation. Increasing the vascular aquatic plant diversity benefit both overall wetland diversity and the ecosystem services provided, as a higher plant species richness can result in up to 25% more algal biomass, thereby supporting a greater abundance of fish and other wildlife while at the same time retaining up to 30% more polluting nutrients (Engelhardt & Ritchie 2001). Livestock grazing on salt marshes can maintain plant diversity while at the same time providing fodder to human livestock but decrease the invertebrate diversity (Jensen 1985; Andresen et al. 1990).

1.3. COASTAL WETLANDS

Coastal marshes occupy the interface between land and sea, and can be regarded as a highly dynamic terrestrial ecosystem subject to large water level fluctuations and erosion (Adam 1990). Coastal wetlands are essential in stabilizing coastlines and as carbon storage, they act as refuge, breeding and feeding grounds for both marine and terrestrial species including fish, birds, invertebrates and plants (Mcowen et al. 2017).

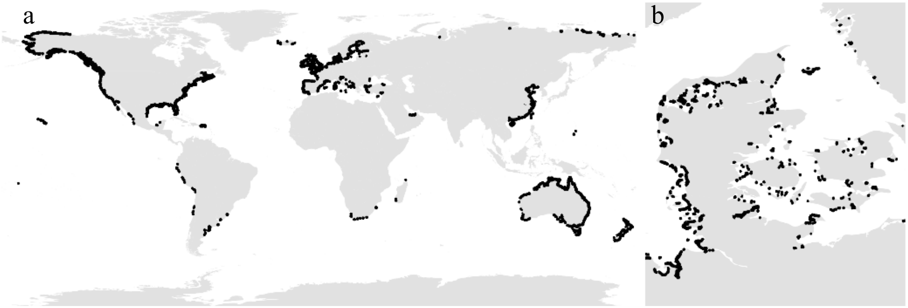


Figure 2 The global distribution of salt marshes (black) (a) and the distribution within Denmark (b) following McOwen et al. (2017).

Coastal wetlands cover a range of habitats including swamps, marshes, mangroves, estuaries, seagrass beds and mud flats. The fieldwork conducted during my Ph.D., presented in **PAPERS I-IV**, were conducted in the coastal wetland habitat *De Østlige Vejler* (Box 1). Therefore, the remaining sections will focus on the coastal wetland types found within *De Østlige Vejler*, salt marshes and reed beds, and their diversity and management.

1.3.1. COASTAL MARSHES

Coastal marshes are marshes located close to the shore. Due to tidal floods, storm surge and salt sprays, salinity is an important factor shaping the coastal marshes. Salinity levels does not necessarily peak closest to the ocean but might become hypersaline in areas less frequently flooded, given the area receives limited inputs of freshwater and thereby dry out between floods with seawater. Another distinct characteristic of the coastal marsh system is the vegetation zonation created in part by the salinity gradient, inundation frequency and in part by competition between plant species (Levine et al. 1998; Hacker & Bertness 1999; Janousek et al. 2014; Veldkornet et al. 2015; Mcowen et al. 2017). Interspecific competition is especially important in dense vegetation, whereas during the colonization stage of bare patches, different plant species facilitate each other (Bertness 1991). Towards the sea, vegetation growth is limited by extreme abiotic conditions including inundation frequency (Balke et al. 2016) and soil salinity (Odum 1988). Glycophytes are excluded from the salt marsh by environmental stressors while halophytes are limited at fresh wetlands by competition (Engels & Jensen 2010). Transplant experiments have shown that in the absence of competition, halophytes grow just as well or even better in fresh compared to salt marshes (Engels & Jensen 2010).

Salt marshes occur worldwide at sheltered coastal locations, primarily in middle to high latitudes, and cover more than 5 million hectares globally (Fig. 2) (Mcowen et al. 2017). The habitat ‘salt marsh’ covers a number of habitats affected by seawater n different ways and to a different extent and therefore, various definitions of salt marshes exist. Definitions focus on various aspects of the marsh including the abiotic conditions, tidal flooding frequency and plant community. According to Odum, the salt marsh is defined by a salinity level averaging 18-35 ppt across the year (Odum 1988). Adam (1990) defined the salt marsh as areas bordering saline waters subject to periodic flooding by tidal submergence and vegetated by herbs, grasses or low shrubs. The tidal cycle might be as short as twice a day or last several years (Adam 1990; Miljøministeriet 2009). Between floods, rainfall reduce soil salinity while evapotranspiration increase soil salinity which means that the highest soil salinity levels can be reached in areas not frequently flooded by seawater (Adam 1990; Moffett et al. 2010). In northern Europe, the zonated *Atlantic and continental salt marshes and salt meadows* is defined by its plant community and divided into four sub-habitats of which three are coastal (European Commission 2013). First the *Salicornia and other annuals colonizing mud and sand (Corine biotype 1310),* dominated by annual plant species growing on mudflats or bare sand on sheltered coastlines (European Commission 2013; Nygaard et al. 2016). Second, the *Spartina swards (Corine biotype 1320)* where perennial grass species capable of tolerating high soil salinity levels thrive (European Commission 2013; Nygaard et al. 2016). Third, the *Atlantic salt meadows (Corine biotype 1330)* which is frequently flooded by the ocean during severe storms, yet protected from most wave activity and erosion (European Commission 2013; Nygaard et al. 2016). If grazed, the plant community consist of salt tolerant graminoids and forbs whereas a lack of grazing creates reed swamps dominated by *Phragmites australis* and *Bolboschoenus maritimus* (Nygaard et al. 2016). In Denmark, reed swamp plants dominate approximately one fifth of the *Atlantic salt meadow* habitat (Nygaard et al. 2016).

In Denmark, the salt marsh is defined as meadows and marshes along the coastline. The plant community and location are key factors in determining whether an area qualifies as a salt marsh (Miljøministeriet 2009). There are no requirements regarding soil salinity levels, and the flooding frequency of *Atlantic salt meadows* range from 10 annual floods to one flood every 10 years (Miljøministeriet 2009). The plant community includes salt tolerant species listed under the Corine biotypes of the *Atlantic and continental salt marshes and salt meadows* (European Commission 2013). The salt marsh, *Bygholmengen*, described in **PAPERS I-II**, is characterized as an *Atlantic salt meadow (Corine biotype 1330)* (Miljøstyrelsen 2005a; Miljøstyrelsen 2005b; Miljøstyrelsen 2011). However, *Bygholmengen* is not an ordinary salt marsh due to its isolation from seawater and tidal floods given its location behind a dike (Box 2).

1.3.2. ISSUES FACING THE COASTAL MARSH

Coastal marshes worldwide face multiple threats related to climate change and anthropogenic uses including sea level rise, coastal squeeze, land reclamation and

BOX 1 De Østlige Vejler

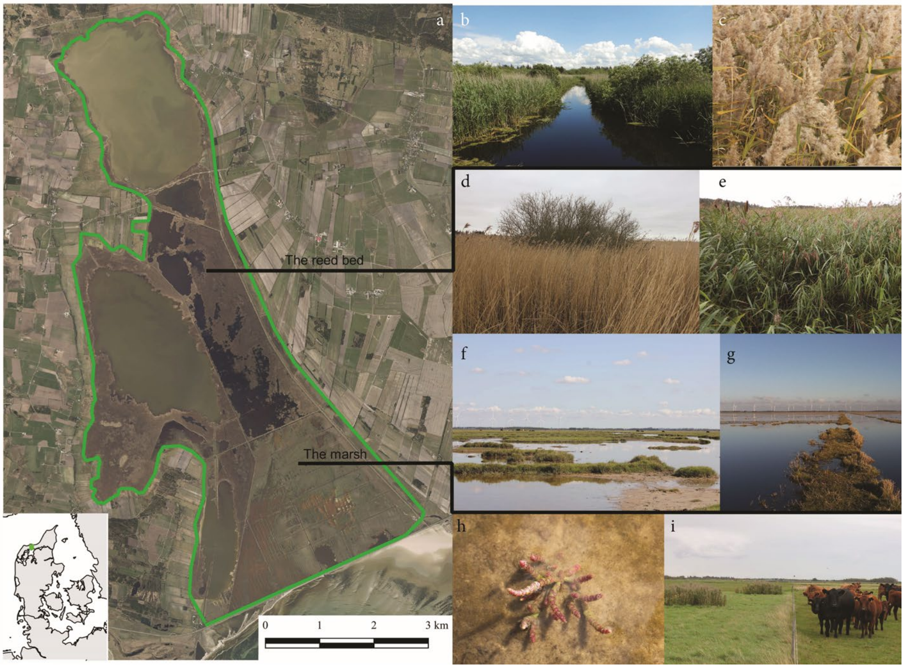


Fig. B1. De Østlige Vejler (a) and the reed bed (b-e) and brackish marsh (f-i).

De Østlige Vejler is part of Vejlerne, Jutland, Denmark (COWI 2000). Vejlerne is a mosaic landscape containing fens, reed beds, lakes and springs, marshes, heaths and grasslands divided in an Eastern and a Western part (Burholt et al. 1994). The Eastern.most part is known as *De Østlige Vejler* and contains a grazed salt marsh *Bygholmengen* (728 ha), several lakes and a large reed bed (522 ha) and is an important natural reserve for breeding and resting birds from all over Europe. As *De Østlige Vejler* is important to birds both on a Danish and European scale, it is a NATURA 2000 Habitat and Bird Directive Site (European Environment Agency 2012). It is also protected under the Ramsar convention (Ramsar Convention Secretariat 2013; Ramsar 2020).

Little is known of *De Østlige Vejler* prior to land reclamations in the 1870ies. During the 1870ies, dams were used to lower the water levels and grazing commenced, even though only a small part of the area was covered in vegetation (Hald-Mortensen 1998). Keeping the water levels low using dams proved problematic, and was abandoned in 1917 (COWI 2000). This resulted in increased water levels, better water quality and good conditions for the biological community (Hald-Mortensen 1998). In 1958, Vejlerne was listed as protected, and in 1960 it was declared a scientific reserve. From this point, the area became closed to the general public. A water-lock (*Centralslusen*) build in 1965 resulted in decreased water levels throughout the area.

Centralslusen separates the salt marsh *Bygholmengen* from the saline *Limfjorden*. The water of *Limfjorden* outside of *Centralslusen* has a salinity of approximately 25-29 ppt. Seawater from *Limfjorden* has not actively been allowed to enter *De Østlige Vejler* since the opening of *Centralslusen* twice during the 1990ies.

In 1993, Aage V. Jensens Naturfond (AVJNF) bought Vejlerne, thereby gaining the responsibility of managing *De Østlige Vejler* (COWI 2000). During spring and summer, it is grazed by cattle with a grazing pressure of less than 1 cattle/hectare. Prior to 2016, the grazing pressure was closer to 0.5 cattle/hectare, and it was necessary to supplement grazing with moving to keep common reed from taking over on the least grazed patches (Nielsen & Clausen 2019a). Grazing pressure was therefore increased during recent years to ensure a low vegetation throughout the meadow. AVJNF actively manage the water levels through water locks in the dam. Fresh water is let onto the *Bygholmengen* once the cattle leaves in autumn, and is therefore submerged during winter.

De Østlige Vejler is a wetland bordering between fresh and saline, where common reed is able to form monocultures on ungrazed areas. *Bygholmengen*, which is characterized as a salt marsh, but given its long isolation from *Limfjorden* salinity levels are low and no vegetation zonation is apparent on the salt marsh. North of *Bygholmengen*, where cattle have no access, the areas is dominated by a large reed bed. The massive reed bed is the largest coherent reed bed in Scandinavia. Approximately 70 ha of the reed bed is harvested annually within the reed beds of *De Østlige Vejler*. The aim of the harvest is to rejuvenate the red bed and limit the build-up of organic materials (Nielsen & Clausen 2019a).

De Østlige Vejler is a scientific reserve, which means that the general public have no access to the area. Walking parts make it possible for visitors to enter the edge of the reed bed (pictured below), and multiple bird watching towers enables visitors to observe the vibrant bird life of *De Østlige Vejler*.

agricultural use, invasive species and building of infrastructure (Gedan et al. 2009). In northwestern Europe, more than 70% of the salt marsh area have been exploited and many are to this day shielded behind made-made structures (Bakker et al. 2002; Bulleri & Chapman 2010). In Denmark, threats facing coastal marshes include a termination of grazing, high intensity summer grazing, drainage, coastal protection and infrastructure (including dikes) and eutrophication (Fredshavn et al. 2019).

Diking: A change in the natural hydrology

Dikes are built for a multitude of reasons including road constructions and land reclamation for agricultural uses (Gedan et al. 2009). Land reclamation is a widespread practice in Europe and has taken place since Roman times (Doody 2008). Regardless the reason for building the dike, dikes pose a threat to salt marsh vegetation as they change the natural hydrology of the salt marsh. Dikes also cause changes in the vegetation (Ganong 1903) where halophytes get replaced by glycophytes and

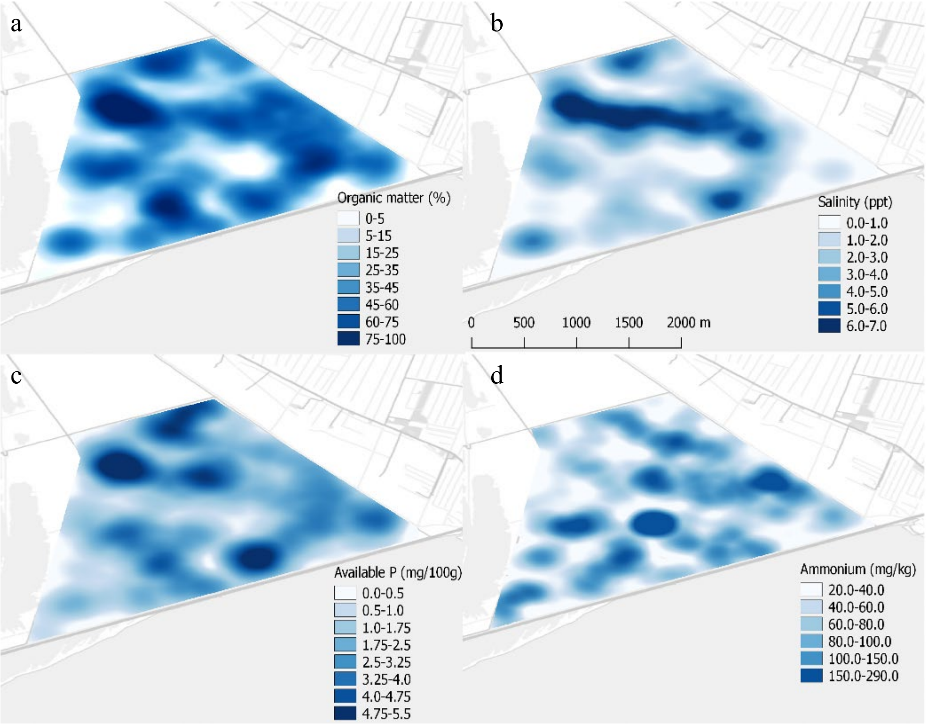
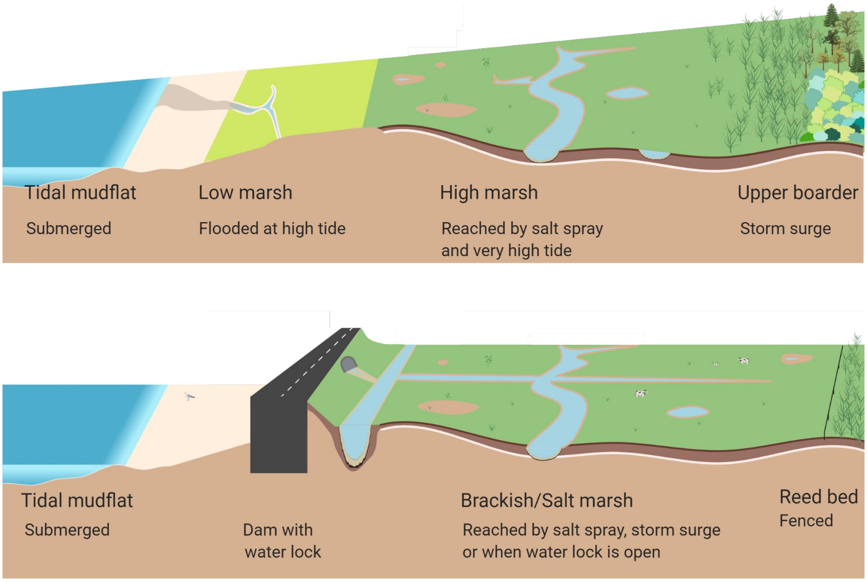


Figure 3 *The spatial distribution of the environmental factors organic matter (a), salinity (b), available phosphorus (P) (c) and ammonium (NH_4^+) (d) on Bygholmengen. Grey areas are water, white areas represent land, the blue area is Bygholmengen. Each map was build by extrapolation of the 80 data points sampled in 2018 in QGIS (QGIS Development Team 2016).*

BOX 2 The salt marsh



Top: Natural salt marsh; Bottom: Bygholmengen. Created under a paid subscription of BioRender.com.

The natural salt marsh (top) has a zonated vegetation. The low salt marsh is dominated by species capable of growing under high salinity level and frequent inundation. The vegetation change as the high marsh is reached, and by the upper border of the marsh, common reed and scrubs will appear, and eventually wooded areas. Zonation is created by inundation frequency, salinity range and minute differences in topography. *Bygholmengen* (bottom), a shielded salt marsh, is exempt from regular tidal flow due to a dike. The marsh receives salt primarily through water spray, during storm surges and from seepage through the water lock. No clear vegetation zonation is apparent.

Bygholmengen is an interesting case study due to its prolonged isolation from tidal floods. It is protected as a salt marsh under the Habitats Directive (Miljøstyrelsen 2005a; Miljøstyrelsen 2005b; Miljøstyrelsen 2011; European Environment Agency 2012). Surveys from made by NOVANA, the national nature surveillance program in Denmark, found that the state of *Bygholmengen* as a salt marsh (H1330) had declined from 2005 to 2011, and stated that natural zonation and hydrology was inhibited by the presence of the dike, which also limit the effects of salt and wind. This leaves the question: Is *Bygholmengen* maintained as a salt marsh, or has the dike changed the natural dynamics to an extent where it no longer qualifies as a salt marsh?

brackish species (Roman et al. 1984). In **PAPER I,** we investigated the vegetation and environmental dynamics of a coastal marsh behind a permanent dike, *Bygholmengen*, *De Østlige Vejler*, Denmark (Box 2). *Bygholmengen* was created during a failed land reclamation, and a dike was built in 1890 separating the marsh from the saline *Limfjorden* (Riis 2009). Today, a highways runs on top of the dike. Since the 1990'ies, where the dike was opened twice towards the fjord and salinity levels on *Bygholmengen* near the dike reached 20.2 ppt, *Bygholmengen* has only received salt water through spray during storms (Kjeldsen, Jørgen Peter 2008; Riis 2009). Eliminating natural tidal floods can alter the plant community as well as physical characteristics of a salt marsh after as little as a one year without tidal flows (Sun et al. 2003).

No clear environmental zonations were found on *Bygholmengen* with increasing distance towards the saline *Limfjorden*, but the environmental factors showed high spatial variation (Fig. 3). It is not uncommon for environmental variables on regularly flooded salt marshes to show different spatial patterns for various environmental parameters (Moffett et al. 2010). Interestingly, the spatial distribution of environmental parameters is better explained by differences in soil texture than differences in hydrology (Moffett et al. 2010), indicating that spatial variations in environmental factors could be found on salt marshes regardless of tidal floods. Soil texture could therefore be a contributing factor to the spatial variation in environmental factors on *Bygholmengen*, where we saw a high correlation between organic matter content and environmental parameters salinity and available phosphorus (P) (Fig. 3).

Several of the environmental parameters measured on *Bygholmengen* fell outside the expected range when comparing with other salt marshes, others were still comparable (**PAPER I-II**). The soil salinity differed from other salt marshes, and reached its maximum at 4.83 ppt (**PAPERS I-II**). This is way below the range defined by Odum (1988), and lower than the recorded soil salinity levels of several other salt marshes (García et al. 1993; Morgan & Adams 2018). We believe the low soil salinity levels is a result of prolonged isolation for *Limfjorden*. This notion is supported by salinity measures made on *Bygholmengen* during the 1990'ies and from 2007 onwards, as the latest peak in salinity was seen in connection with a salt water intrusion (Fig. 4) (Kjeldsen & Nielsen 2008; Kjeldsen 2008; Kjeldsen & Nielsen 2009; Kjeldsen & Nielsen 2010; Kjeldsen & Nielsen 2011; Kjeldsen & Nielsen 2014; Nielsen & Clausen 2019a). In 1995, and once again in 1997, the water lock *Centralslusen* was opened towards *Limfjorden* thereby actively allowing salt water to enter *Bygholmengen*, resulting in a peak in salinity levels in 1996 (Riis 2009) (Fig. 4). The water lock has not been open to allow saltwater intrusion since 1997 (Kjeldsen, Jørgen Peter 2008; Riis 2009). Salinity levels have fluctuated below 10 ppt since 2007, but overall been stable.

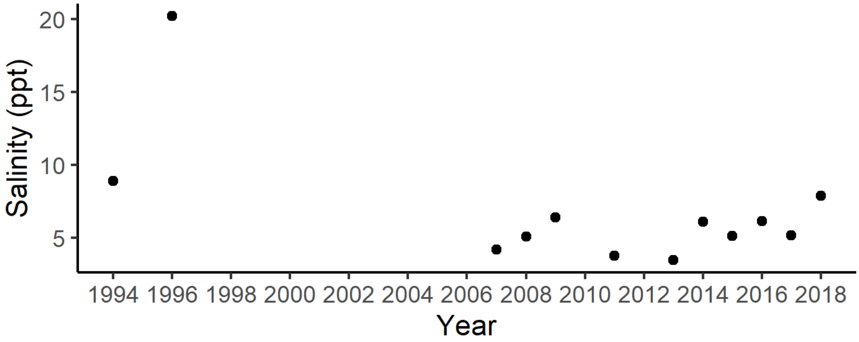


Figure 4 *Salinity levels measured on Bygholmengen at Centralslusen. The water lock was open and let in salt water from Limfjorden in 1995 and 1997. Salinity data from (Kjeldsen and Nielsen 2008, Kjeldsen 2008, Kjeldsen and Nielsen 2009, Kjeldsen and Nielsen 2010, Kjeldsen and Nielsen 2011, Kjeldsen and Nielsen 2014, Nielsen, Henrik Haaning and Clausen 2019).*

Though low compared to the average for Danish salt marshes (3.8 g/100 g) (Nygaard et al. 2016), available P levels on *Bygholmengen* (1.42 mg/100 g soil) (**PAPER I**) were similar to the amount of available P on a New England salt marsh (Theodose & Roths 1999). Total P also resembled that found on other salt marshes found outside of Denmark (**PAPER I**) (Wang et al. 2013; Zhang et al. 2015; Li, J. et al. 2018).

Salt marsh soils outside Denmark contain an average of 6.1 g/kg total nitrogen (N) or less (Morgan & Adams 2018; Li, S. et al. 2018). In comparison, total N levels of Bygholmengen were very high (13.5 g/kg, **PAPER I**). One explanation could be the presence of white clover *Trifolium repens*, which occurred frequently on *Bygholmengen*, as *T. repens* is able to enhance N accumulation rates in grasslands (Deyn et al. 2009). From additional data analysis, we found that plots with *T. repens* had a significantly higher content of total N compared to plots where *T. repens* was absent (Fig. 5). However, even plots without *T. repens* had a higher average content of total N compared to salt marshes outside of Denmark. The surplus of total N might instead be caused by an influx of nitrogen supplied through the feces of the thousands of geese that rest and defecate on the marsh after having fed outside of the marsh (Bazely & Jefferies 1985; Rozema et al. 1999). Finally, eutrophication due to run-off from catchment areas is a concern across Danish and European salt marshes (Rozema et al. 1999; Fredshavn et al. 2014), and as *Bygholmengen* to the east borders agricultural fields, nutrient-rich agricultural run-off could be an issue.

Multiple environmental variables differed between *Bygholmengen* and other salt marshes due to the dike, and we expected that the prolonged tidal exclusion also had affected the plant community and differentiated it from regular salt marsh vegetation.

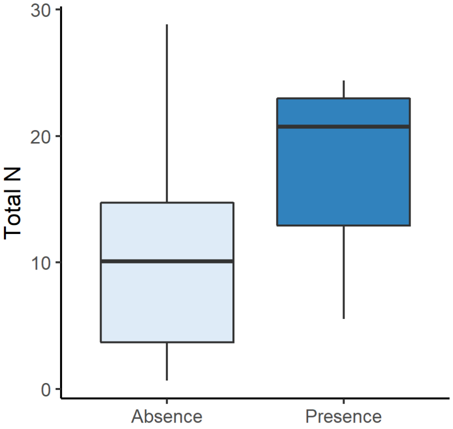


***Figure 5** Soil total N (g/kg) content where Trifolium repens was present or absent. The soil contained a significantly higher content of total N in plots where T. repens was present as oppose to plots where it was absent (Kruskal Wallis, p < 0.001, n = 80, data from 2018). Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles.*

The plant community of *Bygholmengen*, which was dominated by a low vegetation consisting of grass and forbs, differed significantly from that of other Danish salt marshes (**PAPER I**). A common species on Danish salt marshes, *Tripolium pannonicum*, was only seen sporadically on *Bygholmengen* and never occurred in any of our vegetation plots whereas *Salicornia europaea*, a plant associated with Corine biotype 1310, occurred on mudflats (Fig. 6). *Agrostis stolinifera*, *Juncus gerardii* and *Anserina argentina*, on the other hand, were abundant across both *Bygholmengen* and other Danish salt marshes including (**PAPER I**, (Nygaard et al. 2016). Thus, in agreement with previous studies (Ganong 1903; Mitchell 1981; Roman et al. 1984; Sun et al. 2003), we found that salt marsh vegetation behind a dike differ from natural salt marsh vegetation (**PAPER I**).

Entrapping salt marshes behind dikes can result in the invasion of brackish species such as *Phragmites australis* and *Typha augustifolia* (Sinicrope et al. 1990). Even though *P. australis* occurred on 92.5% and 75.0% of investigated plots on *Bygholmengen* in 2017 and 2018, respectively, it most often had a low vegetation cover when found, and *Bygholmengen* was far from dominated by *P. australis* (Fig. 7). Entrapment can also result in the salt marsh evolving into a fresh meadow (Vestergaard 2000; Warren et al. 2002) which has been the goal of numerous agricultural projects (Nixon 1982). Since the plant community of the *Bygholmengen* was significantly different from other salt marshes, we were interested in investigating whether it resembled a fresh meadow community (Corine biotype 6410, the Molinia meadow) (**PAPER I**). The Molinia meadow was chosen for comparison as it is described as a habitat with varying levels of moisture (from part-time flooded to wet or even flooded) and dominated by grass and forbs (Nygaard et al. 2016). However, we found that the plant community of the *Bygholmengen* differed significantly from the Molinia meadow plant community (**PAPER I**). *Bygholmengen* contained none of the species characteristic to the Molinia meadow but did contain several species indicative of the Molinia meadow including *Carex nigra* and *Juncus effusus* (**PAPER**

***Figure 6** Tripolium pannonicum (a) was rarely seen on Bygholmengen. Salicornia europaea (b) was found sporadically on mudflats.*

I, Miljøstyrelsen 2016). Further, *Festuca rubra* was one of the four most abundant species on the Molinia meadow and also occurred on almost every plots on *Bygholmengen* (**PAPER I**, Miljøstyrelsen 2016).

The mean species richness on Danish salt marshes is in decline and had dropped to 12.0 species in 2015 with an average drop of 0.1 species/year since 2011 (Nygaard et al. 2016). On *Bygholmengen*, species richness was only 11.4 in a dry year (**PAPER I**) but 14.0 in a wet year (**PAPER II**) and within the reed bed it was even lower (**PAPER III**). One fifth of all Danish salt marshes have turned into reed beds (Nygaard et al. 2016), and reed beds have a lower species richness than grazed salt marshes (**PAPERS I, II, III**). By including the richness from the reed beds into the Danish salt marsh (habitat 1330) average (Nygaard et al. 2016), the average would have decreased, potentially explaining the higher than average species richness recorded on *Bygholmengen* in 2017. The lower than average species richness recorded in 2018, on the other hand, could have been caused by the very warm and dry conditions experienced during spring and summer of 2018 (**PAPER II**), as droughts often decrease plant species richness (Tilman & El Haddi 1992). We found a mean Shannon diversity of 0.59-0.63 on *Bygholmengen* (**PAPERS I-II**) depending on the year of the survey. The Shannon diversity of US salt marshes range from 0.3-1.8 (Perry & Atkinson 1997; Theodose & Roths 1999; Gedan & Bertness 2009), sometimes exceeding 2.5 (Morgan & Adams 2018). Overall, species diversity of *Bygholmengen* fell within the lower range of other salt marshes. As species richness and diversity on salt marshes is often higher in areas of low (less than 8 ppt) compared to high salinity areas (García et al. 1993; Morgan & Adams 2018), it is somewhat

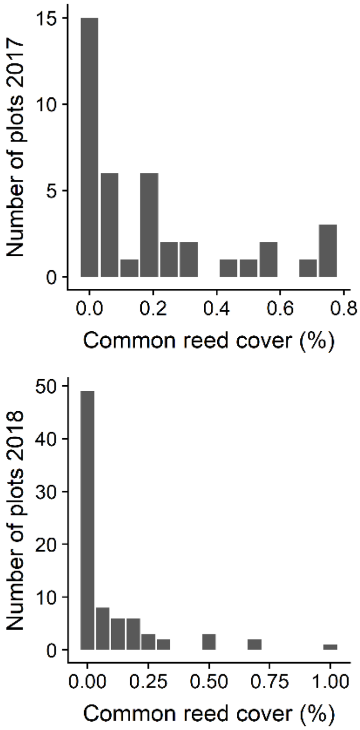


***Figure** 7 Common reed Phragmites australis cover in 2017 and 2018. On the x-axis is the cover of common reed, on the y-axis the number of plots out of 40 (2017) and 80 (2018) with that specific reed cover.*

surprising that the Shannon diversity on *Bygholmengen*, which does not have a high soil salinity, was lower than average. The low salinity level could, however, potentially be an additional factor explaining the high species richness recorded on the marsh during 2017 (**PAPER II**).

In conclusion, the plant community of *Bygholmengen* no longer resembles a natural salt marsh plant community, but has not evolved into a fresh meadow community either after 20 years without any connection to *Limfjorden* and more than 100 years of being kept behind a dike (**PAPER I**). Neither has it turned into a reed monoculture, likely due to grazing. *Bygholmengen* still contains a number of halophytes, as is often seen on salt marshes even long after land reclamation (Min & Kim 1999) and salt marsh restoration projects indicate that should the dike be removed and tidal flooding reinstated, the vegetation of *Bygholmengen* would gradually become more similar to a salt marsh vegetation (Warren et al. 2002; Wetzel & Kitchens 2007). The species composition of *Bygholmengen* resemble that of summer polders, which are salt marshes behind low dams only partly restricting tidal events, that are flooded during high/very high tides (Bakker et al. 2002; Barkowski et al. 2009) (**PAPER I**). Both contain a high number of species preferring brackish conditions as well as several glycophytes, including *Agrostis stolinifera* and *Anserina argentina*. This shows that as long as marsh communities sporadically receive salt-water inputs, either through salt spray or during high tides, they will evolve into similar, brackish dominated plant communities.

Interannual climate fluctuations

Where we in **PAPER I** looked at the effects of a man-made structure on salt marsh vegetation, our focus in **PAPER II** shifted towards examining a different kind of threat facing the salt marsh vegetation, namely climate change. Climate change is expected to have a large impact on vegetation and plant communities across habitats (van Vuuren et al. 2006; Chelli et al. 2017; Rogora et al. 2018). One aspect of global climate change is a forecasted increase in extreme weather event like droughts, floods and heatwaves, as well as large interannual climate variations (Easterling et al. 2000; Orlowsky & Seneviratne 2011). Interannual precipitation variability changed the functional diversity of grassland plant species by decreasing the plant-leaf-nitrogen concentration and increasing the leaf dry matter content during a drought while at the same time altering the species composition (Chen et al. 2019). Severe drought and heat spells significantly reduce the primary production across habitats (Ciais et al. 2005). In salt marshes, climatic extremes can cause rapid large-scale changes in the vegetation (McKee et al. 2004) and experimental evidence show that warmer temperatures decrease salt marsh plant diversity, plant cover and species richness and cause a shift in plant species composition (Gedan & Bertness 2009). In **PAPER II**, we examined the effects of interannual climatic fluctuations in the field by comparing the vegetation of two consecutive years; one wet and cold (2017), the other warm and dry (2018) (Fig. 8) (Cappelen 2018a; Cappelen 2018b; Cappelen 2019). We found that the heat and drought indeed caused both species richness and diversity to decline (**PAPER II**). Drought is associated with salt marsh diebacks (Alber et al. 2008) in agreement with our finding of a significant decrease in vegetation cover during the year of the drought (**PAPER II**). Further, the warmer and drier conditions of 2018 created a habitat where the soil was saltier and drier and with a higher content of available P and NH_4^+ compared to 2017 (**PAPER II**). Palomo et al. (2013) showed that an experimental drought salt marsh resulted in a change in soil oxygen penetration, followed by an increased soil retention of available P but decreased the pools of NH_4^+ and NO_x. This explains why available P levels increased during the drought, but not why NH_4^+ increased (**PAPER II**). Studies from grasslands found that NH_4^+ pools respond differently to drought between grassland sites depending on soil organic matter content, total nitrogen pools and absolute water content (Fuchslueger et al. 2014). In case just one of the parameters (organic matter content, total N or soil moisture) differed between *Bygholmengen* and the salt marsh substrate used by

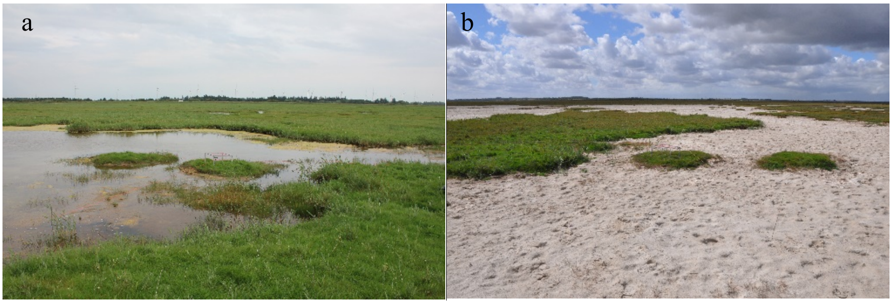


***Figure 8** The salt marsh Bygholmengen during the wet conditions of 2017(a) and dry conditions of 2018 (b). Photo credit (b): Thomas Bo Sørensen.*

Palomo et al. (2013), it could explain why NH_4^+ increased in one study but decreased in the other.

Plans' ability to use available nutrients change during salt and drought stress (Hu & Schmidhalter 2005; Bista et al. 2018) in agreement with our findings that during the wet 2017, the correlation between species richness and nitrogen availability was four times stronger than in dry and saltier 2018 (**PAPER II**). Further, halophytes made up a larger proportion of the plant community during warm, dry and more saline conditions than during wet conditions and we saw a large species turnover between years (**PAPER II**). Salt marsh species (halophytes) are adapted to living under stressful conditions but are poor competitor compared with many terrestrial species (Pennings et al. 2005; Veldkornet et al. 2015; Veldhuis et al. 2018), and an ability to withstand harsh physical conditions is a part of their biology (Bertness et al. 1992). However, as the competitive ability of plants change in response to environmental stress (Pugnaire & Luque 2001), the competitive advantage of the glycophytes could have decreased during the stressful conditions in 2018 thereby giving the salt marsh species an advantage. The richness of species specifically linked to the Atlantic salt meadow habitat (Corine biotype 1330) increased during the drought and the relative abundance of salt marsh specific species compared to other species also increased (**PAPER II**). For example, *Juncus gerardii* increased in frequency and was found on 86.25% of plots during dry condition in 2018 but only on 67.5% during the wet conditions of 2017.

To sum up, interannual climate fluctuations had large impacts on salt marsh plant communities, and both increased precipitation and heatwaves can be problematic. Increased precipitation posed a potential threat to the salt marsh plant community of *Bygholmengen*, as the lowered salinity levels during the wet year resulted in a higher proportion of glycophytes that have the potential to outcompete halophytes (**PAPER II**). The increasingly harsh conditions during the drought increased the amount of salt marsh specific species on a diked salt marsh with a low soil salinity content, but also reduced overall species richness, vegetation cover and height (**PAPER II**). On other salt marshes, severe drought have resulted in hypersaline conditions, severe vegetation diebacks and a decline in species diversity (McKee et al. 2004; Gedan & Bertness 2009; Ibarra-Obando et al. 2010).

1.3.3. REED BEDS

Where **PAPERS I-II** focused on the open vegetation of the salt marsh, we moved the fieldwork into the tall, dense vegetation of the reed bed in **PAPERS III-IV**. The reed bed is a succession driven habitat representing the stage between open water and woodland (Fig. 9) (Hawke & José 1996). There are two types of reed beds: the reed swamp that is permanently waterlogged and the reed fen that has water levels below the ground surface during the summer (Hawke & José 1996). Reed beds have several important functions in landscape ecology including providing habitat for a highly specialized fauna, by acting as a structural element, as food and in bank protection, where the extensive root system of common reed stabilize the substrate protecting the shore from erosion (Ostendorp 1989; Ostendorp 1993). Since the 1950'ies, reed beds have declined in Europe, a phenomenon known as reed dieback (Ostendorp 1989; Hartog et al. 1989; van der Putten, Wim H 1997). The dieback has been ascribed to several factors including eutrophication and water table management, whereas it is speculated that stands with low genetic diversity are more vulnerable, and that mechanical reed harvest can have a detrimental effect on the reed bed (Brix 1999).

Aptly named after its dominating species, common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) is by far the most abundant plant of the reed bed habitat. Common reed is a tall, cosmopolitan, perennial grass (Bastlová et al. 2006). Common reed form dense monocultures and is highly competitive, partly because of its ability to exclude other plants by competitive exclusion of light (Ungar 1998) and partly because of its ability to release gallic acid through its root system inhibiting the growth of other plants (Rudrappa et al. 2007; Rudrappa & Bais 2008). Growth and survival of common reed is limited by soil salinity (Hellings & Gallagher 1992) with salinity levels above 7.5 ppt limiting both seedling germination and growth (Mauchamp & Mésleard 2001).

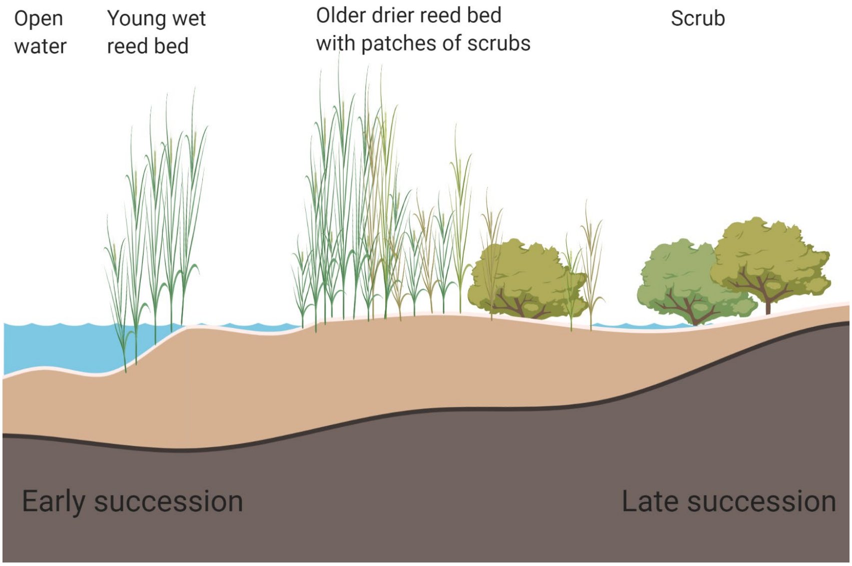


Figure 9 *Reed bed from an early succession stage with open water and common reed to a dry late successional stage with scrub growth. Image created under a paid subscription to Biorender.*

***Figure 10** Many birds nest in the reed bed as it provides shelter and protection from predation.*

Reed beds are home to a rich fauna (Hawke & José 1996). A large number of birds, including passerines, geese and the in-Denmark-red-listed Eurasian bittern *Botaurus stellaris*, breed and feed in the reed habitat (Fig. 10) (Kristiansen 1998b; Jenkins & Ormerod 2002; Trnka & Prokop 2006; Trnka et al. 2014; Mérő et al. 2015; Polak 2016). The bittern, as well as the reed warbler and bearded tit, are especially dependent on the reed beds (Hawke & José 1996). Several mammals including the otter *Lutra lutra* and the harvest mouse *Micromys minutus* can be found in the reed bed, though they do not exclusively depend on the reed bed habitat (Ostendorp 1993; Surmacki et al. 2005; Pertoldi et al. submitted). Frogs and toads are also found in the reed bed where they prefer the open parts of the reed bed and decrease in abundance with increasing reed cover (Mester et al. 2015). Further, the reed bed is home to several species of plants (**PAPER III**) and an abundance of invertebrates (**PAPER IV**).

1.3.4. REED BED MANAGEMENT AND ITS EFFECT ON COMMON REED

Without management, reed beds eventually dry out due to an accumulation of litter from common reed itself (Hawke & José 1996). The reed bed will be colonized by other species of plants and eventually develop into scrub or woodland and reed bed specialists will be lost (Hawke & José 1996; Valkama et al. 2008). Reed management can reverse or halter the natural succession. Several management methods exist and while some focus solely on reed bed management, other methods have commercial interests in mind (Hawke & José 1996). Harvest (reed removed), cutting (reed left behind), burning and grazing are all common methods of reed bed management (Valkama et al. 2008). Winter harvest has commercial interests in mind whereas summer harvest is intended for conservation purposes (Decleer 1990).

Different management methods affect the reed bed vegetation differently as they result in various degrees of litter accumulation and opening up the habitat at different extents. For instance, while reed harvest had no effect on reed stem height, a decrease in reed height is observed after burning (Valkama et al. 2008) and cutting (**PAPER III**). The reed stems left behind in cut as oppose to harvested reed beds could potentially limit light availability at the ground and hinder reed growth, thereby reducing the reed height (**PAPER III**). Reed burning affect not only reed height but also the entire reed bed habitat structure by decreasing the reed density and increasing the number of green stems compared to unmanaged reed (Trnka & Prokop 2006). Mester et al. (2015) also found burning to rejuvenate the reed bed by eliminating the old reed. Grazing differ from winter harvest and burning by causing a shift in the vegetation structure towards a habitat less dominated by common reed whereas common reed remains dominant with both harvesting and burning (Ausden et al. 2005, **PAPER III**).

With few exceptions (Kristiansen 1998a; Hardman et al. 2012; Mester et al. 2015), most reed bed management studies compared managed reed beds to an unmanaged controls not taking into account that the unmanaged controls might represent different successional stages (Decleer 1990; Cowie et al. 1992; Poulin & Lefebvre 2002; Schmidt et al. 2005; Ausden et al. 2005). Due to the successional character of the reed bed habitat, reed bed age, here defined as time since last management, could have a large effect of the reed bed and its inhabitants, which is not taking into account when only comparing managed to unmanaged reed beds. For example, time since last burning affect the vegetation, as the vegetation structure immediately following burning was more heterogeneous, but became more homogenous just a few years after a burning event (Mester et al. 2015). Time since last harvest affect bird nesting preference, where the graylag goose *Anser anser* prefer reed left unmanaged for 5-6 years and avoids newly managed reed and reed beds left unmanaged for more than 16 years (Kristiansen, J. N. 1998v). In **PAPERS III-IV**, we included time since last management (the reed bed age) as a factor in the analysis by surveying four reed treatments: recently harvested reed, recently cut reed, reed harvested 3 years ago and reed harvested 25 years ago (Fig. 11).

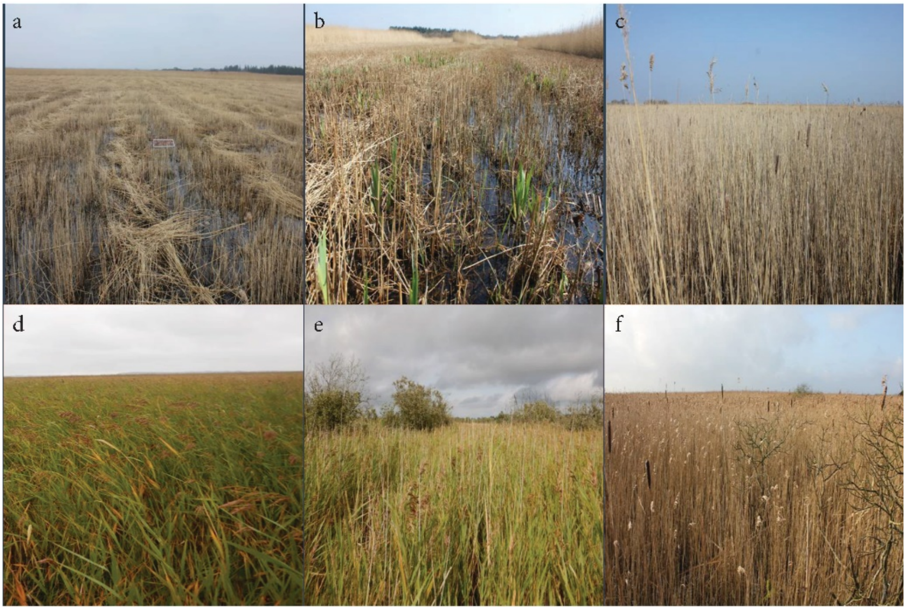


***Figure 11** The reed bed areas of De Østlige Vejler according to management strategy. The cut reed bed in spring (a), harvested reed bed in spring (b), 3-year-old reed bed in spring (c), harvested reed bed in summer (d) and 25-year-old reed bed in summer (e) and 25-year-old reed bed in spring (f).*

Reed management promote reed bed rejuvenation and the growth of new, green reed stems compared to unmanaged reed (Björndahl 1985; Ostendorp 1999; Deák et al. 2015). We found that reed bed age influenced several characteristics of common reed rejuvenation (**PAPER III**). The density of green reed decreased from the 0-year-old to the 25-year-old reed bed, and the ratio of green to brown reed stems also significantly decreased with reed bed age (**PAPER III**). This makes sense, as reed winter harvest commonly increase the reed stem density compared to unmanaged controls (Ostendorp 1999) potentially due to increased light penetration (Granéli 1989). As reed harvest change the microclimate of the reed bed, winter harvest can either reduce shoot mortality due to increased light penetration or increase shoot mortality during late winter frost (Granéli 1989; Packer et al. 2017). The 3-year-old reed bed had a similar green biomass as the 0-year-old harvested, similar number of green reed stems and green stem diameter in August as the 0-year-old harvested (**PAPER III**). However, the 3-year-old reed bed appear to be in transition, as it had a similar height as the 25-year-old reed, and similar brown biomass and brown reed stem density in May as the 25-year-old (**PAPER III**). These results indicate that reed bed age affected the growth of new reed beyond the year of management action, highlighting the importance of including reed bed age and the problem of merging 'unmanaged' reed beds of different ages in one category.

The changed reed bed habitat structure following management has a large impact on reed bed inhabitants. Overall, passerine birds prefer tall, thick reed and were found at smaller densities at burnt compared to unmanaged sites (Trnka & Prokop 2006). However, different passerine species prefer nesting in slightly different reed bed habitats with some preferring drier and others wetter parts of the reed bed (Martínez-Vilalta et al. 2002). We found no difference in water coverage between any of the reed treatments during our surveys in May and August, though we had expected that the 25-year-old would have been drier due to years of accumulated reed biomass (**PAPER III**). By maintaining reed beds in a mosaic of different ages, a range of reed densities and heights becomes available, creating a suitable habitat for several species of birds.

1.3.5. REED BED PLANTS

Even though common reed is by far the most abundant species of the reed bed, the reed bed also contains a number of other plant species. The plants coexisting with common reed often occur at a low frequency resulting in a habitat with a low floral diversity (Keller 2000). Cowie (1992) found 99 plant species within British reed beds. We found 66 plant species in the reed bed in addition to common reed (**PAPER III**). The average number of plant species found in a circle with a radius of 5 m were 8.87 ± SD 3.48. Common plants within the reed bed included *Typha augustifolia*, *Sium latifolium*, *Lycopus europaeu*, *Cardamine pratensis ssp. Dentate*, *Galium palustre* and *Lemna minor*. We found unique species in each reed bed treatment with 7 species found solely in the 0-year-old harvested reed bed, 5 in the 0-year-old cut, 1 in the 3-year-old and 9 in the 25-year-old. Only 22 of 66 species occurred across all four reed treatments; therefore, in order to obtain the highest possible species richness throughout the reed bed, all possible reed treatments should be maintained (**PAPER III**).

It is not uncommon to find significant differences between plant communities experiencing different management regimes (Moog et al. 2002; Kahmen et al. 2002; Kitazawa & Ohsawa 2002). We saw these differences reflected in differing Ellenberg values between treatments (**PAPER III**). In spring, for example, the plant communities of the 0-year-old harvested and 3-year-old harvested reed beds had a significantly lower Ellenberg N than the cut and 25-year-old reed beds. Harvest remove reed stems thereby reducing the amount of litter and the nutrients it contain that would otherwise have been released to the reed bed (Hosoi et al. 1998), explaining the lower Ellenberg N of recently harvested reed beds. Common reed is known to suppress other plants by competitive exclusion through limiting the light availability (Ungar 1998) and harvest open up the reed and increase the light penetration (Granéli 1989). We found that management method and reed bed age influenced the Ellenberg L of the plant community. During spring, we found that Ellenberg L of the cut reed bed, where reed stems were left behind inhibiting light penetration, was significantly lower compared to all the other reed treatments, whereas in August, the 0-year-old harvested had a plant community with a significantly higher Ellenberg L than any other treatment (**PAPER III**). We can therefore conclude that whereas harvest open up the habitat and let in more light, cutting does not.

Different studies have come up with varying and contradictory effects of reed management on plant species richness and diversity. Sometimes, plant species richness and Shannon diversity are positively affected by reed winter harvest compared to unmanaged controls (Cowie et al. 1992), other times, harvest does not affect plant species richness (Poulin & Lefebvre 2002; Schmidt et al. 2005). The effect of harvest depends on the timing of the harvest with summer harvest having a far greater positive effect on species richness compared to winter harvest (Decleer 1990). Grazing increase plant species richness but cause a shift in the vegetation away from common reed and create a tall-herb fen featuring common reed amongst other plants (Ausden et al. 2005). A meta-analysis analysing a broad definition of reed beds found no overall effect of management on plant species richness, regardless of management method (Valkama et al. 2008). Valkama et al. (2008) did show that when subdividing into fresh and saline reed beds, plant species richness responded positively to management in fresh environments but did not respond to harvest in saline marshes. We found that the effect of reed management on species richness depended both on the management method, the time of sampling and the age of the control reed bed

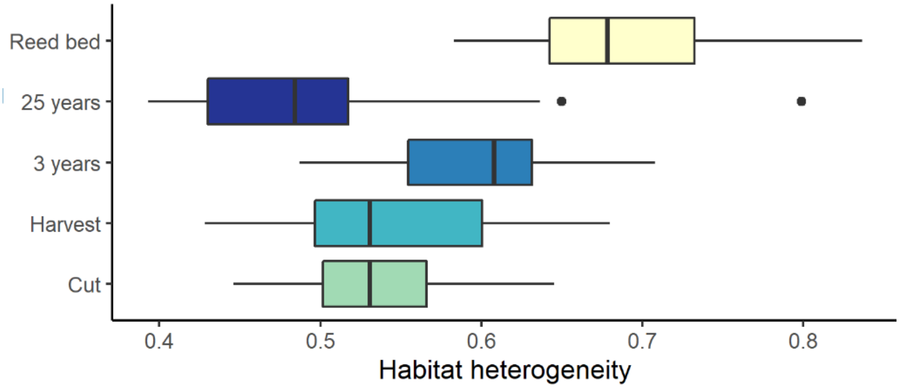


Figure 12 *Habitat heterogeneity in each of the four reed bed treatments in both spring and summer (n = 40 in each treatment) as well as in the reed bed as an entity (n = 160). Habitat heterogeneity is discussed in greater detail in* ***PAPER III****. Statitical analysis showed that the habitat heterogeneity differed between groups (Kruskal Wallis, p < 0.001) and a post hoc Dunn test with sequential Bonferroni correction found that the habitat heterogeneity was significantly larger at the reed bed as an entity than in either of the different treatments in themselves. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers.*

(**PAPER III**). In spring, for instance, harvest increased species richness compared to the 25-year-old control reed bed but decreased it compared to the 3-year-old control, whereas cutting had no effect on species richness (**PAPER III**). In late summer, however, no significant differences in species richness were found between any reed bed treatment regardless of management method or reed bed age (**PAPER III**). The inclusion of both reed bed age and the timing of the fieldwork (**PAPER III**) are likely candidates in explaining why previous studies (Cowie et al. 1992; Poulin & Lefebvre 2002; Schmidt et al. 2005) disagree on the effect of winter harvest on species richness.

In order to secure the highest possible diversity it is sometimes necessary to manage an area in a way that preserves every successional stage of a habitat (Primack 2010). In tall grasslands, management that varied in space and time and included both grazing, burning and grazing created the most heterogonous landscape with multiple stages of succession thereby creating breeding habitats suitable for several species of birds (Rahmig et al. 2009). In heathlands, where most management regimes strive to retain the heathland in an early successional stage, the ant diversity increase if part of the heathland was left unmanaged and allowed to reach later successional stages (Hansen et al. 2020). Mester at al. (2015) found that if unmanaged, the reed habitat becomes homogenous due to the spread of common reed. We found that multiple management methods and several reed bed ages in different successional stages created the widest range of habitat heterogeneity in the reed bed (**PAPER III**). Additional analysis showed that the habitat heterogeneity increased significantly when maintaining all four reed bed treatments compared to having any treatment in itself (Fig. 12). This speaks towards maintaining a mosaic of red bed ages.

In conclusion, we recommend maintaining reed beds managed using different methods and unmanaged reed beds of different ages. Even though plant diversity was highest in the 25-year-old unmanaged red bed, it still only contained 38 of 66 plant species found across the entire reed bed. Maintaing a range of reed bed ages will conserve the highest number of plant species in the reed bed overall and result in the most heterogeneous habitat (**PAPER III**).

1.3.6. REED BED INVERTEBRATES

Many terrestrial invertebrates are found in aquatic or semi aquatic habitats with both Diptera, Coleoptera and Hymenoptera being numerous in wetlands (Batzer & Wu 2020). Even though not all invertebrates are able to withstand severe wetland floods,

Figure 13 *The reed bed contained a high diversity of invertebrates including Hemiptera: Hydrometridae (left), Hymenoptera (middle) and Coleoptera: Carabidae (right).*

many species of Aranea and Carabidae quickly recolonize wetlands following severe floods (Lafage et al. 2015), and flooding even increase the diversity of both Collembola and Carabidae (Lessel et al. 2011). A high diversity of species can be found within individual wetlands across the world; for example, 50-100 carabid species were recorded within one wetland, in another 50-100 species of Diptera and yet another counted more than 500 species of Hymenoptera and 400 species of Lepidoptera (Liebherr & Song 2002; Bettacchioli et al. 2012; Batzer & Wu 2020). Reed beds also contain many invertebrate species (Fig. 13), and in the UK, more than 700 species of invertebrates have been found within reed beds (Hawke & José 1996).

Natural disturbances or human management that change and open up the habitat structure can have a positive effect on invertebrate abundance. For example, beetles were 26% more abundant in beaver disturbed wetlands compared to wetlands without beaver disturbance, as beavers create a range of habitats making room for species that would otherwise have been absent (Willby et al. 2018). Reed bed management also affects both invertebrate abundance and species composition (Decleer 1990; Schmidt, M. H., Lefebvre, Poulin and Tscharntke 2005a; Hardman et al. 2012; Hoffmann et al. 2016). When conducted at a large scale, reed winter harvest decrease invertebrate abundance (Schmidt et al. 2005). However, the effects of small-scale reed harvest on the invertebrate community has only received little attention (Trnka et al. 2014). In **PAPER IV**, we wanted to determine how the time since last reed winter harvest affected invertebrate biomass, diversity and community composition when harvesting only a small part of the reed bed. We investigated both flying and ground-dwelling invertebrates at the Order level and for Coleoptera at the family and species level (Fig. 14). Fieldwork were conducted in *De Østlige Vejler*, where only a small section of the reed bed is subject to commercial harvest.

We found reed bed age significantly affected the invertebrate biomass (**PAPER IV**). The flying invertebrate biomass was significantly higher in the 0-year-old reed bed compared the 3-year-old, which again was significantly higher than the biomass in the 25-year-old. For ground-dwelling invertebrates, no significant difference was found

***Figure 14** Invertebrates were sampled in pit fall traps (a, b) and cross vane window traps (c). The pitfall traps had a dimeter of 8.5 cm, and consisted of two cups, the bottom one lined with cement to keep it from exiting the water logged soil. Cross vane window traps consisted of two transparent, perpendicular vanes each measuring 50x80 cm.*

in the biomass of the 3-year-old and 25-year-old, whereas both had a significantly lower biomass than the 0-year-old (**PAPER IV**). In wetlands, management that set back the succession generally increase invertebrate biomass (Davis & Bidwell 2008). In grasslands, burning increase the invertebrate biomass with up to 50% compared to homogenous, grazed plots as burning create a mosaic landscape (Engle et al. 2008). We found that in August, habitat heterogeneity was significantly higher in the 0-year-old reed bed (**PAPER III**), and as a larger habitat diversity increase invertebrate abundance (Engle et al. 2008; Willby et al. 2018), it could potentially explain the peak in biomass in this reed bed age (**PAPER IV**). In streams, the invertebrate biomass was twice as high in streams in areas disturbed by logging, placing the forest in an ealier successional stage, compared to reference streams (Stone & Wallace 1998). Stone and Wallace (1998) hypothesized that logging broke down leaf detritus into smaller pieces, thereby enhancing nutrient availability, which resulte in the increased invertebrate biomass. Though reed biomass, and thereby nutrients, were removed during reed winter harvest, the heavy machinery used during harvest likely broke up part of the reed left behind, resulting in an abundance of small pieses of commen reed. Chopped reed is sometimes used as a fertiliser (Köbbing et al. 2013), and could have contributed to increasing the invertebrate biomass.

Reed winter harvest affected the diversity at the invertebrate Order level. We found that reed harvest decreased the ground-dwelling Order level Shannon diversity of the 0-year-old reed bed compared to the 25-year-old reed bed (**PAPER IV**). Reed bed age had no effect on the Shannon diversity of flying invertebrates at the Order level (**PAPER IV**). Some invertebrate communities have a higher spatial turnover than others (Corti & Datry 2016), and flying species have a larger movement rate than ground dwelling species (Brouwers & Newton 2009). The lack of difference in Shannon diversity between reed bed ages of the flying invertebrates, as oppose to ground dwelling invertebrates, could be that the flying invertebrates had a lower spatial turnover and were able to recolonize the disturbed habitats faster than the ground dwelling. It could also be that data at the Order level was not sufficient to evaluate the effect of reed bed age on flying invertebrates.

We found that the Shannon diversity of Coleoptera decreased following harvest, and that it was still low even three years after the harvest compared to in the 25-year-old reed bed (**PAPER IV**). The decline in species richness of carabids in wetlands following anthropogenic disturbances has been explained by a decrease in the number of specialist species (Bettacchioli et al. 2012). Natural disturbance do not always decrease the diversity, as Willby et al. (2018) found no difference in Coleoptera diversity between wetlands either with or without beaver disturbance present. Other times, wetland management increase beetle diversity. In a fen, where common reed made up less than 20% of the vegetation cover, fen rewetting increased carabid species richness and changed the carabid assemblage so it no longer resembled that of drained and near-natural fens (Görn & Fischer 2015). In the reed bed, however, harvest increased only the biomass of Coleoptera, not the diversiy (**PAPER IV**).

Regardless of the limited ability for Order level data to detect differences in biodiversity, at least for flying invertebrates, the response to reed bed age was Order specific. For example, Hymenoptera and Thysanoptera were positively correlated with the 0-year-old harvested reed bed whereas Diptera: Brachycera correlated positively with the 3-year-old reed bed and Hemiptera correlated positively with the 25-year-old reed bed (**PAPER IV**). Hemiptera is a very diverse group of herbivorous invertebrates whose diverse trophic requirements make them sensitive to changes in the plant composition, likely explaining why their relative abundance was highest in the 25-year-old reed bed (Moir & Brennan 2007). However, sometimes it is difficult to infer why some Orders were more abundant only from data at the Order level, due to the wide range of life strategies present within most Orders. Order Thysanoptera, for example, includes species living interstitially (closely concealed within e.g. young leaves or flowers) and species living on exposed surfaces (e.g. dwelling on flowers or grass) (Shull 1914), and this wide range of life strategies makes it difficult to access why Thysanoptera were especially abundant in the 0-year-old harvested reed bed. Here, data at the family or even species level is much more informative.

We found distinct Coleoptera communities in each reed bed age (**PAPER IV**), which could be explained by different Coleoptera families being able to use different wetland microhabitats. For example, distinct Carabid species assemblages can be found within the same wetland complex in adjacent areas due to their ability to utilize microhabitats (Liebherr & Song 2002). Even though the Coleoptera biomass peaked in the 0-year-old, the relative abundance of Coleoptera within the 0-year-old reed bed was lower than in both the 3-year-old and 25-year-old (**PAPER IV**). However, this was not the case across all Coleoptera families. Staphylinidae (Coleoptera), commonly known as rove beetles, are non-specific predators feeding on soil arthropods (Bohac 1999). Staphylinidae abundance changed with reed bed age and was positively correlated with the 0-year-old reed bed (**PAPER IV**), and also responded positively to management by grazing in grasslands (Hofmann & Mason 2006). Hofmann and Mason (2006) explained the increase with an increased moisture level in connection with management. Older reed beds are commonly drier than recently managed reed beds in earlier successional stages (Hawke & José 1996), though we saw no difference in surface water cover in either May or August across our three red bed ages (**PAPER III**), we did not record moisture levels of the reed bed ages. Our result are nonetheless in disagreement with results by Hoffmann et al. (2016) who found winter harvest to have a negative impact on Staphylinidae and recommended that reed beds should not be managed. They also found that lower water levels favoured Staphylinidae, while a high abundance was linked to a low vegetation and a high richness to a high vegetation. As reed harvest initially decrease the the height of common reed (**PAPER III**), it could explain the increased abundance of Staphylinidae (**PAPER IV**).

Leiodidae, the round fungus beetles, were positively associated with the 25-year-old reed bed (**PAPER IV**). Leiodidae is a functionally diverse family feeding on fungus or decaying materials (Leschen 1999), and though decomposition occur at the same rate across managed and unmanaged red, the litter layer is thicker in the old reed bed (Cowie et al. 1992) thereby containing more decaying matter explaining the high abundance of Leiodidae in the 25-year-old reed bed. These examples show some of the information that can be gained from working at the taxonomic level family rather than Order.

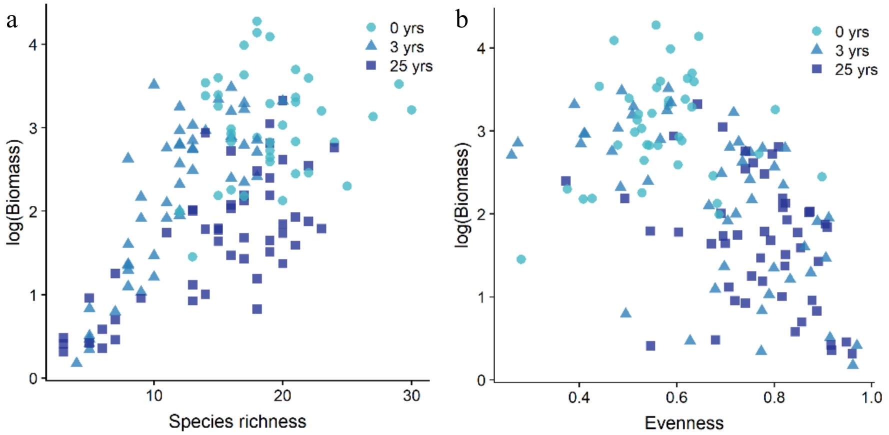


Figure 15 *The relationship between Coleoptera biomass (g, wet weight) and Coleoptera species richness (a) and Coleoptera evenness (b) across weeks 26-35. Coleotera biomass were obtained as described in* ***PAPER IV****. The evenness was calculated using package vegan (Oksanen et al. 2017) in R (R Core Team 2017). There was a significant positive correlation between species richness and log(biomass) (linear model (lm),* $p < 0.0001$*) and a significant negative correlation between evenness and log(biomass) (lm,* $p < 0.001$*).*

The biodiversity crisis, resulting in species extinctions and change in species compositions, have resulted in a need to investigate the relationship between biodiversity and ecosystem functioning (Maureaud et al. 2019). Traditionally, this relationship has been tested experimentally by comparing species richness to total productivity (Tilman et al. 1996) with the overall conclusion from meta-analyses of experimental studies that species richness has a positive impact on ecosystem productivity (Cardinale et al. 2012; Duffy et al. 2017). However, this might not hold true in real ecosystems as Maureaud et al. (2019) found no link between species richness and biomass but found that the ecosystems with the highest biomass was dominated by a few generalist species whereas ecosystems with a higher level of evenness were less productive. Using **unpublished data** on the Coleoptera community across 10 weeks of sampling, we found a significant positive relationship between biomass and species richness (Fig. 15a), but also a negative relationship between evenness and biomass (Fig. 15b). From graphical inspection, we found that the Coleoptera community of the 25-year-old reed bed had the lowest biomass but the most even community whereas evenness was lower and biomass higher in the 0-year-old reed bed (Fig. 15). This indicates that the reed bed communities with the highest invertebrate biomass contain a high number of species yet are dominated by just a few species.

To ensure reed beds are managed the best possible way, managers need efficient tools to evaluate the effect of the management. Invertebrates are often used as bioindicators for evaluating management, but it is time consuming and require a high level of expertise to reach the species level in invertebrate taxonomy (Rainio & Niemelä 2003; Schipper et al. 2010). Sometimes, coarse taxonomic data at a high taxonomic level are able to provide a good indication of the effect of various environmental factors (Hewlett 2000; Caruso & Migliorini 2006; Schipper et al. 2010). Other times, data at the species level provide valuable information not obtained by using coarser taxonomic levels (Verdonschot 2006; Smith et al. 2007). To managers, it is highly relevant to know what taxonomic levels is sufficient to detect the effect of management.

In the reed bed habitat, data at the Order level already showed that the invertebrate communities differed between reed bed ages (**PAPER IV**). For ground-dwelling reed bed invertebrates, the differences between the invertebrate communities of the three reed bed ages were noticeable already at the Order level, and the differences were even more pronounced at the family level (**PAPER IV**). For the flying invertebrates, however, Order level data found no difference in the Shannon diversity, whereas for the ground-dwelling invertebrates, the overall trends were similar regardless of whether data was analysed at an Order, family or species level (**PAPER IV**). Further, the response to management was family specific. Aside from information on red listed species, little new information were gained by analysing Coleoptera at the genus or species level compared to the family level (**PAPER IV**). We therefore recommend managers of reed beds to focus their effort on reaching the family level, but also stress that data at the Order level, at least for ground-dwelling invertebrates, can also be used to determine whether reed harvest affect the invertebrate community.

To sum up, reed bed age affected both biomass and species composition of flying and ground-dwelling invertebrates at the Order level and Coleoptera at the family and species level (**PAPER IV**). Harvest increased the invertebrate biomass but change the community composition and caused a shift in the relative abundance of different invertebrate groups at both the Order, family and species level. The diversity peaked in the 25-yeear-old reed bed, whereas red listed carabid *Carabus clathratus* occurred at the highest abundance in the 0-year-old harvested. Therefore, reed bed management should maintain a mosaic reed bed of different ages to cater for different invertebrate Orders and Coleoptera families, which both ensure a high diversity, high biomass and a suitable habitat for the red listed species.

1.4. EVIDENCE-BASED NATURE MANAGEMENT OF SALT MARSH PLANTS AND REED BED PLANTS AND INVERTEBRATES IN *DE ØSTLIGE VEJLER*

What can biologists do to limit the biodiversity crisis? According to David Western in his 1992 paper (Western 1992), biologists provide knowledge but face several challenges:

> *'First, the action depends on the manager, not the scientist. Ideas must, for this reason, be comprehensible to the user. Second, the manager wants simple workable solutions, not the hypotheses, controversies and contradictions which scientists thrive on.'*

It is therefore important to ensure that scientific ideas and hypothesis are translated into useable solutions. Proper management is of urgent importance in Denmark where a recent report found that 95% of habitat types, including almost all coastal habitats, is in unfavourable or very unfavourable condition (Fredshavn et al. 2019). My Ph.D. project is one part of a large project aiming at creating a management plan for the entire ecosystem *De Østlige Vejler*. The results presented in **PAPERS I-IV** therefore have to be translated into practical use aiding the management of coastal marshes and reed beds, first of all within *De Østlige Vejler*, but with potential to be extended to coastal management elsewhere. In this part of my thesis, I will provide an overview of how my results can be used to make practical management decisions within *De Østlige Vejler*. My work in *De Østlige Vejler* has focused on plants on the salt marsh and plants and invertebrates in the reed beds, and therefore, they are also the focal organisms of this section. I will include additional **unpublished results** when applicable. In the reference map at the beguinnin of the thesis, the location of all the places within *De Østlige Vejler* mentioned within this section can be found.

1.4.1. MANAGEMENT OPTIONS

Current management of *De Østlige Vejler* include reed harvest in a limited part of the extensive reed bed, cattle grazing of *Bygholmengen* and water level management affecting water levels on the salt marsh. The results obtained throughout this thesis can help evaluate the following practices:

- Grazing: Grazing on *Bygholmengen* occur at a grazing pressure that fluctuates between years but stayed below 1 cattle/ha: 0.81 cattle/ha in 2017 and 0.72 cattle/ha in 2018. The cattle is rotated between different parts of the marsh ensuring an even grazing pressure across the hole area. The recommended grazing pressure on Danish salt marshes is 0.3-1.2 animals/ha, and current management of *Bygholmengen* is therefore in line with the recommendations (Buttenschøn 2014). Grazing should ensure an overall low vegetation to accommodate birds but retain a structurally diverse vegetation (Buttenschøn 2014).
- Water level management: Water levels on *Bygholmengen* fluctuate throughout the year. During winter and autumn, management aim for maximum water levels (-4 cm DVR90) whereas during summer, lower water levels are maintained (-19 cm DVR90) (Nielsen & Clausen 2019b). This

Figure 16 *Different water levels on Bygholmengen during the August, 2017 (a) May 2018 (b), June 2018 (c) and during November 2017 (d).*

***Figure 17** Reed harvest within De Østlige Vejler during February 2018.*

means that large parts of *Bygholmengen* are flooded during winter but dry outside of the channels and indents during summer (Fig. 16).
Water levels can be increased by opening the water lock towards *Lund Fjord Kanal*, which result in fresh water being let onto *Bygholmengen*. Water levels are decreased by opening the water lock at *Centralslusen*. In practice, water level management requires specific weather conditions and for instance, water levels can only be decreased when water levels in *Limfjorden* is lower than on *Bygholmengen* due to eastern winds. Flooding with fresh water pose two major management concerns to be considered:

  - Potential eutrophication due to high nutrient levels in the fresh water.
  - Dilution of the salinity levels on *Bygholmengen*.

- The dike and closed water lock to *Limfjorden*: The dike separate *Bygholmengen* from *Limfjorden*. A water lock makes it possible to let water from *Limfjorden* enter the salt marsh when the water level in *Limfjorden* is higher than that on *Bygholmengen*. Since 1995 and 1997, the water lock at *Centralslusen* towards *Limfjorden* has not been open to actively allow salt water onto *Bygholmengen* (Hald-Mortensen 1998). Therefore, current management strategies result in *Bygholmengen* lacking natural salt marsh hydrology.

Figure 18 *The ungrazed control areas had a significantly higher vegetation than the grazed areas (a). Three out of four of the ungrazed control areas were covered in Phragmites australis (b).*

- Reed harvest: Commercial, mechanical winter harvest has been conducted by a Dutch company since 2014 (Fig. 17). Various areas have been harvested throughout the years, but as only reed stems aged one or two years are of commercial interest, some areas have been harvested repeatedly. Only a small part of the reed bed is subject to harvest as approximately 70 ha out of the 522 ha is harvested annually.

Grazing

Grazing affect the vegetation through trampling which can result in better seed germination, and trimming of the vegetation which increase species richness as the decreased plant height provide better light conditions for small plants (Treweek et al. 1997; Rannap et al. 2004). In Denmark, grazing on salt marshes is a widespread practice and have occurred so long that only few salt marshes are left unaffected (Jensen 1985). In the absence of grazing, Jensen (1985) found that salt marsh characteristic species *Salicornia maritima*, *Suaeda maritima* and *Glaux maritima* disappeared.

In **unpublished data**, the effect of grazing on *Bygholmengen* was assessed. In 1987, four control areas each of approximately 25x25 m were fenced thereby completely eliminating grazing by cattle (Fig. 18) (Riis 2009). I did monthly surveys from August 2017 to November 2017 of the ungrazed control areas compared to the grazed salt marsh (**unpublished data**). Each month, a total of eight vegetation analyses were conducted in two of the ungrazed control areas using the pinpoint and 5 m circle approach (Levy & Madden 1933; Nygaard et al. 2016). On a grazed section of *Bygholmengen* adjacent to the ungrazed control areas, another eight vegetation analyses were conducted each month. The vegetation analyses were not repeated measures but conducted within the same section of *Bygholmengen* every month. From

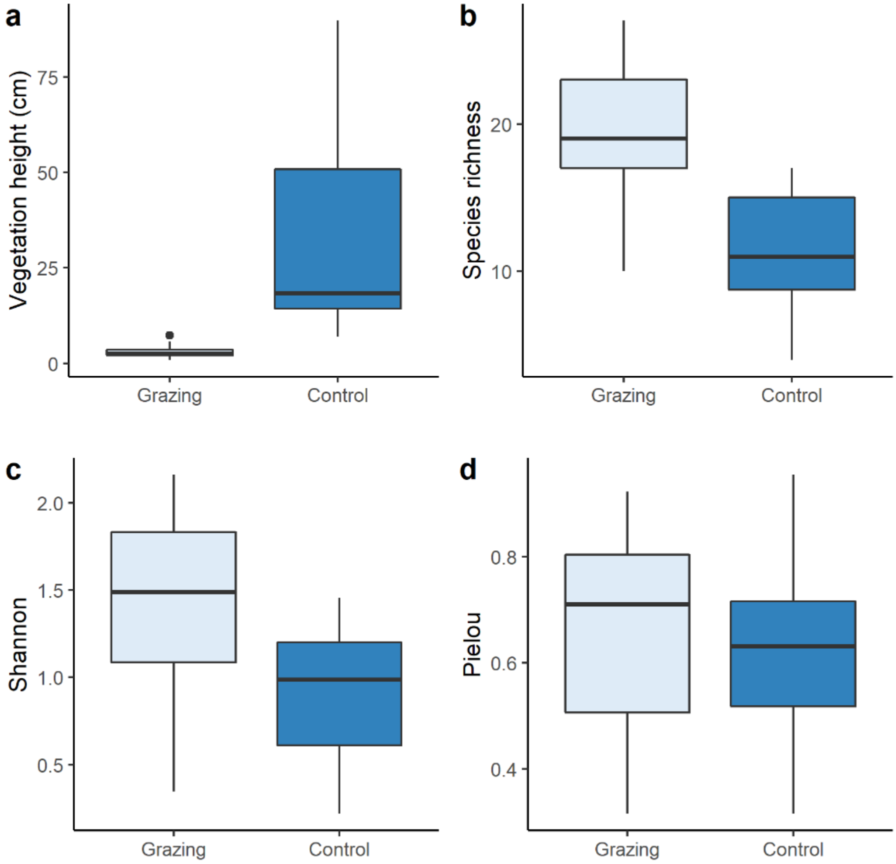


Figure 19 *Results from unpublished fieldwork comparing the vegetation of the grazed Byhgolmengen to ungrazed controls. During August to November 2017, eight grazed and eight control plots were examined each month using the pinpoint method, in total 32 plots per treatments. Plots examined each month were not repeated measures, but randomly sampled plots in either a grazed or a control area. Using a Wilcoxon test followed by Bonferroni correction, significant differences were found for vegetation height (a, $p < 0.001$), species richness (b, $p < 0.001$) and the Shannon diversity (c, $p < 0.001$) but not for Pielou (d, $p > 0.05$).*

these vegetation analyses, it was possible to evaluate the effects of grazing on vegetation height, species richness, species diversity and evenness.

Grazing on *Bygholmengen* decreased vegetation height but increased the mean species richness and the Shannon diversity significantly (Fig. 19). *Glaux maritima* was found on both grazed and ungrazed plots in contrast to results by Jensen (1985). Some species were found only when grazed, including *Trifolium fragiferum* and *Spergularia media*. Other were found only on the ungrazed control areas, including *Solanum* *dulcamara* and *Sium latifolium* (Fig. 20). Median Ellenberg values for moisture (F), light (L), nutrients (N) and salinity (S) were calculated for the species only occurring in either the grazed or ungrazed control plots. Only Ellenberg F differed between the areas, and were significantly higher in the ungrazed control plots (Fig. 20).

Grazing animals are able to keep the landscape open and keep coastal meadows from turning into reed beds or other monocultures (Bakker et al. 1993; Rannap et al. 2004), and we did indeed find that the ungrazed plots were dominated by common reed – three of four fenced plots were completely covered in common reed. Studies conducted in *Vejlerne* in the 1960'ies found that 3 years without grazing were sufficient for common reed to establish, but that even after 13 years without grazing, reed had not completely eliminated the growth of other graminoids (Schierup 1986). Therefore, to avoid the open marsh vegetation turning into a reed bed, continued grazing is recommended. Current grazing pressure appear suitable to maintain an open habitat as well as to keep the distribution of common reed at a minimum. Further, summer grazing at a high stocking rate of 1 cattle/ha creates a salt marsh habitat more suitable for grazing geese than a lower stocking rate of 0.5 cattle/ha, as geese prefer a low vegetation height (Mandema et al. 2014). Contuned grazing therefore both benefit plant species richness and grazing geese.

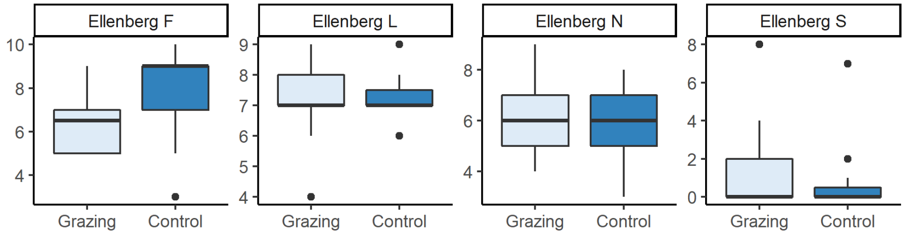


Figure 20 *Median Ellenberg values of the plants only occurring in the ungrazed control areas or the grazed areas. Kruskal Wallis with Bonferroni correction showed that only Ellenberg F (moisture) differed significantly between treatments (p < 0.05). List of species only found on the grazed area: Plantago major ssp. Intermedia, Sagina procumbens, Cerastium fontanum, Lolium perenne, Rumex acetosa, Carex flacca, Cardamine pratensis, Myosotis scorpioides, Plantago major ssp. Winteri, Cirsium vulgare, Trifolium fragiferum, Alopecurus geniculatus, Ranunculus reptans, Trifolium pratense, Sagina nodosa ssp. Nodosa, Ranunculus sceleratus, Lychnis flos-cuculi, Juncus bufonius, Bellis perennis, Taraxacum sect. Taraxacum, Spergularia media. List of species only found in the ungrazed control area: Sonchus arvensisCirsium arvense, Scutellaria galericulata, Cerastium fontanum, Solanum dulcamara, Sium latifolium, Erigeron canadensis, Poa compressa, Cicuta virosa, Rumex crispus, Epilobium hirsutum, Tripleurospermum inodorum, Galeopsis bifida, Atriplex prostrata, Halimione pedunculata, Bolboschoenus maritimus, Lycopus europaeus, Carex disticha, Rumex hydrolapathum, Mentha aquatic, Hippuris vulgaris.*

Water level management: Eutrophication

Apart from grazing, water level management is one of the key management options on *Bygholmengen*. First, there is the issue of flooding *Bygholmengen* with fresh water.

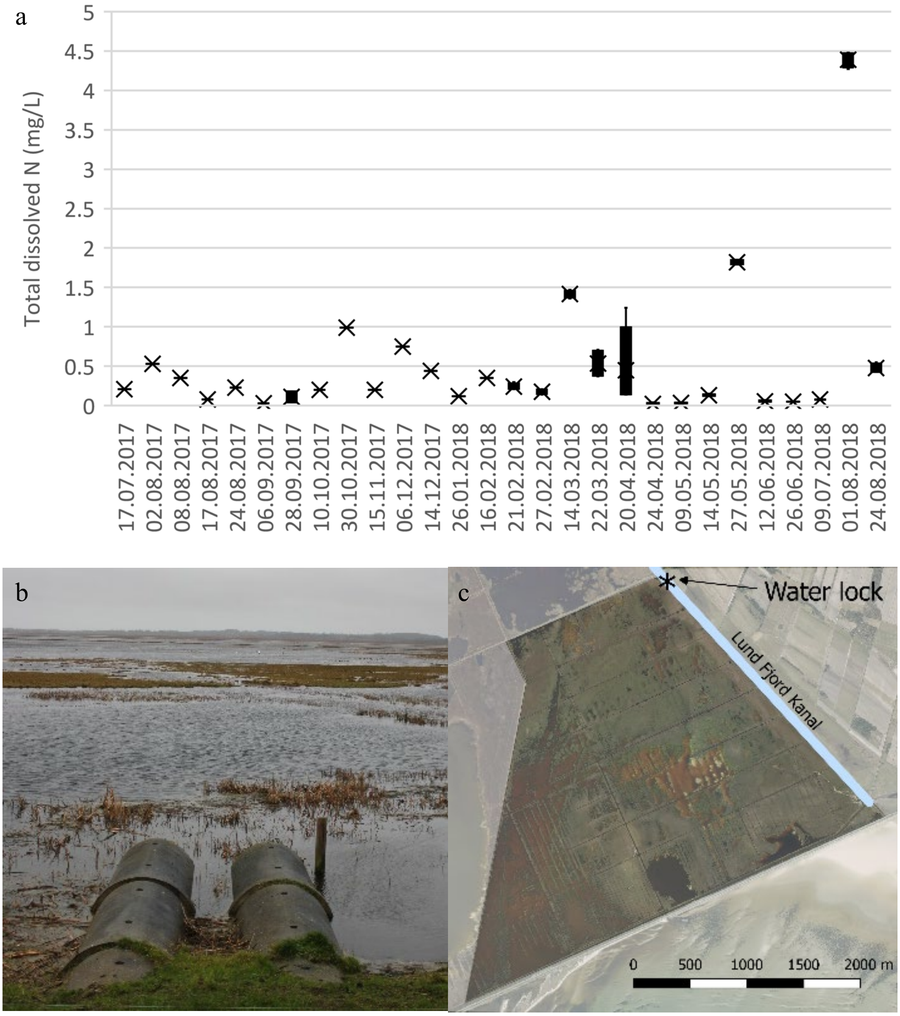


***Figure 21** Total content of dissolved NH_4^+, NO_2^- and NO_3^- (mg/L) measured at the canal adjacent to Bygholmengen (a). Water is let onto Bygholmengen from Lund Fjord kanal via pipes to increase the water level at late autumn or winter (b). Water samples were taken in Lund Fjord Kanal at the water lock (c). Nitrogen content was determined following Danish standard (Danish Standards Association 1975; Danish Standards Association 1991). At each point in time, four samples were collected and analysed. Figure shows the mean (x), median and standard deviation.*

When the water lock is open towards the canal *Lund Fjord Kanal*, fresh water enters the *Bygholmengen* (Fig. 21). As *Lund Fjord Kanal* and *Bygholmengen* is surrounded by agricultural land, concerns have been raised as to whether the water in the canal has a high nutrient content due to agricultural runoff that could increase the nutrient content of *Bygholmengen*. The concern is valid as eutrophication is a general problem on Danish salt marshes due to runoff from catchments areas (Fredshavn et al. 2014). Nitrogen enrichment increase net primary productivity while decreasing plant species richness whereas phosphorus enrichment has little effect on species richness (Soons et al. 2017). By measuring the total dissolved nitrogen content of the water (Fig. 21), we found that the dissolved nitrogen level of the canal fluctuated throughout the year with a peak in August 2018, but was below 2 mg/L most of the year. This corresponds to nutrient levels of Danish canals in natural areas (Thodsen et al. 2019). In Danish canals in agricultural lands, the total dissolved nitrogen content is on average four times higher than in canals of natural areas and exceeds 4 mg/L (Thodsen et al. 2019). The low content of dissolved nitrogen in the canal indicate that water from the *Lund Fjord Kanal* will likely not result in an increased eutrophication of the coastal meadow *Bygholmengen*. Nitrogen levels in the canal should not deter managers from inundating *Bygholmengen* with water from the canal. Further, ammonium levels are not especially high in the area near the water lock (Fig. 3) indicating that this area does not receive an increased nitrogen load from the water from *Lund Fjord Kanal*. It

BOX 3 Biological status (*Naturtilstand*)

The Danish NOVANA framework monitor the quality of Danish habitats and how it change over time. In the Danish NOVANA framework, a habitat specific method to estimate the biological status of the habitat has been developed (Fredshavn & Ejrnæs 2009). The framework makes it possible to make objective and comparable estimates of an areas status across time and space by accessing both species presence and habitat structures. Once a species index and a structural index have been calculated, they are used to calculate the biological status.

The species index is calculated based on the presence of species. Species are ranked for each habitat type, and high rankings are given to species that requires a pristine environment whereas invasive and problematic species are given a negative value. The structural index is based on the presence or absence of structural qualities, that are specified for each habitat type. On salt marshes (habitat type 1330), they include the natural hydrology or its obstruction behind manmade structures including dikes, the presence of salt pannes and vegetation zonation as well as estimating the cover of common reed (Fredshavn & Ejrnæs 2009). Using information on both species composition and the status of the habitat structures, the habitat is awarded a biological status on a scale from 0 to 1 with 1 being the best possible biological status and 0.5 corresponding to a mediocre habitat quality.

is also worth noting that Ellenberg N averaged 4.8 (2017) and 5.4 (2018) on *Bygholmengen* (**PAPER II**) which is lower than the Danish average for salt marshes, where Ellenberg N averages 5.8 (Fredshavn et al. 2014).
We did not measure phosphorus levels in the *Lund Fjord Kanal*, but found that available phosphorus levels were high in the vicinity of the water lock (Fig. 3) and suggest that future monitoring of the *Lund Fjord Kanal* should include phosphorus levels.

Water level management: Fresh water input and restricted salt water flooding

Though eutrophication does not appear to be a problem in association with fresh water flooding of *Bygholmengen*, the fresh water in itself might be problematic. A high fresh water input dilute the soil salinity (Adams & Bate 1994). Studies of the vegetation on *Bygholmengen* during a cold, wet year and a warm, dry year provided some insights into the effect of average and high water levels on *Bygholmengen*. Though the results can not definitively say anything about the effects of water level management, it is possible to use the results to make some observations that can be useful in the management of *Bygholmengen* regarding the effects of a high and average water table. It would require a controlled experiment, as well as longer time series, to confirm the results. A severe drought hit Denmark (Cappelen 2019) during the summer of 2018, resulting in the *Bygholmengen* drying out. The vegetation surveys during the summer of 2018 gave an indication of what *Bygholmengen* would look like if water level management aimed for a lower water table, as water levels during the summer of 2018 had dropped below -40 cm DVR90 where management aim for -19 cm DVR90 (Nielsen & Clausen 2019b). The summer of 2017 had been especially wet (Cappelen 2018a), but did not results in a water level higher than -19 cm DVR90 on *Bygholmengen* in 2017 (Nielsen & Clausen 2019a). With some caution, the fieldwork of 2017 and 2018 provided a way of estimating the effects of current water level management and the effects of a lowered water table on *Bygholmengen* (**PAPER II**). However, as the results only show the effects of a low water table during one year, we cannot make conclusion on the long-term effects of lowering the water table.

A high fresh water input pose a problem if aiming to achieve a salt marsh in a favorable habitat quality and high biological status. Fresh water can change the salt marsh plant community and even turn it into a fresh water community (Vestergaard 2000). In Denmark, assessments of the biological status of selected habitats are conducted continuously (Box 3) and during NOVANA surveys in 2005 and 2011, the biological status of *Bygholmengen* was assessed (Miljøstyrelsen 2005a; Miljøstyrelsen 2005b; Miljøstyrelsen 2011). In 2005, the biological status was estimated to 0.62 (n = 1) corresponding to good biological status, and the obstruction of the natural hydrology was noted (Miljøstyrelsen 2005b). By 2011, the biological status had decreased to 0.55 (n = 1), classified as a mediocre biological status, and a lack of natural vegetation zonation as well as a strong obstruction of the natural hydrology was noted (Miljøstyrelsen 2011). During the fieldwork on *Bygholmengen*

in 2017 and 2018, we found that the biological status was still mediocre (mean biological status 2017: 0.57 ± SD 0.06, n = 40; mean biological status 2018: 0.59 ± SD 0.05, n = 80). The lack of natural hydrology and presence of the dike, as well as a lack of natural zonation contribute to the biological status only being mediocre.
When comparing the wet summer of 2017 to the dry summer of 2018, we found that the biological status increased marginally during dry conditions. We saw in increase in the number of species indicative of the Atlantic salt meadow (Corine biotype 1330) during the dry conditions of 2018 compared to the wet conditions of 2017 (**PAPER II**). However, we found that the species composition on *Bygholmengen* in 2018, where most salt marsh species were present, differed significantly from that of other Danish salt marshes (**PAPER I**). Further, soil salinity levels increased significantly during dry condition (**PAPER II**). If aiming towards achieving higher soil salinity levels and thereby a habitat containing more species indicative of the Atlantic salt meadow, water level management should strive to reduce the input of fresh water and lowering the water table. Alternatively, to open the water lock at *Centralslusen* towards *Limfjorden* thereby letting in salt water. Opening the water lock have previously been found to increase the soil salinity levels which further resulted in a vegetation change towards salt tolerant plant species (Kjeldsen 2008). Opening the water lock to restore natural hydrology would automatically increase the structural quality of *Bygholmengen*, potentially increasing the biological status as a salt marsh. A 2017 NOVANA survey of *Bygholmengen*, that mistakenly listed that the natural hydrology was not restricted in any way, estimated the biological status to 0.84 (Miljøstyrelsen 2017), showing that the presence of a natural hydrology can have a large impact on the biological status. However, whether the biological status would actually increase following an opening of the dike also depends on how the vegetation would respond. When a dike is removed and tidal flooding reinstated, the restoration of salt marsh vegetation and soil characteristics can take decades (Garbutt & Wolters 2008; Santín et al. 2009; Mossman et al. 2012). It could therefore take a long time before the species index increased given the dike at *Centralslusen* was opened.

Another management option is to maintain current water level management with a high water table during winter. The high water table can be achieved by opening the water lock at *Lund Fjord Kanal*, which allows fresh water to flood *Bygholmengen*. Care must be taken in this approach as flooding by fresh water could benefit common reed and result in a higher cover by common reed (Mesléard et al. 1999), but current grazing levels appear to be able to counteract the growth of common reed. The plant community during dry conditions did not resemble a Danish Molinia meadow (**PAPER I**), but during the wetter and less saline conditions of 2017, where water levels were closer to that aimed for by managers, the plant community, in regards of its ability to cope with salt and moisture, had moved closer towards the fresh Molinia meadow plant community (Fig. 22). Therefore, keeping current water level

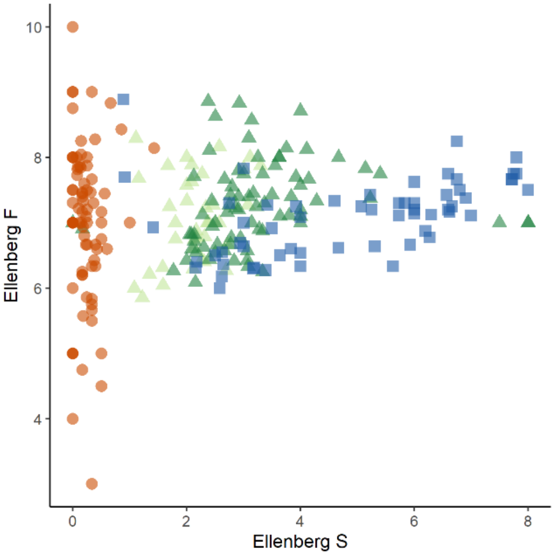


Figure 22 *Ellenberg F (moisture) and Ellenberg S (salinity) for the plant communities on Danish Molinia meadows (red circles, n = 80), Danish salt marshes (blue squares, n = 80) and Bygholmengen in 2017 (light green triangles, n = 40) and 2018 (dark green triangles, n = 80). Each data point represent the mean Ellenberg value of all plants within a 5 m circular plot.*

management plans could result in the plant community gradually becoming less and less well adapted to coping with high salinity levels, and more like a Molinia meadow.

Reed winter harvest

Another important management option in *De Østlige Vejler* is the use of winter harvest in a part of the reed bed. Current management of the reed beds of *De Østlige Vejler* varies across both space and time, as different areas of the reed bed are harvested or cut each year, creating a mosaic of reed beds in different stages of succession (**PAPERS III-IV**). This spatiotemporal variable management is suitable for breaking up habitat homogeneity and create a more heterogeneous landscape with a variety of structural properties suitable for a multitude of species (Christensen 1997; Mester et al. 2015). Based on our results, a continuation of current management including harvest and/or cutting at differing areas across time is recommended for a number of reasons. The take home message regarding the flora and invertebrates is that a reed bed mosaic including reed beds in various successional stages will result in the overall highest plant species richness, create the most heterogeneous habitat and the most diverse invertebrate community (**PAPER III-IV**). Less than half of the plant species found in the reed bed were present across all reed bed treatments, as unique plant species were present in reed beds either harvested or cut and in different reed bed ages (**PAPER III**). The plants differed in their ability to cope with light limitation due to the shadowing effect of common reed and their ability to cope with nutrients (**PAPER III**). The invertebrate biomass peaked in the newly harvested reed bed, declined in the reed bed left unmanaged for three years and was at its lowest in the reed bed left unmanaged for 25 years (**PAPER IV**). The increased biomass in response to harvest was apparent in both aerial invertebrates, ground-dwelling invertebrates and Coleoptera (**PAPER IV**). It would be interesting to include diet analyses of birds in future studies of invertebrates in *De Østlige Vejler* to determine whether the increased biomass of the newly harvested reed bed consist of species that make up a large part of the diet of insectivorous reed bed birds. Many reed bed passerines including the reed warbler *Acrocephalus scirpaceus* as well as the Eurasian bittern *Botaurus stellaris* feed on invertebrate prey (Bibby & Thomas 1985; Paracuellos 1997; Schmidt et al. 2005; Polak 2016). When insect abundances fall, so does the abundance of insectivorous birds (Møller 2019). Previous studies found that large scale reed harvest caused a decrease in the preferred invertebrate prey species of several passerine birds (Schmidt et al. 2005). Even though invertebrate diversity increased with reed bed age, and peaked in the reed bed left unmanaged for 25 years, the invertebrate Orders and Coleoptera families occurred at different relative abundances in each reed bed age (**PAPER IV**). Worth notin, is that when the Coleoptera biomass increased, the evenness of the community decreased (Fig. 15) showing that communities of a high biomass were also dominated by a few Coleoptera species. One redlisted species of Coleoptera was more abundant in the newly harvested, 0-year-old reed bed than in the reed beds left unmanaged for either 3 or 25 years (**PAPER IV**). To accommodate a wide range of invertebrate orders and families, harvest on a small scale is encouraged. It is important to note that these results apply to a reed bed where only a small part of the reed bed at a landscape level is subject to harvest, in agreement with previous studies also advocating for harvest at a small scale (Burgess & Evans 1989; Trnka et al. 2014). Large-scale, mechanical harvest does not necessarily have a positive impact on the invertebrate community (Schmidt et al. 2005).

De Østlige Vejler is designated as a Birds Directive site due to its importance to birds on a European scale (European Environment Agency 2012). Due to this designation, it is important to consider how a management scheme optimal for increasing overall plant diversity and habitat heterogeneity as well as a diverse invertebrate community will impact the birds. High habitat diversity within wetlands is considered optimal for wetland birds (Sjöberg and Danell 1983), and also secured a high plant diversity (**PAPER III**) and invertebrate diversity (**PAPER IV**). Different species of birds, nonetheless, prefer different degrees of structural heterogeneity (Baldi and Kisbenedek 1999; Mero et al. 2018), and previous studies have shown that the structural heterogeneity within reed beds may decrease as a result of reed harvesting due to higher reed expansion and exclusion of other species (Deák et al. 2015). A few years after management, the reed bed becomes a homogenous habitat dominated by common reed (Mester et al. 2015). However, we found that a mixture of reed bed areas either harvested, cut, or left unmanaged for a varying amount of time, created the most heterogeneous habitat at the landscape level (fig. 12, **PAPER III**). Our result therefore indicate that managing the reed bed for a high plant and invertebrate diversity does not clash with management suitable for the birds. It should, however, be noted that some species of birds, for instance the Eurasian bittern, avoid breeding in newly harvested areas (Nielsen & Clausen 2019a), but given only a small part of the reed bed is subject to harvest each year, there should still be plenty of suitable breeding habitat left. Finally, reed management creates edges and fragments the reed bed habitat (Báldi 1999). Báldi (1999) found an edge effect on multiple species of birds in reed-dominated wetlands with *Acrocephalus schoenobaenus* and *A. scirpaceus* preferring the edge habitat and *A. arundinaceus* preferring the reed interior. Should harvest cease in *De Østlige Vejler*, it is therefore important to consider the effect on species living at the reed bed edge.

Hands-off management

Finally, imagine a complete hands-off management scenario. How would the salt marsh and reed beds of *De Østlige Vejler* look if all active management stopped? Likely, natural succession would take over ultimately resulting in a more homogenous landscape. In the absence of grazing, the open and low marsh vegetation would gradually become dominate by common reed. This would decrease the floral diversity of *De Østlige Vejler* immensely as the open marsh area contained a far greater floral diversity than the reed bed (**PAPERS I-III**). It would decrease the areas value as a birding reserve as numerous species, including thousands of geese and ducks, centre their visit on the open marsh rather than the reed bed. The most recently harvested reed bed areas would lose the light-loving pioneer plant species that occur following harvest (**PAPER III**). The reed bed would become more homogenous and dominated by reed, whereas an increased litter build-up would gradually result in a drier habitat. The scrubs in the older parts of the reed beds would become more dominant, and eventually even turn into woodland. The invertebrate community would also change, and since some Orders of invertebrates, as well as a red listed carabid beetle, were considerably more abundant in the recently managed areas, they would likely decline in abundance (**PAPER IV**). Thus, a lack of management would result in habitat homogenization, decreased diversity and a decreased habitat quality for an abundance of species.

1.5. CONCLUSIONS AND PERSPECTIVE

As habitats are deteriorating, species are in decline and the biodiversity in crisis (Small 2011; Fischer et al. 2018; Kennedy et al. 2019; Fredshavn et al. 2019), it is important to assess the state of our protected nature reserves and manage them accordingly. Protected areas are considered a key element in species and habitat protection (Geldmann et al. 2013) and within the terrestrial realm, local biodiversity levels are approximately 10% higher inside than outside protected areas (Gray et al. 2016). In Denmark, 261 areas are protected within the Natura 2000 framework and of these, 95% are in an unfavorable condition (Fredshavn et al. 2019). The coastal habitats, including the Atlantic salt meadow (habitat 1330), are among the habitats least affect by man but are nonetheless in an unfavorable state due to eutrophication, limitations of natural hydrology, invasive species and sea level rise (Fredshavn et al. 2019). Several of these issues can be recognized within *De Østlige Vejler* (**PAPERS I-II**). In **PAPER I**, we found that the Atlantic salt meadow *Bygholmengen*, on which the natural hydrology is highly restricted, no longer had a vegetation resembling that of other Danish salt marshes. The mismatch between the vegetation of *Bygholmengen* and other salt marshes partly explains its deteriorating status as a salt marsh. Further, high levels of N indicated some degree of eutrophication, though the plant community had a lower Ellenberg N that the average Danish salt marsh, and levels of P were not above average.

Sea level rise and coastal squeeze is an eminent threat to salt marshes but recent studies have found that salt marshes are more resilient towards sea level rise than previously expected (Kirwan & Megonigal 2013; Kirwan et al. 2016; Zhu et al. 2020). In **PAPER II**, we looked at another climatic factor likely to have an influence the salt marsh vegetation: interannual climate fluctuations. We found that weather fluctuations coincided with a large species turnover, showcasing the importance of weather fluctuations on short-term vegetation dynamics. On a diked temperate salt marsh, high precipitation levels resulted in fewer halophytes while a heat wave resulted in a decreased vegetation cover but a higher proportion of halophytes (**PAPER II**).

One way to mitigate the loss of biodiversity is by nature management. In **PAPERS III** and **IV**, we evaluated how management affect the reed bed habitat. In **PAPER III**, we found that reed bed management and time since last management affect the plant diversity at multiple levels by impacting species richness, diversity and habitat heterogeneity. We found that the effect of reed management is complex and depend on management method, age of the unmanaged reed bed and the time of the year. Reed harvest rejuvenates the reed bed as it promotes the growth of new reed and new reed stems were still more abundant three years following harvest compared a reed bed left unmanaged for 25 years. Maintaining reed beds of different ages will result in the highest plant species richness and habitat heterogeneity.

In **PAPER IV**, we found that reed harvest also had a large impact on the reed bed invertebrate community. We saw that biomass increased with reed management and that the oldest examined reed bed contained the smallest biomass of invertebrates. As the invertebrate community worldwide is facing a decline (Hallmann et al. 2017; Møller 2019; van Klink et al. 2020; Arzel et al. 2020; Roth et al. 2020), it is important to consider management strategies that maintain a high invertebrate biomass. While Valkama et al. (2008) found that reed management spanning multiple years decreased the invertebrate abundance, we found that harvest increased the biomass even though the area in question had been harvested annually since 2014. We found that harvest and time since last harvest impacted the invertebrate community composition at both the Order level and at the species level of Coleoptera. Some invertebrate Orders and Coleoptera families responded well to harvest while others had a significantly higher abundance in the areas left unmanaged for either a short or a long time.

In conclusion, the salt marsh vegetation on *Bygholmengen* benefit from grazing but suffer due to the dike restricting natural hydrology. Commercial reed harvest changed the plant and invertebrate composition of *De Østlige Vejler*, but when conducted at a small scale, had a positive impact on the species richness of plants and invertebrates at a landscape level.

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PAPER I

COASTAL MEADOW VEGETATION FOLLOWING A CENTURY OF SHIELDING BEHIND A DIKE

Resubmitted to Estuaries and Coasts following major revision

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Coastal meadow vegetation following a century of shielding behind a dike

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ABSTRACT

Diking of salt marshes for agricultural uses is still common practice in Europe, and impacts both the vegetation and physical environment of the marsh. Fieldwork on a shielded marsh (in this case, an enclosed coastal marsh which had been behind a dike since 1890) was conducted to assess the effect of the dike on the plant community, environmental conditions, as well as the correlations between vegetation cover and diversity with environmental factors. Vegetation data from both salt marshes without dikes and fresh meadows were sampled by the Danish Environmental Protection Agency and used to assess whether the plant community of the shielded marsh resembled that of either salt marshes or fresh meadows. The century long elimination of tidal- and storm flooding has resulted in low salinity levels (0.4-5.13 ppt), low available P (0.36-4.90 g/100 g soil), and high total N (0.68-28.82 g/kg). The plant community demonstrated a mean species richness (11.4) similar to that of other salt marshes but were no longer characterized by the same composition of halophytes as the nearby unshielded marshes (ANOSIM, *p*-value > 0.001). The century long shielding by the dike has not yet resulted in vegetation resembling that of the nearby fresh meadow community (ANOSIM, *p*-value > 0.001). Diking that does not allow tidal floods does not therefore protect the salt marsh habitat but results in a habitat which contains both halophytes and glycophytes.

INTRODUCTION

The salt marsh is a widely distributed coastal habitat which is most common in temperate and higher latitudes (Murray et al. 2011). Flooding by salt water through either tidal flow or storms shape abiotic conditions of the salt marsh and seawater creates a zonation of salinity and is the natural supply of nutrients to the salt marsh (Rozema et al. 1999). The salt marsh vegetation is shaped by both interspecific competition and extreme abiotic conditions and is dominated by both halophytes and plants adapted to cope with saline conditions (Hacker and Bertness 1999, Levine et al. 1998, Ungar 1998).

Since Roman times, it has been common practice to enclose and drain salt marsh areas to make land suitable for agricultural use (Doody 2008a). This practice is still common in Europe but is rarely seen in North America (Gedan et al. 2009). Diking of salt marshes that partly or totally restrict tidal flooding is often done to facilitate road construction, reclaim agricultural land, or reduce insect nuisance (Sun et al. 2003) while shielding coastal marshes from erosion (Van Loon-Steensma and Slim 2013). Today, salt marshes that are untouched by man are rare and more than 70% of north-western European salt marshes have been agriculturally exploited (Bakker et al. 2002) with many being shielded behind various man-made structures (Bulleri and Chapman 2010).

Some types of dikes eliminate tidal flooding completely while others, such as berms and summer polders, only limit it (Bakker et al. 2002; Mora and Burdick 2013). Tidal flooding might naturally be excluded from salt marshes for years as is the case in hundreds of naturally, temporarily open/closed estuaries in South Africa (Riddin and Adams 2008) and salt marshes sheltered behind naturally occurring structures (Moreira 1992).

Dikes eliminating tidal- and storm flooding have several effects on the coastal marsh ecosystem. The coastal marsh shielded behind a dike may experience a disrupted salinity gradient, altered hydrology and soil chemistry (e.g. soil pH), increased build-up of organic matter, and decreased dissolved nitrogen (N) and phosphorus (P) (Gedan et al. 2009; Portnoy and Giblin 1997, Roman et al. 1984). All of these are edaphic conditions that affect vegetation (Cañadas et al. 2010; El-Sheikh and Abbadi 2004; Min and Kim 1999a; Min and Kim 1999b; Zhao et al. 2017). Tidal restriction also results in a replacement of halophytic vegetation by brackish species and glycophytes (Roman et al. 1984), and entrapping the coastal meadow behind dikes can result in the marsh turning into a fresh meadow (Vestergaard 2000). Hence, diking may result in severe loss and degradation of salt marsh habitats (Doody 2008b).

Salt marshes are protected habitats in both Europe (Council of the European Commission 1992) and North America (Zedler 2004). Denmark holds more than 25% of the salt marsh habitat within Europe (Doody 2008a); even so, the conservation status for Danish salt marshes is declining due to disruptions of natural dynamics, increased moisture levels, and increased nutrient input from surrounding areas (Fredshavn et al. 2014).

It is important to understand how the plant community correlates with edaphic factors at a coastal meadow shielded by a dike. *Bygholmengen* in Denmark is an example of a coastal marsh that has been shielded behind a dike for over a century (since 1890). Since 1997, this marsh has only received salt water by seepage through the dike and via spray (Riis 2009). Our aim was to determine the vegetation and environmental conditions of *Bygholmengen*. We first examined the vegetation (cover, number of halophytes, species richness and Shannon diversity) and edaphic environment (moisture, salinity, nutrients) of the diked, coastal meadow. We then examined how they correlated. In Denmark, vegetation data is sampled every year through the NOVANA framework (Nygaard et al. 2016). From the NOVANA data, it is possible to obtain plant species lists from a selected number of habitat types including salt marshes (habitat type 1330, (European Commission 2013; Fredshavn 2012; Nygaard et al. 2016)) and fresh meadows (habitat type 6410 (European Commission 2013; Fredshavn 2012; Nygaard et al. 2016)). To determine whether the coastal meadow vegetation of *Bygholmengen* still resembles true salt marsh vegetation or now resembles the vegetation of a fresh meadow, we compiled vegetation data from adjacent salt marshes and fresh meadows from the NOVANA database. In the face of lacking edaphic samples from the NOVANA data, we used Ellenberg values which are bioindicators values linked to each plant representative of the edaphic environment, and calculated using the realized niche of each plant species (Ellenberg et al. 2001). The Ellenberg values were used in addition to the vegetation data to evaluate similarity in the plant communities.

MATERIALS AND METHODS

Field study area – a shielded marsh

This study took place in 2018 on the shielded marsh, *Bygholmengen* (728 ha), in De Østlige Vejler, Denmark (Fig. 1a, b). *Bygholmengen* is characterized as an Atlantic Salt meadow (Corine Biotype 1330) (Danish Environmental Protection Agency 2005a; Danish Environmental Protection Agency 2005b; Danish Environmental Protection Agency 2011). The marsh is protected by a dike from the adjacent brackish fjord, *Limfjorden* (salinity 25-29 ppt outside the dike). The area is vital to breeding and resting wading birds, geese, and ducks on a European scale and is protected by both the Ramsar Convention and the Birds and Habitats Directive (European Environmental Agency 2019; Ramsar 2020). Due to its importance (Nielsen and Clausen 2019), water level management is used to secure water levels suitable for the numerous birds feeding, breeding and resting on the marsh. The management of the water level keeps *Bygholmengen* partly flooded with rainwater from the surrounding catchment area during winter which results in wave activity. This only occurs when the fjord is lower than the shielded marsh due to easterly winds.

Bygholmengen was initially created as part of a failed land reclamation project at the end of the 19th century. The building of a dike enclosed the marsh and shielded it from the fjord, but the dike was breached multiple times until the year 1900 (Jakobsen and Sørensen 1993). In this manuscript, *Bygholmengen* is referred to as 'the shielded marsh'. This shielded marsh does not get flooded at regular high tides or when there are storms because of the dike. The dike is used to control the water levels of the marsh via a canal lock between canals surrounding the shielded marsh and the adjacent fjord. In the 1990s, the dike was opened twice (1995 and 1997) towards *Limfjorden* which actively allowed salt water to enter the marsh which inundated the salt pannes and pools (Riis 2009). This practice has since been abandoned (Riis 2009).

Today, *Bygholmengen* is only affected by salt water through salt spray during storms and by limited seepage through the main canal lock of the dike (Kjeldsen 2008). Salinity at the main canal lock peaked at 20.2 ppt in 1996 after which it has declined and fluctuated between 3.8-7.9 ppt from 2007-2018 (Kjeldsen 2008; Kjeldsen and Nielsen 2008; Kjeldsen and Nielsen 2009; Kjeldsen and Nielsen 2010; Kjeldsen and Nielsen 2011; Kjeldsen and Nielsen 2014; Nielsen and Clausen 2019).

The marsh is grazed from late spring to October each year and approximately 525 cattle were present in 2018 resulting in a stocking rate of 0.72 cattle/ha.

Vegetation analysis at the shielded marsh

Prior to the fieldwork, 80 sampling plots were randomly distributed on the shielded marsh using QGIS v2.18.11 (QGIS Development Team 2016) ensuring a minimum distance of 200 m between sampling plots (Fig. 1). Plots were distributed randomly instead of along a transect as no clear vegetation zonation was apparent. Each sampling plot consisted of a circle with a radius of 5 m, and all species present in the circle were determined to species level (Frederiksen et al. 2006; Schou 2006, Schou et al. 2010; Faurholdt and Schou 2012; Schou et al. 2014). The pinpoint method provides an objective measure of species cover within the pinpoint frame by counting the number of pins touched by vegetation (Levy and Madden 1933; Kent 2011). At the center of each 5 m circle, a pinpoint frame of 0.5x0.5 m with 16 grid points was positioned, and a pin was inserted in each grid. All plants touching the pin were noted and measured, and we counted the total number of interactions between the pin and vegetation.

Data from the pinpoint frame provided frequency data for each species within a 0.5x0.5 m square while data from the 5 m circle provided presence/absence data for an area of 78.5 m^2. Vegetation cover, density, and height were calculated from the pinpoint data, and cover was defined as the percentage of the pins touched by vegetation. Vegetation density was calculated as the number of times vegetation touched the pin in a given pinpoint frame. Mean vegetation height was calculated per pinpoint frame, and total species richness and number of halophytes were calculated from the 5 m circle data. Halophytes, listed in Table 1, are defined as species indicative of the Corine Biotype 1330 and of Danish salt marshes and include species connected to the middle/high marsh (European Commission 2013; Danish Environmental Protection Agency 2016). Shannon diversity (Shannon and Weaver 1949) was calculated on basis of the pinpoint data using the R package vegan v2.5.4 (Oksanen et al. 2017).

Comparison of the shielded marsh with salt marshes and fresh meadows in the region

The Danish Environmental Protection Agency (DEPA) collects vegetation data within a number of habitats, including salt marshes (Corine Biotype 1330) and Molina meadows (Corine Biotype 6410) by using the 5 m circle approach (Nygaard et al. 2016) where all plant species present in a circle with a radius of 5 m are noted. A Molina meadow, here called a fresh meadow, is characterized as a graminoid- and forb-dominated habitat, moist or part-time flooded with fresh water that is often managed by grazing (European Commission 2013). In the Corine Biotypes, the salt marsh is divided into three zones, the '*Salicornia* and other annuals colonizing mud and sand' (1310), '*Spartina* swards' (1320) and 'the Atlantic salt meadow' (1330) (European Commission 2013). We work exclusively with the Atlantic Salt meadow (1330), here called the salt marsh. This type of marsh has been described as an often grazed high marsh habitat which is frequently flooded by the ocean during storms but is protected from significant wave activity and hence erosion as it is on higher ground compared to biotopes 1310 and 1320 (European Commission 2013; Nygaard et al. 2016). In Denmark, the Atlantic Salt meadow (1330) is flooded at a frequency of ten times a year to once every decade (Miljøministeriet 2009).

To test whether the shielded marsh in this survey was similar to either salt marshes or fresh meadows, data from salt marshes not behind dikes and fresh meadows from Northern Jutland which were sampled by EPA was downloaded (http://naturdata.miljoeportal.dk/) (Fig. 1a, c). From the downloaded data, we randomly selected 80 salt marshes and 80 fresh meadows to be compared to the shielded marsh. We used the species lists from the 5 m circles to calculate the mean Ellenberg F (EIV F) and Ellenberg S (EIV S) (Ellenberg et al. 2001) for each of the 80 plots in the shielded marsh, the 80 salt marsh plots, and the 80 fresh meadow plots (total n = 240). Ellenberg indicator values (EIV) of plants are commonly used as bioindicators of their environment (Fanelli et al. 2006; Godefroid 2001; Ling 2003) and exist for a number of environmental variables including salinity (EIV S) and moisture (EIV F) (Ellenberg et al. 2001). Ellenberg F, for example, ranges from 1-12. A plant with a value of 1 means the plant is adapted to very dry condition, 5 means that the plant grows under moist soil conditions and 12 means that the plant is an aquatic plant.

To test whether the plant communities of the shielded marsh, the salt marshes, and fresh meadows differed from each other, we ran an analysis of similarities (ANOSIM) using R package *vegan* (Oksanen et al. 2017). As species data were on a presence/absence level, we used the Jaccard distance on the species matrix prior to ANOSIM analysis.

To visualize the relationship between species, the three habitat types and Ellenberg values, a Redundancy analysis (RDA) was conducted in XLSTAT version 2020.1.1. The presence/absence species matrix was used as the explanatory factor in the RDA analysis. We excluded species that occurred in less than 5% of the plots as we were interested in overall differences between habitats and not the potential noise from rare species (McCune and Grace 2002). Both categorical and continuous response variables were included in the RDA. The categorical response was the habitat type (salt marsh, fresh meadow, or shielded marsh). The continuous responses were the EIV F and EIV S. Build-in centering and standardization were applied. Using the RDA scores on the first two axes, the 10 species most connected to each habitat were determined as those having the smallest overall distance to each habitat.

Environmental factors on the shielded marsh

For each of the 80 plots on the shielded marsh *Bygholmengen*, soil organic matter, soil water content, root zone depth, salinity, total Phosphorus (P), available P (PO_4^{3-}), total Nitrogen (N) as well as NH_4^+-, and NO_2^--NO_3^--concentrations were determined. At the circumference of each 5 m circle, a soil spike was used to extract a core of soil and we measured the soil depth where there were no longer roots (root zone depth). At the edge of each 5 m circle, four soil samples were collected and stored at -20°C until analysis. Soil samples were collected over a short period of time to minimize the effect of weather fluctuations on the environmental factors. Each sample was analyzed separately, and the mean per plot was calculated. Soil water content was determined by placing samples at 105°C until stable weight was reached, and organic matter content was determined by placing the dry samples in a muffle furnace (550°C) for 4 hours according to the Danish Standard (Danish Standards Association 1980). The soil salinity was determined in a 1:5 (distilled water:soil) solution (Hardie and Doyle 2012) with a Cond 340i. Available P was determined using the molybdate method after extraction with 1 N KCl following the international standard (ISO 6878 2004). Available N (NH_4^+, NO_2^--NO_3^-) was determined using spectrometric detection after extraction in 0.001 M H_2SO_4 following the Danish Standard (Danish Standards Association 1975; Danish Standards Association 1991). Total N was determined using the international standard (ISO 16948 2015). For total P, the four soil samples collected at each sampling plot were mixed before analysis and total P content determined using the ICP-OES method with HNO_3 extraction following the Danish Standard (Danish Standards Association 2003).

Interactions between vegetation and environmental factors on the shielded marsh

To visualize and test correlation between environmental variables and selected vegetation parameters (vegetation cover, species richness, number of halophytes, and Shannon diversity) on the shielded marsh, a redundancy analysis (RDA) and a multivariate multiple regression (MMR) were conducted. The RDA was conducted in XLSTAT version 2020.1.1 (Addinsoft 2019). As some parameters used in the analysis were considerably larger than others, internal centering and standardization of parameters were chosen. The edaphic parameters were used as explanatory variables while the vegetation parameters, vegetation cover, number of halophytes, species richens, and Shannon diversity were the response variables. The RDA visualized the relationship between vegetation parameters and environmental factors. MMR is a method of modelling more than one response variable with a set of explanatory variables. Multivariate analysis of variance (MANOVA) were used to evaluate which of the environmental parameters should be included in the final model (Fox and Weisberg 2011) and found that moisture (p-value > 0.001), salinity (p-value > 0.001), available P (p-value = 0.048) and NH_4^+ (p-value = 0.039) had significant influence on the vegetation. The Pillai statistic (Fox and Weisberg 2011) was used to determine that the partial model with fever predictors fit the predictors just as well as the full model (p-value = 0.18) and determined to use the partial model.

All data analyses except the RDAs were conducted in R v3.5.2 (R Core Team 2017) and results were plotted in R using ggplot2 v3.1.1 (Wickham 2016).

RESULTS

Vegetation, plant richness and diversity of the shielded marsh

A total of 85 species were found across the shielded marsh *Bygholmengen* with a maximum of 28 species within a single plot (Online Resource 1). Of the 85 species, 12 were considered salt marsh halophytes (Table 1). The species occurring on most plots were *Agrostis stolonifera*, *Juncus gerardii*, *Glaux maritima*, *Argentina anserine*, *Phragmites australis*, *Spergularia media*, and *Eleocharis uniglumis*. These species were all observed on more than 50% of the plots. *Agrostis stolinifera*, *Juncus gerardii*, *Glaux maritima*, *Argentina anserine*, and *Eleocharis uniglumis* are considered salt marsh (1330) specific halophytes (Table 1).

Mean vegetation cover was 62.5% and the average species richness was 11.4 species of which more than half (6.9) were halophytes (Table 2). The mean Shannon diversity was 0.59 (Table 2). Mean vegetation height was 3.49 cm and mean vegetation density was 41.1 vegetation touches per pinpoint frame (Table 2).

Comparison of the shielded marsh with salt marshes and fresh meadows in the region

The mean species richness - 24.4 in the fresh meadow, 12.0 in the salt marsh and 11.9 in the shielded marsh - differed between habitat types (ANOVA, p-value < 0.001, n = 240). A complete list of species present in each type of habitat is available in Online resource 1. The plant communities of the shielded marsh differed from the plant communities of salt marshes and fresh meadows (ANOSIM, p-value > 0.001, R = 0.978, n = 240). In an ANOSIM analysis, R ranges from 0-1 with 1 indicating a high degree of separation between groups. There was a high degree of separation as indicated by the high R-value.

The RDA based on species presence/absence explained 81.00% of the variation between habitats on the first two axes with 60.06% of the variation of the data explained by axis 1 and 20.94% by axis 2 (Fig. 2). The fresh meadow was positively correlated with axis 1 while the salt marsh was correlated positively with axis 1 and negatively with axis 2 (Fig. 2). The shielded marsh was negatively correlated with both axis 1 and axis 2 (Fig. 2). EIV S-values correlated negatively with axis 1 and positively correlated with axis 2 while EIV F-values was negatively correlated with axis 1 (Fig. 2). Of the ten species most closely associated with each habitat, EIV S-values for species from the salt marsh species were higher than for species from the shielded marsh while fresh meadow species had the lowest Ellenberg S-values (Table 3). Overall, the fresh meadow plant community consisted of plants adapted to fresh, moist conditions, the salt marsh to saline and moist conditions, and the shielded marsh to intermediary saline conditions (Online resource 2).

Environmental factors of the shielded marsh

Soil salinity ranged from 0.1-5.13 ppt with a mean of 1.68 ppt (Table 4). Mean soil moisture was 60.99%, mean pH was 5.5, and mean organic matter content was 34.05%. Available P averaged 1.42 mg/100 g dry soil, mean NH_4^+ was 61.98 mg/kg and mean NO_3^--NO_2^- was 1.02 mg/kg. Total P averaged 609.60 mg/kg and total N 13.49 g/kg (Table 4).

Interactions between vegetation and environmental factors on the shielded marsh

The RDA explained 85.9% and 11.9% of the variation in the data by axes 1 and 2, respectively (Fig. 3). The environmental variables moisture, total N and organic matter (OM) content explained most of the variation on the first axis while salinity, NH_4^+ and NO_2^-- NO_3^- explained most variation on axis 2. Cover and number of halophytes were primarily explained by axis 1. Species richness and Shannon diversity were also primarily explained by axis 1 but axis 2 also had explanatory power for these parameters (Fig. 3).

Multivariate multiple regression revealed positive relationships between vegetation cover as well as both moisture (p-value < 0.001, n = 80) and NH_4^+ (p-value $= 0.035$, n = 80) (Table 5). The number of halophytes correlated negatively with moisture (p-value < 0.001, n = 80). Species richness was negatively correlated with salinity (p-value < 0.001, n = 80) and positively correlated with moisture (p-value < 0.001, n = 80) and NH_4^+ (p-value < 0.01, n = 80). The Shannon diversity was also negatively correlated with salinity (p-value $= 0.019$, n = 80) and positively correlated with moisture (p-value < 0.001, n = 80) and NH_4^+ (p-value $= 0.029$, n = 80).

DISCUSSION

Vegetation, plant richness and diversity on the shielded marsh, the salt marsh and the fresh meadow

Mean species richness (11.4 species/5 m circle) of the shielded marsh was similar to that of other Danish salt marshes (Corine biotype 1330) which averaged 12 species in a 5 m circle (Nygaard et al. 2016). By comparison, Danish molina meadows (Corine Biotype 6410) have on average 21 species per 5 m sample circle (Nygaard et al. 2016).

Danish salt marshes are characterized by low, open vegetation with a mean vegetation height of 42 cm across grazed and ungrazed areas (Nygaard et al. 2016). The shielded marsh in this study had a mean vegetation height of only 3.5 cm in the summer as a result of grazing cattle and geese (Nielsen and Clausen 2019). Grazing (Tessier et al. 2003) as well as potential erosion during winter due to inundation by rainwater from the catchment area may have caused the low vegetation cover of 62.5% which is lower than on sheep grazed Danish salt marshes (Jensen 1985).

It has long been known that the plant community of diked- and natural salt marsh differ (Ganong 1903). Even a one-year-long tidal flood restriction due to a dike causes changes in both vegetation and the physical environment (Sun et al. 2003). Though the vegetation rapidly changes following tidal restrictions, halophytic plants can still be found 30 years after land reclamation and seizure of tidal floods (Min and Kim 1999a). It is therefore not surprising that the plant community of the shielded marsh no longer has a high resemblance to true salt marshes after approximately 20 years with only sporadic inputs of saltwater spray even though halophytes are still present.

The plant communities of the salt marsh, the shielded marsh, and the fresh meadow were adapted to different environmental conditions as indicated by their different position in relation to Ellenberg values (Fig 3, Online resource 2). The species of the shielded marsh were not as well adapted to saline conditions as those of the salt marsh but were still considerably better adapted to saline conditions than the fresh meadow community was (Fig. 2, Table 3). The shielded marsh and salt marshes had an equal number of salt marsh halophytes indicative of Corine Biotype 1330 (Tables 1 and 5). Nevertheless, the species associated with the salt marsh were far better adapted to living under saline conditions overall than those of the shielded marsh as indicated by the higher Ellenberg S values. The lower Ellenberg S of the species most associated with the shielded marsh indicates that the marsh could be in transition towards a plant community far less adapted to salt exposure; nonetheless, the lack of overlap between the fresh and shielded marsh (Fig. 2) implies that this transitions is far from complete.

Agrostis stoloniefera, *Juncus gerardii,* and *Anserina argentina* were among the most common species on both Danish salt marshes (Nygaard et al. 2016) and the shielded marsh. However, other common species of the Danish salt marshes *Tripolium pannonicum* and *Puccinellia maritima* (Nygaard et al. 2016) were not found on the shielded marsh. Both plant species were common in 1994 on the shielded marsh (Burholt et al. 1994) when salinity levels were considerably higher than today (peak 20.2 ppt in 1996) (Kjeldsen 2008) which indicates that the plant community has changed with the decline in salinity levels at the shielded marsh. Overall, the dominating species *Agrostis stolonifera*, *Juncus gerardii*, *Glaux maritima*, *Anserina argentina* and *Phragmites australis* correspond to a brackish marsh community rather than a salt marsh community (Jensen et al. 2018; Morgan and Adams 2018; Odum 1988).

Summer polders, which are marshlands shielded from most flooding events by low dikes, have vegetation that resembles high marsh vegetation and includes many glycophytic species (Bakker et al. 2002; Barkowski et al. 2009). Many of the same vegetation differences found between the shielded marsh and the salt marsh can be found in the summer polders and salt marshes (Bakker et al. 2002). *Juncus gerardii,* in particular, is abundant in the middle marsh zone of summer polders (Barkowski et al. 2009) and was one of the most common species on the shielded marsh. The most common species on the shielded marsh included the brackish adapted species *Agrostis stolinifera* and *Anserina argentina* which were found to overlap the species that dominated the summer polders (Bakker et al. 2002; Scherfose 1990). *Argentina anserine* was observed to be a key species for the high marsh (Barkowski et al. 2009). *Leontodon autumnalis* is abundant in both summer polders and on the shielded marsh whereas *Salicornia europaea*, *Suaeda maritima,* and *Atriplex prostata* are far more abundant on the salt marsh compared to both the summer polder (Bakker et al. 2002) and the shielded marsh. It can therefore be concluded that the species composition of the permanently shielded marsh is similar to other marshes that are more or less permanently shielded behind man-made structures.

Environmental factors on the shielded marsh

Excluding tidal flooding can either result in either brackish or hyper-saline conditions depending on the inflow of fresh water and evaporation (Adams and Bate 1994; Ibarra-Obando et al. 2010). At the *Bygholmengen* salinity has decreased considerably since its most recent peak of 20.2 ppt in 1996 (Kjeldsen 2008). With current salinity levels below 5 ppt, the shielded marsh does not qualify as a salt marsh according to international definitions but is a brackish or oligohaline marsh (Morgan and Adams 2018; Odum 1988).

Eutrophication from catchment areas is a problem on Danish and European salt marshes as it poses a threat to the plant community (Fredshavn et al. 2014; Rozema et al. 1999). Total N levels (13.49 g/kg) at the shielded marsh were high compared to salt marshes outside of Denmark (6.1 g/kg and below) (Li, S. et al. 2018; Morgan and Adams 2018). Thousands of geese use the shielded marsh for resting and defecating after having foraged on and around the marsh, and thereby represent a potential influx of N to the marsh explaining the elevated total N levels (Bazely and Jefferies 1985; Rozema et al. 1999). Feces from geese contain approximately 7 times more nitrogen than phosphorus (Ayers et al. 2010) and did not appear to cause increased phosphorus levels as available P (1.42 mg/100 g soil) of the shielded marsh was low compared to the average Danish salt marsh (3.8 mg/100 g soil) (Nygaard et al. 2016). Total P of the shielded marsh (Table 4) fell within the range of salt marshes outside of Denmark (160-1071 mg/kg) (Wang et al. 2013; Zhang et al. 2015; Li et al. 2018).

Compared to other salt marshes both in Denmark and internationally (Morris and Jensen 1998, Feagin et al. 2009; Veldkornet et al. 2016) the organic matter content of

Bygholmengen, which primarily consisted of plant roots, was high but variable (Table 4) and more similar to that of ombrogenic Atlantic salt marshes which contain a peat layer (Cott et al. 2013). As there is a direct link between salt marsh erosion and mean wave power (Leonardi et al. 2016), and a negative relationship between organic matter content and water depth (Patrick Jr 1990), the lack of wave activity during spring, summer, and autumn may explain the increased build-up and sedimentation rate of organic matter compared to less sheltered salt marshes. Sedimentation rates are also higher in naturally sheltered salt marshes when compared to marshes subject to tidal flooding (Moreira 1992). In agreement with results by Veldkornet et al. (2016), we found that high moisture levels correlated with high organic matter content (Fig. 3). We further found that organic matter content was positively related to total N and total P and, to a lesser extent, nutrient availability and salinity (Fig. 3). As these factors are vital in determining vegetation cover, species richness and Shannon diversity (García et al. 1993; van Wijnen and Bakker 1999), it is important to know how each environmental factor is related to the others as a change in one environmental variables may have repercussions for other variables.

Interactions between the vegetation and environmental factors on the shielded marsh

The distribution of halophytes is limited by extreme abiotic conditions near the ocean and competition from glycophytes on land (Egan and Ungar 2001; Hacker and Bertness 1999; Pennings et al. 2005; Purer 1942) with soil salinity being a limiting factor for overall plant species richness (García et al. 1993; Cañadas et al. 2010; Zhao et al. 2017). Despite the overall low salinity levels, we found salinity to correlate negatively with total species richness but not with halophyte richness on the shielded marsh (Table 5). Glycophyte cover and survival is limited by salinity levels, but the halophyte cover is not (Crain et al. 2004; Pennings et al. 2005; Veldkornet et al. 2015). We found no link between vegetation cover and soil salinity (Fig. 3, Table 3) which could be explained by either the overall low salinity levels of the shielded marsh or by presence of halophytic species able to grow on the brackish substrate.

As the year of the study was especially dry (Andersen et al. 2020), the positive relationship between moisture and each of the vegetation parameters (cover, species richness, number of halophytes, Shannon) was not surprising. These results agree with species richness-moisture trends in saline arid habitats (Zhao et al. 2017) but are opposite the trend for semi-arid to not arid, saline habitats (Cañadas et al. 2010; Shaltout et al. 1995).

Both nitrogen availability and total N have a large impact on salt marsh vegetation growth and biomass (Kiehl et al. 1997; Rozema et al. 1999; van Wijnen and Bakker 1999; Liu et al. 2018). We saw a positive relationship between cover and nitrogen availability. Species richness of the shielded salt marsh also correlated positively with nitrogen availability (Fig. 3, Table 5) in agreement with previous findings from salt marshes (Kiehl et al. 1997; van Wijnen and Bakker 1999; Morgan and Adams 2018).

Phosphorus availability can limit the biodiversity of salt marshes (Theodose and Roths 1999), but we found no correlation between the Shannon diversity and phosphorus (Table 5).

Conclusion

We found that with elimination of tidal and storm flooding, vegetation and soil characteristics of the shielded marsh no longer resemble that of true salt marshes. Rather, they resemble that of a brackish marsh with the potential of becoming a fresh meadow in the future. Thus, obligations to protect the salt marsh habitat (Council of the European Commission 1992) are not fulfilled when a dike almost completely excludes seawater inputs. Should the dike be removed or opened, it would likely take a long time to create natural salt marsh vegetation as previous studies have shown that species community and soil characteristics still differ from that of natural salt marshes even decades after restoration (Garbutt and Wolters 2008; Mossman et al. 2012; Santín et al. 2009).

Author contribution LHA, DB, CP, SB and KT conceived the ideas for the study. LHA, DB, ASKS, JSK and TBS planned the field and laboratory work. JSK, TBS and LHA conducted the fieldwork under guidance of DB. JSK and TBS assisted with the laboratory work. LHA and ASKS gathered data from DEPA. LHA conducted the data analyses and wrote a first draft to the manuscript under the supervision of DB. CP assisted and advised on the statistical analyses. All authors commented on the results and manuscript.

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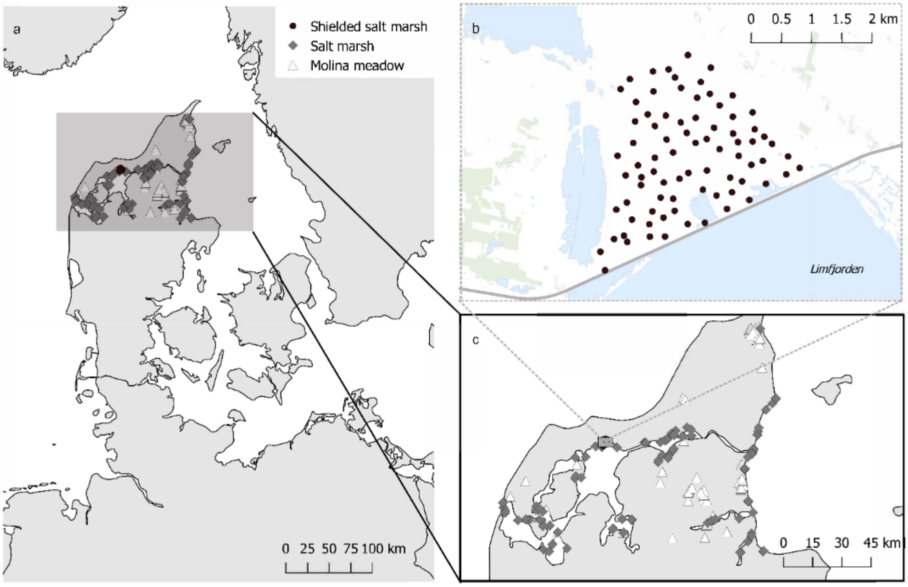


Figure 1 Map of Denmark (a) including the data points sampled on the shielded marsh *Bygholmengen* (b). The data points from salt marshes (Corine biotype 1330) and fresh meadows (Corine biotype 6410) sampled by DEPA are depicted in (c)

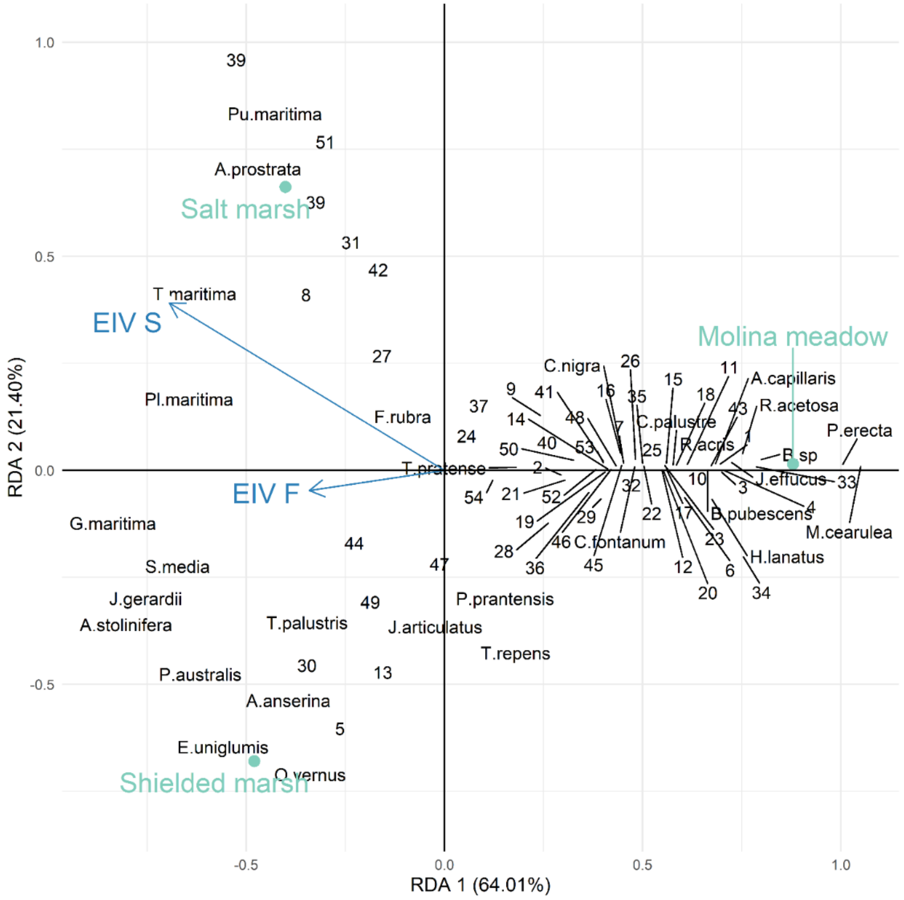


Figure 2 Redundancy Analysis (RDA) results including species occurring on at least 5% of plots in the three habitats, shielded marsh, salt marsh and fresh meadow as well as Ellenberg values (EIV) for moisture (F) and salinity (S). Each habitat was represented by 80 data points. The 30 most abundant species are listed with names, the rest with numbers: *Achillea millefolium* (41), *A. ptarmica* (45), *Agrostis capillaris (*A.capillaris), *A. stolonifera* (A.stolinifera), *Anthoxanthum odoratum* (10), *Argentina anserine* (A.anserina), *Atriplex littoralis* (42), *A. prostrata* (A.prostrata), *Avenella flexuosa* (3), *Bellis perennis* (54), *Betula pubescens* (B.pubescens), *Bolboschoenus maritimus* (30), *Briza media* (7), *Bryopsida sp.* (B.sp), *Calluna vulgaris* (20), *Carex echinata* (32), *C. flacca* (53), *C. ovalis* (54), *C. nigra* (C.nigra), *C. panacea* (33), *Cerastium fontanum ssp. vulgare var. vulgare* (C.fontanum), *Cirsium palustre* (C.palustre), *Danthonia decumbens* (26), *Deschampsia cespitosa* (1), *Dryopteris carthusiana* (17), *Eleocharis uniglumis* (E.uniglumis), *Erica tetralix* (12), *Eriophorum angustifolium* (21), *Festuca rubra* (F.rubra), *Filipendula ulmaria* (22), *Galium palustre* (28), *Galium saxatile* (4), *Glaux maritima* (G.maritima), *Holcus*

lanatus (H.lanatus), *Hydrocotyle vulgaris* (16), *Juncus articulatus* (J.articulatus), *J. conglomeratus* (23), *J. effusus* (J.effucus), *J. gerardii* (J.gerardii), *Leontodon autumnalis* (5), *Lolium perenne* (24), *Luzula multiflora* (43), *Lychnis flos-cuculi* (2), *Molinia caerulea* (M.cearulea), *Myrica gale* (46), *Nardus stricta* (6), *Odontites vernus* (O.vernus), *Phragmites australis* (P.australis), *Plantago lanceolata* (29), *Plantago major* (47), *Plantago maritima* (Pl.maritima), *Poa humilis* (49), *P. pratensis* (P.prantensis), *Potentilla erecta* (P.erecta), *Prunella vulgaris* (35), *Puccinellia maritima* (Pu.maritima), *Ranunculus acris* (R.acris), *Ranunculus flammula* (50), *Ranunculus repens* (36), *Rhytidiadelphus squarrosus* (18), *Rumex acetosa* (R.acetosa), *R. crispus* (37), *Sagina procumbens* (13), *Salicornia europaea coll.* (51), *Salix aurita* (14), *Salix repens* (11), *Schoenoplectus maritimus* (8), *Schoenoplectus tabernaemontani* (44), *Scorzoneroides autumnalis* (9), *Seriphidium maritimum* (31), *Spergularia media* (S.media), Sphagnum (52), *Stellaria graminea* (25), *Suaeda maritima* (39), *Succisa pratensis* (15), *Taraxacum officinale coll.* (40), *Trifolium pratense* (T.pratense), *T. repens* (T.repens), *Triglochin maritima* (T.maritima), *T. palustris* (T.palustris), *Tripolium pannonicum subsp. tripolium* (39), *Vicia cracca* (19), *Viola palustris* (48)

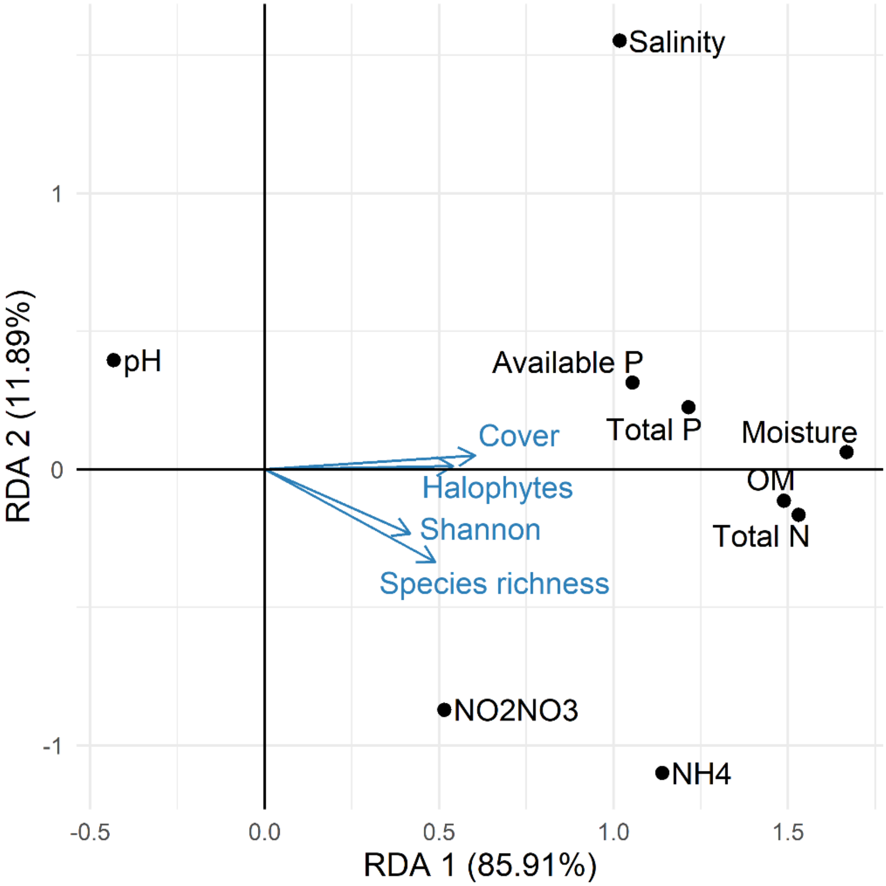


Figure 3 Redundancy Analysis (RDA) results with environmental parameters as explanatory variables and the vegetation parameters vegetation cover, species richness, number of halophytes and Shannon diversity as response variables. OM is the organic matter content

Table 1 List of halophyte species. Species in bold were found in this study. Halophyte species are here defined as species listed as indicative for habitat type 1330 in the NATURA 2000 framework as well as species listed as characteristic for Danish salt marshes (European Commission 2013, Danish Environmental Protection Agency 2016)

List of halophyte species
Agrostis stolonifera, Argentina anserine, *Armeria maritima, Artemisia maritima, Aster tripolium,* ***Atriplex hastate, A. littoralis,*** *Beta maritima, Blysmus rufus, Carex extensa, Centaurium littorale,* ***Centaurium pulchellum****,* ***Eleocharis spp.****,* ***Festuca rubra****, Frankenia laevi,* ***Glaux maritima****, Halimione pedunculatar, H. portulacoides,* ***Juncus gerardii****, Limonium sp., Lotus tenuis, Matricaria maritima, Odontites litoralis, Puccinellia distans, P. fasciculata, P. maritima, P. retroflexa,* ***Plantago maritima****, Samolus valerandi, Spergularia marina,* ***Trifolium fragiferum****,* ***Triglochin maritima***

Table 2 Mean, standard error (SE) and range of each biotic factor measured across the 80 sampling plots on the shielded marsh, *Bygholmengen*. Part of dataset also included in (Andersen et al. 2020)

	Mean ± SE	Range [min ; median ; max]
Species richness	11.4 ± 0.44	[0.0 ; 11.0; 28.0]
Halophytes	6.9 ± 0.21 ()	[0.0 ; 7.0 ; 12.0]
Cover (%)	62.5 ± 0.03 ()	[0.0 ; 93.8 ; 100.0]
Vegetation height (cm)	3.5 ± 0.2 ()	[0.0 ; 2.2 ; 21.0]
Vegetation density	41.9 ± 2.8 ()	[9.0 ; 49.0 ; 150.0]
Shannons diversity	0.59 ± 0.047 ()	[0 ; 0.63 ; 1.85]

Table 3 The ten species most closely related to each of the three habitat types according to the RDA (Figure 3). Ellenberg S (Ellenberg et al. 2001) values are indicated in brackets

Shielded marsh	Salt marsh	Fresh meadow
Agrostis stolonifera (0)	*Atriplex littoralis (7)*	*Agrostis capillaris (0)*
Argentina anserine (1)	*Atriplex prostrata (-)*	*Avenella flexuosa (-)*
Bolboschoenus maritimus (2)	*Puccinellia maritima (8)*	*Bryopsida sp. (-)*
Eleocharis uniglumis (5)	*Salicornia europaea* coll. *(8)*	*Carex panicea (1)*
Leontodon autumnalis (0)	*Schoenoplectus maritimus (2)*	*Deschampsia cespitosa (0)*
Odontites vernus (0)	*Seriphidium maritimum (5)*	*Galium saxatile (0)*
Phragmites australis (0)	*Elytrigia repens (-)*	*Juncus effusus (0)*
Sagina procumbens (2)	*Suaeda maritima (8)*	*Molinia caerulea (0)*
Poa humilis (-)	*Tripolium pannonicum (8)*	*Potentilla erecta (0)*
Triglochin palustris (3)	*Triglochin maritima (8)*	*Rumex acetosa (0)*

Table 4 Mean, standard error (SE) and range of each abiotic factor and Ellenberg values. Results are based on 80 sampling points on the salt marsh. Part of dataset also included in (Andersen et al. 2020)

	Mean ± SE (median)	Range [min ; max]
Root zone depth (cm)	12.91 ± 0.47	[0.00 ; 14.00 ; 25.00]
Moisture (%)	60.99 ± 1.41	[23.83 ; 65.43 ; 88.43]
Organic matter (%)	34.02 ± 1.82	[0.61 ; 32.72 ; 83.5]
pH	5.52 ± 0.045	[4.63 ; 5.47 ; 7.84]
Salinity (ppt)	1.68 ± 0.10	[0.1 ; 1.28 ; 5.13]
Available P (mg/100g dry soil)	1.42 ± 0.083	[0.36 ; 1.16 ; 4.90]
NH_4^+ (mg/kg)	61.98 ± 3.05	[20.90 ; 53.35 ; 289.40]
NO_3^--NO_2^- (mg/kg)	1.02 ± 0.036	[0.00 ; 1.00 ; 2.50]
Total P (mg/kg)	609.60 ± 32.00	[100.00 ; 530.00 ; 1800.00]
Total N (g/kg)	13.49 ± 0.66	[0.68 ; 13.30 ; 28.82]

Table 5 Multivariate multiple regression results including parameter estimates and standard deviation (St.d.), a corresponding *p*-value and the R^2 of the model. The multivariate multiple regression was built on 80 data points from the shielded marsh *Bygholmengen*.

		Estimate (St.d.)	*p*-value	R^2
Cover				0.40
	Intercept	-0.24 (0.15)	0.13	
	Moisture	0.011 (0.0036)	0.0034	
	Salinity	0.028 (0.042)	0.51	
	Available P	0.010 (0.047)	0.83	
	NH_4^+	0.0025 (0.0011)	0.035	
Halophytes				0.37
	Intercept	1.018 (0.97)	0.30	
	Moisture	0.098 (0.022)	$3.61 \cdot 10^{-5}$	
	Salinity	-0.26 (0.26)	0.32	
	Available P	-0.13 (0.30)	0.67	
	NH_4^+	0.0089 (0.0072)	0.22	
Species richness				0.48
	Intercept	-1.92 (1.84)	0.30	
	Moisture	0.24 (0.043)	$2.63 \cdot 10^{-7}$	
	Salinity	-1.99 (0.50)	0.00016	
	Available P	-0.58 (0.56)	0.30	
	NH_4^+	0.046 (0.014)	0.0013	
Shannon				0.30
	Intercept	-0.55 (0.22)	0.018	
	Moisture	0.021 (0.0052)	0.00012	
	Salinity	-0.15 (0.061)	0.019	
	Available P	-0.091 (0.069)	0.19	
	NH_4^+	0.0037 (0.0017)	0.029	

SUPPLEMENTARY MATERIALS FOR PAPER I

Online Resource 1 Species list (presence/absence) for the habitats salt marsh, fresh meadow and shielded marsh

Online Resource 2 Ellenberg S and F of the three plant communities of the salt marsh, fresh meadow and shielded marsh

Online Resource 1 Complete list of species present (1) or absent (0) from the three habitats fresh meadow, salt marsh and shielded marsh. Species were recorded across 80 circles with a radius of 5 m in each type of habitat

Species	Molinia/ fresh meadow	Salt marsh	Shielded marsh
Acer pseudoplatanus	1	0	0
Achillea millefolium	1	1	0
Achillea ptarmica	1	0	0
Agrostis canina	1	0	1
Agrostis capillaris	1	1	0
Agrostis stolonifera	1	1	1
Agrostis vinealis	1	0	1
Alnus glutinosa	1	0	0
Alopecurus geniculatus	1	1	0
Anagallis minima	1	0	0
Andromeda polifolia	1	0	0
Anemone nemorosa	1	0	0
Angelica archangelica ssp. litoralis	0	1	0
Angelica sylvestris	1	0	1
Anthoxanthum odoratum	1	0	1
Anthriscus sylvestris	0	1	0
Arenaria serpyllifolia	1	0	0
Argentina anserina	1	1	1
Armeria maritima	1	1	0
Armeria maritima ssp. maritima	0	1	0
Arrhenatherum elatius var. elatius	0	1	0

Artemisia vulgaris	0	1	0
Atriplex glabriuscula	0	0	1
Atriplex littoralis	0	1	0
Atriplex longipes ssp. longipes	1	0	1
Atriplex patula	0	0	1
Atriplex pedunculata	0	1	0
Atriplex portulacoides	0	1	0
Atriplex prostrata	0	1	1
Avenella flexuosa	1	0	0
Avenula pubescens	1	0	0
Bellis perennis	1	1	1
Berula erecta	0	1	0
Betula pendula	1	0	0
Betula pubescens	1	0	0
Bidens cernua	0	1	0
Blysmus compressus	1	0	0
Blysmus rufus	0	1	0
Bolboschoenus maritimus	0	0	1
Brachythecium rutabulum	1	0	0
Briza media	1	0	0
Bryopsida	1	1	0
Bryum pseudotriquetrum	1	0	0
Calamagrostis canescens	1	1	0
Calamagrostis epigejos	1	0	0
Calliergonella cuspidata	1	0	0
Calluna vulgaris	1	0	0

Caltha palustris	1	0	0
Calystegia sepium	0	1	0
Campanula rotundifolia	1	0	0
Campylopus introflexus	1	0	0
Cardamine pratensis	1	1	0
Carex acutiformis	1	0	0
Carex arenaria	1	1	0
Carex canescens	1	0	0
Carex demissa	1	0	0
Carex disticha	1	1	0
Carex echinata	1	0	0
Carex elata	1	0	0
Carex flacca	1	0	0
Carex hirta	1	0	0
Carex hostiana	1	0	0
Carex lepidocarpa	1	0	0
Carex nigra	0	0	1
Carex nigra var. nigra	1	1	0
Carex nigra var. recta	1	0	0
Carex oederi	1	0	0
Carex otrubae	0	1	0
Carex ovalis	1	1	0
Carex pallescens	1	0	0
Carex panicea	1	1	1
Carex paniculata	1	0	0
Carex pilulifera	1	0	0

Carex pulicaris	1	0	0
Carex rostrata	1	0	0
Carex serotina	0	0	1
Carex vesicaria	1	0	0
Carex viridula	1	0	0
Centaurea jacea	1	0	1
Centaurium pulchellum	0	0	1
Cerastium fontanum	0	0	1
Cerastium fontanum ssp. vulgare var. vulgare	1	1	0
Cerastium glomeratum	0	0	1
Chamaenerion angustifolium	1	0	0
Cirsium arvense	1	1	1
Cirsium oleraceum	1	0	0
Cirsium palustre	1	1	1
Cirsium vulgare	0	1	0
Cladina sp.	1	0	0
Cladonia sp., s.l.	1	0	0
Cladonia sp., s.s.	1	0	0
Climacium dendroides	1	0	0
Cochlearia officinalis ssp. officinalis	0	1	0
Comarum palustre	1	0	0
Crataegus laevigata	1	0	0
Crataegus monogyna	1	0	0
Crepis paludosa	1	0	0
Cynosurus cristatus	1	1	0

Cytisus scoparius	1	0	0
Dactylis glomerata ssp. glomerata	1	0	0
Dactylorhiza	1	0	0
Dactylorhiza maculata ssp. maculata	1	0	0
Dactylorhiza majalis	1	0	0
Danthonia decumbens	1	1	0
Daucus carota	0	0	1
Deschampsia cespitosa	1	0	0
Dicranum bonjeanii	1	0	0
Dicranum scoparium	1	0	0
Dolomedes Fimbriatus	1	0	0
Drepanocladus aduncus	0	1	0
Drosera rotundifolia	1	0	0
Dryopteris carthusiana	1	0	0
Dryopteris cristata	1	0	0
Dryopteris filix-mas	1	0	0
Eleocharis palustris ssp. vulgaris	0	1	0
Eleocharis uniglumis	1	1	1
Elymus repens	0	0	1
Elytrigia	0	1	0
Elytrigia juncea	0	1	0
Elytrigia juncea x repens	0	1	0
Elytrigia repens	1	1	0
Empetrum nigrum	1	1	0
Epilobium adenocaulon	1	0	0

Epilobium hirsutum	1	1	0
Epilobium montanum	1	0	0
Epilobium obscurum	0	1	0
Epilobium palustre	1	1	0
Epilobium tetragonum	1	0	0
Equisetum arvense	1	0	1
Equisetum fluviatile	1	0	0
Equisetum palustre	1	0	0
Erica tetralix	1	0	0
Eriophorum angustifolium	1	1	1
Eriophorum vaginatum	1	0	0
Eupatorium cannabinum	1	0	0
Euphrasia micrantha var. micrantha	1	0	0
Euphrasia stricta	0	0	1
Fagus sylvatica	1	0	0
Festuca ovina	1	0	0
Festuca rubra	1	1	1
Filipendula ulmaria	1	1	0
Fissidens adianthoides	1	0	0
Frangula alnus	1	0	0
Galeopsis	1	1	0
Galeopsis ladanum	0	0	1
Galeopsis tetrahit	1	0	0
Galium aparine	1	0	0
Galium boreale	1	0	0
Galium palustre	0	0	1

Galium palustre ssp. palustre	1	1	0
Galium saxatile	1	0	0
Galium uliginosum	1	1	0
Galium verum	1	0	0
Genista anglica	1	0	0
Gentianella uliginosa	0	1	0
Geum rivale	1	0	0
Glaux maritima	0	1	1
Glyceria fluitans	1	1	0
Gnaphalium uliginosum	1	0	0
Hepaticopsida	1	0	0
Hieracium umbellatum	1	0	0
Hierochloe odorata	0	0	1
Hippuris vulgaris	0	0	1
Holcus lanatus	1	1	1
Holcus mollis	1	0	0
Honckenya peploides	0	1	0
Hordeum vulgare	0	1	0
Hydrocotyle vulgaris	1	1	0
Hylocomium splendens	1	0	0
Hypericum maculatum	1	0	0
Hypnum cupressiforme	1	0	0
Hypochaeris radicata	0	0	1
Hypochoeris glabra	0	0	1
Hypochoeris radicata	1	1	0
Iris pseudacorus	1	0	0

Jacobaea aquatica	1	0	0
Jasione montana	1	0	0
Juncus anceps var. atricapillus	0	1	0
Juncus articulatus	1	1	1
Juncus bufonius	1	0	0
Juncus conglomeratus	1	0	0
Juncus effusus	1	1	0
Juncus filiformis	1	0	1
Juncus gerardii	1	1	1
Juncus maritimus	0	0	1
Juncus pygmaeus	0	0	1
Juncus ranarius	0	0	1
Juncus squarrosus	1	1	0
Juniperus communis	1	0	0
Juniperus communis ssp. communis	1	0	0
Lathyrus sp.	1	0	0
Lathyrus japonicus ssp. maritimus var. maritimus	0	1	0
Lathyrus linifolius	1	0	0
Lathyrus pratensis	1	0	0
Lemna	0	0	1
Lemna minor	1	1	0
Leontodon autumnalis	0	0	1
Leontodon hispidus	0	0	1
Lepeta sp.	1	0	0
Leymus arenarius	0	1	1

Lichenes sp.	1	0	0
Lichenes sp. (eksl. Cladonia sp., s.l.)	1	0	0
Limonium vulgare	0	1	0
Linum catharticum	1	0	0
Lolium perenne	1	1	1
Lonicera periclymenum	1	0	0
Lotus corniculatus	1	1	0
Lotus pedunculatus var. pedunculatus	1	0	0
Lotus tenuis	0	1	0
Luzula campestris	1	0	0
Luzula multiflora	1	1	0
Luzula pilosa	1	0	0
Lychnis flos-cuculi	1	1	1
Lycopus europaeus	1	1	0
Lysimachia europaea	1	0	0
Lysimachia thyrsiflora	1	0	0
Lysimachia vulgaris	1	1	0
Lythrum salicaria	1	0	0
Maianthemum bifolium	1	0	0
Mentha aquatica	1	1	0
Mentha citrata	0	0	1
Mentha x verticillata	1	0	0
Menyanthes trifoliata	1	0	0
Molinia caerulea	1	0	0
Myosotis laxa ssp. caespitosa	1	1	0

Myosotis scorpioides	1	0	0
Myrica gale	1	0	0
Nardus stricta	1	0	1
Odontites vernus	0	1	1
Oenanthe lachenalii	1	0	0
Pedicularis palustris ssp. palustris	1	0	0
Pedicularis sylvatica	1	0	0
Persicaria amphibia	1	1	0
Persicaria hydropiper	1	1	0
Persicaria lapathifolia	0	0	1
Persicaria minor	1	0	0
Peucedanum palustre	1	0	0
Phalaris arundinacea	0	1	0
Phleum pratense ssp. pratense	1	0	0
Phragmites australis	1	1	1
Picea abies	1	0	0
Picea sitchensis	1	0	0
Pilosella lactucella	1	0	0
Pilosella officinarum	1	0	0
Pinus mugo	1	0	0
Pinus sylvestris	1	0	0
Plagiomnium ellipticum	1	0	0
Plantago lanceolata	1	1	1
Plantago major	1	1	1
Plantago major ssp. winteri	1	0	0
Plantago maritima	0	1	1

Plantago media	0	0	1
Pleurozium schreberi	1	0	0
Poa angustifolia	0	0	1
Poa annua	1	0	1
Poa humilis	0	1	1
Poa pratensis	1	1	1
Poa pratensis ssp. pratensis	1	0	0
Poa trivialis	1	1	1
Polygala serpyllifolia	1	0	0
Polygala vulgaris	1	0	0
Polygonum aviculare	0	1	1
Polygonum aviculare ssp. neglectum	0	0	1
Polygonum aviculare ssp. rurivagum	0	0	1
Polytrichum commune	1	0	0
Populus tremula	1	0	0
Potentilla erecta	1	0	0
Potentilla reptans	0	1	0
Prunella vulgaris	1	0	0
Prunus cerasifera	1	0	0
Prunus serotina	1	1	0
Prunus spinosa	1	0	0
Pseudoscleropodium purum	1	0	0
Pteridium aquilinum	1	0	0
Puccinellia distans	0	1	0
Puccinellia maritima	0	1	0
Quercus robur	1	0	0

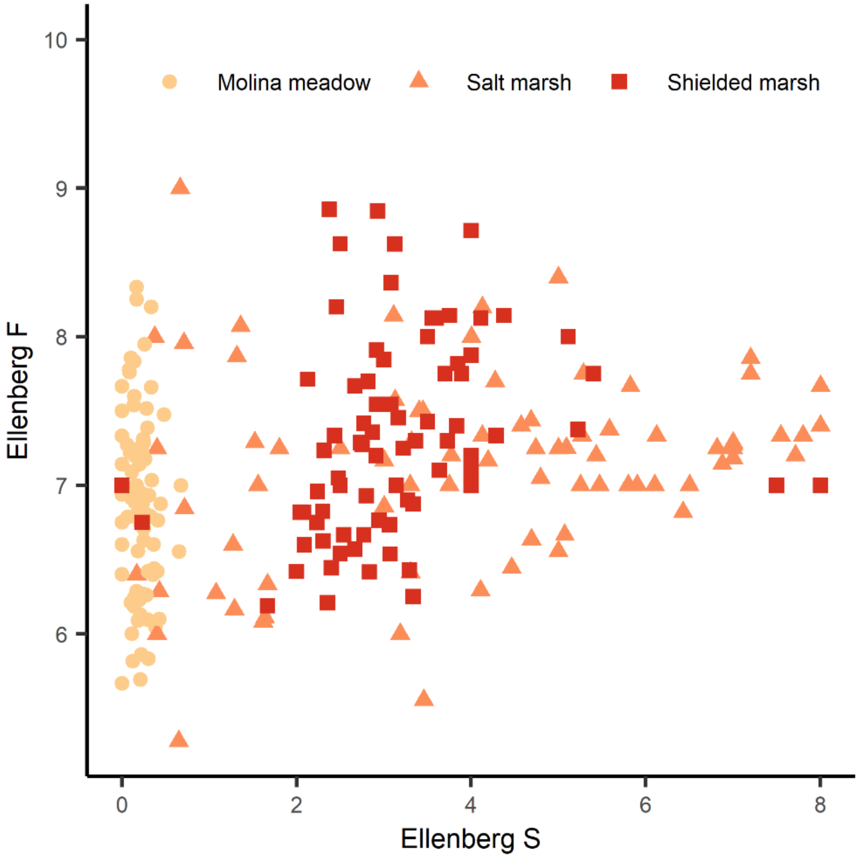
Ranunculus acris	1	1	0
Ranunculus auricomus	1	0	0
Ranunculus bulbosus	0	1	0
Ranunculus flammula	1	1	0
Ranunculus peltatus ssp. peltatus	0	0	1
Ranunculus repens	1	1	1
Ranunculus sceleratus	0	0	1
Rhinanthus minor	1	1	0
Rhinanthus serotinus	1	0	0
Rhytidiadelphus squarrosus	1	0	0
Rosa rubiginosa	0	1	0
Rosa rugosa	1	1	0
Rubus idaeus	1	0	0
Rubus sect. Rubus	1	0	0
Rumex acetosa	1	1	0
Rumex acetosella	1	0	0
Rumex crispus	1	1	0
Rumex hydrolapathum	0	0	1
Rumex maritimus	0	0	1
Rumex obtusifolius	1	1	0
Sagina maritima	0	0	1
Sagina nodosa	1	0	0
Sagina procumbens	1	1	1
Salicornia europaea	0	0	1
Salicornia europaea coll.	0	1	0
Salix aurita	1	0	0

Salix cinerea	1	1	0
Salix repens ssp. repens var. argentea	1	1	0
Salix repens ssp. repens var. repens	1	0	0
Schedonorus arundinaceus	1	1	0
Schedonorus pratensis	1	1	0
Schoenoplectus lacustris	0	0	1
Schoenoplectus maritimus	0	1	0
Schoenoplectus tabernaemontani	1	1	1
Scorzonera humilis	1	0	0
Scorzoneroides autumnalis	1	1	0
Scutellaria galericulata	1	0	1
Selinum carvifolia	1	0	0
Senecio viscosus	0	1	0
Seriphidium maritimum	0	1	0
Silene dioica	1	0	0
Sonchus arvensis	0	1	0
Sonchus oleraceus	1	1	0
Sonchus palustris	0	1	0
Sorbus aucuparia	1	0	0
Spartin sp.	0	1	0
Spartina alterniflora x maritima	0	1	0
Spergularia	0	1	0
Spergularia media	0	1	1
Spergularia salina	0	1	0
Sphagnum sp.	1	0	0

Sphagnum cuspidatum	1	0	0
Sphagnum magellanicum	1	0	0
Sphagnum palustre	1	0	0
Sphagnum rubellum	1	0	0
Sphagnum squarrosum	1	0	0
Stachys palustris	1	0	0
Stellaria alsine	1	0	0
Stellaria graminea	1	1	0
Stellaria holostea	1	0	0
Stellaria media	1	0	0
Stellaria palustris	1	0	0
Suaeda maritima	0	1	0
Succisa pratensis	1	1	0
Tanacetum vulgare	0	1	0
Taraxacum officinale coll.	1	1	0
Taraxacum sect. Taraxacum	0	0	1
Trichophorum cespitosum	1	0	0
Trichophorum cespitosum ssp. germanicum	1	0	0
Trifolium dubium	1	0	0
Trifolium fragiferum	0	1	1
Trifolium medium	1	0	0
Trifolium pratense	1	1	1
Trifolium repens	1	1	1
Triglochin maritima	1	1	1
Triglochin palustris	1	1	1

Tripleurospermum inodorum	0	1	0
Tripleurospermum maritimum	0	1	0
Tripolium pannonicum subsp. tripolium	0	1	0
Trollius europaeus	1	0	0
Typha sp.	1	0	0
Typha latifolia	0	1	0
Ulex europaeus	1	0	0
Urtica dioica	1	1	0
Urtica urens	0	0	1
Vaccinium myrtillus	1	0	0
Vaccinium oxycoccos	1	0	0
Vaccinium uliginosum	1	0	0
Vaccinium vitis-idaea	1	0	0
Veronica arvensis	1	0	0
Veronica beccabunga	0	1	0
Veronica chamaedrys	1	0	0
Veronica officinalis	1	0	0
Vicia cracca	1	1	1
Vicia sativa ssp. nigra	1	1	0
Viola canina	1	0	0
Viola palustris	1	0	0
Viola tricolor ssp. curtisii	0	1	0
Warnstorfia fluitans	1	0	0

Online resource 2 The Ellenberg S (salinity) and F (moisture) for the plant community within each of the three habitat types salt marsh, Molina meadow and the shielded marsh (*Bygholmengen*). A total of 240 data points are plotted, 80 for each habitat



PAPER II

TURNOVER AND CHANGE IN PLANT SPECIES COMPOSITION IN A SHIELDED SALT MARSH FOLLOWING VARIATION IN PRECIPITATION AND TEMPERATURE

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RESEARCH ARTICLE

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Turnover and change in plant species composition in a shielded salt marsh following variation in precipitation and temperature

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Abstract

Questions: Temperature and precipitation variation between years may affect plant species composition directly or indirectly. We wish to investigate whether salt marsh edaphic conditions and plant species composition change as a result of climatic variation. Further, whether areas with the largest edaphic variations also experience the largest change in species composition and turnover. Finally, do temperature and precipitation variations change the way the plant community is able to respond to natural edaphic gradients?

Location: Bygholmengen, a shielded salt marsh in Vejlerne, Denmark, Northern Europe.

Methods: Botanical surveys were conducted and soil samples collected from 40 plots during a wet and dry summer to register changes in vegetation cover, species richness composition and edaphic factors (moisture, nutrients, salinity). These data were used to calculate dissimilarities in species composition, temporal turnover and environmental dissimilarity between years. A linear mixed-effects model was used to link species richness with the measured edaphic factors.

Results: We found that the precipitation and temperature variations altered the edaphic conditions; furthermore, the vegetation cover and species richness decreased when conditions were dry whereas the number of salt marsh species increased. Further, species composition changed significantly between years, and sampling plots that experienced the least edaphic change also retained more species between years. Species richness responded more to changes in nutrient availability during wet than dry conditions.

Conclusion: Our results pointed toward the climatic variations, and subsequent change in edaphic conditions, being responsible for the significant change in species composition as areas with the least change in edaphic factors retained most species between years. Dry conditions favored salt marsh-adapted species and the extent to which increased nutrient levels led to a higher species richness decreased in dry compared to wet conditions.

KEYWORDS

biodiversity, coastal habitat, Denmark, environmental dissimilarity, salt meadow, species richness, temporal turnover, vegetation

1 | INTRODUCTION

Salt marsh, a threatened coastal habitat, is estimated to decline on a global scale due to sea-level rise (Blankespoor, Dasgupta, & Laplante, 2014; Craft et al., 2009; Crosby et al., 2016; Spencer et al., 2016), and is also vulnerable to interannual variations in precipitation and temperature (Dunton, Hardegree, & Whitledge, 2001; Hanson et al., 2016; Osland et al., 2016). Interannual variation in the climate can result in changes in the species composition as abiotic stressors like flooding, warming and increased salinity affect the biodiversity, species composition and distribution of coastal plant communities (Gedan & Bertness, 2009; Hook, Buford, & Williams, 1991; McKee, Mendelssohn, & Materne, 2004). Dunton et al. (2001) showed that an increase in precipitation changed the species composition and increased the biomass in a salt marsh, while droughts in estuaries are associated with dieback of salt marsh vegetation and a decrease in biomass (Alber, Swenson, Adamowicz, & Mendelssohn, 2008; McKee et al., 2004; Paudel, Milleville, & Battaglia, 2018; Wetz & Yoskowitz, 2013). Shifts in rainfall regimes can cause the vegetation structure to shift between salt flats, mangroves and salt marshes (Osland et al., 2016). Further, droughts alter the soil chemistry and result in more saline conditions (Chapple & Dronova, 2017; Forbes & Dunton, 2006; Palomo, Meile, & Joye, 2013). Stressful conditions not only affect the physical environment but both salt and drought stress impact plant ability to utilize nutrients (Bista, Heckathorn, Jayawardena, Mishra, & Boldt, 2018; Hu & Schmidhalter, 2005).

Historically, many salt marshes have been shielded by dams and while some dams have been removed many still remain (St. Omer, 1994; Zedler & Nordby, 1986). Dams may alter the hydrology and vegetation of the marsh area (St. Omer, 1994; Van Loon-Steensma & Slim, 2013; Weis & Butler, 2009). Despite the long-term presence of dams salt marsh species can still be present (St. Omer, 1994) and such salt marsh areas still fall under the protection by the European Habitats Directive (Council of the European Commission, 1992). Without regular tidal intrusions, dammed salt marshes are even more dependent on water gained through precipitation and a lack of precipitation can have large consequences for the vegetation (Zedler, Covin, Nordby, Williams, & Boland, 1986; Zedler & Nordby, 1986). Given that interannual climatic variations resulting in droughts and floodings are likely to become more frequent (Jongejans, De Kroon, Tuljapurkar, & Shea, 2010; Salinger, 2005), and as these extreme climatic events have shown negative impacts on plants across habitat types including coastal habitats (Ciais et al., 2005; Maxwell et al., 2019), it is important to know how the shielded salt marshes respond to climatic variation in precipitation and temperature. While multiple studies have described how salt marsh vegetation cover and biomass is affected by drought (Alber et al., 2008; McKee et al., 2004; Paudel et al., 2018; Wetz & Yoskowitz, 2013), the effects of precipitation and temperature variation on the shielded salt marsh plant communities are not yet explained. It is therefore important to determine whether the response of shielded salt marshes to precipitation and temperature variations is equal to that of tidal salt marshes, information that will be of special interest to salt marsh managers. Here, we studied the effect of precipitation and temperature variation on the plant community of a shielded salt marsh in a wetter than average year (2017) followed by a year drier and warmer than average (2018), which created an optimal study setting, with the aim of quantifying changes in the vegetation (Cappelen, 2018a, 2019).

By taking advantage of the between-year climatic fluctuations, we intended to investigate how the plant community responds to variations in temperature and precipitation. We aimed at answering the following questions: (a) can precipitation and temperature variations between years change the edaphic conditions (moisture, salinity, nutrient levels) of a salt marsh? We expected a change in the abiotic environment following the drought toward more saline conditions (Chapple & Dronova, 2017; Forbes & Dunton, 2006; Palomo et al., 2013). As increased precipitation on salt marsh habitats influences plant species composition (Dunton et al., 2001), we expected species composition during a year of drought to be different from that of a wet year, leading to the questions: (b) does species composition respond to extremes in precipitation and temperature on a year-to-year basis during current climatic conditions? We expected the species composition to change toward being adapted to drier and more saline condition during the dry year compared to the wet year; and (c) is species turnover linked to environmental dissimilarity? As both salt and drought stress impact the ability of plants to utilize nutrients (Bista et al., 2018; Hu & Schmidhalter, 2005), we expected plants to react differently to the edaphic gradient during wet and dry years.

2 | METHODS

2.1 | Study area

This study took place in the salt marsh Bygholmengen (728 ha), in De Østlige Vejler, Denmark, which is protected under the European Habitats Directive as a Natura 2000 site (H1330) (Appendix S1A; Miljøstyrelsen, 2005a, 2005b, 2011). Bygholmengen was created in 1868 in a land reclamation project but due to repeated problems with flooding and drainage, the idea of using the land in agriculture was quickly abandoned (Riis, 2009). Today, the salt marsh is a scientific reserve (area to which the general public has no access) shielded by a dam and exempt from regular tidal intrusion. The construction of the dam together with pumping enables water-level management to some extent in the salt marsh. Though dams may shield salt marshes from sea-level rise and erosion (Van Loon-Steensma & Slim, 2013), shielded salt marshes may be increasingly susceptible to drought events as they do not experience regular tidal inundations.

In 2017, 590 cattle grazed the meadow resulting in a grazing pressure of 0.81 cattle/ha while in 2018 the number of cattle was decreased to 525, corresponding to 0.72 cattle/ha.

2.2 | Climate data

To quantify the climatic differences between 2017 and 2018, data on the climate of Northern Jutland for 2017 and 2018 were obtained from reports of the Danish Meteorological Institute (DMI).

2.3 | Botanical surveys

Botanical surveys were conducted in order to determine the vegetation's cover, density, species richness and biodiversity. A total of 40 non-permanent sampling plots were randomly distributed over the marsh, ensuring a distance of at least 200 m between plots and located using a GPS (Garmin Etrex 10). These sampling plots were examined in both August 2017 and August 2018. Given the flat terrain, we believe that the plots were relocated with high accuracy; in a different study, the GPS relocated pit fall traps dug into the ground with great accuracy.

Each sampling plot consisted of a circle with a radius of 5 m (Nygaard et al., 2016) in which all plants were determined at the species level to create a comprehensive species list using Frederiksen et al. (2006); for graminoids recent literature was used (Schou, 2006; Schou, Wind, & Lægaard, 2010, 2014). We determined total species richness as the number of species within the 5 m circle and counted the number of salt marsh species within each circular plot to obtain the salt marsh species richness. We define salt marsh species as species specific for habitat type 1330 in the NATURA 2000 framework as well as species listed as characteristic for Danish salt marshes (European Commission, 2013; Miljøstyrelsen, 2016) (Appendix S2).

At the center of each plot, we positioned a pinpoint frame. Within the pinpoint frame of 0.5 m × 0.5 m with 16 intersection points (Levy & Madden, 1933) we determined vegetation cover, height and density and registered the frequency of plant species.

2.4 | Edaphic factors

To determine whether the abiotic environment changed between years, we tested the soil in both 2017 and 2018. At the circumference of each 5 m circle, four soil samples were collected. They were analyzed for content of total phosphorus (P) by extraction in HNO_3 using the ICP-OES method (Danish Standards Association, 2003) and for available phosphorus (P) using the molybdate method after extraction in 1 M KCl (ISO6878, 2004). Total nitrogen (N) was determined using a LECO model 628 (ISO, 16948, 2015). The content sof ammonium (NH_4^+) (Danish Standards Association, 1975), nitrite (NO_2^-) (Danish Standards Association, 1991) and nitrate (NO_3^-) (Danish Standards Association, 1991) were determined spectrometrically after extraction in 0.001 M H_2SO_4. Moisture content was determined by placing a soil sample at 105°C until constant weight following the Danish Standard (1980) and organic matter content was determined by adding dry samples to a muffle furnace for 4 hr (Dansk Standardiseringsråd, 1980). Soil salinity levels were determined in a 1:5 distilled water : soil solution (Hardie & Doyle, 2012).

TABLE 1 The mean, standard error (*SE*) and range for each edaphic and biotic factor measured in 2017 and 2018 on Bygholmengen

	2017		2018		
	Mean ± *SE*	**[min; max]**	**mean ± *SE***	**[min; max]**	***p*-value**
Moisture (%)	75.7 ± 1.7	[38.5; 89.9]	59.3 ± 2.1	[27.8; 84.0]	***
Organic matter (%)	41.3 ± 2.8	[2.7; 83.5]	31.7 ± 2.8	[1.1; 68.8]	m.s.
Salinity	1.34 ± 0.13	[0.17; 4.40]	1.42 ± 0.15	[0.1; 4.83]	n.s.
Available P (mg/100 g)	0.92 ± 0.10	[0.10; 2.94]	1.30 ± 0.10	[0.35; 3.51]	*
NH_4^+ (mg/kg)	33.19 ± 1.67	[17.45; 73.3]	61.58 ± 5.80	[23.55; 289.4]	**
NO_2^-–NO_3^- (mg/kg)	1.24 ± 0.06	[0.80; 2.73]	1.02 ± 0.07	[0; 2.5]	n.s.
Total P (mg/kg)	742 ± 47	[150; 1700]	543 ± 42	[100; 1400]	n.s.
Total N (g/kg)	14.34 ± 0.92	[1.3; 26.7]	12.40 ± 0.99	[0.83; 25.98]	n.s.
Ellenberg *N*	4.83 ± 0.04	[4.14; 5.64]	5.41 ± 0.05	[4.5; 6.11]	*
Ellenberg *F*	7.07 ± 0.09	[5.86; 8.29]	7.17 ± 0.08	[6.25; 8.57]	n.s.
Ellenberg *S*	2.18 ± 0.08	[1.07; 4]	3.05 ± 0.13	[0.17; 5.40]	**
Species richness	14 ± 0.74	[6; 33]	11.69 ± 0.66	[0; 23]	*
Salt marsh species richness	5.76 ± 0.20	[2; 9]	7.05 ± 0.30	[0; 11]	*
Cover (%)	0.81 ± 0.04	[0; 1]	0.63 ± 0.05	[0; 1]	*
Vegetation density	73.8 ± 5.9	[0; 163]	42.5 ± 4.8	[0; 150]	*
Vegetation height (cm)	6.5 ± 0.9	[0.1; 35.5]	3.5 ± 0.5	[0; 21.0]	*
Simpson's diversity	0.44 ± 0.04	[0.02; 1]	0.54 ± 0.04	[0; 1]	n.s.
Shannon's diversity	0.63 ± 0.03	[0.00; 1.38]	0.70 ± 0.04	[0; 1.85]	n.s.
Pielou's evenness	0.48 ± 0.02	[0.08; 0.84]	0.61 ± 0.03	[0; 1]	n.s.

Note: A *t* test with Bonferroni correction was conducted to test for significant differences between the two years and the *p*-values for the test are provided: n.s. (not significant), $p > 0.1$; m.s. (marginally insignificant), $p < 0.01$; $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

For all edaphic factors apart from total P, the four samples were analyzed separately and the mean was calculated, whereas for total P the four soil samples were mixed prior to analysis.

2.5 | Data analysis

2.5.1 | Edaphic factors

t Tests were conducted to test for between-year differences in the edaphic variables. To avoid type 1 errors, we further did a Bonferroni correction of the *p*-values to account for multiple testing.

2.5.2 | Vegetation cover, species richness, species composition and turnover rates

The cover was calculated as the percentage of the number of pins touched by any vegetation within the pinpoint frame, thereby distinguishing between ground covered in vegetation or other (incl. water, bare ground and decomposing organic materials). The vegetation density was calculated as the number of times the pinpoint pin was touched by the vegetation.

We calculated Simpson's diversity (Simpson, 1949), Shannon's diversity (Shannon, 1948) and Pielou's evenness (Pielou, 1966) as measures of biodiversity for each pinpoint frame using the R package vegan (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). In vegan, Simpson's diversity is defined as $1-\sum p_i^2$, Shannon's diversity (*H*) is defined as $1-\sum p_i \log(p_i)$ and Pielou's evenness is defined as *H*/log(*S*). Here, p_i is the proportional abundance of species *i* and *S* is the total species count.

For all plant species present in the 5-m circle, Ellenberg values on moisture (*Ellenberg F*), salinity (*Ellenberg S*) and nutrients (*Ellenberg N*) were used to calculate average Ellenberg values for each sampling plot (Ellenberg, Weber, Düll, Wirth, & Werner, 2001).

We divided the species lists for each circular sampling plot into three groups. First, we counted how many species were present in 2017 only but had disappeared in 2018 (species lost). Second, we counted how many species appeared in 2018 that were not present in 2017 (species gained). Third, we counted the number of species present on a given sampling plot in both 2017 and 2018 (the species overlap.) We calculated the recurrence rate as the percentage of plots in which a species occurred in 2018, given that it had been found there in 2017; further, we determined whether the plant was annual or perennial using Frederiksen et al. (2006). This was done for the most common species (more than 10 occurrences across 2017 and 2018) as well as all species.

Aiming to determine whether species composition in the 5-m circle (presence/absence) had changed significantly between 2017 and 2018 on both a larger, salt marsh scale and on a plot level scale, we followed the approach presented by Finderup Nielsen et al. (2019). First, a turnover matrix based on the binary Jaccard dissimilarity was created using betadisper (R Core Team, 2017). Next, we used a Principal Coordinate Analysis (PCoA) approach to visualize the data with a polygon symbolizing each of the years 2017 and 2018. In order to test for differences in species composition between years, we computed a PERMANOVA based on the Jaccard metric using Adonis2 in R with 999 permutations (McArdle & Anderson, 2001; R Core Team, 2017). Next, to determine the identity of the species that contributed most to the potential difference between years, we did an indicator species analysis using the indicspecies package in R with 999 permutations and a significance level of 0.05 (Cáceres & Legendre, 2009).

We further calculated the temporal species turnover to quantify whether the species composition had changed as (species gained + species lost)/(total number of species observed on a given sampling plot during both years) (Cleland et al., 2013; Diamond, 1969). Linear models were made of the relation between the species turnover and the total species richness in each sampling plot across years.

The environmental dissimilarity is a measure of the variability across all edaphic factors between plots (Lloyd, Mac Nally, & Lake, 2005; Qian & Ricklefs, 2012). We calculated the environmental dissimilarity between individual plots in 2017 and 2018 using the Canberra distance (Lance & Williams, 1967) using a matrix containing information on all edaphic variables. The Canberra distance internally standardizes the contributions of each variable thereby accounting for large differences in numerical values of the individual variables (Lloyd et al., 2005). We made linear models of the relation between the environmental dissimilarity and the species turnover.

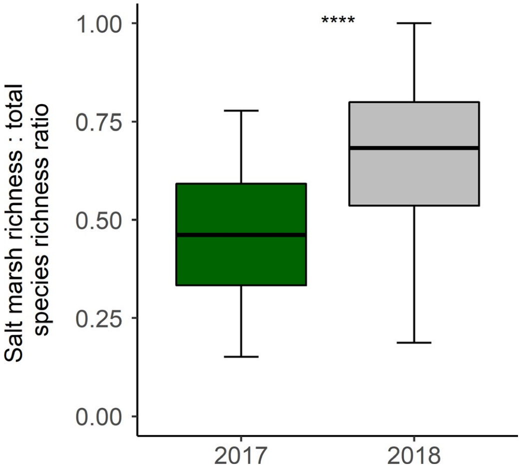

FIGURE 1 Boxplot of the ratio between the number of salt marsh species (Appendix S2) and the total species richness in 2017 (green) and 2018 (grey), respectively. A value of 1 indicates that all species were salt marsh-adapted species while 0 indicates that none were salt marsh-adapted species. The medians are plotted together with the 25% and 75% quantiles while the whiskers show the maximum and minimum. ****, *p*-value < 0.0001

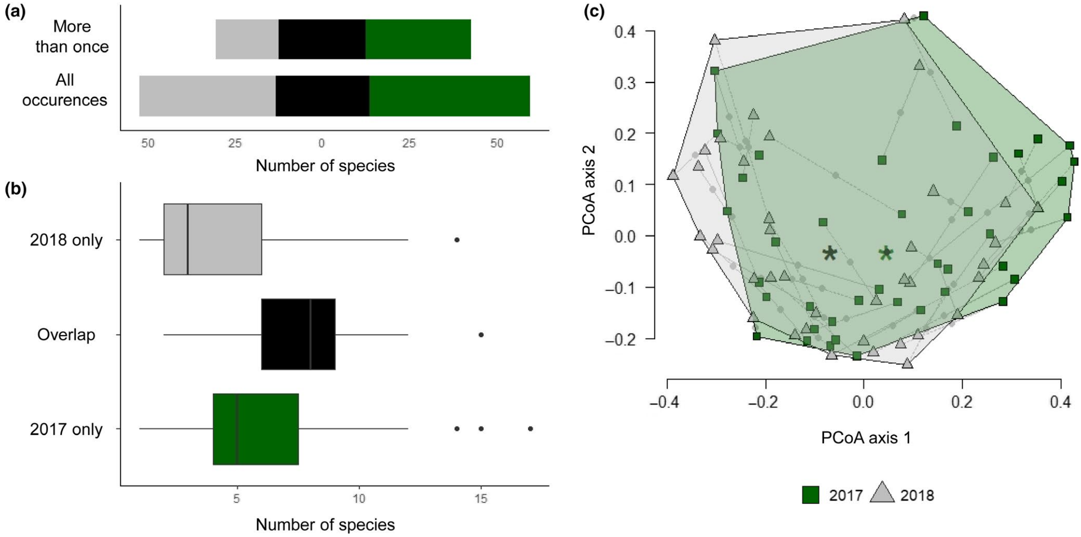

FIGURE 2 The species composition of Bygholmengen across 40 plots sampled in both 2017 and 2018. In (a) and (b), the species overlap (species occurring in both 2017 and 2018) is depicted in black, the species present in 2017 only in green (species lost), those of 2018 only in gray (species gained). In (a), the total number of species found across all plots on Bygholmengen is shown including both all occurrences and when excluding species that only occurred once (more than once). In (b), the species distribution is shown per sampling plot, where the boxplot depicts the median and the 25 and 75% quantiles, minimum, maximum and outliers. Here, all occurrences are included. In (c), species compositional change between years 2017 (green, squares) and 2018 (gray, triangles) is illustrated based on the PCoA using Jaccard dissimilarity on the binary data for 40 plots. When a line connects a green square and a gray triangle, they represent the same sampling plot in 2017 and 2018. Eigenvalues for PCoA axes 1 and 2 are 3.89 and 2.36, with 16.71% of variance explained on axis 1 and 9.49% on axis 2

2.5.3 | Correlations between the edaphic factors and species richness and salt marsh richness

To test for correlations between species richness and salt marsh richness of the circular plots and the edaphic factors within and between the two years, linear mixed-effects models with random slope and intercept for year was used. Models were created for both the total species richness and the salt marsh species richness, each including all edaphic variables. Year was a fixed factor in the model. Plot was a random factor to account for the repeated measures. A parameter was considered significant at the 0.05 level given the *t*-value exceeded ±1.96.

All statistical analyses described above were performed in R 3.4.1 (R Core Team, 2017). Graphs were created using ggplot2 (Wickham, 2016).

3 | RESULTS

3.1 | Climate data

Since 1874, only 10 summers have been wetter than that of 2017, while the spring rainfall was among the three highest rainfalls during the past 10 years (Cappelen, 2018a, 2019; DMI, 2011). Meanwhile, 2018 had the most hours of sun since 1920, with spring temperatures being among the top ten measured since 1953 and the mean summer temperature being the highest since 1953 (Cappelen, 2018a, 2019).

All climatic comparisons presented below are in comparison to the 10-year average (referred to as the “average”). In 2017, Northern Jutland experienced a 7% higher rainfall than average and 12% fewer hours of sun (Cappelen, 2018a). In contrast, both spring and summer of 2018 were significantly warmer and drier than average (Cappelen, 2018b, 2018c), and overall, 2018 experienced 11% more hours of sun and 25% less rainfall compared to the average (Cappelen, 2019). Comparing spring–summer rainfall of Northern Jutland it was 468 versus 255 mm in 2017 and 2018, respectively (Cappelen, 2018a, 2019). These differences caused visible alterations to the landscape with more bare sand being present in the dry year 2018 than in 2017 (Appendix S1B–E).

3.2 | Edaphic factors

Soil moisture levels were significantly lower in 2018 compared to 2017 (Table 1). The soil nutrient levels were significantly higher in 2018 compared to 2017 for available P and NH_4^+ (Table 1). Soil salinity did not change significantly between years, nor did the organic matter content, total P or total N.

3.3 | Vegetation cover, species richness, species composition and turnover

Both vegetation cover, height and density decreased significantly from 2017 to 2018 (Table 1). The vegetation height was almost halved. Across all 40 plots, total species richness was significantly higher in 2017 compared to 2018 (Table 1). In contrast, a significantly higher salt marsh species richness was found per plot in 2018 compared to 2017 and a significantly larger percentage of species were salt marsh species in the dry compared to the wet year (Figure 1).

The total species richness was 73 in 2017 of which 46 were not seen in 2018. The total species richness in 2018 was 66 species and 39 of these species had not been found in 2017 (Figure 2a). On average, 45.7% of the species on a given sampling plot were found in both 2017 and 2018, corresponding to 7.6 species reoccurring on any given plot. An average of 6.3 species found in 2017 had disappeared from the plot in 2018 while an average of 3.7 new species occurred on any given plot in 2018 in which it was not found in 2017 (Figure 2b). The overall most abundant species across years were the perennial species *Juncus gerardii* (recurrence rate 96.2%), *Agrostis stolonifera* (recurrence rate 90.0%), *Glaux maritima* (recurrence rate 93.8%), *Phragmites australis* (recurrence rate 83.3%) and *Potentilla anserina* (recurrence rate 94.1%). Of all species found at least 10 times across 2017 and 2018, the perennials recurred in 65.0% (standard error *SE* 8.8%) instances while annuals recurred on 50.6% (*SE* 15.9%) of sampling plots. However, there was no significant difference in the recurrence rate of annuals and perennials, neither when considering the species occurring at least 10 times nor when considering the entire species pool (Mann–Whitney *U* test, $p > .05$).

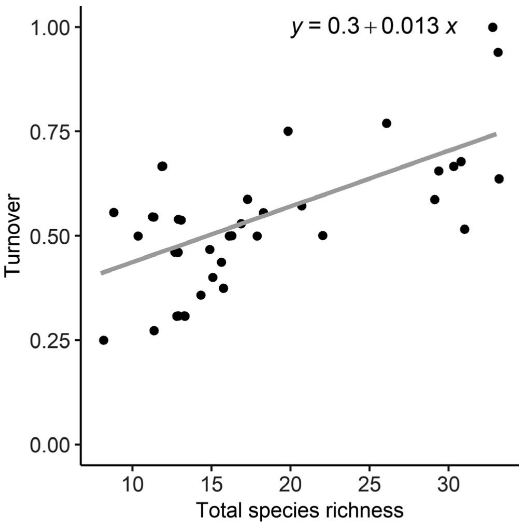

FIGURE 3 The temporal turnover rate plotted against total species richness. $R^2 = 0.31$

The biodiversity did not change significantly from the wet to dry year (Table 1), but there were changes in plant community composition. The plant community had a significantly higher Ellenberg *S* and Ellenberg *N* value in 2018 than in 2017, while the Ellenberg *F* value remained similar between years (Table 1). The change in species composition was significant on both the small sampling plot scale (Figure 2c; PERMANOVA, $p < 0.01$) and on the large salt marsh scale (Figure 2c; PERMANOVA, $p < 0.01$). The indicator species analysis selected six species that were associated to either 2017 or 2018. Three were associated with the wet year 2017: *Juncus bufonius* (annual), *Centaurium pulchellum* (annual) and *Trifolium pratense* (perennial) and three with the dry year 2018: *Poa annua* (annual), *Atriplex glabriuscula* (annual) and *Carex nigra* (perennial). This means that *Juncus bufonius* was more likely to be found in 2017 and that if located on a given site, there is a greater probability that the site was surveyed in 2017.

The temporal species turnover ranged from 0.25–1.00 with a mean turnover of 0.54. The turnover rate and species richness had a significant positive correlation (Figure 3; $p < 0.001$, $R^2 = 0.316$). The temporal environmental dissimilarity ranged from 0.02 to 0.50 and was significantly negatively correlated with the species overlap ($p < 0.01$, $R^2 = 0.38$) (Figure 4a) while we found no significant correlation between the environmental dissimilarity and the turnover rate ($p > 0.05$; Figure 4b).

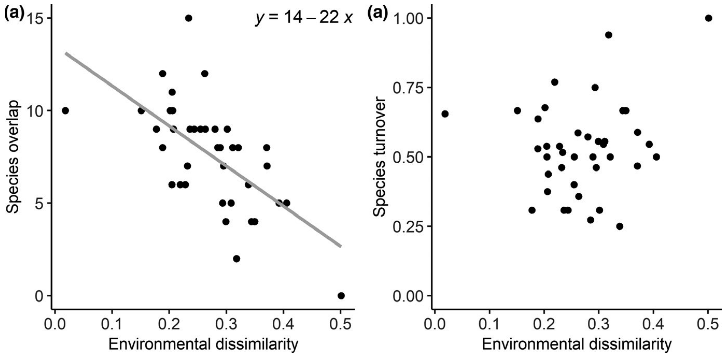

FIGURE 4 The environmental dissimilarity between years was significantly negatively correlated with the species overlap ($p < 0.01$, $R^2 = 0.38$) (a). No significant correlation was found between the species turnover and the environmental dissimilarity (b)

3.4 | Correlations between the edaphic factors and species richness and salt marsh richness

From the linear mixed model, we found species richness to correlate significantly with salinity, available P and available N across years as indicated by $t > \pm 1.96$ (Table 2). The response to all nutrients was stronger in the wet year compared to the dry year (Table 2). The salt marsh richness was not explained well across years by the edaphic factors (Table 2). We did, however, find that salt marsh species responded positively to moisture in the wet year and negatively to moisture in the dry year (Table 2). Further, the salt marsh species reacted more strongly to available N and total P in the wet year 2017 compared to dry 2018.

4 | DISCUSSION

As drought and high rainfall are likely to become more frequent in many regions under future climate changes, it is important to know if and how these affect the vegetation in salt marsh areas. Here, we found that the climatic variations between wet and dry conditions affected the shielded salt marsh vegetation by decreasing the vegetation cover and height in dry as opposed to wet conditions as well as altering the species composition. As the study was limited to two years, however, we do not know if the trends observed here will apply in a long-term perspective and as such, are limited to drawing conclusions regarding how current variations in precipitation and temperature can affect the plant community within the current climate.

4.1 | Edaphic factors

Following a drought, increased soil oxygen penetration may result in changes in soil chemistry (Palomo et al., 2013). Indeed, the shielded salt marsh in our study was drier and with a higher nutrient availability in low-precipitation 2018 compared to high-precipitation 2017 (Table 1). Where we found NH_4^+ levels to increase and NO_2^-/NO_3^- levels to decrease, Palomo et al. (2013) found the opposite response in an experimental salt marsh experiencing drought. The increased soil available N and available P might, however, partly be a result of the plants' decreased ability to acquire nutrients during a drought (Bista et al., 2018). Soil salinity levels are known to increase during a drought (Chapple & Dronova, 2017; Forbes & Dunton, 2006), as was also the case in this study, although not significantly (Table 1).

4.2 | Vegetation cover, species richness, species composition and turnover

A decrease in biomass and vegetation height is a common vegetation response to drought (Forbes & Dunton, 2006; McKee et al., 2004; Paudel et al., 2018; Tilman & El Haddi, 1992; Zedler et al., 1986) corresponding to the decrease in plant cover, height and density we found during dry conditions (Table 1). Despite the increased nutrient content of the salt marsh, which commonly results in an increase in the above-ground biomass (Crain, 2007; Darby & Turner, 2008), the vegetation height and cover decreased in connection with the drought indicating that the drought stress was stronger than the increased nutrient availability. Further, as grazing pressure was lower during the dry year compared to the wet, the decreased cover, density and height cannot be ascribed to the altered grazing pressure; if anything, the lowered grazing pressure could even have confounded the effect of the drought on the vegetation cover, density and height.

Salt marsh species are adapted to coping with stressors including salt stress (Veldhuis, Schrama, Staal, & Elzenga, 2018), and the distribution of salt marsh vegetation is primarily limited by competition (Veldkornet, Adams, & Potts, 2015). At increasingly extreme edaphic conditions, abiotic stressors, such as an increased salinity, will limit the distribution of non-salt marsh vegetation due to their decreased competitive advantage compared to salt marsh species

TABLE 2 The results of the linear mixed model with random slope and intercept for year

	Species richness			Salt marsh species richness		
	2017	2018	*t*-value	2017	2018	*t*-value
Intercept	8.87	7.11	2.87 (*)	3.98	5.71	2.82 (*)
Moisture	−0.029	0.0035	−0.25 (n.s.)	0.0015	−0.0018	−0.009 (n.s.)
Organic matter	0.098	0.089	1.30 (n.s.)	0.043	0.081	1.57 (n.s.)
Salinity	−2.019	−2.007	−3.75 (*)	0.26	0.26	0.98 (n.s.)
Available P	−2.079	−1.54	−2.00 (*)	−0.30	−0.29	−0.70 (n.s.)
Available N	0.20	0.048	1.97 (*)	0.016	0.0067	0.93 (n.s.)
Total P	−0.0040	0.0026	−0.19 (n.s.)	0.0015	0.00044	0.79 (n.s.)
Total N	0.27	0.16	0.96 (n.s.)	−0.13	−0.14	−1.35 (n.s.)

Note: Regression coefficients are provided for each year for the correlations between species richness and salt marsh species richness and all edaphic factors, accordingly. Further, *t*-values are provided; a value above ±1.96 indicates a significant correlation. The significance level is noted with n.s. being not significant and *corresponding to a significant correlation.

(Veldkornet et al., 2015). This could explain the increase in the number of salt marsh species during the dry conditions despite the general decrease in species richness. Further, salinity is generally known to limit species richness (García, Marañón, Moreno, & Clemente, 1993; Li et al., 2013); thus, the drop in species richness could also be caused by an increased salinity.

Salt marsh plant communities can shift in response to drought (Wetzel & Kitchens, 2007), as seen in our results by a shift toward more salt marsh species. The change in species composition and identity across the two years (Figures 1, 2) as well as the change in Ellenberg values of the plant community (Table 1) indicate that the decline in species richness could not simply be explained by the species of 2018 being a subset of those found in 2017. Indicator species analysis found that most of the species that were linked only to one year were annuals rather than perennials. The perennial *Carex nigra* appeared more frequently during the dry year. As *C. nigra* has a seed longevity of 15–20 years, often delays germination and exploits gaps in the vegetation (Schütz, 2000), seeds in the ground were likely able to grow where the altered conditions hindered the growth of other plants. However, we did not find perennials to have a higher recurrence rate compared to annuals. Meeks (1969) found that the earlier a marsh community was drained of water during the spring season, the more rapidly perennial species would be replaced by annuals; further, that multiple years of early water drawdown would result in a plant community dominated by annuals. Therefore, the lack of water during spring might have encouraged more annuals to germinate.

As individual species frequently disappear and reappear locally, the annual species turnover can be high (van der Maarel & Sykes, 1993) and several studies have found correlations of varying degrees between overall species turnover and climatic variations between years (Hallett et al., 2014; Letten, Ashcroft, Keith, Gollan, & Ramp, 2013; Noto & Shurin, 2017). Regardless of climatic conditions, species retention is generally lower and species gain higher in salt marshes compared to other habitats (Pakeman & Lewis, 2017). The increasingly dry and saline conditions might further have made competition between species in the salt marsh harsher (Pennings & Callaway, 1992). We found temperature and precipitation variation to coincide with a significant change in species composition and a high species turnover (0.54), in accordance with results by Noto and Shurin (2017) who also linked the species turnover of salt marshes to precipitation. Though we did not find a significant correlation between the species turnover rate and the environmental dissimilarity, results point toward climatic variations in precipitation and temperature leading to high species turnover as more species were retained where the environment changed the least.

While a higher species richness has been associated with a higher community stability in grasslands (Tilman, 1996), the same might not apply for salt marshes (Noto & Shurin, 2017), in agreement with our results. Here, a high species richness did not increase stability in the salt marsh given that we found no evidence that areas with more species were less prone to species loss under extreme circumstances (Figures 3 and 4).

4.3 | Correlations between the edaphic factors and species richness and salt marsh richness respectively

Both salt and drought stress alter the ability of plants to utilize nutrients (Bista et al., 2018; Hu & Schmidhalter, 2005). Nitrogen is a main limiting factor for salt marsh vegetation (Kiehl, Esselink, & Bakker, 1997; van Wijnen & Bakker, 1999) and in agreement with results by Morgan and Adams (2018), total species richness in our study was limited by the availability of nitrogen. Our results also showed that N availability has less influence on total species richness during dry and more saline conditions, which could be explained by the results of Ryan and Boyer (2012) who found that overall species richness decreases while the dominance of a few salt marsh species increases when salinity and nitrogen levels increase simultaneously. Soil moisture affects the salt marsh plant community (Alvarez-Rogel et al., 2000) and Theodose and Roths (1999) found that species richness was highest in the moistest areas of a salt marsh.

5 | CONCLUSIONS

As expected, climate variations resulted in significant differences in several edaphic factors In the shielded salt marsh; often, but not always, responding in the same direction as edaphic factors In tidally influenced salt marshes in relation to drought. Equivalently to tidally influenced salt marshes, the drought event in the shielded salt marsh decreased vegetation cover and density compared to wet conditions and changed the overall species composition. While total species richness decreased when going from wet to the dry extreme, the salt marsh species richness increased. Perennials did not recur significantly more often than annuals. We saw a high temporal species turnover in connection with the climatic variations and found that more species recurred when the edaphic conditions changed the least. Finally, we found species richness to be better able to respond to increased nutrient availability during wet conditions. These results show that shielded salt marsh plant communities are likely to respond swiftly to a change in the edaphic conditions due to variation in precipitation and temperature; further, that in shielded salt marshes extreme drought might actually promote salt marsh species and cause a setback in the distribution of non-salt marsh-adapted species.

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AUTHOR CONTRIBUTIONS

LHA, DB, CP and SB conceived the idea fior the research. LHA, ASKS, JSK and TBS collected the data and assisted in the laboratory work. LHA did the statistical analysis with contributions from CP. LHA, with contributions from DB, wrote the first draft to the paper. All authors commented on the results and manuscript.

DATA AVAILABILITY STATEMENT

All data used in this publication are stored in Zenodo, https://doi.org/10.5281/zenodo.3608523.

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SUPPORTING INFORMATION

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

Appendix S1. A map of the study site along with images of the area in 2017 and 2018

Appendix S2. List of salt marsh species

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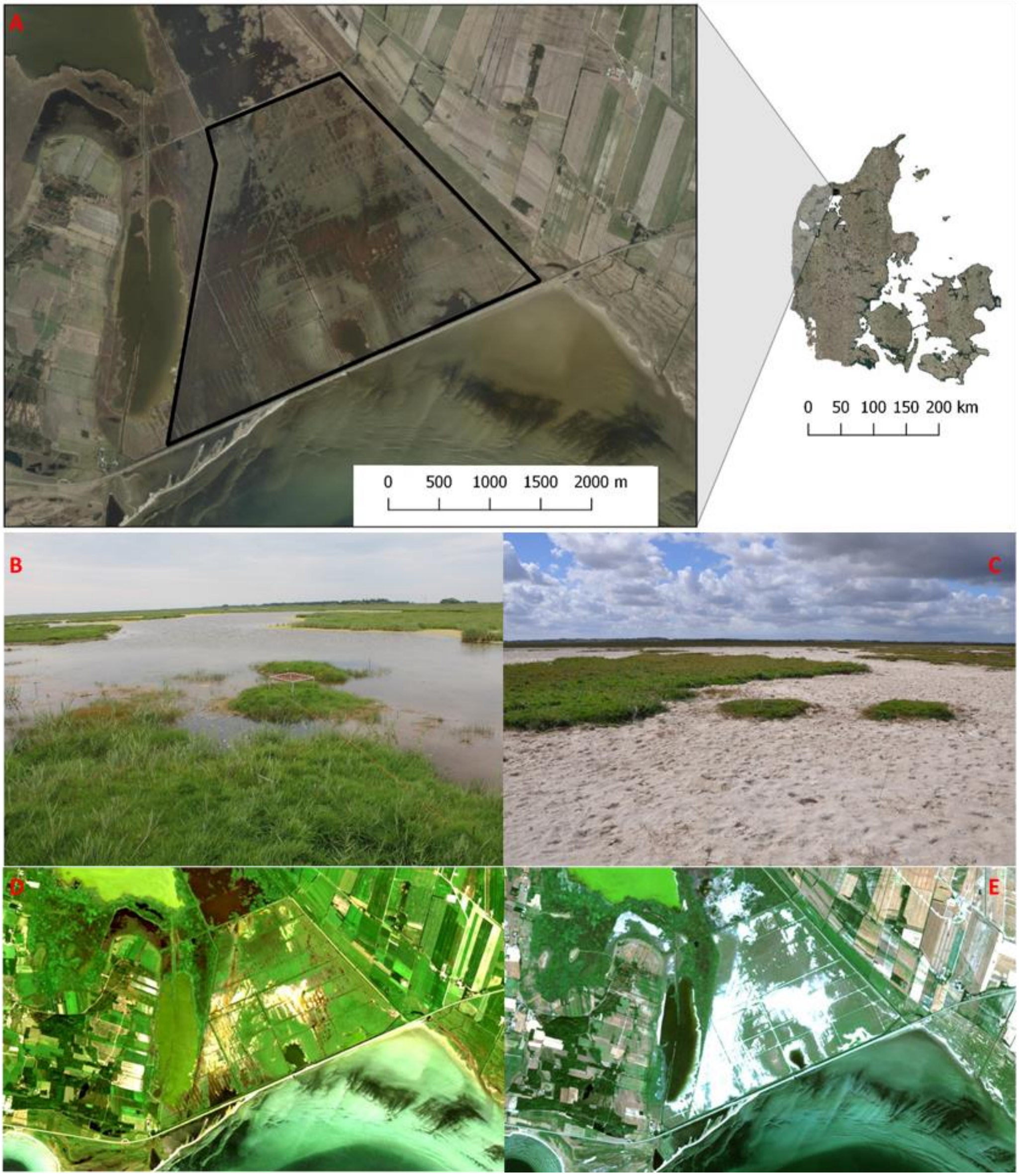
SUPPORTING INFORMATION FOR PAPER II

Appendi S1: Map of Bygholmengen and sampling points

Appendix S2: List of salt marsh species

Supporting information to the paper
Anderse, L.H. et al. Turnover and change in plant species composition in a shielded salt marsh following variation in precipitation and temperature. *Jornal of Vegetation Science*.

Appendix S1. Appendix S1. The geographical location of the salt marsh Bygholmengen (A). The same sampling plot on Bygholmengen in August 2017 (B) and August 2018 (C) photographed from different angles. Photographs by Line Holm Andersen and Thomas Bo Sørensen. Satellite images from July 2017 (D) and July 2018 (E). Satellite images were obtained from satellite Sentinel-2 L2A (EOS Land Viewer, 2018).



References: EOS Land Viewer. (2018). Sentinel-2 L2A (satellite).

Supporting information to the paper:

Anderse, L.H. et al. Turnover and change in plant species composition in a shielded salt marsh following variation in precipitation and temperature. *Jornal of Vegetation Science.*

Appendix S2. List of salt marsh species. Species in bold were found in this study. Salt marsh species are defined as species listed as specific for habitat type 1330 in the NATURA 2000 framework as well as species listed as characteristic for Danish salt marshes (European Commission, 2013; Miljøstyrelsen, 2016).

Agrostis stolonifera
Armeria maritima
Artemisia maritima
Aster tripolium
Atriplex littoralis
Atriplex hastata
Atriplex pedunculata
Atriplex portulacoides
Beta maritima
Blysmus rufus
Carex extensa
Centaurium littorale
Centaurium pulchellum
Eleocharis spp.
Festuca rubra
Frankenia laevi
Glaux maritima
Juncus gerardii
Limonium sp.
Lotus tenuis
Matricaria maritima
Odontites litoralis
Puccinellia distans
P. fasciculata
P. maritima
P. retroflexa
Plantago maritima
Potentilla anserina
Samolus valerandi
Spergularia marina
Trifolium fragiferum
Triglochin maritima
Tripolium pannonicum

References:

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PAPER III

REED BED VEGETATION STRUCTURE AND PLANT SPECIES DIVERSITY DEPEND ON MANAGEMENT TYPE AND THE TIME PERIOD SINCE LAST MANAGEMENT

Under review after first revision at Applied Vegetation Science

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Reed bed vegetation structure and plant species diversity depend on management type and the time period since last management

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Running title: Structural effect of reed bed management

ABSTRACT

Question: Reed beds, dominated by common reed (*Phragmites australis*), have high ecological value. Several studies have examined the differences between managed and unmanaged reed beds without taking into account the time passed since the last management. In this paper, we seek to answer the question: How does the time passed since last management and the management method itself affect the plant community and the habitat structure of reed beds?

Location: 'De Østlige Vejler', Northern Jutland, Denmark

Methods: We examined four reed bed treatments – beds cut or harvested during the year of the study and reed beds harvested 3 and 25 years ago, respectively. The reed bed plant communities and the reed bed habitat structure were determined in May and August. We tested the data for overall between-treatment differences (ANCOVA and PCA) and specific differences in the plant community and habitat structure (Kruskal-Wallis).

Results: The plant community differed significantly between the four reed beds according to treatment, and each reed bed exhibited unique species. Species richness was significantly higher in the recently harvested reed beds (0 and 3 years since harvest) compared with the 25-year-old reed beds. Harvest sparked reed rejuvenation and increased the growth of new reeds. The newly harvested and 25-year-old reed bed exhibited markedly different reed bed habitat structures. The 3-year-old reed bed had a habitat structure that equally resembled that of the newly harvested and the 25-year-old reed beds. Cutting, as opposed to harvesting, created a plant community adapted to less light availability.

Conclusions: To secure most plant species and most variation in habitat structure, reed beds should contain a mosaic of differently aged and differently managed patches. Previous studies have disagreed on the effect of management on plant species diversity, which could be explained either by different reed bed age or different sampling periods.

Key words: *Phragmites australis*, reed swamp, plant community, habitat structure, species richness, biodiversity, harvest, moving, succession

INTRODUCTION

Reed beds, dominated by the sub-cosmopolitan common reed *Phragmites australis* (Cav.) Trin. Ex Steud (Lansdown 2017), are detritus-based wetland ecosystems that represent the early stage of succession from open water to woodland (Cowie et al. 1992; Valkama et al. 2008). Where new wetlands previously were formed at the same rate as others were lost, present-day drainage and eutrophication have halted natural wetland formation, resulting in a net loss of wetland areas (Vadász et al. 2008). Such wetland loss has been especially pronounced in Europe where 60–90% of all wetlands have disappeared during the 20th century (Čížková et al. 2013). Due to the limited herbivore grazing of reed beds, large amounts of litter accumulate and the reed bed eventually dries out and is gradually transformed through natural succession into other types of land cover (Hawke & José 1996). This succession can be stopped or reversed by different reed management methods, such as harvesting or burning of the reed bed, which slow down the litter accumulation rate (Cowie et al. 1992).

In Europe, reed beds have great economic value and common reed is used in a wide range of products, e.g. thatching material, and for the purpose of construction and gardening (Köbbing et al. 2013). In order to secure reed stems of high quality for commercial interests, reed beds should be harvested either annually or bi-annually (Valkama et al. 2008). Reed beds also have great ecological value being home to several rare plant species, numerous species of birds, and more than 700 species of invertebrates (Valkama et al. 2008). Therefore, it is important to evaluate how the management methodologies (i.e. frequency and/or type of management) affect reed bed plant communities and habitat structures.

Several studies have compared managed to unmanaged reed beds, but a potentially important confounding effect arises, namely the fact that the reed bed age (defined as time since last management action) varies considerably between studies (Decleer 1990; Cowie et al. 1992; Poulin and Lefebvre 2002; Schmidt et al. 2005). By merging reed beds of different ages into the same category “unmanaged”, the effect of reed management might be confounded by the different successional stages of the non-harvested reed beds. Thus, it is largely unknown which reed bed age provides a favourable environment for the species inhabiting the reed beds. According to Güsewell et al. (2000), reed bed age is important, andthey found that reed stem length, shoot number and stem diameter differed significantly between reed beds mown annually, every second year and every third year. The reed age also matters to the animals inhabiting the reeds. For example, Greylag Goose (*Anser anser*) avoids both newly cut reed beds and reed beds older than 16 years (Kristiansen 1998). Time since reed management may even be speculated to explain some inconsistencies between studiesm as reed management has been documented to affect plant species richness both positively (Decleer 1990; Cowie et al. 1992) and negatively (Deák et al. 2015), and the effect may also depend on salinity (Valkama et al. 2008).

In the present study, we explored how reed bed age affected the species composition, plant community (species richness, Shannon diversity and habitat heterogeneity as well as Ellenberg indicator values (EIV), vegetation height and density) and reed bed habitat structure (i.e. height, diameter and density of common reed, both new (green) and old (brown)) of the reed bed. The effect on the harvested reed beds was examined for three age stages – time since last management 0 (young), 3 (intermediate) and 25 years (old). Additionally, we examined two management methods reed cutting and reed harvest. When cut, the stems of common reed were left behind and when harvested, the stems were removed. The difference between the four reed bed ages and management treatments was investigated during spring (May) before complete reed regrowth at the managed sites and in late summer (August) after regrowth to full height.

METHODS

Study site

This study took place in a bird sanctuary and protected area with no access to the public in Northern Jutland, Denmark, named ‘De Østlige Vejler’ (57°04’N, 9°03’E). The entire Vejlerne is home to the largest coherent reed bed in Scandinavia, which covers approximately 2000 ha (Riis 2009). The ‘De Østlige Vejler’ contains more than 600 ha of reed bed.

Reed bed treatments

Common reed has been harvested from Vejlerne for more than 100 years, but from 1979 and onwards only in winter. Throughout the years, different areas have been harvested, and it is therefore possible to locate areas with varying time since last harvest – here referred to as reed bed age. During 2018, we investigated four different areas comprising three different ages. The oldest reed bed area was last harvested in 1993, leaving the area unmanaged for 25 years (25-year-old reed bed). The second area was last harvested in 2015 (3-year-old reed bed). Two reed bed areas were managed during the year of the study (0-year-old reed beds) using two different management methods – cutting, where the reed stems are left behind, and traditional harvesting, where the reed stems are removed. Harvesting and cutting took place in February 2018. Thus, in total, four reed bed treatments were investigated.

For each of the four reed bed treatments, data were sampled in circular plots with a radius of 5 m. Twenty plots were sampled per treatment in May and another 20 plots in August, adding up to a total of 160 sampling plots. We did not sample the same 20 per treatment plots in May as in August since our sampling activity caused heavy disturbance within the 5 m circle due to trampling.

Abiotic conditions

During spring (May), salinity was measured in the surface water at four points within each 5 m circle plot using a Cond 340i (WTW) after which average salinity was calculated. Salinity was not measured in August due to absence of surface water caused by a prolonged drought. In both May and August, it was also noted whether the 5 m circle was dry or covered by water (Nygaard et al. 2016), and the percentage coverage of water within the circle was estimated.

The plant community

Twenty plots were established for each reed bed treatment in both May and August, yielding 40 plots per treatment. The plots were distributed randomly within the four differently aged reed beds using QGIS 2.18.11 (QGIS Development Team 2016). Within each plot, consisting of a circle with a radius of 5 m,all plant species were recorded and determined to species level. Plant abundance and species composition were determined using the pinpoint method (Levy and Madden 1933) where a pinpoint frame of 0.5x0.5 m was placed at the centre of each 5 m circle. The pinpoint frame was carefully placed on the vegetation ensuring not to damage it in the process. The pinpoint frame had 16 intersection points at each of which a pin was inserted. All plants in contact with the pin were recorded and if several individuals of the same species touched the pin repeatedly, their total number was counted. The height at which each plant touched the pin was also recorded and if a species touched the pin at different heights, only the maximum height was registered. Plants were identified to species level using primarily Frederiksen et al. (2006) and specific literature on graminoids (Mossberg and Stenberg 2014; Schou 2006; Schou et al. 2010; Schou et al. 2014).

We aimed to determine whether the species composition differed between the four reed bed treatments. First, we computed a PERMANOVA with 999 permutations based on the Jaccard metric using *Adonis2* in order to test for differences in species composition between treatments (McArdle and Anderson 2001; Oksanen et al. 2017). Second, we determined which species were unique to each of the treatments. Unique species are here defined as species occurring only in one of the treatments. Third, an indicator species analysis was used to determine which species were especially related to each treatment using the *indicspecies package* in R (Cáceres and Legendre 2009). This package assesses the statistical significance of the relationship between a number of sites and species on a presence/absence level. The number and identity of unique species may differ from the number of indicator species as a species occurring only once in a treatment is unique but might not qualify as an indicator species. The plant species presence/absence data from the 5 m circle were also used to estimate Ellenberg L (light), F (moisture), S (salinity) and N (nutrient) (Ellenberg et al. 2001) and we calculated the Ellenberg values for the plant community in each 5 m circle. Ellenberg indicator values are used as bioindicators of the environment (Ellenberg et al. 2001). We also calculated the Ellenberg values for the indicator species of each treatment and for the species unique to each treatment.

Data from the pinpoint frame were used to calculate vegetation cover and Shannon diversity (Shannon 1948), while data from the 5 m circle were used to determine species richness and within-treatment habitat heterogeneity. In order to investigate the within-treatment heterogeneity for each of the four treatments, we calculated the dissimilarity for all pairwise combinations of plots within a treatment (Willby et al. 2018). The R package *vegan* (Oksanen et al. 2017) was used to calculate the binary Jaccard dissimilarity as it allowed use of the presence/absence data from the 5 m circles. We calculated the habitat heterogeneity for May and August separately.

Reed bed habitat structure

Two types of observations were made in order to characterise the common reed bed structure within each plot. First, stem density was measured in a 0.5x0.5 m frame where both the number of green (new) and the number of brown (old) stems were counted. This enabled us to calculate the reed density per m^2. Second, the diameter of 20 randomly selected stems within the 0.5x0.5 m frame was measured. When possible, this was done for both green and brown stems; however, as 20 green stems could not be located in some of the frames, such registration was not always possible. Furthermore, data on common reed height obtained during the pinpoint analysis were also used to characterise the reed bed habitat structure.

We estimated the aboveground reed biomass from the aboveground standing reed volume using the number of reed stems (reed stem density) in a square meter (RS) multiplied by the reed stem area (calculated using the reed stem radius (r)) and the reed height (h):

$$Biomass\ (m^3) = RS \cdot \pi \cdot r^2 \cdot h$$

The biomass was estimated for both green and brown reed.

We estimated total plant density within the pinpoint frame as the number of touches of the pinpoint pin. We divided the total density into the reed density (RD) and the density of all other plants. Using the information on the number of green (GR) and brown reed (BR) stems in a pinpoint frame, the new to old ratio was calculated:

$$New\ to\ old\ ratio = GR/BR$$

Data analysis

In order to determine whether the four reed treatments differed significantly, a non-parametric MANOVA with 10,000 permutations was conducted using the R package *npmv* (Burchett et al. 2017). Separate tests were run for May and August and for the plant community parameters (Ellenberg values; vegetation height, density and cover; species richness, Shannon diversity and habitat heterogeneity) and the reed bed habitat structure parameters (reed height; diameter of green and brown shoots; density of green and brown shoots and the green to brown ratio; green and brown biomass). A Principal Component analysis (PCA) (Jolliffe 2002) with parameter scaling ($\mu = 0$, $\sigma = 1$) was conducted to visualise the degree of difference between treatments.

For each reed and plant community parameter in May and August, we tested for significant differences between the four treatments for each parameter using a Kruskal-Wallis test (Hollander et al. 2013). We used the sequential Bonferroni Correction, also known as the Holm correction, to account for multiple testing (Holm 1979). When a significant between-treatment difference was found, a post-hoc Dunn test was performed to determine which treatments differed from each other.

All data analyses were conducted using R v.3.4.1 (R Core Team 2017). Graphs were created in ggplot2 (Wickham 2016).

RESULTS

Abiotic conditions

The mean salinity levels were below 1 ppt in all four reed bed treatments (Appendix S1). The water cover did not differ between the treatments within the same sampling period, but there was a significant decrease in water cover from May (close to 100%) to August (close to 0%) between treatments (Appendix S1).

Plant community

The plant species composition differed significantly between treatments in May (PERMANOVA, $p < 0.01$) and August (PERMANOVA, $p < 0.01$). Thus, in May and August, unique species counted five in the cut reed bed, seven in the 0-year-old harvested bed, one in the 3-year-old reed bed and nine in the 25-year-old bed (Appendix S2). A full species list for each treatment can be found in Appendix S3. The indicator species analysis found that one species was associated with the cut reed bed, four with the harvested and three with the 25-year-old bed across May and August (Table 1), whereas no particular species was mainly associated with the 3-year-old bed. The plant species exclusively found in the 0-year-old harvested treatment exhibited the highest values of Ellenberg L and F but the lowest values of Ellenberg N compared with the other treatments (Table 1 and Appendix S4).

The plant community characteristics differed significantly (*p*-value < 0.001, non-parametric MANOVA) between the three reed bed ages and the two types of management treatments in year-0 in both May and August.

By visual inspection of the PCA plot for May, we found that the plant communities of the 0-year-old harvested and 3-year-old treatments grouped together, distancing themselves from the cut and 25-year-old reed bed treatments that also grouped together (Fig. 1a). In May, the first principal component PC1 and second principal component PC2 explained 24.94% and 15.61%, respectively, of the total variance in the plant community (Fig. 1a). PC1 and PC2 explained 25.15% and 19.92%, respectively, of the total variance in the plant community in August (Fig. 1b). In May, PC1 was best explained by species richness and Ellenberg F, while Ellenberg L and Ellenberg N best described PC2 (Fig. 1a). The same parameters were also among those with the highest loading in August where PC1 was best explained by Ellenberg L and Ellenberg and PC2 by species richness and Ellenberg F . Shannon diversity was the most important parameter on PC3 in both May and August (Fig. 1a, b).

In May, six of the ten plant community parameters differed significantly between treatments (Kruskal-Wallis with sequential Bonferroni correction, $p < 0.05$) (Appendix S5). These were species richness, habitat heterogeneity, cover, vegetation height, Ellenberg N and Ellenberg L. In August, five of ten parameters differed significantly between treatments (Kruskal-Wallis with sequential Bonferroni correction, $p < 0.05$): Shannon diversity, habitat heterogeneity, vegetation height, Ellenberg S and Ellenberg L (Appendix S5).

The post hoc Dunn test showed that the four treatments differed on between 0% and 33.3% of the parameters in question in May and on 22.2-44.4% in August (Appendix S5). Median species richness was significantly higher in the 3-year old reed bed compared with both the 0-year-old harvested bed and the 25-year-old reed bed in May (Fig. 2, Appendix S5). The opposite trend was found for Shannon diversity, which was significantly higher in the 0-year-old and 25-year-old reed beds than in the 3-year-old bed in August (Fig. 2, Appendix S5. Habitat heterogeneity was significantly higher in the 0-year-old cut than in the 0-year-old harvested and 3-year-old harvested reed beds in May, but by August the 0-year-old harvested bed had a significantly higher habitat heterogeneity than all the other treatments (Fig. 2, Appendix S5). Boxplots of the remaining plant community parameters can be found in Appendix S5.

Reed bed habitat structure

The non-parametric MANOVA found a significant difference in reed bed habitat structure characteristics (p-value < 0.001) between the three reed bed ages and the two management treatments in both May and August (Fig 1c and 1d).

Based on visual inspection, the PCA showed only little overlap between the 0-year-old harvested and the 25-year-old reed bed treatments, whereas the 3-year-old reed bed were located in between and overlapped with both the 0- and 25-year-old reed beds in both May and August (Fig. 1c, d). While the 0-year-old harvested plots were associated with new reed growth (higher density, diameter and biomass of green reed), the 25-year-old harvested reed bed was associated with a high density and biomass of brown reed (Fig. 1c, d). The 0-year-old cut reed bed was similar to the 0-year-old harvested, but the overlap was not complete and the cut bed was less correlated with green reed density and had a lower green reed to brown reed density (Fig. 1c). PC1 explained 38.59% and 38.66% of the variance in reed bed habitat structure in May and August, respectively, while PC2 explained 26.3% of the variance in May and 27.08% of the variance in August (Fig. 1c, d). The parameters green reed to brown reed ratio (new:old reed ratio) and the density of green shoots had the highest loadings on PC1 in May, while reed height and brown biomass had the highest loadings on PC2. In August, the green to brown reed ratio and the density of green shoots were still the most important parameters on PC1, while height remained the most important parameter on PC2, with diameter of green shoots being the second-most important parameter on PC2 in August (Fig. 1d).

In both May and August, all eight reed bed structure parameters (100%) differed significantly between treatments (Kruskal-Wallis with sequential Bonferroni correction, $p < 0.05$). The post-hoc Dunn test revealed that of these eight parameters, between 37.5-100% of parameters differed between treatments in May while 12.5-87.5% differed in August (Appendix S5). Reed height was significantly lower in the 0-year-old cut and the 0-year-old harvested reed beds compared with the 3-year-old and 25-year-old harvested beds in May. In August, reed height was only significantly lower in the 0-year-old cut reed bed than in the other treatments (Appendix S5, Fig. 3). The density of green reed shoots was significantly higher in the 0-year-old harvested reed bed compared with the 3-year-old bed, which in turn had a significantly higher number of green reed shoots than the 25-year-old reed bed (Appendix S5, Fig. 3). The 25-year-old reed bed had a significantly lower ratio of green to brown shoots compared with the other reed bed treatments (Appendix S5, Fig. 3). While the green to brown reed ratio was significantly higher in the 0-year-old harvested bed than in the 3-year-old reed bed in May, this difference had disappeared by August (Appendix

S5, Fig. 3). Boxplots of the remaining habitat structure parameters can be found in Appendix S7.

DISCUSSION

Plant community

Management actions that change the habitat structure also radically change the species composition across habitats as seen in both grasslands and abandoned rice fields (Mesléard et al. 1999; Kitazawa and Ohsawa 2002). In correspondence with this, we also found that the species composition of the investigated reed beds differed significantly between treatments. Thus, cutting decreased the Ellenberg L-values of the plant community in May, likely due to the fact that the reed left behind shaded the underlying plants. In contrast, harvesting increased the Ellenberg L-values (Appendix S5). Ellenberg L of grassland plant communities has also been observed to increase with enhanced cutting frequency (Moog et al. 2002). As the Ellenberg values were based on presence absence data, they highlight the characteristics of plants co-occurring with the dominant species common reed rather than focus on common reed itself.

Unique species were found in each of the four reed bed treatments of our study (Appendix S5, Appendix S2) and we therefore suggest that, on a large scale, the most diverse habitat will be achieved by a mosaic of differently managed reed beds. In this context, use of different management treatments seems especially important since less than half of the species were found in all the treatments, the majority occurring in either one, two or three treatments (Appendix S2). Similarly, Kitazawa and Ohsawa (2002) found that different management treatments of rural herbaceous vegetation resulted in dominance of species that were uniquely adapted to the living conditions created by the particular management regimes.

Our results partly explain some of the disagreement about the effect of management on species richness in reed beds as the response of species richness to management is dependent on both reed bed age and time of the sampling. We found that species richness peaked after 3 years since last management, whereas Schmidt et al. (2005) found that species richness did not differ between managed and 5-year-old reed beds. In accordance with our result, Decleer (1990) found a higher species richness in managed compared with old (35-year-old) reed beds, which is also in agreement with our finding that species richness was higher in the recently harvested than in the 25-year-old reed bed. This indicates that species richness is positively affected by management, but that the effect only lasts for a few years before it abates, and we therefore encourage more studies to be undertaken including reed beds of intermediary age. In tall-herb fens, species richness increased after 2-4 years of grazing due to a decrease in the abundance of common reed (Ausden et al. 2005), and in our study the initial increase in species richness following management could be explained by the removal of common reed and decreased reed density in the young compared with the old reed beds. In our case, grazing of the reed bed would likely also result in reed bed drawback since the area adjacent to the study reed beds is a grazed marsh where common reed growth is limited (Andersen et al. 2020). We only observed an age effect on species richness in May, where the species richness was significantly higher in recently harvested (0- and 3-year-old) compared to the 25-year-old reed bed, and by August species richness no longer differed between the treatments. One explanation could be that the increases in species richness seen during spring in the younger reed beds, where the reed density was lower compared to the 25-year-old reed bed, had already been reduced by late summer due to the high competitive ability of common reed. The timing/season of the fieldwork may therefore also explain the inconsistencies across studies on the effect of management on species richness.

As suggested by Valkama et al. (2008), we looked at species richness and diversity relative to two management methods, which is yet a rare subject of study. We found that the methods of management did not affect species richness but that cutting led to a lower Shannon diversity than harvesting. According to Cowie et al. (1992), cutting also results in lower species diversity compared with burning, another reed management practice that also increases species richness.

An equal proportion of plant community parameters differed between the 0-year-old harvested and 3-year-old harvested as between the 3-year-old and 25-year-old harvested, which indicates the importance of including reed bed age of unmanaged reed beds (Appendix S5). None of the selected plant community parameters differed significantly between the 0-year-old harvested and 3-year-old reed bed in May. This highlights the importance of age of the reed bed used as a control. Had we only conducted fieldwork in either May or August, or only included either the 3-year-old or 25-year-old reed bed as a control, the results would have been significantly different.

Habitat structure

We found that harvesting promoted reed bed rejuvenation as the growth of new reed was strongly related to both reed age and management, which is in agreement with previous studies (Björndahl 1985; Ostendorp 1999; Deák et al. 2015). Further, the rejuvenation effect following management seems to last for at least three years, which highlights the importance of taking time since last management into account when studying reed beds and the effects of harvesting. In other investigations, winter harvesting was found to increase reed density compared with unmanaged reed beds (Bresciani et al. 2011; Valkama et al. 2008; Ostendorp 1999). This is partly in agreement with our finding that green reed density was significantly higher in the recently managed reed beds and in the early successional stage compared with reed beds left unmanaged for many years. We encourage more studies to include multiple ages of unmanaged reed beds to confirm this observed trend and discuss the optimal period for leaving reed beds unmanaged; however, based on the results of the present study and those of Schmidt et al. (2005) plant richness seems to peak 3-5 years following harvesting.

No clear habitat structure responses of reed beds to management treatments such as harvesting, cutting, burning and grazing have been identified (Valkama et al. 2008). In our study comparing two management treatments, we found that cutting and harvesting created different habitat structures; thus, the growth of green reed and reed biomass and height were significantly smaller in the 0-year.old cut reed bed than in the 0-year-old harvested bed. The reduced reed growth in the cut compared with the harvested reed bed can likely be explained by light limitations.

Reed beds are home to numerous birds and invertebrates that all depend on different habitat structures, a high habitat heterogeneity and various plant species (Sjöberg & Danell 1983; Baldi & Kisbenedek 1999; Valkama et al. 2008; Mero et al. 2018) with several species of birds avoiding newly harvested reed beds (Nielsen and Clausen 2019; Vadász et al. 2008). Denser vegetation protect nests from discovery by predators (Polak 2016; Wang et al. 2019), lead to higher breeding success (Mérő and Žuljević 2014) and a higher number of fledglings (Ille and Hol 1995). As harvest increased green shoot density in our study, it could have increased nest protection in May though it is important to consider that the reed height was lower thereby exposing nests. However, reed density dropped over the season, with the lowest die off in the old reed bed that had the highest density in August. Thus, higher protection in old reed beds in August might be expected although this is outside the breeding season.

In conclusion, we found that management method affects the plant community and that cutting resulted in a community with a significantly lower Ellenberg L compared with harvesting. Furthermore, the two management methods created different reed bed habitat structures with higher regrowth in the harvested than in the cut reed beds. We observed that plant species richness peaked 3-5 years after last harvesting; this finding may, though, be dependent on the timing of the fieldwork. While reed harvesting resulted in reed bed rejuvenation and increased green shoot density, reed die off throughout the season meant that the highest overall reed density occurred in the old reed bed and that this therefore provided the best protection for breeding birds. Thus, in order to create optimal conditions and favourable habitats for most species in reed beds comprising both heterogeneous and homogenous areas, a mosaic of beds exhibiting different management treatments and time since last management is likely the most optimal.

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Author contribution

DB, KT, SB, TLL and LHA conceived the idea of the research. LHA, MPK, JF and CMSF collected the data. LHA analysed the data under the guidance of CP and discussed first results with DB and PN. LHA wrote the first draft of the manuscript with contributions from DB. All authors discussed and commented on the final manuscript.

Data availability statement

Data available on zenodo.org.

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Figure 1. Separation of the four reed bed treatments into 0-year-old cut, 0-year-old harvested, 3-year-old harvested and 25-year-old harvested reed beds. The top row represents separation of the four reed bed treatments relative to plant community parameters in May (a) and August (b) and the bottom row the separation of the four reed bed treatments relative to habitat structure parameters in May (c) and August (d). Abbreviations used are SR: species richness; SD: Shannon diversity; HH: habitat heterogeneity; D: density of plants other than reed; EIV L: Ellenberg Indicator Value for light; EIV N: Ellenberg Indicator Value for nutrients; EIV F: Ellenberg Indicator Value for moisture; EIV S: Ellenberg Indicator Value for salinity; h: height; GR: green reed density, BR: brown reed density; GR:BR: green reed to brown reed ratio; B(g): biomass, green reed; B(b): biomass, brown reed; d(g): diameter, green shoots; d(b):diameter, brown shoots.

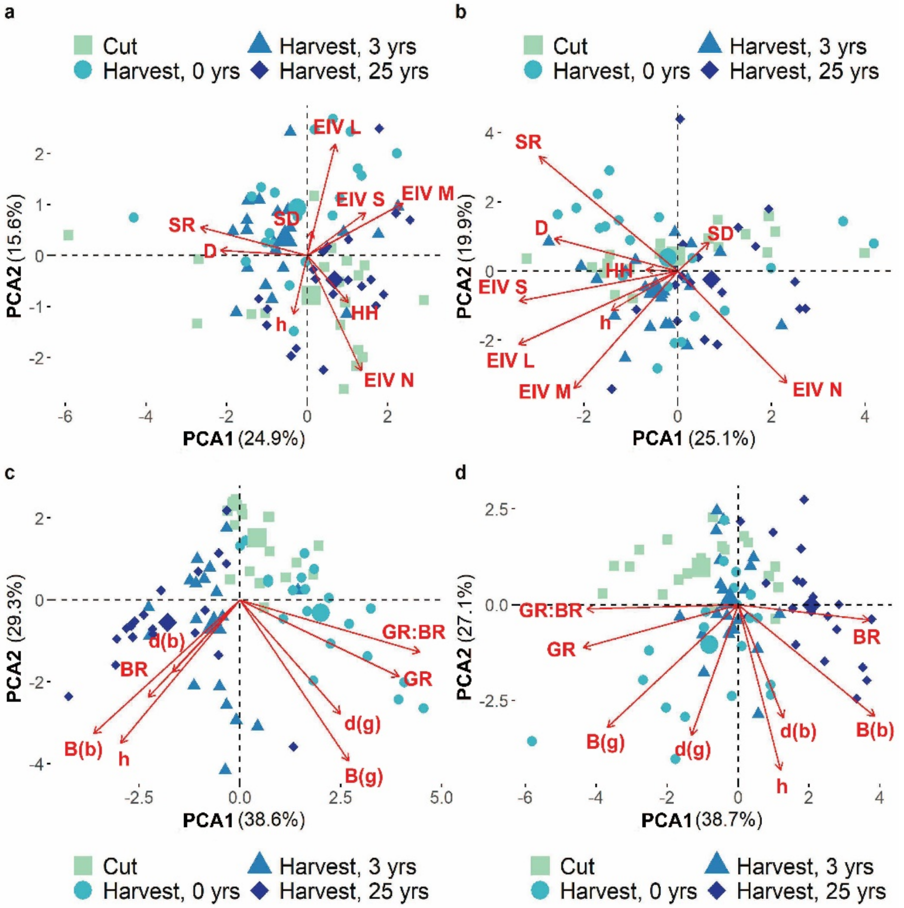


Figure 2. Median species richness, Shannon diversity and habitat heterogeneity for each of the four reed bed treatments in May and August. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers. Letters indicate whether two reed bed treatments are significantly different (different letter) or not (same letter) within May or August.

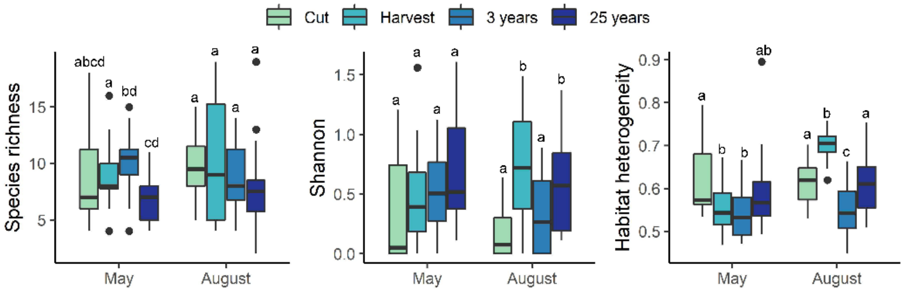


Figure 3. Median reed height (cm), density of green shoot and new to old shoot ratio for each of the four reed bed treatments in May and August. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers. Letters indicate whether two reed bed treatments are significantly different (different letters) or not (same letter) within May or August.

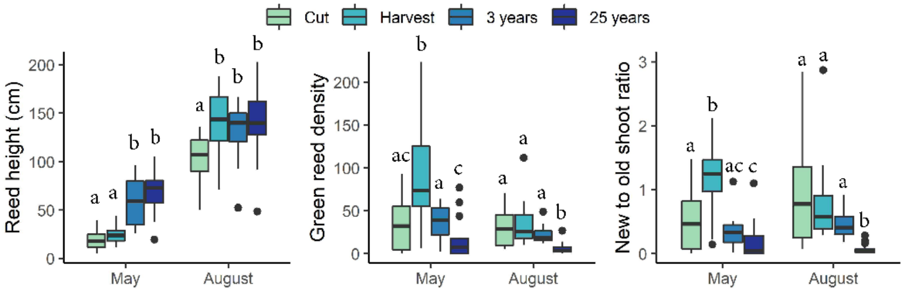


Table 1. Results of indicator species analysis. One species was linked to the cut, four to the harvested, none to the 3-year-old and three to the 25-year-old habitats. A/P: annual/perennial, EIV: Ellenberg Indicator Value, L: Ellenberg value for light, F: moisture, N: nutrients, S: salinity. All species are listed as least concern on the Danish Red List (Wind and Pihl 2010).

	Species	***p*-value**	**A/P**	**EIV L**	**EIV F**	**EIV N**	**EIV S**
Cut	*Alisma plantago–aquatica*	0.005	P	7	10	8	0
Harvested	*Carex elata*	0.005	P	8	10	5	0
Harvested	*Myosotis laxa ssp. caespitosa*	0.015	A	7	9	7	0
Harvested	*Carex disticha*	0.015	P	8	9	5	0
Harvested	*Eriophorum angustifolium*	0.015	P	8	9	2	0
25-year-old	*Solanum dulcamara*	0.005	P	7	8	8	0
25-year-old	*Cicuta virosa*	0.015	P	7	9	5	0
25-year-old	*Phalaris arundinacea*	0.025	P	7	8	7	0

SUPPLEMENTARY MATERIALS FOR PAPER III

Appendix S1: Water cover and salinity levels across treatments in May and August

Appendix S2: Venn Diagram depicting the number of species within each habitat

Appendix S3: A complete species list with frequencies for each reed bed treatment

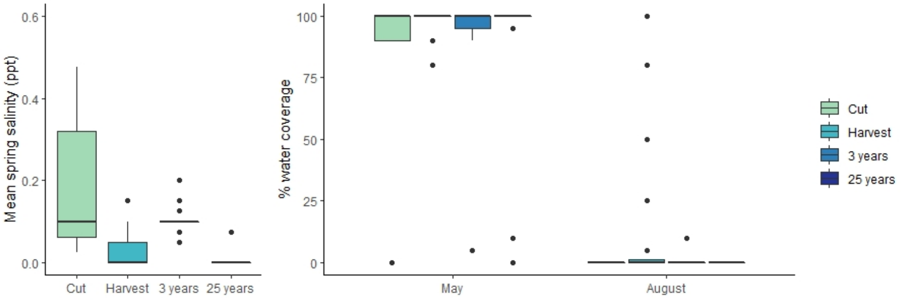
Appendix S4: Unique species per treatment

Appendix S5: Between-treatment differences

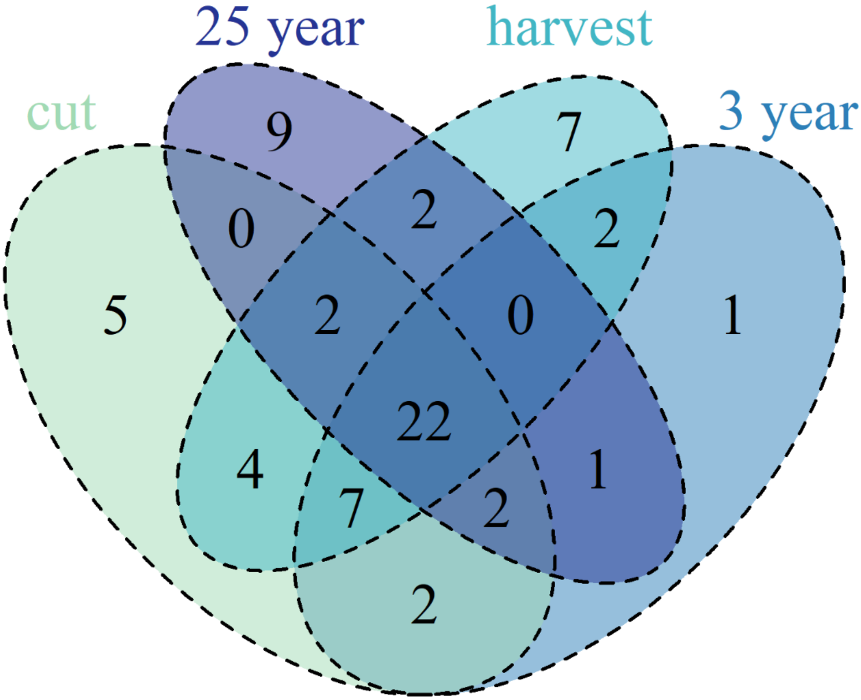
Appendix S6: Boxplots, plant community

Appendix S7: Boxplots, reed bed habitat structure

Appendix S1. The spring salinity across treatments in May and the water cover (%) of the 5 m circles in both May and August across treatments. Boxplots show median values as well as the 25th and 75th percentile, the whiskers are the largest and smallest value within 1.5 times the interquartile range from the 75th and 25th percentile, and points represent outliers.



Appendix S2. A Venn Diagram depicting the number of species present across all plots in each treatment as well as the number of overlapping species between habitats.



Appendix S3. A complete species list of species found in each reed bed and their frequency (%). The frequency is based on how often the species occur in a 5 m circle. The frequency is calculated across both May and August.

Species	Cut	Harvested	3-year-old	25-year-old
Agrostis stolonifera	42.5	40	70	2.5
Argentina anserina	2.5	0	0	0
Bolboschoenus maritimus	52.5	22.5	60	5
Cardamine pratensis ssp. Dentata	70	42.5	32.5	17.5
Carex panicea	0	2.5	0	0
Carex rostrata	15	20	10	0
Cicuta virosa	2.5	0	0	15
Cirsium palustre	10	0	2.5	0
Deschampsia cespitosa	0	0	0	2.5
Epilobium palustre	5	40	12.5	25
Equisetum arvense	0	0	2.5	10
Equisetum fluviatile	0	2.5	0	2.5
Equisetum fluviatile	0	10	0	2.5
Galeopsis bifida	0	0	0	2.5
Galium palustre	47.5	40	67.5	27.5
Galium uliginosum	7.5	2.5	0	0
Hierochloë odorata	5	0	2.5	2.5

Hippuris vulgaris	0	2.5	0	0
Hydrocharis morsus-ranae	12.5	2.5	25	27.5
Hydrocotyle vulgaris	7.5	7.5	10	5
Juncus effusus	2.5	5	0	0
Lemna trisulca	20	37.5	10	2.5
Lycopus europaeus	60	57.5	70	27.5
Lysimachia thyrsiflora	12.5	10	25	12.5
Mentha aquatica	22.5	12.5	37.5	5
Menyanthes trifoliata	0	5	0	0
Myosotis laxa	2.5	17.5	2.5	0
Myriophyllum verticillatum	5	0	0	0
Phalaris arundinacea	0	0	0	10
Phragmites australis	100	100	100	100
Polygonum amphibium	7.5	0	2.5	0
Potentilla palustris	2.5	10	7.5	0
Ranunculus sceleratus	2.5	2.5	0	0
Ribes nigrum	0	0	0	5
Rumex hydrolapathum	42.5	20	22.5	12.5
Rumex palustris	5	2.5	0	0
Salix sp.	2.5	20	5	42.5
Schoenoplectus lacustris	0	10	5	0

Stratiotes aloides	2.5	0	0	0
Triglochin maritima	0	0	0	2.5
Utricularia minor	10	17.5	5	0
Vicia cracca	0	0	0	5

Appendix S4. Unique species for each of the four reed bed treatments listed along with a number of the plants characteristics. All species are listed as least concern on the Danish Red List (Wind & Pihl 2010). Mean Ellenberg values per treatments can be found in the bottom of the table. A/P states whether the plant is an annual (A) or perennial (P) plant. EIV is the Ellenberg Indicator value for light (L), moisture (F), nutrient (N) and salinity (S).

Treatment	Species	A/P	EIV L	EIV F	EIV N	EIV S
Cut	*Carex pseudocyperus*	P	7	9	5	0
Cut	*Stratiotes aloides*	P	7	11	6	0
Cut	*Argentina anserina*	P	7	6	7	1
Cut	*Festuca rubra*	P	x	6	x	0
Cut	*Ranunculus acris*	P	7	6	x	0
Harvest	*Hippuris vulgaris*	P	7	10	x	0
Harvest	*Lathyrus pratensis*	P	7	6	6	0
Harvest	*Eleocharis palustris ssp. vulgaris*	P	8	10	?	0
Harvest	*Carex panicea*	P	8	8	4	1
Harvest	*Menyanthes trifoliata*	P	8	9	3	0
Harvest	*Carex nigra*	P	8	8	2	1
Harvest	*Eriophorum angustifolium*	P	8	9	2	0
3-year-old	*Dryopteris carthusiana*	P	5	x	3	0
25-year-old	*Urtica dioica*	P	x	6	9	0
25-year-old	*Triglochin maritima*	P	8	7	5	8
25-year-old	*Deschampsia cespitosa*	P	6	7	3	0

25-year-old	*Filipendula vulgaris*	P	7	3	2	0
25-year-old	*Galeopsis bifida*	A	7	5	6	0
25-year-old	*Myriophyllum verticillatum*	P	5	12	8	0
25-year-old	*Phalaris arundinacea*	P	7	8	7	0
25-year-old	*Vicia cracca*	P	7	6	x	1
25-year-old	*Ribes nigrum*	P	4	9	5	0
Cut			7	7.6	6	0.2
Harvest			7.7	8.6	3.4	0.3
3-year-old			5	-	3	0
25-year-old			6.4	7	5.6	1

References: Wind P, Pihl S (2010) The Danish Red List. The National Environmental Research Institute, Aarhus University

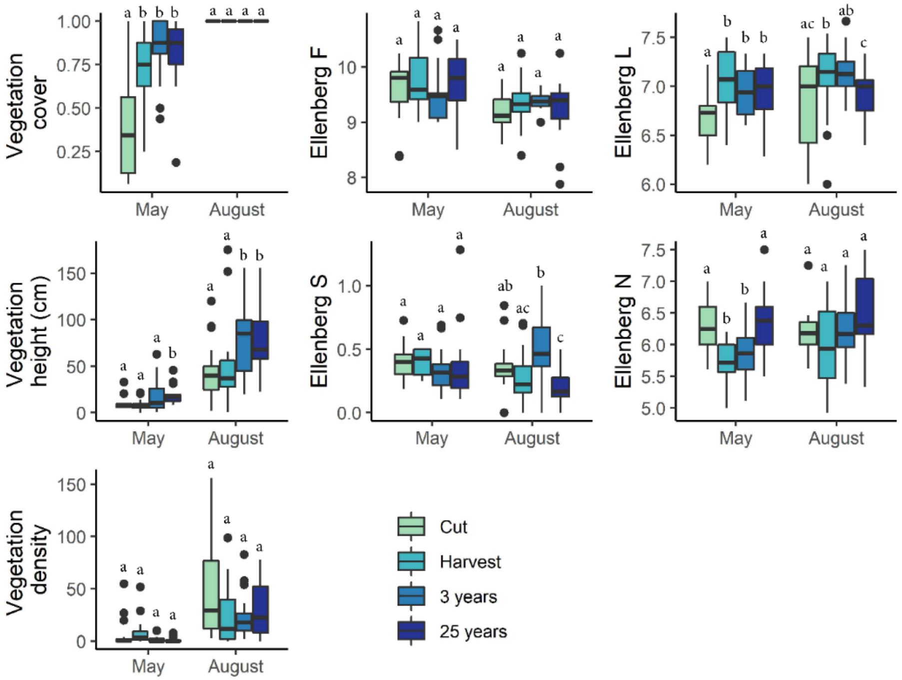
Appendix S5. Between-treatment differences in plant community and reed bed habitat structure parameters. If Kruskal-Wallis with sequential Bonferroni correction was significant, post hoc Dunn test results for between-treatment differences are shown. The accumulated difference show the percentage (%) of parameters that differ between the reed bed treatments. Non-significant Kruskal-Wallis results are indicated by '-'. *** $p < 0.001$, ** $p < 0.01$, *$p < 0.05$, m.n.: marginally non-significant $p < 0.1$, n.s.: non-significant.

	Month	Cut: Harvest	Cut:3-year-old	Cut:25-year-old	Harvest: 3-year-old	Harvested:25-year-old	3-year-old:25-year-old
Plant community							
Species richness	May	n.s.	m.n.	n.s.	n.s.	*	***
	August	-	-	-	-	-	-
Shannon	May	-	-	-	-	-	-
	August	***	n.s.	***	*	n.s.	*
Habitat heterogeneity	May	**	***	n.s.	n.s.	n.s.	n.s.
	August	***	*	n.s.	***	***	*
Cover	May	**	***	***	n.s.	n.s.	n.s.
	August	-	-	-	-	-	-
Veg. height	May	n.s.	n.s.	**	n.s.	*	**
	August	n.s.	**	*	**	**	n.s.
Ellenberg N	May	***	**	n.s.	n.s.	***	**
	August	-	-	-	-	-	-

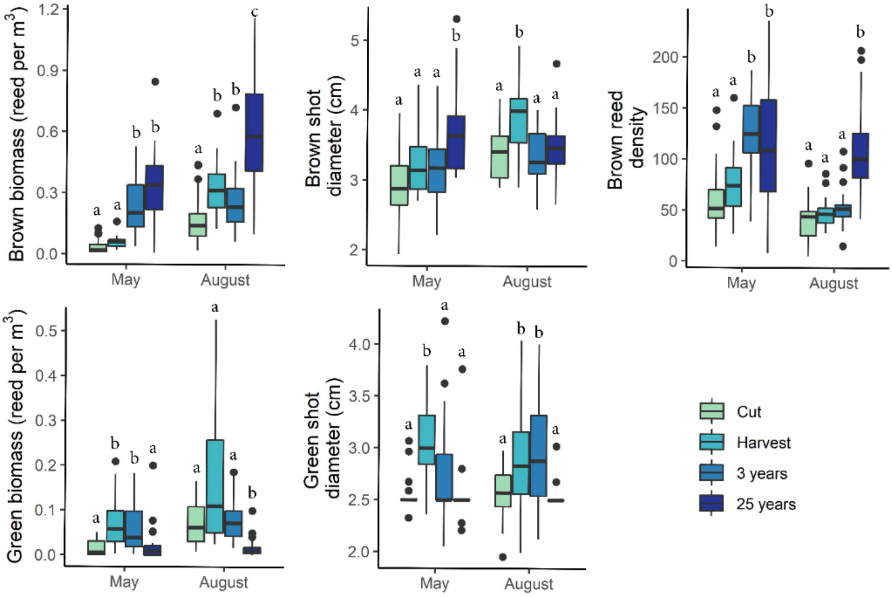
Ellenberg S	May	-	-	-	-	-	-
	August	n.s.	n.s.	**	**	n.s.	***
Ellenberg L	May	***	*	**	n.s.	n.s.	n.s.
	August	*	m.n.	n.s.	n.s.	*	*
Ellenberg F	May	-	-	-	-	-	-
	August	-	-	-	-	-	-
Accumulated difference (%)	May	44.4	44.4	33.3	0.0	33.3	33.3
	August	33.3	22.2	33.3	44.4	33.3	44.4
Reed bed habitat structure							
Green biomass	May	***	**	n.s.	n.s.	***	**
	August	m.n.	n.s.	***	n.s.	***	***
Brown biomass	May	n.s.	***	***	***	***	n.s.
	August	**	n.s.	***	n.s.	*	***
Green density	May	***	n.s.	m.n.	**	***	*
	August	n.s.	n.s.	***	n.s.	***	***
Brown density	May	n.s.	**	**	**	*	n.s.
	August	n.s.	n.s.	***	n.s.	***	***

Green diameter	May	***	n.s.	n.s.	**	***	n.s.
	August	*	*	n.s.	n.s.	**	**
Brown diameter	May	n.s.	n.s.	***	n.s.	*	*
	August	**	n.s.	n.s.	***	**	n.s.
Reed stem ratio	May	**	n.s.	*	***	***	m.n.
	August	n.s.	n.s.	***	n.s.	***	***
Reed height	May	n.s.	***	***	***	***	n.s.
	August	***	**	***	n.s.	n.s.	n.s.
Accumulated difference (%)	May	50.0	50.0	62.5	75.0	100	37.5
	August	50.0	25.0	75.0	12.5	87.5	75.0

Appendix S6. The median plant community parameters in May and August. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers. Letters indicate whether two reed bed treatments are significantly different (different letters) or not (same letter) within May or August.



Appendix S7. The median reed bed habitat structure parameters. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers. Letters indicate whether two reed bed treatments are significantly different (different letters) or not (same letter) within May or August.



PAPER IV

TIME SINCE LAST HARVEST AFFECT BOTH BIOMASS AND DIVERSITY OF INVERTEBRATES

In preparation

LINE HOLM ANDERSEN, PETRI NUMMI, JEPPE RAFN, CECILIE MAJGAARD SKAK FREDERIKSEN, MADS PRENGEL KRISTJANSEN, KRISTIAN TRØJELSGAARD, CINO PERTOLDI, DAN BRUHN AND SIMON BAHRNDORFF

Effects of reed bed management on invertebrate biomass and diversity

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ABSTRACT

1. Reed beds host a unique flora and fauna including species of conservation concern and red listed invertebrate species. Reed beds are harvested during winter, mainly for commercial purposes, and effects seems to vary across taxonomic levels.

2. In the present study we access how time since last reed harvest influenced invertebrate biomass and community across taxonomic levels in the largest coherent reed bed of Scandinavia. We sampled ground-dwelling and aerial invertebrates continuously for 10 weeks in a reed bed harvested during the year of the study (0-year-old), one harvested three years prior (3-year-old) and one harvested 25 years prior (25-year-old). Biomass was estimated and a subset of the data was sorted to Order level and Coleoptera to the species level.

3. We found that biomass of both aerial and ground-dwelling invertebrates, as well as Coleoptera, peaked in the 0-year-old reed bed and was lowest in the 25-year-old reed bed. The Shannon diversity, on the other hand, peaked in the 25-year-old reed bed.

4. Reed winter harvest changed the invertebrate community composition and relative abundance of the different invertebrate Orders and Coleoptera families, and the three reed beds each had distinct invertebrate communities. Further, we found data at the coarse taxonomic level Order provided valuable information on the effect of time since last reed harvest,

but that the response to harvest was family specific at least for Coleoptera. Data at the species level provided valuable information on red listed species, but did not

5. *Synthesis and applications:* Our findings highlight the importance of successional stages and management practices on the invertebrate community in reed beds. We suggest that it is possible to ensure high insect biomass and diversity by creating a mosaic pattern of reed bed through harvest. Small-scale reed harvest is thus a useful tool in reed bed management and can be used to increase the biomass of invertebrates, thereby increasing the food supply to insectivorous reed inhabitants, but also increasing the habitats for particular invertebrate orders and Coleoptera families through increasing reed bed age.

Keywords: biodiversity, management, insects, reedbeds, ramsar, ecological succession

INTRODUCTION

Reed beds are habitats of high value to both human and wildlife and host a unique flora and fauna (Holland et al. 1990; Costanza et al. 1997). Reed beds provide habitat for a rich invertebrate fauna with more than 700 species of invertebrates, multiple reed specialists, and with at least 40 insect species depending entirely on the reed bed habitat in the United Kingdom alone (Hawke & José 1996; Hardman et al. 2012). Generally, several species of local or global conservation concern are found in high numbers in reed beds including aquatic warbler (*Acrocephalus paludicola)* and Eurasian bittern (*Botaurus stellaris)*, as well as reed specialist moths (*Phragmataecia castaneae*, *Chortodes brevilinea* and *Pelosia muscerda)*, all depending on the reed stems or the reed bed as habitat (Hawke & José 1996; Hardman et al. 2012). Numerous species depend not only on reed beds as shelter/habitats, but also as food source. Many reed bed passerines as well as the Eurasian bittern feed on invertebrate prey (Bibby & Thomas 1985; Paracuellos 1997; Schmidt, M. H., Lefebvre, Poulin and Tscharntke 2005b; Polak 2016) and a drop in insect abundance can result in a decrease in insectivorous birds (Møller 2019).

Reed beds are often harvested for conservation or commercial purposes (Decleer 1990). Harvest and other management methods affect the invertebrate community and previous studies highlight how invertebrate abundance as well as different taxonomic groups respond differently when comparing newly managed reed to unmanaged controls (Ditlhogo et al. 1992; Schmidt, M. H., Lefebvre, Poulin and Tscharntke 2005a; Valkama et al. 2008). Spider biomass and richness, for example, were not affected by harvest according to Decleer (1990), whereas Schmidt et al. (2005a) found reed harvest to have a negative impact on spider as well as Coleoptera abundance. Contrary to this, Görn et al. (2014) found winter harvest to positively impact Coleoptera: Carabidae. According to a meta-analysis, harvest only decreased invertebrate abundances when repeated over several consecutive years (Valkama et al. 2008). Furthermore, the successional stage of the reed bed, which is reset by harvest, has also been shown to be important (at least for moths and Diptera) (Hardman et al. 2012). We therefore hypothesize that some of the contradictory findings among previous studies of reed bed invertebrates (Decleer 1990; Schmidt, M. H., Lefebvre, Poulin and Tscharntke 2005a; Görn et al. 2014) might be explained if the successional stage of the reed bed was included rather than just comparing managed to unmanaged reed beds. The previous results suggests species specific responses and that successional stage of the reed bed may affect the invertebrate community, but also highlight the need for more holistic approaches where both reed management and time since last management action are taken into account.

Similarly, results suggest that the taxonomic resolution when evaluating the effects of reed harvest may affect the outcome. Whereas some studies have discovered effects of reed management at the family level (Ditlhogo et al. 1992), others at the species level (Decleer 1990) and there seems to be no consensus on the most suitable taxonomic level to evaluate management practices for invertebrates in reed beds. Invertebrate species are often used as bioindicators to monitor the effects of management practices (Rainio & Niemelä 2003; Schipper et al. 2010), but it is both time consuming and require taxonomic expertise to reach the species level. Higher taxonomic levels are therefore sometimes used as surrogates for evaluating species responses (Gaston & Williams 1993; Andersen, A. N. 1995; Schipper et al. 2010). Regardless, there is still debate on whether higher taxonomic levels are suitable surrogates for species and while some studies find a high degree of overlap between higher and lower levels of diversity (Hewlett 2000; Caruso & Migliorini 2006), other find that species level data is far better than data on higher taxonomic levels (Verdonschot 2006; Smith et al. 2007).

We aim to assess the effects of reed bed age, here defined as time since last reed harvest, on the flying and ground-dwelling invertebrate community. We compare the invertebrate community across three ages of reed beds, a 0-year-old in an early successional stage (newly harvested, reed removed for commercial use), a 3-year-old at an intermediary stage of succession and a 25-year-old in a late stage of succession. Based on previous studies we expect harvest to either have no impact on or decrease the invertebrate biomass (Ditlhogo et al. 1992; Schmidt, M. H., Lefebvre, Poulin and Tscharntke 2005a). Second, we investigated the invertebrate diversity across the three different reed bed ages at the Order level and for Coleoptera also at family, genus and species level as we expected that the effect of reed bed age could differ across taxonomic levels. We chose Coleoptera because they are good bioindicators that respond quickly to anthropogenic disturbances and habitat alterations (Rainio &

Niemelä 2003; Avgın & Luff 2010), thereby making them optimal for studying what taxonomic level is required in order to access the effect of reed management.

METHODS

Study site

The study took place in reed beds in Vejlerne, Denmark (57°04'N, 9°03'E) during the summer (June 25th to August 29th, weeks 26-35) of 2018 (Fig. 1). *Vejlerne*, Denmark, (a Birds- and Habitat Directive site protected under the Ramsar convention), contain the largest coherent reed bed of Scandinavia and is protected primarily due to its importance for resting, breeding and feeding wading birds, passerines, geese and ducks on an European scale (Ramsar Convention Secretariat 2013; Nielsen & Clausen 2019b; Ramsar 2020). The area contains approximately 2000 ha of reed bed, and mechanical, commercial reed harvest has taken place during wintertime since 1979. Only a limited part of the reed has been subject to harvest, and different areas has been harvested throughout the years resulting in a mosaic of reed bed with different ages. Three areas with different ages were chosen for the study (Fig. 1): 0-year-old (harvested in 2018), 3-year-old (harvested in 2015), and 25-year-old (harvested in 1993). The 0-year-old reed bed, which has been harvested annually since 2014, had a vegetation dominated by common reed, *Phragmites australis* (Cav.) Trin. Ex Steud, but with patches of forbs requiring open conditions. The 3-year-old reed bed was the most homogenous and consisted mainly of common reed while the 25-year-old reed bed was dominated by common reed, but with significant scrub (*Salix* spp.) growth (for an in-depth analysis of the vegetation see Andersen et al. unpublished). The mean salinity levels were below 0.2 ppt across reed bed stands, and surface water cover did not differ between reed bed ages in May or August.

Sampling design

Terrestrial invertebrates are abundant and highly diverse within wetlands (Batzer & Wu 2020). We used two kinds of traps to target them. Flying invertebrates were sampled using cross vane window traps, also known as flight interception traps, as they are highly efficient and are safe to use in comparisons of diversity and relative abundance between collecting sites as long as the same size interception surface is used (Bouget et al. 2008; Yi et al. 2012; Anderson et al. 2013). Pitfall traps were used to target ground-dwelling invertebrates (Kotze et al. 2011; Anderson et al. 2013). An odorless solution of detergent, salt and water was added to all traps to minimize attraction of insects and ensure preservation of caught invertebrates (Koivula et al. 2003).

Twelve cross vane window traps were placed randomly using QGIS (QGIS Development Team 2016) in each of the three reed beds ages ensuring a minimum distance between traps of 100 m. The traps were modified following Nageleisen and Bouget (2009). Each cross vane window trap consisted of two transparent, perpendicular panels each measuring 50x80 cm. The perpendicular panels were placed on top of a black barrel Ø50 cm. As it was not possible to suspend the trap from the vegetation as is commonly done with cross vane window traps, the black barrel was placed on top of a wooden frame. In the field, the top of the black barrel was approximately 150 cm above ground.

Pitfall traps were placed randomly at 10 dry sites in each reed bed age ensuring a distance of at least 80 m between sites. At each site, we placed five pitfall traps in a straight line with 5 m between individual traps and the five traps are collectively referred to as a pitfall station. The contents of each of these five traps were pooled during the biweekly collections. Because of the high water table in reed beds, pitfall traps were constructed with two plastic cups (Ø8.5 cm), one taller than the other, with concrete filling the gap between them to ensure they would not float away.

Whereas cross vane window traps were emptied every week, pitfall traps were emptied every other week (Duelli et al. 1999). All traps were first emptied in week 27, 2018, and sampling continued until week 35. By week 35, pitfall traps in the 0-year-old reed bed had been flooded and no ground-dwelling invertebrates could be sampled. All collected specimens were stored in 70% ethanol solution at 5°C before subsequent taxonomical sorting in the laboratory.

Biomass estimates

We measured the biomass individually for the cross vane window traps and the pitfall traps. Further, after having estimated the weight of the total pitfall trap content, we searched their content across the sampling period (weeks 26-35 2018) for Coleoptera and estimated their biomass separately. The biomass of the invertebrates in an alcohol-wet state was estimated following a modified method of Hallmann et al. (2017). After ensuring a constant alcohol content 70% for at least 24 hours using a densitometer, the wet invertebrate biomass was obtained by placing the invertebrate content in a sieve (Ø0.2 mm) at 70° angle to allow most of the ethanol to sieve through. Once there was 10 seconds between the drops of ethanol, the invertebrate biomass was weighed. The content of two traps were each measured ten times to estimate the potential measurement error and we found that the final weight fluctuated with less than 2% (1.96%) between measurements.

Data were analysed separately for the biomass of cross vane window traps, pitfall traps and Coleoptera. We build a generalized linear model (GLM) to determine whether biomass differed between areas with different reed bed ages and through time. The influence of repeated measures was accounted by using the trap or trap station as a random factor in a Generalized Linear Mixed Effect Model using the *lme4* package v1.1-21(Bates et al. 2014) for R version 3.5.3. The package *MASS v. 7.3-51.1* (Venables & Ripley 2002) revealed that the lognormal distribution showed the best fit to the data, and log links were therefore specified in the models. We obtained *p*-

values from a Wald test. If significant, least square means were used to determine which reed bed ages that differed significantly from each other (Searle et al. 1980).

Invertebrate community composition

A subset of the biomass was selected for further analysis. We selected the content of cross vane window traps collected in week 31, 2018, and pitfall traps collected in weeks 30-31, 2018, to be sorted to the Order level (Whiting 2014). Additional taxonomic analyses were carried out for Coleoptera specimens caught in the pitfall stations which were sorted to species level according to relevant literature (Lindroth & Bangsholt 1985; Lindroth 1986; Hansen, M. 1987; Holmen 1987; Nilsson & Holmen 1995).

To test whether the relative abundance of the invertebrates reed beds harbored different between reed bed ages, we used a Chi square test followed by a post hoc chi square test with an overall Bonferoni correction following Beasley (1995) to determine which invertebrate Orders were statistically linked to each reed bed age.

A distance based Redundancy Analysis (dbRDA) (Legendre et al. 2012) was conducted in R using the package *vegan v2.5-4* (Oksanen et al. 2017) to assess the relationship between reed bed age and the invertebrate community. We conducted dbRDA's on an Order level for the content of cross vane window traps and pitfall traps as well as on a Family, genus and species level for Coleoptera. Using rank correlations between dissimilarity indices and gradient separation (Faith et al. 1987), we found Bray Curtis to be the best distance measure across invertebrates caught in cross vane window and pitfall traps. Centering and scaling were applied. Following the dbRDA, permutation test with 500 permutations were run to assess the significance of the model, axes and reed bed age (Legendre et al. 2012).

We conducted the statistical analyses (chi-square, dbRDA) separately for the contents of cross vane window traps and pitfall traps (Order and Coleoptera: Family, genus, species level), respectively. Orders/families/genus/species that occurred with a mean abundance of less than 5 individuals across all traps within a given reed bed age were excluded from the dbRDA.

Invertebrate diversity

Based on the abundance data from week 30 at the Order level (cross vane window traps) and weeks 30-31 at the Order level and species (Coleoptera) level (pitfall traps), we calculated the Shannon diversity (Shannon 1948) and evenness using the package *vegan* (Oksanen et al. 2017) for R (R Core Team 2017). We used a Kruskal Wallis test to determine whether the diversity and evenness differed between the reed bed ages.

RESULTS

Biomass

Biomass of flying invertebrates were significantly affected by both reed bed age ($p < 0.001$), sampling week ($p < 0.001$) and the interaction between age and week ($p < 0.001$) (Fig. 2a). The biomass from the flying invertebrate traps was significantly higher across time in the 0-year-old compared to the 3-year-old ($p < 0.001$) and 25-year-old ($p < 0.001$) and higher in the 3-year-old compared to the 25-year-old ($p < 0.001$) (Fig. 2b). The biomass of the pitfall traps were also significantly affected by reed bed age ($p < 0.001$), sampling week ($p < 0.001$) and the interaction between age and sampling week ($p < 0.001$) (Fig. 2c). While the biomass of the 0-year-old was significantly higher across sampling weeks than the biomass of the 3-year-old ($p < 0.001$) and the 25-year-old ($p < 0.001$), no significant difference was found between biomass of the 3-year-old and 25-year-old reed bed ($p > 0.05$). (Fig. 2d).

The biomass of the Coleoptera collected in the fit fall was significantly different between reed bed ages ($p < 0.001$) and there was a significant interaction between reed bed age and sampling time ($p < 0.001$) (Fig. S1). Sampling time in itself had no significant impact on Coleoptera biomass ($p > 0.05$). The Coleoptera biomass was significantly larger in the 0-year-old compared to the 3-year-old ($p < 0.001$) and the 25-year-old ($p < 0.001$) and the biomass in the 3-year-old was significantly larger than that of the 25-year-old ($p < 0.01$).

Invertebrate community composition

A total of 41,712 invertebrates were sorted to the Order level from the cross vane window traps. Nineteen invertebrate Orders were present and ten of them occurred at least five times on average per trap (Fig. S2). The composition of flying invertebrates at the Order level differed significantly between the three reed bed ages ($\chi^2 = 367.2$, df = 36, $p < 0.001$). In the pitfall traps, 82,303 invertebrates were sorted to the Order level. Sixteen Orders were found in the pitfall traps and 11 of them occurred at least five times on average per trap (Fig. S3). The composition at the Order level also differed between the three reed bed ages for the ground-dwelling invertebrates ($\chi^2 = 534.9$, df = 38, $p < 0.001$). A total of 9,000 Coleoptera were determined to the species level. The species composition did not differ between habitats ($\chi^2 = 217.9$, df = 400, $p > 0.05$). Of the 92 species present (full list in table S1), most occurred at a very low abundance and only ten species of Coleoptera remained when excluding species that occurred at an average abundance of less than five individuals per pitfall station per habitat (Fig. S4). The Coleoptera composition of species occurring at least fine times on average per pitfall station differed significantly between reed bed ages ($\chi^2 = 156.9$, df = 18, $p < 0.001$).

The dbRDA was used to plot the multidimensional relationship between the invertebrate Orders collected in the flying traps and the reed bed ages. A significant amount of variation was explained on both axis 1 (permutational ANOVA with 999 permutations, $p < 0.001$) and axis 2 (permutational ANOVA with 999 permutations, $p < 0.05$) (Fig. 3). Habitat also significantly influenced the insect abundance on an Order level (permutational ANOVA, 500 permutations, $p < 0.001$). In total, the constrained RDA explained 19.18% of the variance in the data. Of the variation explained, the constrained RDA explained 73.3% on axis 1 and 26.7% on axis 2 (Fig. 3).

Hymenoptera was positively correlated with the 0-year-old reed bed (Table S2). Brachycera (suborder within Diptera) was negatively correlated with the 0-year-old and positively correlated with the 3-year-old and Coleoptera correlated negatively with the 0-year-old and positively with the 3-year-old and 25-year-old reed bed (Table S2). More order specific responses can be seen in figures S2 and tables S2.

The dbRDA found the ground-dwelling invertebrates at the Order level differed significantly between the reed bed ages (permutation test with 999 permutations, $p < 0.001$) (Fig. 4). Both axis 1 (permutational ANOVA, $p < 0.001$) and axis 2 (permutational ANOVA $p < 0.01$) were significant. The constrained dbRDA explains 26.38% of the variation in the data. The constrained dbRDA explained 74.85% on axis 1 and 25.15% on axis 2.

Aranea correlated negatively with the 0-year-old reed bed but positively with the 3-year-old and 25-year-old reed beds (Table S2). Both Collembola and Opiliones correlated negatively with the 0-year-old reed bed, and Opiliones correlated positively with the 25-year-old reed bed. More order specific responses can be seen in figures S3 and tables S2.

The constrained dbRDA for Coleoptera at the family level explained $R^2 = 39.35\%$ of the variation in Coleoptera abundance (Fig. 5). Both axis 1 ($p < 0.001$) and axis 2 ($p < 0.01$) were significant and explained 70.20% and 29.80% of the variation, respectively. The three red bed ages had significantly different Coleoptera communities at the family level ($p < 0.001$). At the genus level, the dbRDA explained 36.95% of the variation in the data (Fig. S5). Both axis 1 ($p < 0.001$) and axis 2 ($p < 0.01$) were significant with 77.10% explained on axis 1 and 22.90% explained on axis 2. At the species level, the dbRDA explained 36.15% of the variation in the data (Fig. S6). Both axis 1 ($p < 0.001$) and axis 2 ($p < 0.01$) were significant with 77.05% explained on axis 1 and 22.95% explained on axis 2. As the family-level analysis had the highest R^2, Family specific responses can be found in figure S4 and table S3.

Invertebrate diversity

For the flying invertebrates, the Shannon diversity did not differ between reed bed ages (Kruskal Wallis, $p = 0.33$) (Fig. 6a) whereas a significant difference was found in the Shannon diversity of the ground-dwelling invertebrates ($p < 0.05$) (Fig. 6b). Post hoc testing showed that the Shannon diversity was significantly lower in the 0-year-old compared to the 25-year-old reed bed (Dunn with Bonferroni correction, K = 3, $p < 0.05$). For the Coleopterans (Fig. 6c), the Shannon diversity differed significantly between the three reed bed ages (Kruskal Wallis, $p < 0.05$). A post hoc test showed that the 25 year old reed bed had a significantly higher Shannon diversity than the 3 year old (Dunn with Bonferroni correction, K = 3, $p = 0.021$). Results were similar if the Shannon diversity was calculated using Family level data rather than species level data (Fig. S7)

For the cross vane window trap content, evenness differed significantly between reed ages (Kruskal Wallis, $p < 0.01$) and was significantly higher in the 25-year-old compared to the 0-year-old (post hoc Dunn with sequential Bonferroni correction, $p < 0.05$) and marginally insignificantly higher than the 3-year-old old (post hoc Dunn with sequential Bonferroni correction, $p < 0.054$) (Fig. S8a). Evenness also differed significantly for the pitfall trap content at Order level (Fig. S8b) (Kruskal Wallis, $p < 0.001$). The evenness was higher in the 3-year-old than the 0-year-old ($p < 0.001$) and almost higher than the 25-year-old ($p < 0.07$) while also almost being significantly higher in the 25-year-old compared to the 0-year-old (post hoc Dunn with sequential Bonferroni correction, K = 3, $p < 0.051$). Evenness did not differ between ages for the Coleoptera ($p > 0.05$) (Fig. S8c).

Two species of Coleoptera found in the reed beds were listed on the Danish Red list as near threatened: *Carabus clathratus* and *Dytiscus circumcinctus*. *D. circumcinctus* was only recorded once in the 25-year-old reed bed whereas *C. clathratus* was more abundant in the 0-year-old and 3-year-old compared to the 25-year-old (Fig. S9).

DISCUSSION

Reed bed age affected not only invertebrate biomass but also community composition. Contrary to former results indicating that reed management decrease or have no impact on invertebrate abundance (Ditlhogo et al. 1992; Schmidt et al. 2005), we found that the biomass of invertebrates decreased with time since last harvest. This was the case for both the biomass of aerial invertebrates, ground-dwelling invertebrates and Coleoptera, that all peaked in the 0-year-old reed bed. Our results are in agreement with results from wetlands dominated by monocultures of cattail *Typha* spp., where removal of biomass through mowing or burning increased the abundance of invertebrates (Ball & Nudds 1989). The response to harvest is likely scale dependent and our results support previous results that harvest of a small fraction of a reed bed benefit invertebrate abundance (Burgess & Evans 1989; Trnka et al. 2014) as oppose to large scale harvest (Schmidt et al. 2005). As invertebrate populations are experiencing a global scale decline (Hallmann et al. 2017; Møller 2019; Powney et al. 2019; van Klink et al. 2020; Arzel et al. 2020) with implications for the invertebrate diversity (Forister et al. 2019; Wagner 2020) and for insectivorous species (Møller 2019), it is important to consider management strategies that maintain a high invertebrate biomass. However, we found that even though biomass for ground-dwelling invertebrates was lowest in the 25-year-old reed bed, it had the highest Shannon diversity, showing that a high biomass is no guarantee for a high diversity. Further, the invertebrate biomass in Vejlerne fluctuated throughout the season, in agreement with previous findings (Bibby & Thomas 1985; Ball & Nudds 1989; Bedford & Powell 2005), and the effect of reed bed age therefore differs depending on time of the season.

We detected an effect of reed bed age on the invertebrate community already at the Order level. For example, Hymenoptera, which has previously been found to be more abundant in cut as oppose to unmanaged reed beds (Trnka et al. 2014), was associated with the 0-year-old reed bed, which could be explained by Hymenoptera's overall resilience to disturbance (Christie & Hochuli 2009; Arthur 2017). Brachycera (Diptera) was associated with the 3-year-old and Hemiptera with the 25-year-old. Hemiptera are mostly herbivorous and have diverse trophic requirements making them sensitive to changes in habitat structure and floral composition (Moir & Brennan 2007), which might explain why their relative abundance peaked in the undisturbed 25-year-old reed bed. Opiliones are omnivores that are sensitive to disturbance (Stašiov et al. 2020), potentially explaining why they were positively associated with the 25-year-old reed bed.

The response to reed winter harvest and reed bed age was highly family dependent, at least for Coleoptera. Data at the family level showed that while some families responded negatively to recent harvest, one (Silphidae, large carrion beetles) did not respond at all, and some even increased in abundance. Data at the genus or species level did not increase the models ability to distinguish between reed bed ages. We found that staphylinid beetle abundance was positively impacted by reed harvest and decreased with reed bed age, whereas winter harvest impact the staphylinid beetle abundance negatively compared to alternative management methods summer harvest and grazing (Hoffmann et al. 2016). Leiodiae, which we found to be positively correlated with the 25-year-old reed bed, consists of species feeding on fungus or decaying materials (Leschen 1999), and as the litter layer is thicker in old reed beds (Cowie et al. 1992) this could explain why Leiodiae was especially abundant in the oldest reed bed. The relative abundance of Carabidae was low in the 0-year-old harvested and high in the 3-year-old. Other studies have found reed winter harvest to have a beneficial impact on Carabids when compared to other management methods (Görn et al. 2014), but we found that when comparing to unmanaged stands, the effect of winter harvest was actually negative. Reed bed stripping, a management method that opens up the reed bed and slows down succession, resulted in distinctly different water beetle assemblages across areas with varying time since last stripping (Knoblauch & Gander 2020), in agreement with our findings that Hydrophilidae, the water scavenger beetles, had a high relative abundance in the 0-year-old harvested.

Data at the species level added one significant finding, namely that the red listed species *Carabus clathratus* (Wind & Pihl 2010) was most abundant in the 0-year-old and 3-year-old reed bed and rarely occurred in the 25-year-old reed bed. *C. clathratus* prefer living in wet habitats, and even hunt under water (Lindroth & Bangsholt 1985). Its low abundance in the old successional 25-year-old reed bed could be explained by years of accumulated litter making the habitat drier. Therefore, *C. clathratus* is an example of a species that would likely decline in abundance if harvest stopped and natural succession took its course.

As it requires time and expertise to identify invertebrate specimens to species level, it is highly relevant for managers to know which taxonomic level that provide sufficient information in order to detect the effect of management actions. Order level data is sometimes sufficient to indicate how various environmental factors affect the invertebrate community (Hewlett 2000; Caruso & Migliorini 2006; Schipper et al. 2010). We found that regardless of taxonomic levels, the Shannon diversity of ground-dwelling invertebrates peaked in the old reed bed, whereas Order level data for flying invertebrates were not sufficient to show a potential difference in the Shannon diversity between ages. Data at the Order level were, however, sufficient to determine that the invertebrate communities differed between reed bed ages. Data at a finer taxonomic level sometimes provide valuable information compared to coarse taxonomic data (Verdonschot 2006; Smith et al. 2007). Several studies have found the effect of reed management on invertebrates to be family specific (Decleer 1990; Ditlhogo et al. 1992). The taxonomically well-resolved Coleopetera data support the idea that family specific responses can occur. We showed that even though Coleoptera biomass decreased with reed bed age (Fig. S1), the relative abundance of Coleoptera compared to other Orders actually increased with reed bed age (Table S2). In conclusion, data at the Order level was sufficient to determine overall trends in species composition, but data at the family level was necessary to ensure that the effect on the diversity was discovered. While data on the species level provided information on rare species, it did no

Overall, our results show that commercial reed harvest at a small scale is compatible with sustaining invertebrate communities. Small-scale commercial harvest is compatible with ensuring a high invertebrate biomass, thereby creating a food supply for insectivorous birds, including multiple warblers of conservation interest (Hawke & José 1996; Schmidt et al. 2005). However, harvest decreased the Shannon diversity changed the invertebrate community and the relative abundance of invertebrate Orders and Coleoptera families across reed bed ages. By ensuring reed beds of multiple reed bed ages, managers can maintain a higher diversity at the landscape level, even though species diversity and evenness increased with time since last harvest. The period of time an area is left unmanaged also impact the invertebrate community, and though only few Orders and Coleoptera families mainly correlated positively with the 3-year-old reed bed, it had an invertebrate community significantly different from both the 0-year-old and 25-year-old reed bed. We therefore suggest that while the majority of reed patches should remain unmanaged, other parts can be harvested at a rotational scheme allowing a mosaic pattern of reed ages to be present.

Author contributions statement

LHA, KT, CP, DB and SB came up with the idea for the study. LHA, JR, CMSF and MPK collected the data in the field. JR identified all Coleoptera specimens to species level. LHA identified invertebrates at the order level and did the biomass estimates. LHA wrote a first draft of the manuscript in collaboration with SB. All authors commented on the results and the manuscript prior to submission.

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Figure 1. Map of the reed bed area in *De Østlige Vejler*.

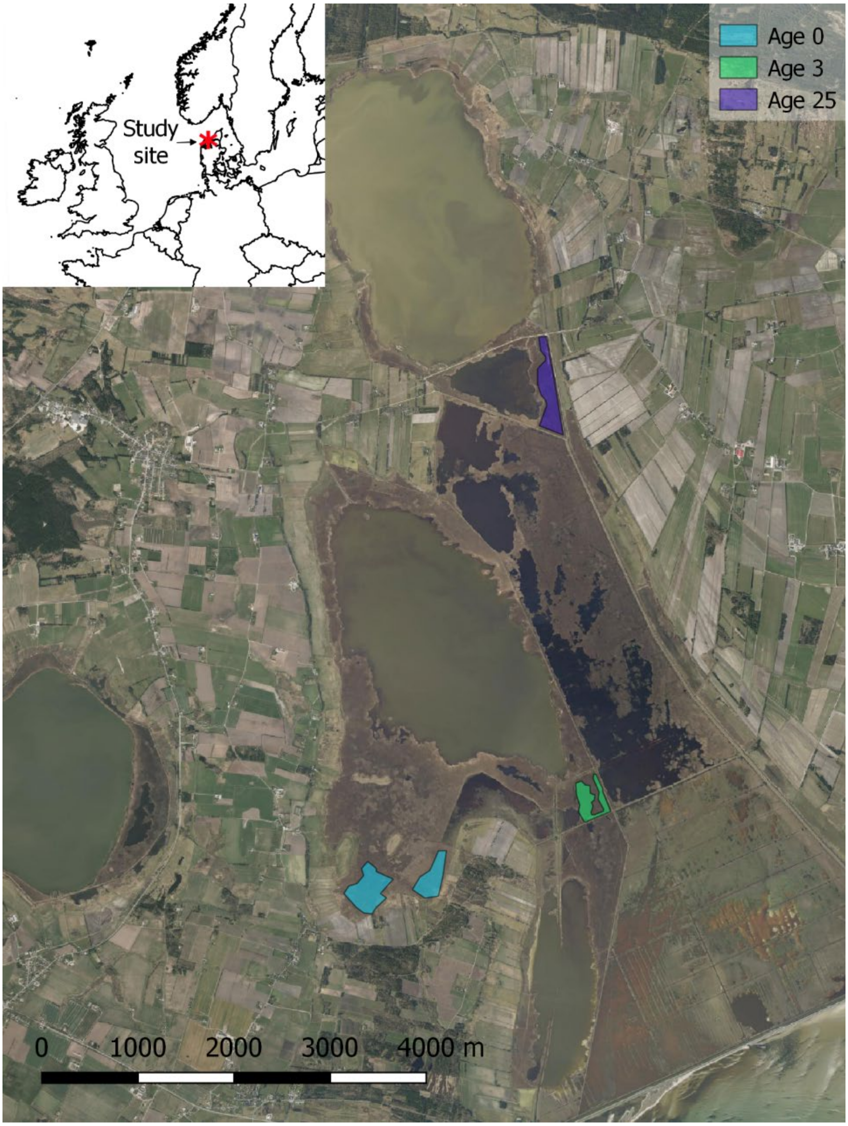


Figure 2. The biomass of the invertebrates captured in the cross vane window traps (a, b) and in the pitfall stations (c, d). While a and c show the biomass on a weekly basis, b and d depict the average weekly biomass. Boxes represent 25th and 75th percentiles, whiskers extend to the smallest/largest value within 1.5 times the interquartile range. Dots are outliers (more than 1.5 times beyond either interquartile range).

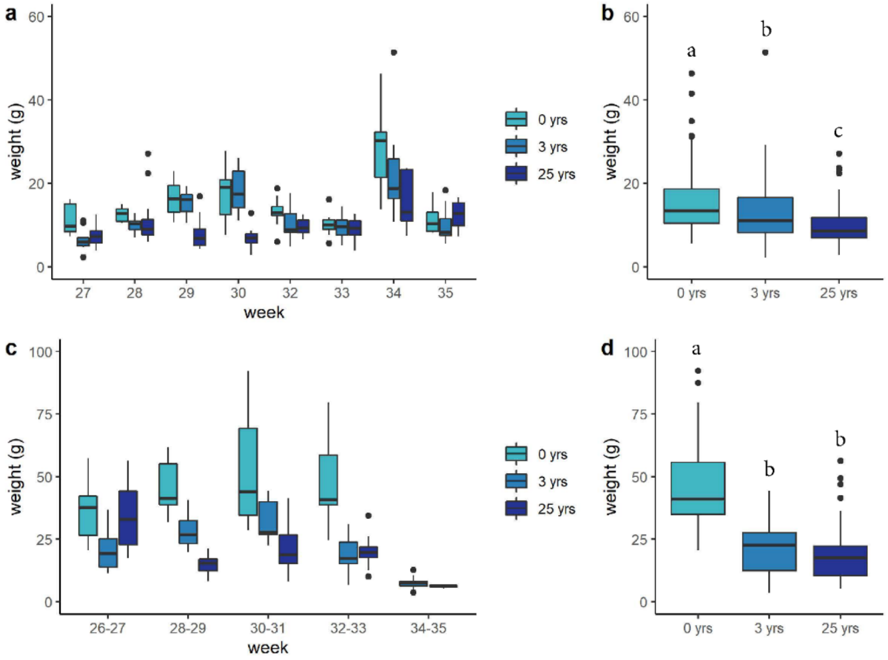


Figure 3. Distance based Redundancy Analysis of flying invertebrate abundance at the Order level for the three reed bed ages ($R^2 = 0.19$). The polygons represent the outer position of plots for each reed bed age with the reed bed age positioned as the centroid. Invertebrate orders occurring with a minimum of 5 individuals/trap in at least one reed bed age were included.

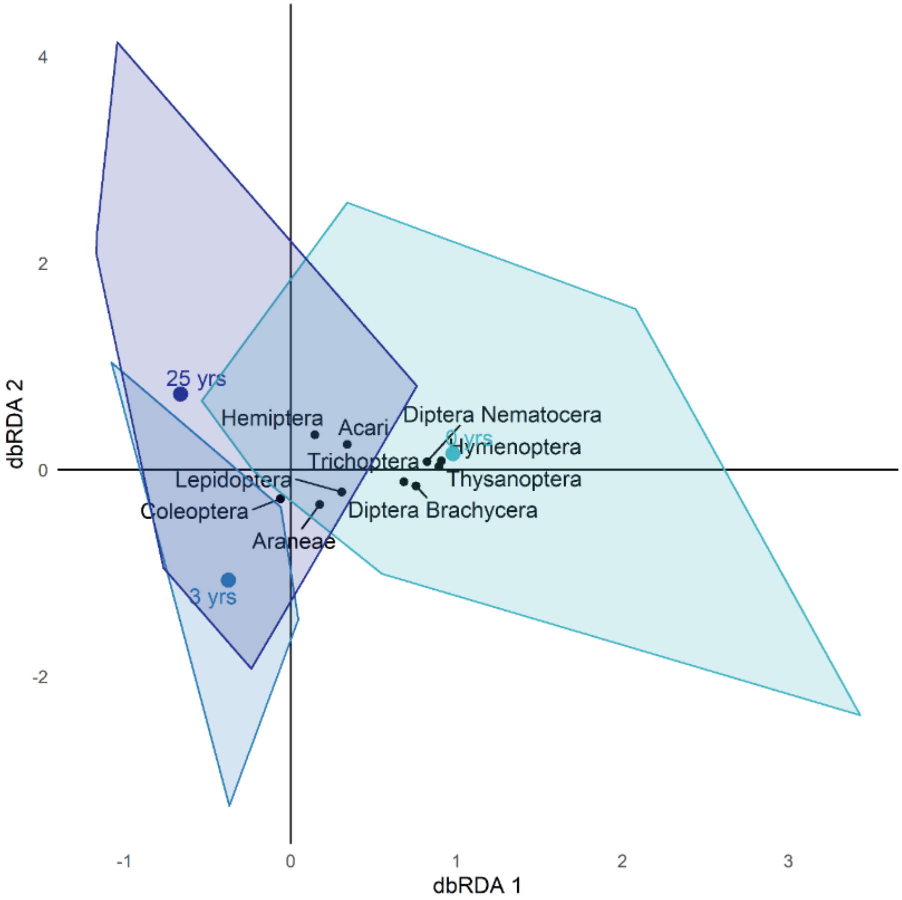


Figure 4. Distance based Redundancy Analysis of ground-dwelling invertebrate abundance at the Order level for the three reed bed ages ($R^2 = 0.26$). The polygons represent the outer position of plots for each reed bed age with the reed bed age positioned as the centroid. Invertebrate orders occurring with a minimum of 5 individuals/pitfall station in at least one reed bed age were included.

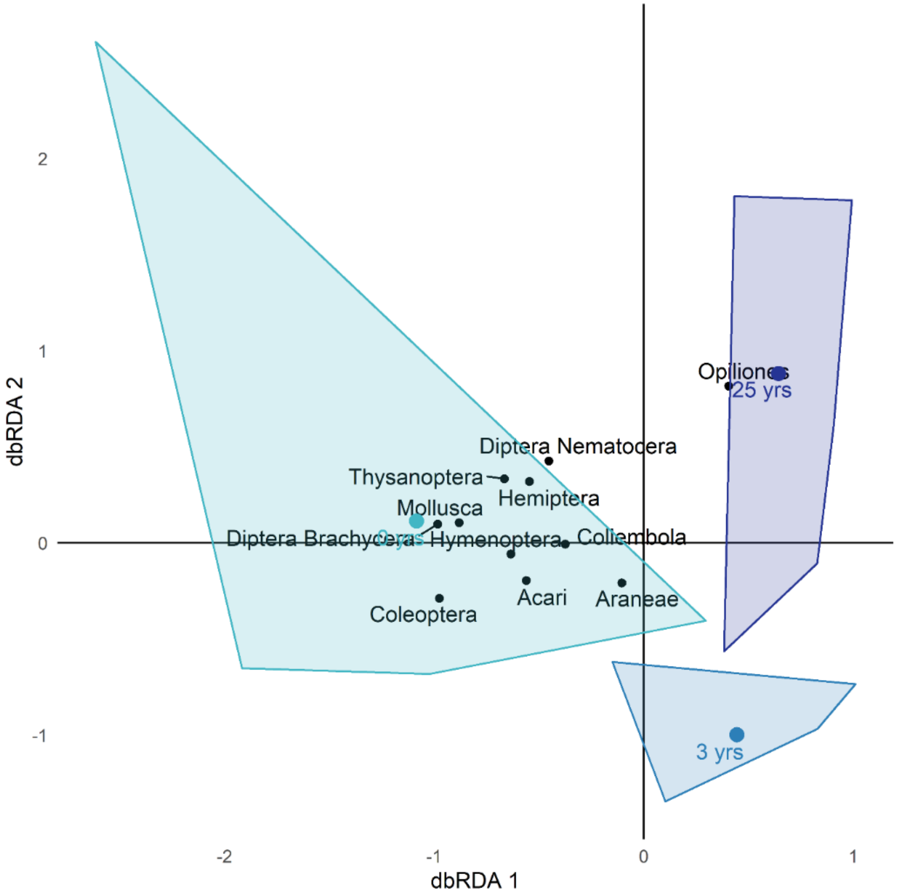


Figure 5. dbRDA for Coleoptera on a family level for families that had a minimum mean abundance/pitfall station of 5 individuals in at least one reed bed age ($R^2 = 0.39$). The polygons represent the outer position of plots for each reed bed age with the reed bed age positioned as the centroid. Coleoptera families occurring with a minimum of 5 individuals/pitfall station in at least one reed bed age were included.

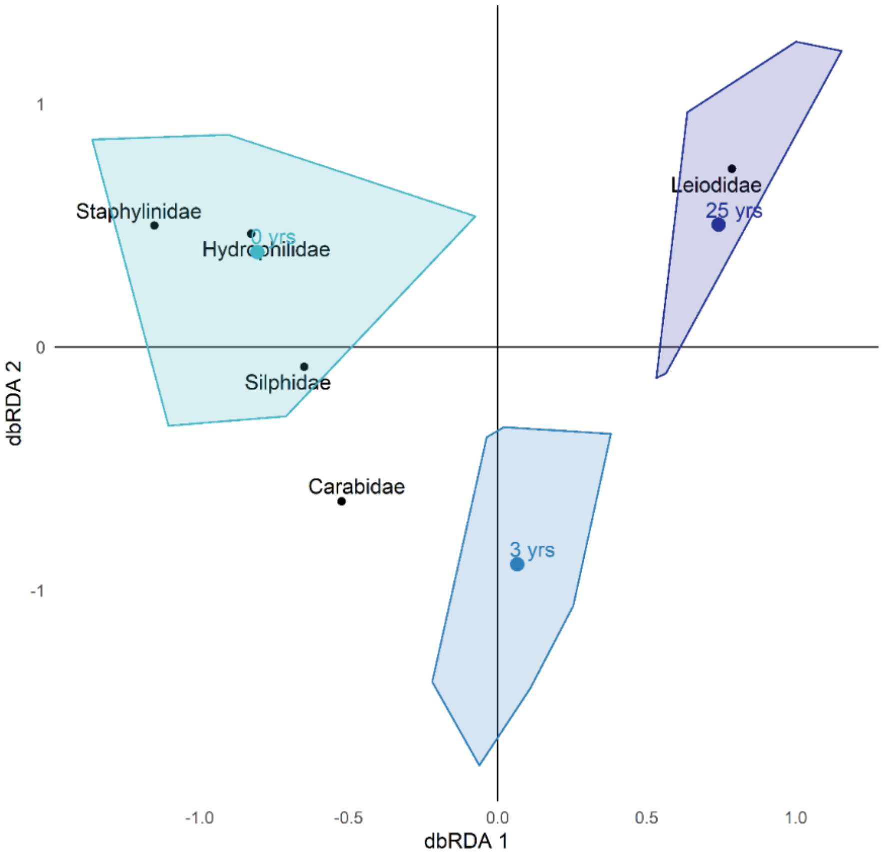
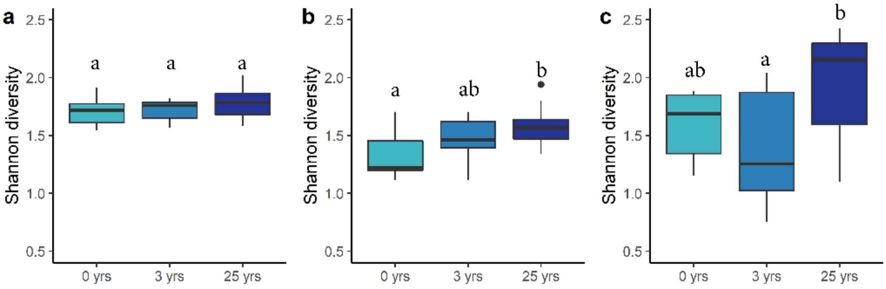


Figure 6. The Shannon diversity at the Order level of the invertebrate community collected in the cross vane window traps (a) and pitfall traps (b) and on the species level for Coleopterans collected in pitfall traps (c). Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers (more than 1.5 times beyond either interquartile range).



SUPPORTING INFORMATION FOR PAPER IV

Figure S1. Coleoptera biomass

Figure S2: Abundance, Order level, cross vane window trap

Figure S3: Abundance, Order level, pitfall trap

Figure S4: Abundance, Family level, Coleoptera

Figure S5: dbRDA Coleoptera, genus level

Figure S6: dbRDA Coleoptera, species level

Figure S7: Shannon diversity, Coleoptera family level

Figure S8: Evenness

Figure S9: *Carabus clathratus* abundance

Table S1: Coleoptera species list

Table S2: Post hoc chi square, Order level

Table S3: Post hoc chi square, Family level: Coleoptera

Figure S1. Coleoptera biomass from the pitfall traps across time during weeks 26-35, 2018 (a) and averaged across time (b).

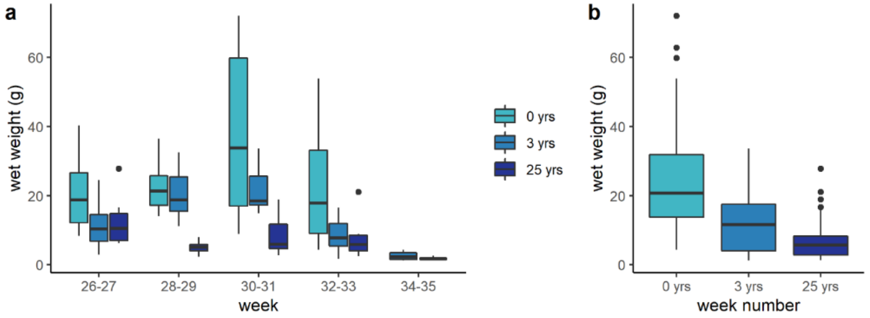


Figure S2. Invertebrate abundance from the cross vane window traps listed for each reed bed age. Each box represent the median abundance based on the content of 12 traps. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers.

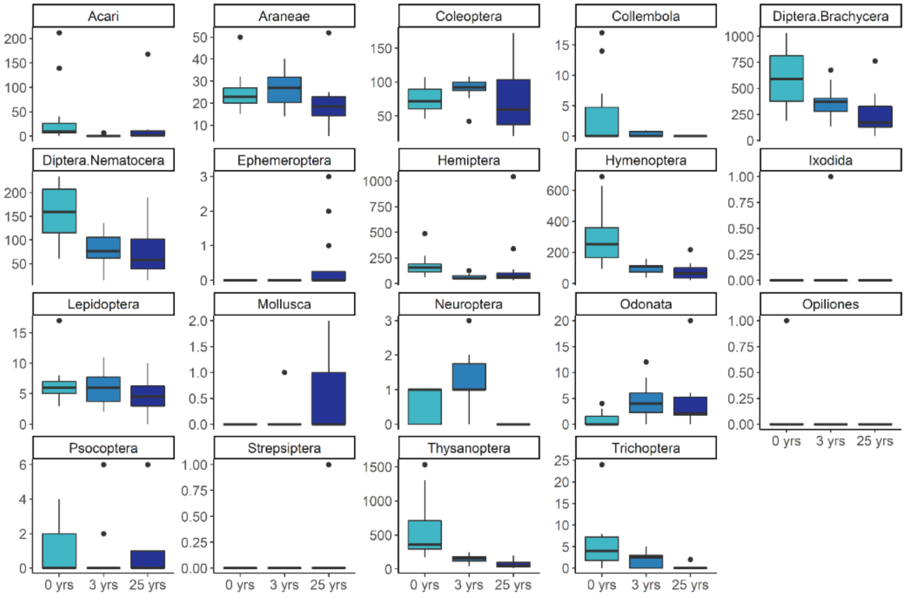


Figure S3. Invertebrate abundance from the pit fall traps at the Order level. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers.

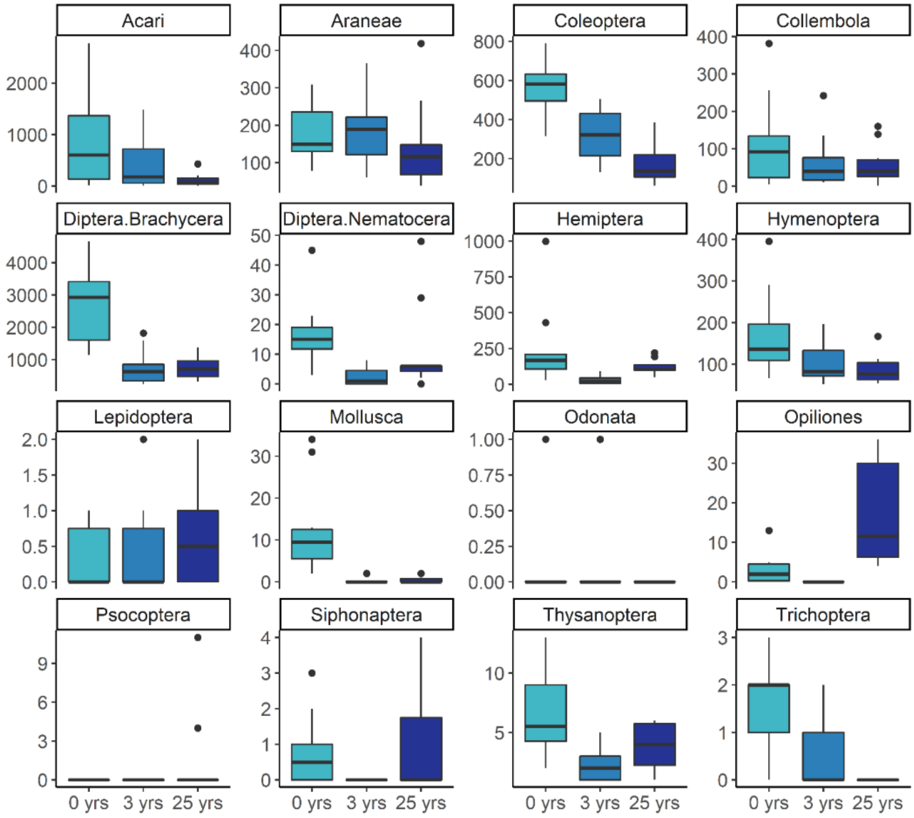


Figure S4. Coleoptera Family level abundance from pit fall traps. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers.

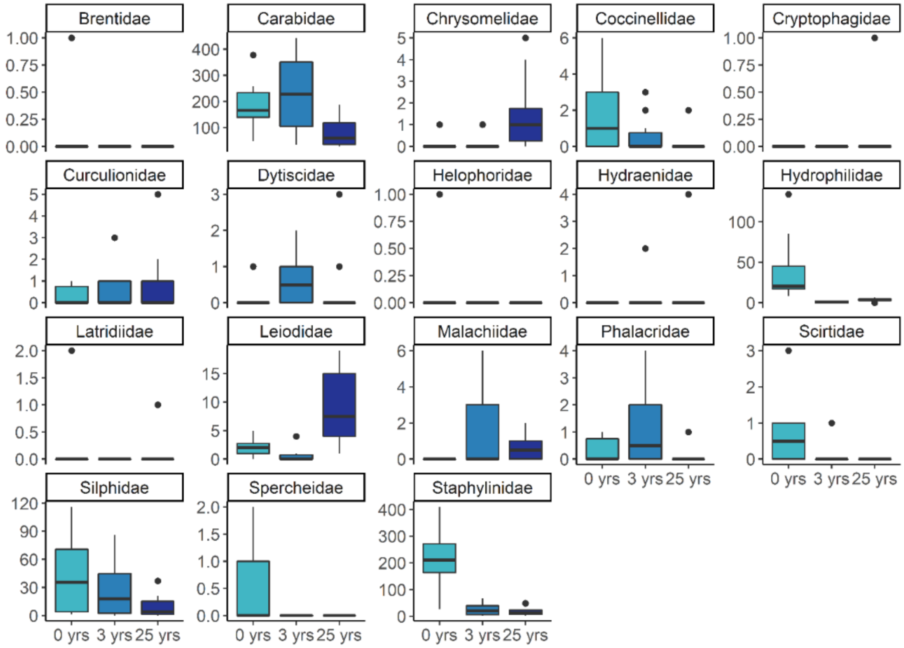


Figure S5. Genus level separation of Coleoptera. $R^2 = 0.3695$, dbRDA1 significant ($p < 0.001$), dbRDA2 significant ($p < 0.001$), habitat significant ($p < 0.001$).

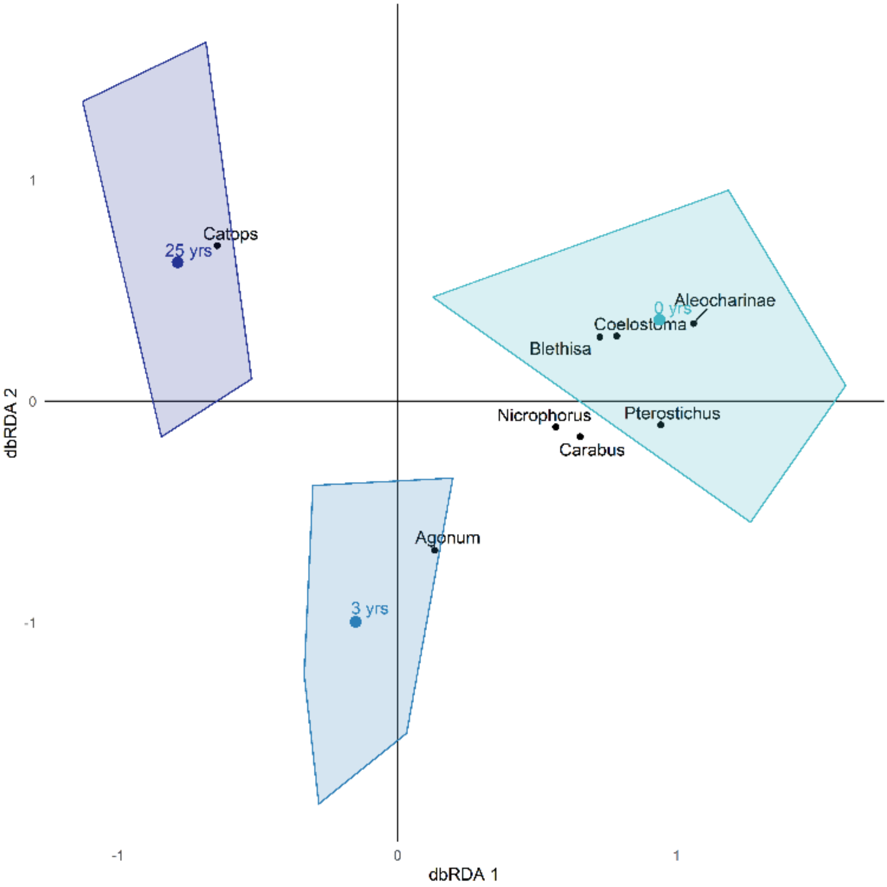


Figure S6. Species level separation of Coleoptera in the three reed bed ages 0, 3 and 25 years. Only species occurring with a minimum of 5 species per trap per habitat were included in the analysis. $R^2 = 0.3615$, RDA1 significant ($p < 0.001$), RDA2 significant ($p < 0.002$), habitat significant ($p < 0.001$).

Figure S7. The Shannon diversity calculated using Coleoptera data at the family level. The Shannon diversity differed significantly between reed bed ages (Kruskal Wallis, *p* < 0.01).

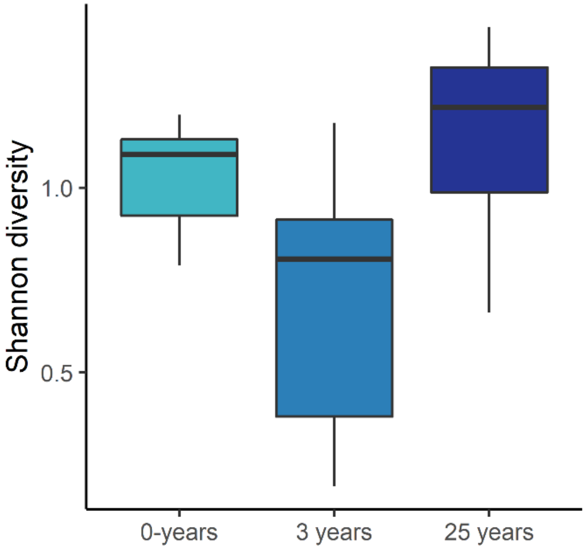


Figure S8. Evenness at the Order level for the content of cross vane window traps (a) and pit fall traps (b) and at the species level for Coleoptera (c). Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers. For the cross vane window trap content, evenness differed significantly between reed ages (Kruskal Wallis, $p < 0.01$) and was significantly higher in the 25-year-old compared to the 0-year-old (post hoc Dunn with sequential Bonferonni correction, $p < 0.05$) and marginally insignificantly higher than the 3-year-old old (post hoc Dunn with sequential Bonferonni correction, $p < 0.054$). Evenness also differed significantly for the pit fall trap content at Order level (b) (Kurskal Wallis, $p < 0.001$). The evenness was higher in the 3-year-old than the 0-year-old ($p < 0.001$) and 25-year-old ($p < 0.07$) while almost being significanlt higher in the 25-year-old compared to the 0-year-old (post hoc Dunn with sequential Bonferonni correction, $p < 0.051$). Evenness did not differ between ages for the Coleoptera (c) ($p > 0.05$).

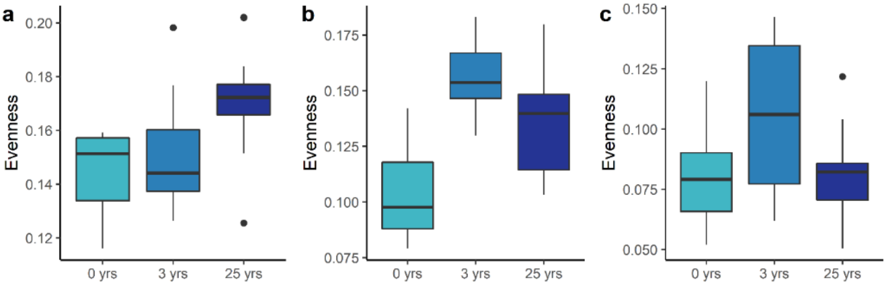


Figure S9. Mean abundance per pitfall station of near threatened *Carabus clathratus* within the three reed bed ages. There is a significant difference in the abundance between reed bed ages (Kruskal Wallis, $p < 0.05$). A subsequent Dunn test found that the 0-year-old ($p <0.001$) and the 3-year-old ($p < 0.01$) both had a significantly higher abundance of *C. clathratus* than the 25-year-old reed bed.

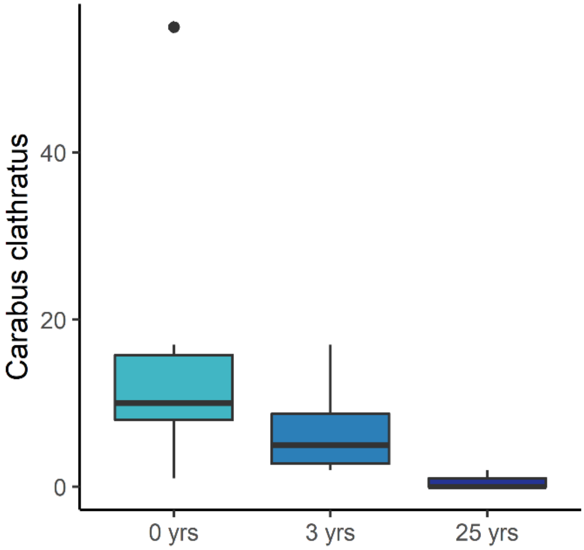


Table S1. List of Coleoptera species found in the pitfall traps of weeks 30-31 2018 across habitats.

Agabus sturmii

Agonum emarginatum

Agonum thoreyi

Agonum viduum

Aleocharinae sp

Altica oleracea

Amara apricaria

Amara lucida

Anacaena limbata

Anisosticta novemdecimpunctata

Anotylus rugosus

Anthocomus rufus

Aphthona nonstriata

Apion viciae

Arpedium brachypterum

Atomaria atricapilla

Bagous glabrirostris

Bembidion fumigatum

Blethisa multipunctata

Calathus micropterus

Carabus clathratus

Carabus granulatus

Cassida flaveola

Catops morio

Cercyon tristis

Cercyon ustulatus

Chaetocnema concinna

Coccidula rufa

Coccinella septempunctata

Coccinella undecimpunctata

Coelostoma orbiculare

Colymbetes paykulli

Cryptorhynchus lapathi

Cymbiodyta marginella

Cyphon padi

Cyphon variabilis

Dytiscus circumcinctus

Dytiscus marginalis

Elaphrus cupreus

Enicmus transversus/histrio

Enochrus affinis

Enochrus testaceus

Galerucella nymphaeae

Helophorus brevipalpis

Hydraena palustris

Hydrobius fuscipes

Hydroporus angustatus

Ilybius quadriguttatus

Laccobius biguttatus

Loricera pilicornis

Nicrophorus vespillo

Nicrophorus vespilloides

Notaris scirpi

Ochthebius minimus

Odacantha melanura

Olophrum fuscum

Olophrum piceum

Oulema melanopus

Paederus riparius

Pelenomus quadrituberculatus

Phaedon armoraciae

Phalacrus corruscus

Philonthus binotatus

Philonthus cruentatus

Philonthus fumarius

Philonthus laminatus

Philonthus politus

Philonthus quisquiliarius

Phyllobrotica quadrimaculata

Phyllotreta exclamationis

Poecilus cupreus

Propylea quatuordecimpunctata

Psyllobora vigintiduopunctata

Pterostichus melanarius

Pterostichus niger

Pterostichus nigrita

Rhinoncus inconspectus

Silpha tristis

Sitona lineatus

Spercheus emarginatus

Stenus cicindeloides

Stenus juno

Stenus palustris

Stephostethus lardarius

Stilbus oblongus

Tachinus marginellus

Tachinus rufipes

Tachyporus dispar

Tanysphyrus lemnae

Tetartopeus terminatus

Thanatophilus rugosus

Thanatophilus sinuatus

Table S2. Post-hoc chi square test with Bonferroni correction following Beasley (1995) on the relationship between each reed bed age and invertebrate Order. Response shows whether the correlation between the reed bed age and invertebrate Order was positive (+) or negative (-).

		Pitfall			Cross vane window		
Order		0	3	25	0	3	25
Lepidoptera	*p*-value	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
	Response	NA	NA	NA	NA	NA	NA
Hymenoptera	*p*-value	< 0.001	>0.05	>0.05	<0.01	>0.05	>0.05
	Response	+	NA	NA	+	NA	NA
Diptera Brachycera	*p*-value	< 0.001	< 0.001	>0.05	<0.001	<0.001	>0.05
	Response	-	+	NA	-	+	NA
Diptera Nematocera	*p*-value	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
	Response	NA	NA	NA	NA	NA	NA
Hemiptera	*p*-value	>0.05	< 0.001	< 0.001	<0.001	<0.001	>0.05
	Response	NA	-	+	-	-	NA
Thysanoptera	*p*-value	>0.05	>0.05	>0.05	<0.001	<0.001	<0.001
	Response	NA	NA	NA	+	-	-
Coleoptera	*p*-value	<0.01	<0.001	>0.05	<0.001	<0.001	<0.01
	Response	-	+	NA	-	+	+
Aranea	*p*-value	<0.001	<0.001	<0.001	<0.05	>0.05	>0.05
	Response	-	+	+	-	NA	NA
Odonata	*p*-value	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
	Response	NA	NA	NA	NA	NA	NA
Acari	*p*-value	>0.05	<0.001	<0.001	>0.05	<0.01	>0.05
	Response	NA	+	-	NA	-	NA

Trichoptera	*p*-value	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
	Response	NA	NA	NA	NA	NA	NA
Psocoptera	*p*-value	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
	Response	NA	NA	NA	NA	NA	NA
Mollusca	*p*-value	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
	Response	NA	NA	NA	NA	NA	NA
Opiliones	*p*-value	<0.01	>0.5	<0.001	>0.05	>0.05	>0.05
	Response	-	NA	+	NA	NA	NA
Collembola	*p*-value	<0.05	>0.05	>0.05	>0.05	>0.05	>0.05
	Response	-	NA	NA	NA	NA	NA
Ephemeroptera	*p*-value	NA	NA	NA	>0.05	>0.05	>0.05
	Response	NA	NA	NA	NA	NA	NA
Strepsiptera	*p*-value	NA	NA	NA	>0.05	>0.05	>0.05
	Response	NA	NA	NA	NA	NA	NA

Table S3. Post-hoc chi square test with Bonferroni correction following Beasley (1995) on the relationship between each reed bed age and Coleoptera family level. Response shows whether the correlation between the reed bed age and Coleoptera family was positive (+) or negative (-).

Order		0	3	25
Carabidae	*p*-value	<0.001	<0.001	>0.05
	Response	-	+	+
Hydrophilidae	*p*-value	<0.001	<0.001	>0.05
	Response	+	-	-
Leiodidae	*p*-value	>0.05	>0.05	<0.001
	Response	-	-	+
Silphidae	*p*-value	>0.05	>0.05	>0.05
	Response	-	+	-
Staphylinidae	*p*-value	<0.001	<0.001	<0.01
	Response	+	-	-

APPENDICES

Appendix A: A list of papers co-authored during the Ph.D., published or in review, but not part of the Ph.D. thesis

Appendix A. List of papers co-authored during the Ph.D., published or in review, but not part of Ph.D. thesis

Peer reviewed, English:

Andersen, L. H., Pellegrino, I., Sunde, P., Loeschcke, L. and Pertoldi, C. 2017. Integrating population viability analysis, genomics and spatial data using the European population of Little Owl *Athene noctua* as a model species. Ecology and Evolution, 7: 10987-11001.

Pertoldi, C., Schmidt, J. B., Thomsen, P. M., Nielsen, L. B., Elmeros, M., Muro, F., Iacolina, L., Nielsen, J. L., Trøjelsgaard, K., Lauridsen, T. L., **Andersen, L. H.**, Lukassen, M. B., Dan Bruhn. Comparing DNA meta-barcoding with faecal analysis for diet determination of the Eurasian otter (*Lutra lutra*) in Vejlerne, Denmark. Submitted at Mammal Research.

Peer-reviewed, Danish:

Andersen, L. H. 2018. Tilbagegang og øget isolation i den danske kirkeuglebestand (*Athene noctua*) 2009-2016. Flora og Fauna, 124 (1+2): 22-29.

Popular scientific communications:

Alstrup, A.K.O., Pertoldi, C. and **Andersen, L.H.** 2018. Kirkeuglen: Sidste udkald hvis kirkeuglens tilbagegang i Danmark skal vendes. Habitat, 17: 54-61.

Lauridsen, T. L., Jeppesen, E., Søndergaard, M., Fox, A., Clausen, P., Balsby, T., Bruhn, D., **Andersen, L. H.**, Pertoldi, C., Bahrndorff, S., Trøjelsgaard, K., Nielsen, H. H. 2018. Optimeret forvaltning af De Østlige Vejler. Vand og Jord, 25:66-69.

Dataset

Andersen, L.H., Skærbæk, A.S.K., Sørensen, T.B., Knudsen, J.S., Pertoldi, C., Bahrndorff, S. and Bruhn, D. 2020. Dataset accompanying Andersen et al. 2020 Journal of Vegetation Science [Dataset]. http://doi.org/10.5281/zenodo.3608523

SUMMARY

Across the globe, the biodiversity is declining and habitats are deteriorating. Coastal wetlands are no exception, and face multiple threats including land reclamation, eutrophication and diking, while they are also likely to be affected by climate change.

This thesis investigates anthropogenic effects on coastal wetlands with focus on the salt marsh and reed bed habitats. The work is centered on De Østlige Vejler, Denmark, which is a protected area comprising lakes, salt marsh and reed beds. Here, I first examine the vegetation of the salt marsh and its response to anthropogenic disturbances. I investigate the effects of a century long tidal flood exclusion due to a dike, as well as the response of the salt marsh vegetation to interannual weather fluctuations. Second, I explored how plants and invertebrates in the reed bed response to reed bed management. I look into the effects of reed winter harvest, reed cutting and time since last harvest.

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