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Hydrology and dune slack habitat: in-depth assessment of the relationship between hydrological regime and plant communities

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Hydrology and dune slack habitat:

in-depth assessment of the relationship between hydrological regime and plant communities

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Declaration and consent

‘I hereby declare that this thesis is the result of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

I confirm that I am submitting this work with the agreement of my supervisor(s)’.

‘Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw’r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o’r blaen ar gyfer unrhyw radd, acnid yw’n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

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The following research papers have been produced from this body of work and have been published, or submitted for publication, in a peer-reviewed journal:

All data chapters, with the exception of the literature review in this thesis, have been written and prepared as publications for peer-reviewed scientific journals, currently awaiting submission.

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Summary

To safeguard dune wetlands and to provide sustainable management practices into the future, there is a critical need to increase our knowledge around the factors which regulate dune slack plant communities, and to design science-led interventions to protect these high conservation habitats from current and emerging threats. The primary aim of this thesis was to explore the spatial and temporal dynamics of the hydrology regime and its associated dune slack plant communities at Newborough Warren, in an effort to improve our fundamental understanding of dune ecosystem functioning and to contribute to the formulation of improved dune slack management and conservation practices. By integrating field monitoring, statistical analysis and numerical modelling, this thesis sets out to gain a better understanding of the relationship between dune slack vegetation and underlying hydrological regime. First, our study confirmed the potential of using 3D-hydrological modelling to run and evaluate scenarios of forest management which may affect groundwater levels within the dune system. The hydrological model allowed for successful predictions of management interventions, and therefore, shows how model and field monitoring can be combined to predict the impact of current and future management interventions. Secondly, this thesis highlights the role of hydrology as a driver of dune slack vegetation change. We analysed the relationships between vegetation and hydrology metrics, with the intention of their utilisation for management and conservation. The 5-year average mean spring level (MSL) was the metric which best explained and predicted overall dune slack plant community responses to hydrological regime. We conclude that vascular plant dune slack community responses can be predicted with a range of hydrology metrics and that these can provide a valuable management tool to monitor and interpret observed changes. Further, we revealed that species composition significantly moderated the relationship between hydrology and vegetation response within groups of dune slack communities. This moderating effect was evident for both vascular plant and bryophyte communities, with different multi-year metrics for bryophytes (8-year average rather than 5-year average for vascular plants), highlighting the importance of accounting for species assemblages in statistical analyses of vegetation response in dune wetlands. This finding highlights that ideally dune slack vegetation should not be treated as a homogeneous entity in terms of hydrological responses, and it enables a more refined understanding of the dune slack hydrology-vegetation linkages. And lastly, this thesis also addresses important questions regarding dune slack vegetation response and the effect of the inter-annual dynamics, as well as moderating factors such as soil organic matter

content which influences the responses of dry dune slack communities to hydrological change. As a result, we now have a better understanding of the short- and medium-term dynamics behind the drivers of the hydrological relationship within and between dune slack communities. However, to fully understand the dynamics behind vegetation response on all levels, more research is needed to better understand the resilience and recovery response of dune communities to climate change for future management and dune slack conservation. To get a more complete understanding of the dynamics around tipping points on different levels, we do need to incorporate the full range of dune slack communities, in excellent- or poor-conditions, and potentially beyond the tipping points to understand the full extent of resilience. Our results also suggest that more research is needed to understand bryophyte dynamics, as they often play a vital role within dune slack communities, but are poorly understood. Therefore, the findings in this thesis conclude that long-term monitoring is necessary, especially with repeated measures, to determine the short-term and long term dynamics and how they affect vegetation response around hydrological change in the future.

Contents

All photos are made by Lisanne van Willegen

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of Tables

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Appendix

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Acronyms

EbF	Ellenberg indicator of soil moisture
MSL	Mean spring water level (m)
MAX	Maximal water level (m)
MIN	Minimum water level (m)
Mean	Average water level (m)
Median	Median water level (m)
LOI	Loss-on-ignition (%)
SOM	Soil organic matter
pH	Potential of hydrogen
NVC	National Vegetation Classification

Chapter 1

Chapter 1

1. Overview

1.1. Introduction

Wetlands provide numerous valuable ecosystem services, however, they are facing unprecedented threats from climate change across Europe. Rising temperatures, declining rainfall, and more extreme weather events are expected to severely degrade wetland ecosystems in many regions. This highlights the urgent need to protect and restore these habitats against further damage and loss (Čížková et al., 2013; Pörtner et al., 2022). The effect of climatic change is related to geographical location and also wetland type (Salimi et al., 2021), with the risk generally increasing with smaller areas and habitat fragmentation (Haddad et al., 2015; Oliver et al., 2015). Anthropogenic influences, like drainage, pollution and groundwater extraction have already been shown to have a negative influence on the wetland ecosystems, potentially limiting mitigation possibilities and decreasing their resilience against future threats. Coastal wetlands are viewed as one of the most sensitive wetland ecosystems to anthropogenic disturbance, with habitat types ranging from inter-tidal to sand dunes predicted to lose 20-90% of their habitat before 2100 under RCP8.5 (Bindoff et al., 2022). The high risk of damage is related to a combination of both sea level rise and global warming, although most of the assessments to date have focussed on mangroves, salt marshes and sea-grass habitats. Dune slacks or humid dune grasslands have received comparatively little attention, but are equally vulnerable to changes affecting groundwater availability and evapotranspiration processes. Dune slacks are seasonal wetlands within sand dune systems, known for their ability as habitats to support high diversity plant communities which are strongly influenced by the dynamics of the local groundwater regime (Grootjans et al., 2004). Within Europe, the Atlantic-region countries contain 66% of the humid dune slack habitat in Europe (France and Portugal excluded, ~112 km^2): none of which were classed as favourable during the Natura 2000 assessment of 2018, and the future prospects of these habitats were ranked as bad or poor (E28). The condition of dune slack habitat in the UK has also been classed as ‘unfavourable and bad’ and with the decline still evident over the last decade (Stratford, 2014). Future climate conditions are expected to influence and change current groundwater dynamics (Kløve et al., 2014), which is likely to have a high impact on dune slack habitat (Curreli et al., 2013; Rhymes et al., 2016). Overall, the general direction of change in the composition of dune slack habitat is likely to shift towards dry grassland communities by the end of 2100 based on current climate change and sea level rise predictions (Curreli et al., 2013). In order to ensure the survival of coastal wetlands into the future, we need a better understanding of how and when dune slack habitats will respond to climate change. Therefore, there is an urgent need to expand our knowledge of the relationship between dune slack habitat and hydrology, with a special focus towards variability linked to climate (Martins et al. 2018). Gaining knowledge on the dynamics of hydrology which drives plant community responses will help to improve management and ultimately, lead to a better protection of the vulnerable dune slack habitat in response to future climate change.

1.2. Aims and objectives of the study

In order to safeguard dune wetlands and to provide sustainable management in the future, there is an urgent need to increase our knowledge on the factors which regulate dune slack communities, and how to protect the habitat from current and emerging threats.

The aim of this research is to gain a better understanding of the underlying mechanisms and drivers of dune slack vegetation, especially in relation to hydrology. By combining field monitoring, statistical analysis and numerical modelling, a more integrated view can be formed, leading to a better understanding of ecosystem functioning.

Overarching scientific questions guiding this thesis are:

- Over what timescales does hydrological regime influence dune slack vegetation?
- Do all dune slacks respond the same, or do different plant communities vary in their response to hydrological change?
- Can a better understanding of hydrology-vegetation relationships inform management of dune systems ?

To support the aim of the thesis four key objectives have been formulated as follows:

- To develop a representative 3-D hydrological model of the dune water table at Newborough Warren, using existing long-running hydrological monitoring data, hourly meteorological data, topography and previous studies and published literature. The validated model can be used to test the influence of different forest management scenarios on groundwater regime.

- To assess and explore the influence of climate induced intra- and inter- annual variation of the hydrological regime as a driver of dune slack vegetation assemblages.
- To identify the role of vascular plant and bryophyte community species composition in the vegetation response to hydrological regime.
- To utilise hydrology metrics to predict the vegetation response of dune slack vegetation, which is of high importance for the future design of better management and conservation practices.

This thesis supplements previous work by Davy et al. (2006) and Davy et al. (2010), who characterised the underlying hydrological and ecological requirements in dune slacks, and created eco-hydrological guidelines (themselves also building on work by dune pioneers such as Derek Ranwell (Ranwell, 1959)). This thesis also builds on work by Curelli et al. (2013), who outlined a more robust approach to producing eco-hydrological guidelines, with much of the new data coming from Newborough Warren. The initial starting 3-D hydrological model was developed by Adam Taylor and Rob Low for (NRW).

1.3. Thesis outline

The individual chapters of this thesis focus on addressing the research objectives.

Chapter 1 is the introduction to the thesis and set outs the aims and structure of the thesis.

Chapter 2 represents a review of published literature, which provides a summary of dune slack ecology as well as expected climate change impacts on hydrology in Wales.

Chapter 3 is a showcase of the 3D hydrology model of Newborough using MODFLOW and Groundwater Vistas software, in which the groundwater level has been predicted for the period of 1989-2019 and validated against long term monitoring data. The ability to predict the behaviour of dune slack habitat is of high importance for management and conservation. As coastal wetlands are considered to be highly vulnerable in the future, there is a need for accurate model predictions, that are able to incorporate not only climate conditions, but potential vegetation change or management interventions. The model incorporated 27 different vegetation types, detailed evapotranspiration calculations in which hourly climate data has been used to increase accuracy of the output, and improved spatial resolution of calculations and outputs. This chapter aims to present the hydrology model outputs using the long-term monitoring data as validation and 2 model scenarios incorporating “forest felling” and a “zero management” scenario.

In this study, I examine

- hydrological numerical modelling as a tool for management, quantifying the impact of different woodland management within a dune wetland ecosystem. I expect that different woodland management scenarios (forest felling and a zero management) have an impact on the hydrological regime, leading to a change in the groundwater level on the long-term, with forest felling leading to increased water tables, and the zero management scenario showing lower water tables than current status baseline.

Chapter 4 explores the relationship between hydrology and dune slack vegetation using hydrology metrics and indicators, analysing a variety of approaches to understand and characterise the relationship between hydrology and dune slack vegetation. Mean Ellenberg indicator values for soil moisture (EbF) were used to characterise vegetation status or response of dune slack communities. EbF as a proxy for vegetation community response was tested against a wide selection of hydrology metrics to understand the timescales and nature of inter- and intra- annual variation in both hydrology and vegetation, and to find the best hydrology metrics suited to describe and predict the relationship between the two. This chapter aims to improve hydrology monitoring for future management and gain a better understanding of the relationship between hydrology and dune slack vegetation.

Specifically, I address the following questions:

- Which hydrology metrics have the strongest affinity to dune slack vegetation mean EbF values?
- How does inter-annual variability affect the relationship?
- Which hydrological year best represents the relationship between vegetation and hydrology?

Chapter 5 is dedicated to building linear mixed models to explore the role of soil and plant community characteristics in modifying the mean Ellenberg response of the vegetation. This chapter explores in more detail the variation among different plant communities within the broad umbrella of ‘dune slacks’ and aims to gain an even better understanding of the dynamics of dune slack vegetation over time, by incorporating the NVC classification of dune slack communities as a factor in the analysis. The results can be used to model dune slack vegetation response at the level of dune slack communities or groups of communities. This chapter aims to determine the importance of soil and plant community characteristics in modifying vegetation responses to hydrological regime. To use this information to build a predictive model to predict the response of dune slack communities to changes in hydrological regime and to inform future management regimes.

Specifically, I address the following questions:

- What are the differences in plant community response related to species assemblages to the hydrology regime?
- Which hydrology metrics or other variables influence the plant communities’ responses?

- How is the inter-annual responses within and between the plant communities related to species assemblages?
- How do bryophytes species alter the interpretation of key hydrological relationships? And do they display similar relationships and inter-annual patterns as shown in plant communities?

Chapter 6 provides a general discussion of the thesis, bringing together the findings and making suggestions for future management and research and ends with some final concluding remarks.

All chapters, with the exception of the literature review in this thesis, have been written and prepared as publications for peer-reviewed scientific journals, currently awaiting submission. The contributions of co-authors are described at the end of each chapter in the acknowledgements section. Other published contributions as co-author during this PhD project are mentioned below.

1.4. Study site

In order to conduct the research, a large scale dune system of Newborough Warren (Isle of Anglesey, Wales) has been selected that would be appropriate and suitable for the aims and objectives of this study. The dune system of Newborough Warren represents one of the largest dune habitats in the UK (Figure 1.1) and contains all five main dune slack plant communities (i.e. NVC classes: SD13-SD17; (Rodwell, 2000)). This full range of plant communities types would allow for a more comprehensive analysis of the vegetation, as often research is focussed on a selection of plant communities. Incorporation of all plant communities within this research would increase the opportunity to understand the full scale of the dynamics and drivers of the dune slack habitat. Another aspect of the site selection was driven by hydrology and drought sensitivity. After 1950, many dune systems have been subjected to (partial) afforestation in Europe, which also applied to the dune system at Newborough. Although establishment of the forest brought shelter and protection for many plant species, there is strong evidence that typical dune species, and in particular the species of dune slacks might be negatively affected by the presence of the forest (Stratford et al., 2007). Over time, the dune slacks have shown signs of desiccation and drought stress and there are records that line the appearance of drying slacks with the arrival of the forest (Onyekwelu, 1972). Additional to the afforestation, other factors like grazing, drainage and stabilisation have also impacted the dune system. As a result, researchers have started to monitor the groundwater level and dune slack communities in more detail (Curreli et al., 2013). The hydrology data resulting from this monitoring would be sufficient in both quality and quantity for the analysis of this study.

Figure 1.1 Aerial map of dune system of Newborough, Wales, United Kingdom.

Newborough Warren is located on the SW corner on Anglesey, North Wales (53°08’56”N, 4°21’38”W). The dune system covers around 1295 ha of land owned by Welsh Government and private landowners. Newborough Warren is surrounded by water on three sides and the village of Newborough to the northeast; The Irish Sea in the west, Malltraeth Estuary along the northwest, the agricultural fields of Newborough to the east and the Menai Strait in the southeast. In the middle of the coastline, a small island is connected at low tide, known as Llanddwyn. At the northeast, there is a small lake, Llyn Rhos-ddu, which separates the dunes from the mainland further north. The dune system is enclosed; sided by two estuaries and geological features, consisting of Holocene aeolian calcareous sands that overlie glacial till deposits, resting on Palaeozoic and Precambrian basement (Bristow & Bailey, 1998). Between 1947 and 1965, the western side of the warren was afforested with Corsican pine (*Pinus nigra* ssp. *Laricio*) (Hill & Wallace, 1989). The remaining east side of the site has developed as an open dune grassland with four lines of parabolic dunes containing a high number of dune slacks. The site is managed by livestock grazing with sheep, cattle and Welsh mountain ponies since 1987 (Plassmann et al., 2010). The local climate can be described as mildly oceanic with an long-term average annual rainfall of 872mm between 2006 and 2019 (RAF Valley station (Met Office, 2012)). The prevailing wind in the area has predominantly been southwest during the period 1890-1950 (Ranwell, 1958). The area is officially designated as a Special Area of Conservation (SAC), a National Nature Reserve (NNR) and a Site of Special Scientific Interest (SSSI) and managed by Natural Resources Wales.

1.5. Additional publications and presentations

The following publications were either part of the PhD or resulted from collaboration during the period of the PhD. My role within each project has been stated below each paper.

Callaghan, Des & **van Willegen, Lisanne** & Williams, Graham & Hollingham, Martin & Jones, Laurence. (2020). Pony trails, hydrology and habitat restoration: aspects of the ecology of *Petalophyllum ralfsii* in a Welsh oceanic dune system. Journal of Bryology. doi:10.1080/03736687.2020.1819719.

My contribution to this paper entailed substantial fieldwork, collection and processing of hydrology data and DGPS elevation data, formulation and assisting in the writing of the paper.

Dwyer, Ciara & Pakeman, Robin & Jones, Laurence & **van Willegen, Lisanne** & Hunt, Natalie & Millett, Jonathan. (2021). Fine-scale hydrological niche segregation in coastal dune slacks. Journal of Vegetation Science. 32. doi:10.1111/jvs.13085.

My contribution to this paper entailed training the lead author on use of the MENYANTHES model, assisting with fieldwork and in the writing of the paper.

Dwyer, Ciara & Millett, Jonathan & Jones, Laurence & Bartholomeus, Ruud & **van Willegen, Lisanne** & Chavasse, Anna & Pakeman, Robin. (2022). Patterns of variation in plant diversity vary over different spatial levels in seasonal coastal wetlands. Diversity and Distributions. 28. n/a-n/a. doi:10.1111/ddi.13589.

My contribution to this paper entailed training the lead author on use of the MENYANTHES model, fieldwork and assisting in the writing of the paper.

1.6. Conference presentations

Chapter 3:

British Ecological Society conference, Birmingham, UK 2018. Oral presentation: “Preparing for climate change modelling - MODFLOW model case: optimization of the MODFLOW parameters for dune ecosystem.”

Chapter 4:

Joint British Ecological Society/European Society of Ecology/ GfÖ and NecoV conference, Ghent, Belgium 2017. Poster presentation: “Dune slack communities and Ellenberg: a time lag interaction between competition, plants and bryophytes.”

NAEM conference in Lunteren (Netherlands), 2020. Poster presentation: “Dune slack conservation using Ellenberg”.

Chapter 2

Chapter 2

2. Dune slack habitat

This literature chapter gives an overview of dune slack habitat, which provides a background to and summarises research on dune slack habitat and ecology as well as expected climate change impacts on hydrological regime within dune wetland ecosystems in Wales.

2.1. Dune slack communities

Dune slack communities can be classified according to plant species composition. Dune slacks are low-lying areas in between dune ridges and can vary in shape, size and age, and experience high inter- and intra-annual variation of the water table (Ranwell, 1959; Jones et al., 2006). The fluctuation in the groundwater level is a feature present in all slacks, where the water level rises from autumn until spring and then decreases again over summer, but always within 2 m of the surface (**Figure 2.1**). Dune slacks are formed generally in two ways: primary dune slacks, which form when a newly forming dune ridge cuts the connection with the sea, and secondary dune slacks, which form in the dunes when wind erosion deflates (scours) the sand surface down to the water table (where cohesion of wet sand is high enough to halt further wind scour). The newly formed habitat offers opportunity for colonisation by those plant and moss species which are able to adapt to the dynamic hydro-ecological niche (Ranwell, 1960; Lammerts & Grootjans, 1997). Over time, environmental conditions can be altered by soil pedogenesis, hydrology and other influences like grazing, making the habitat become more suitable for other species (Grootjans et al., 1998; Lammerts et al., 2001). This allows for the development of a variety of dune slack communities, shifting from one community into another by succession, each with its own environmental niche (Grootjans et al., 1991; Berendse et al., 1998; Lammerts & Grootjans, 1998; Sýkora et al., 2004). The dune slack habitat contains a wide range of variation within environmental factors, which allows for many species able to co-exist, often resulting in high species diversity. In the UK, five main dune slack vegetation communities have been described (NVC types: SD13 – SD17), which can also be divided in a number of typical sub communities depending on the vascular plant and bryophyte species assembly (a, b ,c or d) (**Figure 2.2**) (Rodwell, 2000). The dune slack communities each have a distinct hydrology regime: SD13 is a pioneer community, whereas SD14, SD15 and SD17 are considered as a wet type of dune slack community and SD16 as the drier type of dune slack community.

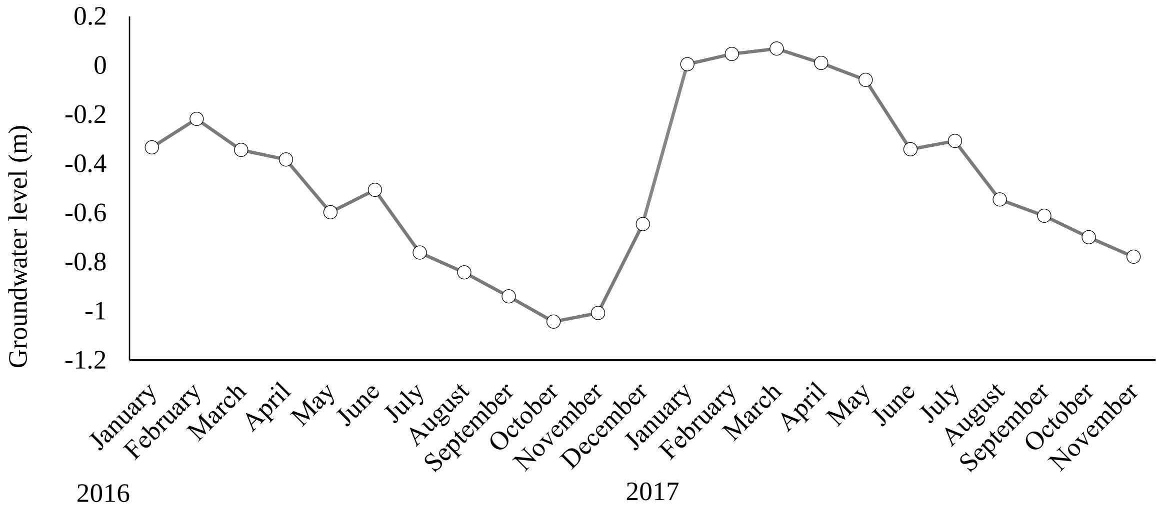

Figure 2.1 Hydrograph of a dune slack groundwater level.

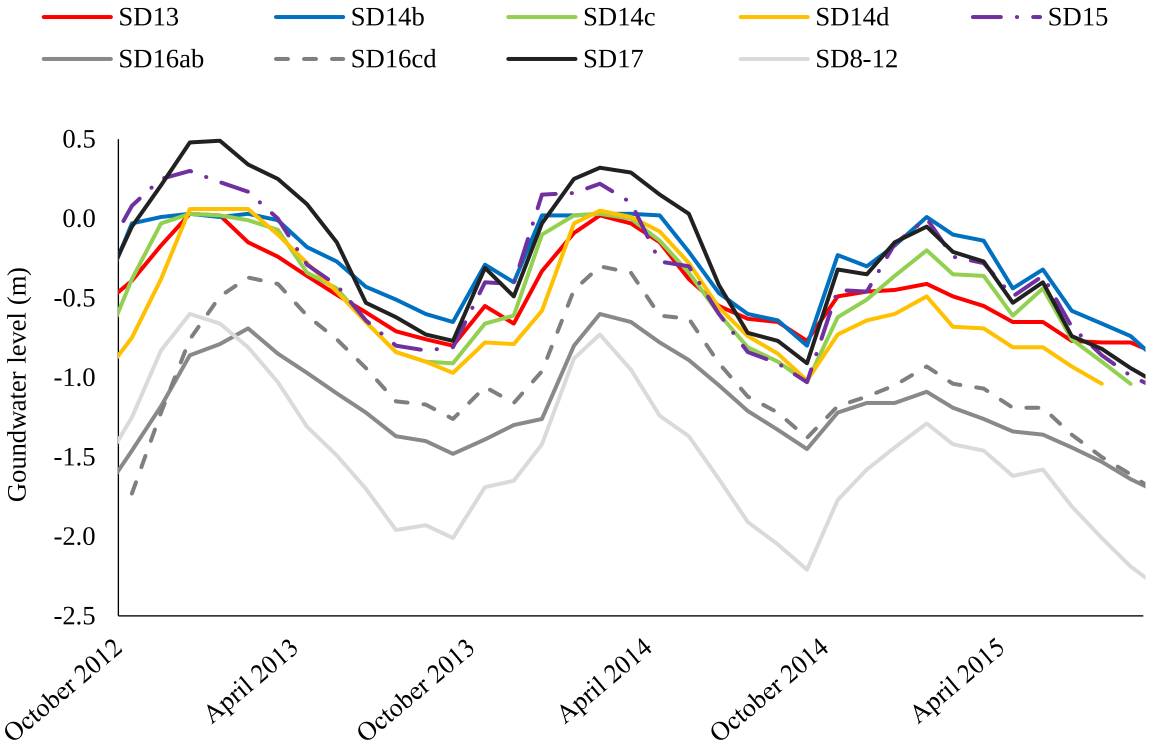

Figure 2.2 Example of a hydrograph of dune slack communities NVC types: SD13 – SD17 and dune grassland communities NVC type: SD8-12 at Newborough, Wales.

2.2. Dune slack succession: Environmental drivers

The successional stages of the dune slack communities are strongly linked to th**e** dynamics of the groundwater level and nutrient availability (Grootjans et al., 1991; Sival & Strijkstra-Kalk, 1999; Curreli et al., 2013). Although there is still discussion on what exact properties drive dune slack communities, there has been research on hydrological thresholds and other environmental drivers related to nutrient availability. The study of Curreli et al. (2013) was able to differentiate between dune slack communities types using the (4-year) mean winter water level, showing that only a difference of 20 cm was enough to separate plant communities. However, the relationship between hydrology, soil- and groundwater- chemistry is complex, as environmental factors often influence each other, leading to indirect (lagged) feedbacks. For example, one of the main chemistry processes that has a high influence on other environmental conditions is the dune slack soil's buffering capacity. The amount of calcium- (Ca^{2+}) and bicarbonate (HCO_3^-) ions in the soil provides a mechanism to create nutrient-poor conditions by binding with solutes containing phosphorus or nitrogen (Sival & Grootjans, 1996). This is beneficial for basiphilous or pioneer dune slack communities, as the depletion of buffering-ions can lift nutrient-limitations in the soil, and will lead to succession into more eutrophic and/or acidophilic vegetation communities (Lammerts & Grootjans, 1997; Sival & Strijkstra-Kalk, 1999; Sýkora et al., 2004). The influx of carbonate-rich seepage during winter flooding can replenish the ions in the soil (Stuyfzand, 1993). Therefore, the buffering mechanism is likely to have a strong relationship with the dynamics of the winter groundwater level, but the effect might be limited in dune slacks without carbonate-rich seepage.

Aside from the buffering process, there are other chemical processes that influence nutrient availability, like the precipitation of cations or the development of soil organic matter (Berendse et al., 1998; Jones et al., 2006; Rhymes et al., 2014; Rohani et al., 2014). Iron-rich groundwater can help to maintain a low availability of phosphorus, by binding phosphate to oxidated forms of iron ($Fe(OH)_3$) (Adema & Grootjans, 2003). This process is controlled by redox-potential in the soil, and allows for the (temporary) storage of phosphorus in the soil in forms which are poorly available to plants (Bakker et al., 2005). The development of soil organic matter is mainly driven by above ground biomass production, a process of plant litter decomposition under aerobic conditions (Rohani et al., 2014). As a result, organic matter development has a high sensitivity for the groundwater intra-annual dynamics. Drought periods can lead to groundwater level reductions as small as 10 cm, which have been found to have a high impact in dune slacks leading to increased availability of nutrients (Rhymes et al., 2016). Despite the strong relationship between hydrology and soil organic matter development, there are still unexplained differences in organic matter accumulation rates between and within dune slack plant communities, which were not explained by hydrology, buffering capacity or community age (Jones et al., 2008; Rohani et al., 2014). More research is needed to fully understand the feedbacks of soil- and groundwater chemistry processes on dune slack plant community succession. The knowledge will improve our understanding of dune slack ecology and functioning over time. This will be of high importance for restoration and conservation in the future, as success of restoration or management depends on the correct assessment of environmental conditions.

2.3. Dune slack succession: Additional factors

Aside from the environmental drivers, there are additional influences that affect the successional dynamics of the dune slack plant communities, which can be of evolutionary origin or a management influence, for example. Plant species can have traits that prolong the lifespan of whole plant communities. Within dune slacks, species like *Schoenus nigricans* have been found to recycle nutrients to maintain N-limiting conditions and *Littorella uniflora* can enhance radial oxygen loss (ROL) through its root system. ROL increases the loss of nutrients from soil via increased denitrification and can also increase iron oxidation by the presence of oxygen within anoxic conditions (Adema & Grootjans, 2003; Rohani et al., 2014). Both abilities have been found in plant communities that display different lifespans in research, creating an “alternative stable state”, preventing plant communities from succession (Adema et al., 2005). Management in dune slacks can control or alter conditions that might have been important in the ecosystem and have been missing over time. Grazing, mowing or sod-cutting can play an important role to maintain or decrease nutrient balances within plant communities, and even to create set-backs to younger plant communities (Hewett, 1985; Sýkora et al., 2004; Plassmann et al., 2010; Millett & Edmondson, 2015). The addition of livestock can also lead to more structural changes in the landscape, for example the soil bulk density can increase along animal tracks, which can be a more favourable condition for rare species like bryophytes (Callaghan et al., 2021). Grazing can also lead to higher heterogeneity in spatial elements, as the pressure can be localised or targeted as a result of behaviour and type of livestock (Plassmann et al., 2010; Millett & Edmondson, 2015). Overall, the impact and effects of grazing can result in a positive feedback to maintain species diversity (Pakeman et al., 2017; Dwyer et al., 2022), but overgrazing needs to be prevented as it can lead to a loss of diversity (Geelen et al., 2020).

2.4. Dune slack succession: Timescales and hydrology metrics

Chronosequence studies report a range of timescales for plant communities and succession, ranging from short time periods up to several decades (Grootjans et al., 1991; Lammerts & Grootjans, 1998; Sýkora et al., 2004; Kooijman et al., 2016b). The successional timescales depend on the feedbacks from the hydrology relationships, and therefore, are sensitive to inter- and intra-annual variation resulting from the climate. To understand the response of plant communities in the context of timescales and successional patterns, hydrology metrics are often used, as they are a good proxy able to summarise hydrology dynamics over time.

The intra-annual variation is often summarised in hydrology metrics, like minimum or maximum water level, representing extremes values of drivers within each hydrology season. The mean winter- and spring water level can be also be a good predictor of succession, as research already has shown (Curreli et al., 2013; Dwyer et al., 2021a). Most plant species are unable to cope with prolonged waterlogging of the rooting zone during the growing season, as this negatively affects both germination and creates anoxic conditions (Grootjans et al., 1998). In addition to negatively affecting root growth, waterlogging also prevents the build-up of nutrient levels in the soil, since mineralisation of organic matter will be reduced under anoxic conditions (Adema et al., 2005; Rhymes et al., 2016). The mean spring water level or the duration of winter flooding could therefore be an important proxy, as this will influence the mineralisation of nutrients in the slack and affect root establishment and survival vital to the more pioneer-type of plant communities. However, above a certain level of winter conditions, some of the drier dune slack communities or species with higher growth rates might experience other limitations for succession. The lowest (summer minimum) level may for example, might also be a good proxy for the influence of biological impacts on dune slacks (via drought, nutrients, and water chemistry) (Curreli et al., 2013; Rhymes et al., 2014).

However, the inter-annual variation within the intra-annual metrics might be the strongest predictor of successional change between plant communities. Understanding the impact of the inter-annual variation of the climate will be important, since the groundwater level is highly influenced by precipitation and evapotranspiration. As small-scale differences in hydrology between plant communities can easily be reached, it is therefore important to determine the resilience and response of plant communities to the inter-annual variation of climate (patters). The climate of the Northwest European dune slacks has a known influence of the ocean currents for example, where there are decades of drier and wetter periods as a result of the Gulf stream (Palter, 2015). There is also atmospheric fluctuations of pressure patterns that adds to these periods near the Northern Atlantic Ocean, which is referred as the North Atlantic Oscillation (Hurrell, 1995). The trend or fluctuation might be minimal over periods of 10 years or even more, however the responses of vegetation to these temporal changes are currently unknown, and may show varying time lags of response. Understanding the impact of climate change and the effect on plant community succession will be important for dune slack management. It remains unclear in what kind of timescales plant communities are able to adapt, chance or disappear, as the succession dynamics have found to be a process of multiple (interacting) factors. More research will help to determine the main drivers of dune slack community dynamics and provide vital information to help devise new management strategies to protect them against future threats.

2.5. Climate change

2.5.1. Climate

The climate has been changing over the last century and known to influence the dynamics and development of a dune ecosystem (Jones et al., 2010; Pye et al., 2014). In the near future, climate change is likely to become even more a serious threat for wetlands habitats, like dune slacks (Čížková et al., 2013; Salimi et al., 2021). Model studies in England and Wales have produced predictions or model simulations, in which climate change will have impact on the inter- and intra- annual patterns of climate variables like precipitation, temperature and wind, but also other measures changes that affect the hydrology regime, like sea level rise (Saye & Pye, 2007; Clarke & Sanitwong Na Ayutthaya, 2010). The result of these studies and their possible impacts are discussed in the next paragraphs in the context of Wales and for the conditions at dune site Newborough.

2.5.2. Precipitation and recharge

The amount and timing of precipitation is an important element of the hydrology regime, as this is the main input of recharge of a dune system and an important driver of the inter- and intra-annual dynamics of the groundwater level, vital to the dune slack ecosystem. Next to precipitation, there is evapotranspiration of the vegetation that controls the amount of recharge, as vegetation can actively withdraw precipitation in the soil before it reaches the groundwater table. The dune system decreases evapotranspiration during the autumn and winter as the vegetation has a short life span (annual) or has reduced or limited evapotranspiration by the drop in temperature, light or aerobic conditions during winter conditions. This creates a moment for the dune system where recharge is highest for the next growing season, which is an essential element of the hydrology regime in dune wetlands. If future conditions lead to a decrease of precipitation, this will consequently lower the ground water table and increase the severity and frequency of droughts, especially if the dune system is mainly fed by precipitation. This could lead to the progressive drying up of the dune ecosystem over time, creating circumstances facilitating more drought-resistant species or species which are able to exploit water lower in the soil profile using deep root systems (Kamps et al., 2008; Witte et al., 2008; Bartholomeus et al., 2015). This will likely impact on native dune slack communities, leaving them prone to being outcompeted in unfavourable dry conditions. However, one of the advantages of increased drought is that the dune system is more vulnerable for soil erosion. The area of bare sand could increase as a result, which would promote mobility of the system and increase the conditions for pioneer communities (Provoost et al. 2011; Pye et al. 2014). For the region of the United Kingdom, drier summers and wetter winter periods are predicted, which might be a limiting factor for the dune system groundwater capacity, especially during summer (Jenkins et al., 2008). In Newborough, the groundwater table is likely to decrease in the future, as precipitation is the main source for the total storage of groundwater. There are indications that the decrease in groundwater storage might be compensated by water from the lake Llyn Rhos ddu which is suggested to feed part of the water table of the dunes system, especially during summer (Stratford et al., 2007). If this will be the case, the water might be nutrient enriched from adjacent high intensity agricultural lands, providing an extra deleterious source of nitrogen (Jones et al. 2004; Rhymes et al. 2014). To understand the impact of the lake, it would be important to evaluate the hydrology regime with a groundwater model capable of simulating these dynamics.

2.5.3. **Temperature rise, evapotranspiration and CO_2**

Climate change is predicted to bring an increase in temperature in Wales (Saye & Pye, 2007). The effect of higher temperatures, will be an increase in atmospheric CO_2 concentrations. This is predicted to have many possible implications for the functioning of dune ecosystems, in which evapotranspiration plays in important role. The temperature rise will likely result in an increase in evapotranspiration, which has been found to be a main driver (Wang et al., 2022). In combination with the elevation in CO_2 could also lead to higher potential evapotranspiration, as the gas exchange in the stomata will use less energy as the CO_2 gradient is higher and increase the maximum of the photosynthesis process (Barnaby and Ziska 2012). The increase in temperature will lead also lead to a longer growing season, and as a result of that, shorter winters and reduced frosts (Barnaby & Ziska, 2012). This could lead to increased vegetation growth, as plants will be able to grow earlier and longer, or able to do a second flowering period. This combination of both the increase of potential evapotranspiration and the longer growing season will decrease the annual recharge that dune systems receive, as there is a higher water usage by the vegetation, and therefore, has an impact on the total storage of groundwater of the dune systems.

However, this increased growth rate might be limited by problems of water shortage as a result of increased evapotranspiration demand or drought stress. Heat stress and intense drought period has also been shown to reduce growth and survival affecting the resilience of dune vegetation systems (Witte et al. 2008; Bartholomeus et al. 2012; Witte et al. 2012). As the temperature will increase, this will also lead to a higher evapotranspiration (Witte et al. 2008), and therefore, to a higher demand of water. The water table needs to be high enough during the growing season, especially for dune vegetation, which relies on adequate water availability in the top layer/unsaturated zone. Therefore, the local groundwater level will likely become a limiting factor for evapotranspiration, as most dune system are only fed by rainwater. Therefore, it is likely that the water table will control total evapotranspiration and the potential to increase with future conditions, limiting the effect on total groundwater storage. If the total groundwater storage would decrease over time, leading to a gradual lowering of water table, a succession towards more grassland communities would be expected (Curreli et al., 2013). This change in plant communities could also affect total evapotranspiration, if plant community evapotranspiration is lower, leading to an increase of the total groundwater storage. Overall, it will be difficult to predict the outcome of elevated temperature and CO_2 without the use of monitoring and computer simulation or modelling.

2.5.4. **Nitrogen deposition and succession**

Another important factor, nitrogen deposition and fixation, is not directly related to climate change, but already has a high impact on dune wetlands, of which the effect is likely to be influenced by climate change (Jones et al., 2008; Provoost et al., 2011). As mentioned before, the stabilisation of the vegetation has been the result of co-occurring factors, of which the nitrogen availability plays a key role (Sival et al., 1998; Rhymes et al., 2014). Welsh dune systems, alongside most systems in northwest Europe, have been negatively affected by overstabilisation of the vegetation in the past 50 years, partly due to the increase in nitrogen deposition and fixation (Jones et al., 2007; Provoost et al., 2011; Kooijman et al., 2016a). Due to the high stabilisation in the dune systems, there are large concerns about the decrease in bare sand and mobility in the systems, leading to the loss of biodiversity and habitat (Arens et al. 2013; Pye et al. 2014). Nitrogen deposition can play a role in the development of soil and above ground biomass in dune systems (Jones et al. 2008; Kooijman et al. 2016; Whiteman et al. 2017). Nitrogen deposition is not always the highest contributing factor in dune systems, as some are less or not limited by nitrogen availability (Jones et al. 2008; Kooijman et al. 2016). Nitrogen fixation can also occur by cyanobacteria, present in soil crusts, which can be formed on dune slack sands and fix up to 25 kg N ha-1 a year in dune grasslands (Provost 2011, Stewart 1967). Other N-fixing species are legumes or shrubs like Hippophea rhamnoides, which were abundantly present at Newborough until 1990 before they were cleared (Jones et al. 2008). Another study indicates that nitrogen deposition could lead to accelerated acidification in the presence of high N-enrichment levels (Aggenbach et al. 2016). This effect is likely to be intensified, especially when water tables are lowered and denitrification decreases (Rhymes et al. 2016).

2.5.5. **Sea level increase**

The influence of sea level can have high impact on the hydrology regime of coastal ecosystems. Differences in topographic locations and geological context will determine the effect of future sea level rise on a dune system. As the amount of annual recharge from precipitation feeds the freshwater belt or dome in dune systems, the actual height of the dome can be controlled by the influence of the sea water level. Sea water has a higher density, which makes fresh water lighter then sea water. The brackish layer in between the different densities is called the infusion layer, the surface of which is also controlled by the sea level. The climate study results of UK 2009 (Jenkins et al. 2009), predicts a rise in absolute sea level of at least between +12 cm and +76 cm at the end of 2100. This scenario has been used to examine the potential implications of the sea level rise in Sefton coast, which predicted a loss of 50 m of shoreline by the end of 2100 (Saye and Pye 2007; Clarke and Na Ayutthaya 2010). This would initially lead to the decrease of the mean ground water level of 1.0 - 1.5 m in the next 90 years. However, this is response is a result to the loss of shore line, which would lower the water tables by 0.18 m per 100 m of erosion (Clarke and Na Ayutthaya 2010). As a result of the sea level rise, the brackish infusion layer in between would increase in gradient, resulting in the possibility of salt water intrusion with the ground water further inland (Oude Essink, 2001). Overall, the ground water table is expected to drop between 1 m and 3 m for the Sefton coast at the end of 2100, based on medium high emission scenario (UKCIP'02).

The response at Newborough, however, remains unclear, and requires a hydrological model to be developed for the site. The sea level rise could have an impact on the groundwater level in the dune slacks, possibly decreasing the level located further away from the sea (Clarke and Na Ayutthaya 2010). This would be the result of sea level rise decreasing the total storage of the groundwater, leading to a lower dome in the middle of the dune site. The increase in sea level might have a different effect closer to the sea, which might locally increase the groundwater level or create new primary slacks. However, there is a high likelihood, that the influence of the sea level rise might be very limited at Newborough as the dune site is underlain by glacial deposits and a bedrock (Bristow, 2003). In the study of Ranwell in 1959, the influence of the sea level was not detected in the dune slacks near the beach, despite the high intertidal change (Ranwell, 1959). This led to the suggestion, that below the slacks near the beach there exists an impermeable layer, which will prevent shoreline erosion inwards of the dune site or limit this effect on the hydrology regime (Betson et al. 2002).

2.5.6. **Wind**

Long term records of the Valley, near Newborough, show that over time there has been a significant reduction in average wind speeds over the last 45 years (Clarke & Sanitwong Na Ayutthaya, 2010; Sexton & Murphy, 2010)). Wind is regarded as one of the three most important drivers of the natural dune mobility (Provoost et al. 2011). When stabilisation has occurred within a dune system, it is more difficult to get the sand moving again as vegetation acts as a natural stabilising agent. More wind energy or disturbance is therefore needed to get the sand moving again, which can favour more pioneer plant communities which often have low evapotranspiration (Provoost et al. 2011; Arens et al. 2013). High wind dynamics are also responsible for the creation of secondary dune slack formation, as mentioned in 2.1. The future predictions suggest that there may be even more reductions in the average wind speed and storms (Sexton DMH 2010). This could facilitate more stability in the dune system, leading to even less pioneer plant communities (Rhind et al., 2007; Tsoar, 2013). This could lead to an increase of evapotranspiration within dune systems. Wind can also lead to higher erosion dynamics at the shoreline, which has been an occurrence at Newborough (Betson et al., 2002). But like discussed earlier in 2.5.6, it is likely the effect of erosion on the shoreline might be limited by underlying geology features.

2.5.7. Pathogens/invasive species

As climate change can dramatically alter the physiological boundaries of species, they can become more vulnerable to a range of other secondary stresses. For example, climate change can create more opportunity for pathogens to gain new territory as climate conditions expand habitat borders, potentially taking barrier away for dispersal. This can allow outbreaks of invasive plant species (e.g. *Cotoneaster simonsi*) or other pathogens, like fungus. Pathogens like the Red Needle Blight (*Dothistroma* species) have been present in the Newborough forest for some time, since its first occurrence in 1986. This fungus is able to infect all ages of pine trees and is present in several Corsican pine stands at Newborough. This disease has already made an impact on the juvenile trees, creating stands with ill and deformed trees. The disease has an impact infecting the needles, which leads to a reduction in evapotranspiration or even loss of the needles (Drenkhan et al., 2016). The true impact of this disease is still unclear and uncertainty still exists on how this disease will develop in the future, however, there are efforts made to change the forest over time into a mixed broadleaf forest, limiting the effect of this disease on evapotranspiration.

2.6. Groundwater model studies

I briefly discuss the model options we use in this study as part of the literature review. This provides background and validation to model selection in Chapter 3.

2.6.1. MODFLOW

In some previous studies on Newborough, the groundwater modelling software of MODFLOW has been used (Betson et al., 2002). MODFLOW is designed as a grid model, in which each cell represents a part of the system. Each cell is computed with a direction (x,y,z) as part of a layer (Harbaugh, 2005). The model is able to use elevation, surface and different layers as inputs to form the dune system. The hydraulic properties can be added, using different zones or layers of conductivity determine the behaviour of the groundwater flow and specific yield which in turn determine the amount of water storage in the soil. The model uses the grid cells to calculate the movement of the water depending on these properties and input. This is a complex way to calculate the groundwater flow, especially after adding relevant soil processes. However, the outputs can reveal spatial patterns and 3D images, which help better understand the spatial context to changes in dune hydrology. MODFLOW has been used in many groundwater studies, including on dunes in Holland (Geelen et al., 2017) and at Braunton Burrows in the UK

(Abesser et al. 2017). As the site of Newborough has complicated geological features, it the numerical model software has been selected to understand the hydrology regime.

2.6.2.**Menyanthes**

Another option to analyse time series groundwater data is the model Menyanthes (von Asmuth et al., 2012). Most time series models are ARIMA (Auto Regressive Integrated Moving Average) time series models, although there has been a diversification of methods. Menyanthes is also able to use another method, the PIRFICT method (Predefined Impulse Response Function In Continuous Time). This is a new method of time series analysis, which as a different method that uses the knowledge of on physical behaviour based on a mathematical algorithm. The method is formulated as a (continuous time) convolution integral, instead as a temporal difference or differential equation. This enables it to model parameters as a continuous process, rather than a time step based model. This could help with data fitting to climatic data, as data is no longer bound to be measured at the same time, which allows for a direct link between time series and spatial/physic models. However, this should be done with caution. Time series models may be influenced by non-causal cross-correlations. The model uses evapotranspiration and precipitation as one of the few explaining variables, which makes it simplistic and strait forward in representing a fit or not. It can also add other explaining variables like trends or step-trends for drainage level change or groundwater abstraction. The main difference with ARIMA models is that physically inspired behaviour, can be implemented *a priori* in the model, instead of adding insight or selection of the results posteriori. With ARIMA models, model order needs to be defined with at least 5 terms of Transfer Noise/deterministic complement. Also, ARIMA models have difficulty dealing with highly irregular data or data gaps. In the scenario with dune slack systems, the model is able to cope with non-linear behaviour of the data, like runoff during flooding periods.

2.7. Summary

This chapter provided a background for this thesis, by summarising dune slack ecology dynamics and discussing mechanisms by which plant communities can respond to hydrological change, and other influences which moderate those vegetation responses. It also summarises the possible impact of climate change and other pressures on the hydrology regime in relation to Newborough and describes modelling approaches which can be used to help address scientific questions around the interactions between hydrology, management and dune slack vegetation. By analysing literature on the topics of dune slack ecology, successional dynamics and hydrology metrics, we can now provide a basis and direction for the research in chapters 3 (groundwater model), 4 (hydrology metrics) and 5 (plant community response). These findings aid to answer the overarching questions posed in the introduction:

- Over what timescales does hydrological regime influence dune slack vegetation?
- Do all dune slacks respond the same, or do different plant communities vary in their response to hydrological change?
- Can a better understanding of hydrology-vegetation relationships inform management of dune systems ?

Based on literature, there are strong indications that plant communities are highly sensitive to the impacts of climate change on the hydrology regime. Research has shown that dune slack vegetation are sensitive to different kind of environmental drivers, soil- and groundwater (chemistry) processes, can be sorted to hydrology thresholds and show successional trends varying between years and decades. It remains unclear how plant communities adapt, chance or disappear, as the succession dynamics have found to be a process of multiple (interacting) factors. The exact responses of dune slack plant communities to short term temporal changes are currently unknown, and may show varying time lags of response as a result of the feedbacks.

Understanding the short term dynamics of plant communities to inter- and intra-annual variation of the hydrology regime will help to improve our understanding of dune slack ecology and functioning over time. These findings were used to form a consensus on the focus of the research and allowed to recognize knowledge gaps. Together, this will help to determine the main drivers of dune slack community dynamics and provide vital information to help devise new management strategies to protect them against future threats from climate change.

Chapter 3

Chapter 3

3. Forest management shows impacts on groundwater levels in adjacent dunes

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Abstract

Introduction: Coastal wetlands are sensitive to changes in hydrological regime. However, dune slack hydrological management can be a difficult process, as site conditions can be complex and be affected by management both on and off-site. Predicting changes to hydrological regimes needs a site-specific approach. Hydrological modelling is a useful tool to estimate groundwater flow predictions that allows for quantification of management actions on site level.

Aim: In this study we explore 3-D hydrological modelling as a tool for assessing site management, quantifying the impact of different woodland management within a dune wetland ecosystem.

Location: Newborough Warren, North Wales, UK.

Methods: A period of 10-year was used to simulate groundwater flow using the MODFLOW hydrological model with a Groundwater Vista interface. The hydrological model was supported by climatic data (rainfall and evapotranspiration) over a 10-year period, with model calibration and validation making use of 30 observation wells. The model incorporates structural and temporal variation among 27 vegetation types. The validated model was used to evaluate the influence of 2 management scenario: forest felling and a zero management scenario, compared with the current-status baseline which incorporates routine thinning and small coupe felling. Forest management scenarios take place on the~50% western side of the dune system that is afforested, while the focus of changes in groundwater levels lies in the un-forested eastern part of the dune system.

Results: The level of temporal and spatial resolution, allowed for the successful prediction of the groundwater flow and seasonal dynamics such as annual flooding to be observed in the model. The different scenarios, forest felling and zero management scenario, both had an impact on the groundwater regime within the dune system compared to the baseline model situation, which contained the management regime present at the site. Zero management would result in water levels 15 – 28 cm lower than they are at present at a distance of 280 m into the dunes from the forest edge. The felling of the forest would result in a rise of water levels by around 75 cm at a similar distance from the forest edge, and a rise of 22 – 32 cm at 1000 m into the dune system.

Conclusion: The hydrological model shows how model and field monitoring can be combined to help improve our ability to predict the impact of current and future management interventions. The results underpin the need for sufficient spatial and temporal resolution to represent the parameters used in hydrological models, to obtain accurate groundwater level predictions. Our results also emphasized that role of woodland management as a valuable tool to mitigate potential effects on the hydrological regime of coastal wetlands. Future research should focus on further improving evapotranspiration calculations and input to future climate conditions within the model, and on exploring a wider range of management scenarios and climate projections to evaluate both future impacts at the site, and possible management options.

Keywords: Hydrology, Groundwater modelling, Forest, Scenario, Management intervention, Dune slacks.

3.1. Introduction

Coastal wetlands are sensitive to changes in water tables, caused by a range of factors including climate change and local management (Curreli et al., 2013). Dune slacks are a particular type of coastal wetland, which is strongly dependent on groundwater regime and hydrochemistry (Jones et al., 2006). Seasonal flooding is part of the hydrological regime to maintain specific dune slack plant communities, ranging from very wet conditions, with almost all year submergence, to drier conditions with only occasional flooding every few years (Ranwell, 1959). The hydrological regime is influenced by the local climate and management, where precipitation is often the main source of water, and evapotranspiration can be modified by site management (Davy et al., 2006). Climate change projections for precipitation, temperature and sea level will affect the local hydrological regime of many coastal wetlands (Saye & Pye, 2007; Kamps et al., 2008; Clarke & Sanitwong Na Ayutthaya, 2010; Oppenheimer et al., 2019). Climate conditions are expected to become also more erratic in the near future based on current IPCC predictions (Pörtner et al., 2022), and are expected to have a major impact on wetland ecosystems (Kløve et al., 2014; Salimi et al., 2021). The predictions could have serious effects on dune slack habitat, as dynamics within the habitat show thresholds between dune slack communities can be as narrow as 20 cm (Curreli et al., 2013), which indicates that the conditions might be difficult to maintain between communities in the future. To get a better understanding of the threats and vulnerabilities of the hydrological regime, there is a need for hydrological models that allow for accurate representation of the sensitive relationship between hydrology and vegetation with current and future ecosystem dynamics.

While climate change provides a very real threat, management of water tables can either exacerbate or help mitigate this to some extent. However, management of dune slack habitat can be a complicated process, as dune slack dynamics are complex and often need a site-specific approach. Although the general process of dune slack succession and the role of hydrology is relatively well known (Grootjans et al., 1991; Davy et al., 2006), it still can be a challenge to understand the full scope of site dynamics within these principles. Hydrology is often recognized as the main driver (Curreli et al., 2013; Martins et al., 2018; Dwyer et al., 2021a), however there are discussions of scale (Felton & Smith, 2017; Dwyer et al., 2022) and the role of other abiotic drivers (Sperandii et al., 2019) which also govern relationships of vegetation with hydrological regimes in wetland systems. Most of the dune slack habitat in the UK is currently in bad or unfavourable condition and is in need of management (Rhind & Jones, 1999; Pye et al., 2014). The poor condition is the result of many factors, including decades of nitrogen pollution, loss of grazing pressure and over-stabilization, which have led to degradation or change of the dune slack habitat and the vegetation types within (Provoost et al., 2011). There are also examples of management interventions that can affect the hydrological regime of coastal systems in different ways. Groundwater extraction has a high impact on coastal systems, typically resulting in a lowering of the overall groundwater level on site (Bakker, 1981). Drainage channels and sluices, often used to manually alter conditions on site, can also have impact on local groundwater level, by intercepting recharge or speeding up drainage away from the site. The precise effects depend on the site conditions, but usually these features result in lower groundwater levels. Overall, multiple factors can be involved, at different time scales, which can influence the hydrological regime to some degree, making it difficult to separate effects and adjust management correctly. Therefore, in the most complex coastal ecosystem, restoration of the dune slack habitat needs to be done with a site-specific approach, and ideally guided by modelling studies.

Hydrological modelling is a tool used to produce groundwater flow predictions and allow assessment of management actions at site level. Depending on the type of model, they can be used for predictions of different scenarios, past or future. Hydrology models can be built upon different strategies, using different levels of input and calculation (numerical process-based) or are more based on statistical approaches including time-series analysis, allowing for a more dynamic incorporation of random behaviour (von Asmuth et al., 2012). To understand site-specific dynamics, numerical models are well suited, as they allow for the incorporation of different layers of zones, for example topographic resolution or different hydraulic zones, to be applied to a grid of cells. This so called “finite difference grid” allows for complicated spatial-temporal changes over time, by using properties and boundaries that can be assigned to grid cells, allowing incorporation of vegetation and geological modifications over time. This type of model has been demonstrated to simulate small scale systems with reasonable accuracy, which can be difficult for hydrological modelling (Abesser et al., 2017). Therefore, in this study we explore hydrological numerical modelling using the MODFLOW model as a tool for management, quantifying the impact of different woodland management within a dune wetland ecosystem. Compared with a baseline representing current levels of forest management (thinning, and felling of small coupes), we expect different woodland management scenarios to have an impact on the hydrological regime: with forest felling resulting in an increase in water table, and a zero management scenario resulting in a lowering of water table compared with current baseline.

3.2. Methods

3.2.1. **Study area**

This study was conducted at Newborough Warren, a large dune system of 1295 ha, located on the Isle of Anglesey, North Wales (53°08’56” N, 4°21’38” W). The dune system is bounded by two estuaries and a rock ridge, consisting of Holocene aeolian calcareous sands that overlie glacial till deposits, resting on Palaeozoic and Precambrian basement (Bristow & Bailey, 1998). The dune system is mainly fed by precipitation and receives little water input from the near environment around the Warren aside from the lake (Stratford et al. 2007; Stratford et al. 2013). The site has an oceanic climate with mild winters and relatively cool summers, with an average long term annual rainfall of 847 mm in the period of 1971-2001 (Stratford et al., 2007) Surface runoff is considered to be minimal. Between 1947 and 1965, the western side of the warren was afforested with Corsican pine (*Pinus nigra* ssp. *Laricio*) (Hill & Wallace, 1989). The remaining east side of the site has developed as open dune grassland with four lines of parabolic dunes containing a high number of dune slacks. The site is managed by livestock grazing with sheep, cattle and Welsh mountain ponies since 1987 (Plassmann et al., 2010). Local climate can be described as mildly oceanic with an long-term average annual rainfall of 872 mm between 2006 and 2019 (RAF Valley station; (Met Office, 2012)). The area is officially designated as a Special Area of Conservation (SAC), a National Nature Reserve (NNR) and a Site of Special Scientific Interest (SSSI) and managed by Natural Resources Wales.

3.2.2. **Hydrological model**

In this study we explore the application of 3-dimensional hydrological modelling as a tool for management, quantifying the impact of different woodland management within a dune wetland ecosystem. For this objective we use a numerical based hydrological model, MODFLOW (Harbaugh, 2005), using the interface of Groundwater Vistas (by Environmental Simulations Incorporation) for model building and simulations. MODFLOW is a numerical model design in which groundwater flow calculations can be done per cell, which is incorporated in a grid that represents the hydrological system (**Figure 3.1**). Each cell is computed with a direction (x, y, z), part of a layer. Multiple grid layers can be added, incorporating top and bottom elevation and different soil layers, allowing for a 3-dimensional structure. Hydraulic properties can be added, boundaries and different zones of vegetation and conductivity can also be set as well as specific yield to determine the amount of water storage in the soil. The precipitation and evapotranspiration rate can be set for the vegetation zones for each time step, allowing groundwater flow to be calculated.

3.2.3. Model description

An initial MODFLOW model was developed for the site by Bristow (Bristow 1998). This initial model has then been re-developed and improved by adding more factors in the model data calculation, including an improved model structure (A. Taylor and R. Low, unpublished). However, a number of elements required substantial improvement before application to evaluate management scenarios at fine scale. These model improvements, conducted as part of this study, included updating the ground surface elevation using up to date LiDAR at 50 cm vertical resolution, increasing the number of vegetation types and particularly forest management classes, improving the bottom elevation with historical data and field observations, and improving temporal resolution of model time steps from monthly to weekly climate input data. The most recent version, with these improvements, based on the model version 96 of MODFLOW will be discussed in the paper.

3.2.4. Model spatial resolution, structure, surface and bottom elevation

The domain of the model consists of 100 by 120 cells, enveloping an area of 5 km by 6 km with a homogenous distribution (equal cell size). The spatial resolution of a grid cell is 50 m by 50 m. The top elevation was converted from topographical LIDAR data with a resolution of 0.5 m resolution for each grid cell. The basement of the dune system consist of Precambrian metamorphic rock, carboniferous limestone and coal, covered by a layer of boulder clay (Betson et al., 2002). The aquifer on top of the basement is considered to be a layer of homogeneous, aeolian sand represented by one layer in the model. The metamorphic basement was considered to be impermeable, and therefore, vertical leakage is assumed to be negligible. Borehole drilling and seismic refraction surveys have been done to get an indication of the depth of the basement rock, however exact measurements were not possible at the time (limitations of the borehole drilling, (Betson et al., 2002)). The bottom elevation has been adjusted to improve fit with the data of the observation wells or as a result of historical geological reports (Colman & Peart, 1993).

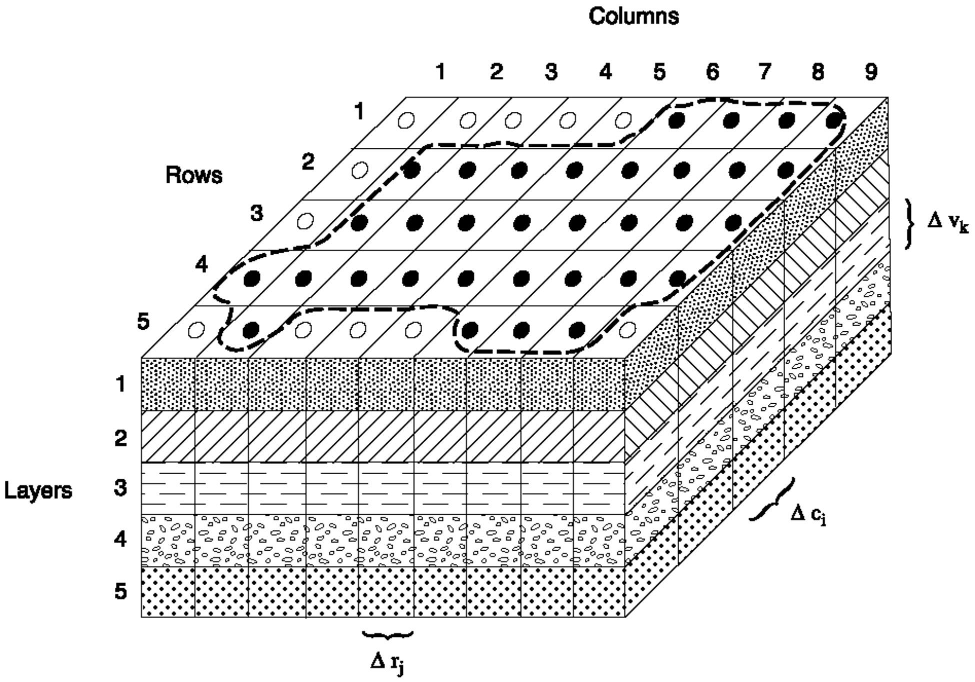

Figure 3.1 Three-dimensional finite difference grid used in MODFLOW (public domain, adjusted from Figure 1, McDonald and Harbaugh (1988), from (Harbaugh, 2005). Dotted black line denotes nominal site boundary and limit of model calculations.

3.2.5. **Boundary conditions**

Figure 3.2 illustrates the site domain used at Newborough, with the topographical boundary of the model indicated with the black line surrounding the active cells of model, no groundwater flow is calculated outside this line. Previous studies (Stratford et al., 2013) have established direction of groundwater flow moving east and south west of the rock ridge which extends north-east to south-west out to the boundary of Llandwyn Island (**Figure 3.2**). The Precambrian metamorphic rock ridge forms the western boundary of the model, this has been assigned as a no-flow boundary. The lake and stream at the northern edge of the model have been assigned as a constant head and river cells, running from 8 m OD to 0 m OD at sea level, according to topography. This stream is connected from the lake to the eastern edge of the system, connecting with the tidal area. As the bottom elevation at the seaside is assumed to be higher than the actual sea level, the cells have been assigned as a constant head boundary at 0 m OD elevation.

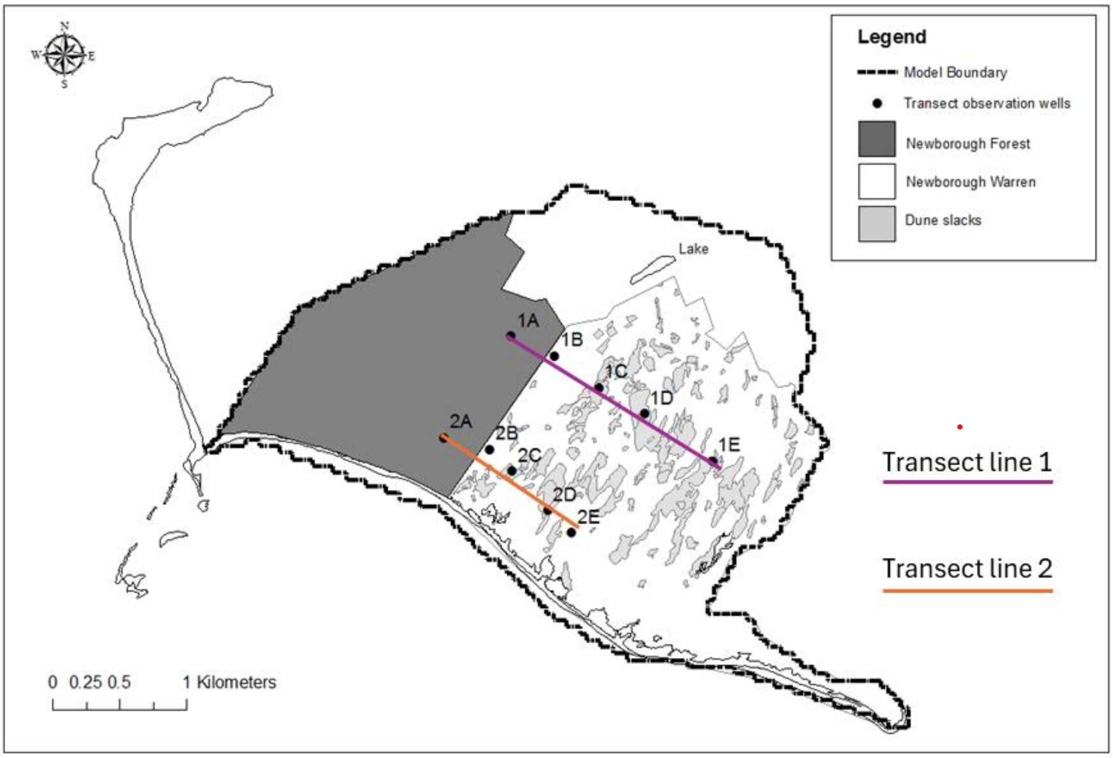

Figure 3.2 Boundary of the hydrological model (black line) surrounds the dune site that is incorporated in the model. The site shows the distinction between the Newborough forest (solid grey), hinterland (white), and Newborough warren (dune area containing the dune slacks), the lake Llyn-Rhos du and both the transect lines of the observation wells (Transect line (1A-1E) and Transect line 2 (2A-2E)).

3.2.6. **Hydrological conductivity zones**

The initial hydraulic conductivity zones had been set according to previous research at the site (Betson et al., 2002), which conducted grain size analysis, permeability and borehole tests and suggested hydraulic conductivity values of between 11.5 m/d and 4.5 m/d. The vertical: horizontal anisotropy was around 1.36 and therefore horizontal flow was assumed to be isotropic in the model (kxx= kyy). The initial parameter values for the model included a 10% porosity based on the permeability samples. The storage of the unconfined aquifer is 21% of fine sands.

3.2.7. **Hydrological validation data and temporal resolution**

The dune system has been monitored with 2 transects of 7 piezometers since 1989 (Bristow, 2003) In 2006 the monitoring has been expanded up to 50 piezometers, measured on a monthly frequency and with hourly data loggers in selected piezometers. Each piezometer has been measured for elevation using a dGPS, with a vertical accuracy of 10 mm. The groundwater level data has been corrected for above Ordnance Datum **(**aOD**)** and used to validate the model predictions in this study. The model had a temporal resolution of monthly stress periods with effectively 10-day time steps.

3.2.8.Model precipitation and evapotranspiration

The key input calculations for the hydrological model are recharge and evapotranspiration rate. Both parameters were calculated outside the model, which are then linked to a vegetation zone in the model, allowing change over time steps. The input climatic data for calculating both these parameters was at daily resolution obtained from the RAF Valley Weather station (Valley, Anglesey, Wales, 10 m above sea level, ~10 km from the site). Potential evapotranspiration was calculated using the Penman Monteith equation. This allowed then for the calculation of the actual recharge and evapotranspiration rates for the model. The actual evapotranspiration was corrected for total water availability in the soil as a function of precipitation and vegetation characteristics (rooting depth, evaporation rate). This allowed calculation of soil moisture deficit (SMD), which in turn adjusts evapotranspiration during periods of water shortage. Recharge was calculated as a function of precipitation and actual evapotranspiration (AET). Evapotranspiration was corrected for recharge, allowing evapotranspiration to reach its potential rate when field capacity is reached in the model. For each vegetation type in the dune system (Appendix,**Table 0.1**) a vegetation zone was developed in the model. Zones were defined to allow for incorporating management like thinning or felling into the model. There was a total of 27 vegetation zones in the model, with each zone having its own recharge and evapotranspiration parameter rate.

3.2.9.Calibration

The model has been validated and calibrated against long term data from the piezometers, which we describe as observation wells. With the use of 30 observation wells, we have calibrated the hydrological data against the model predictions (**Figure 3.2**above). The offsets were calculated as the predicted groundwater level minus the observed groundwater levels. Therefore, if the offset was negative, this would imply that the model underpredicted (drier conditions), whereas positive offsets represent overpredictions (wetter conditions).

3.2.10. Model scenario

Two management scenarios were created: The “zero management” scenario was represented by full forest without any interventions like thinning, felling or replantation. The “forest felling” scenario represents a model without any forest plantation and the area is replaced by semi fixed dune grassland (zone 1, Appendix **Table 0.1**). The baseline represents current management status and includes all thinning and small-scale felling operations that occurred during the model domain timescale.

3.3. Results

3.3.1.Model observation wells

The performance of the model baseline was evaluated for all observation wells, with results visualised using 2 transects of observation wells, which were positioned along a transect from the forest into the dunes, to determine model performance and fit (**Figure 3.2**).

3.3.2.Performance model - baseline

The baseline scenario of the model output showed a good overall fit for the observation wells, with the average offset residuals varying between -0.29 m and +0.33 m for the period of 2007-2018 (**Table 3.1**). The overall fit with the wider set of piezometers across the site (**Figure 3.3**) has varying offset, with average offset residuals between +0.6 m and -0.9 m. To illustrate seasonal dynamics, the summer and winter offsets are shown in **Figure 3.4**. Only three observation wells across the whole evaluated set had a greater average offset than 0.3 m. There were some spatial patterns to the offset, but these were not completely consistent. In the middle of the transect lines in **Figure 3.1**, located between the forest and the centre, the model offset was the smallest around observation well 1C and 2C, with limited variation between the model predicted output and the observed values (**Table 3.1**). This is also observed in **Figure 3.3**, with other observation wells close to the forest, with limited offset between the lake and the seaside, and limited average offset around the seaside east. The highest offset was observed in the forest, close to the forest edge in observation wells 1B and 2B, with minimum offset -1.48 m for 1B and -1.21 m for 2B (**Table 3.1**). The highest offset in the forest was also comparable, with minimum offset values of -1.06 m for 1A and -1.01m for 2A. Nearby wells in the forest showed some differences, with one showing a high average offset between -0.93 m and -0.60, but the other showed very good fit (offset between 0.0 m and 0.1 m, **Figure 3.3**). This suggests the influence of some highly local conditions affecting behaviour of individual wells.

Table 3.1 Model validation results: Average offsets (m) of the baseline scenario of the model per observation well, during the period 2007-2018: highest negative offset MIN (model underpredicted), highest positive offset MAX (model overpredicted) and average offset.

Observation well	1A	2A	1B	2B	1C	2C	1D	2D	1E	2E
MIN offset(m)	-1.06	-1.01	-1.49	-1.21	-1.07	-1.08	-0.92	-1.19	-0.81	-0.65
MAX offset (m)	0.62	0.54	0.21	0.37	0.60	0.43	0.94	0.33	1.07	0.69
Average offset (m)	-0.15	0.08	-0.29	-0.28	-0.08	-0.13	0.11	-0.22	0.33	0.14

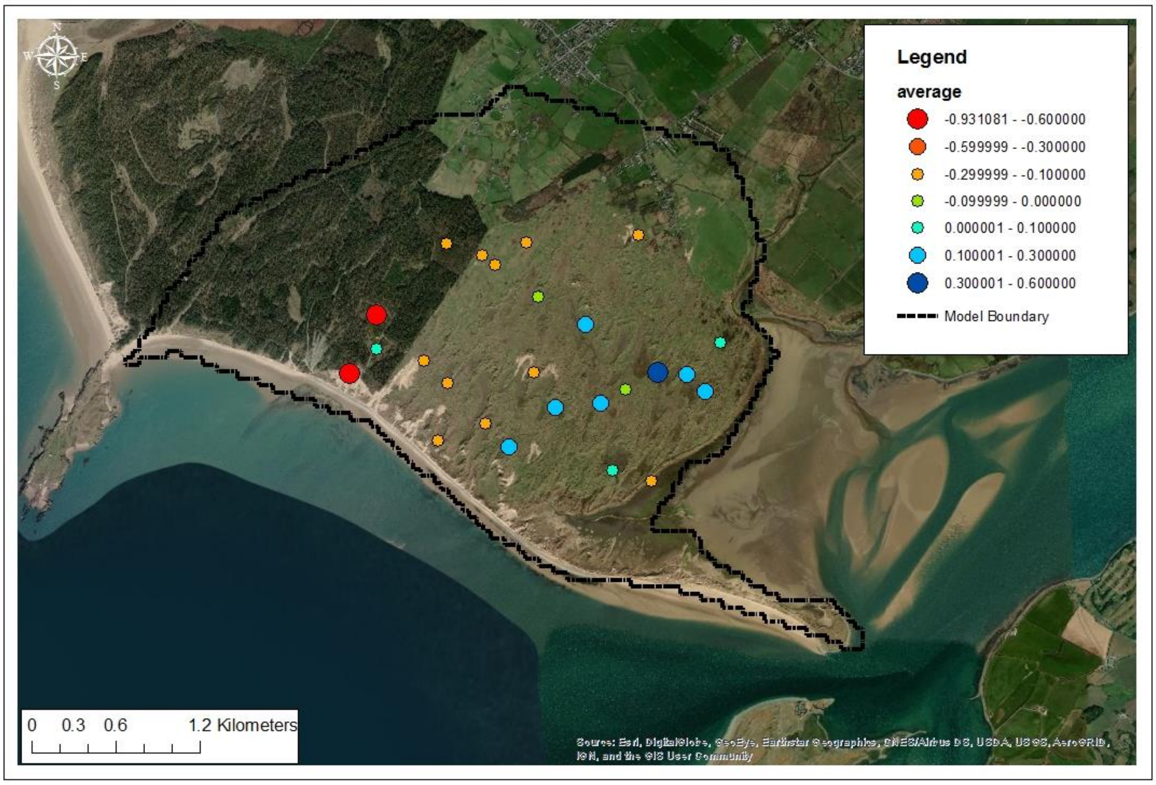

Figure 3.3 Model validation results: Average groundwater level offsets (m) over the period 2007-2018, displayed per observation well (circle locations), in which the colour indicates the model performance. The colour scale represents the offset values (m): red marks the highest underperformance (drier conditions) of the model and dark blue marks the highest overperformance of the model (wetter conditions). Offsets are calculated by the predicted groundwater levels from the standard model minus the observed groundwater levels from the observation wells.

The baseline scenario of the model performed better during summer conditions (**Figure 3.4**, Top), compared to the offset during winter (**Figure 3.4**, Bottom). In summer, eight wells showed a greater offset than ± 0.3 m, while in winter the majority of the wells showed a greater offset than ± 0.3 m. During the winter period, the dune area outside the forest had on average a higher predicted water level, creating a positive offset between 0.6 m and 1.0 m for most observation wells. The observation wells in the forest had a smaller offset in comparison, however the two forest observation wells closest to the sea had again the highest minimum offset (between -0.3 m and -0.8 m), underpredicting during both winter and summer conditions.

The timeseries of full model baseline and observed values of the observation wells 1A-1E and 2A- 2E are displayed in **Figure 3.5** for the period 2007-2017. The time series show that the seasonal pattern of peaks and low points in water table is well represented by the model, both in terms of the relative magnitude of variation and the timing over the ten years. The model performs slightly less well on the extreme high and low values, but the time series suggest a number of effects operating which partially explain some of the observed offsets. In very dry summers a number of the observation wells run dry, resulting in truncation of the observation records (**Figure 3.5**, see 1A, 1C, 2B, 2C). Meanwhile in winter at high water table conditions a number of the slacks show a truncation of the peaks, notably 1D and to a lesser extent 2C, caused by overland flow in a slack where the topography prevents ponding of water table above a certain height.

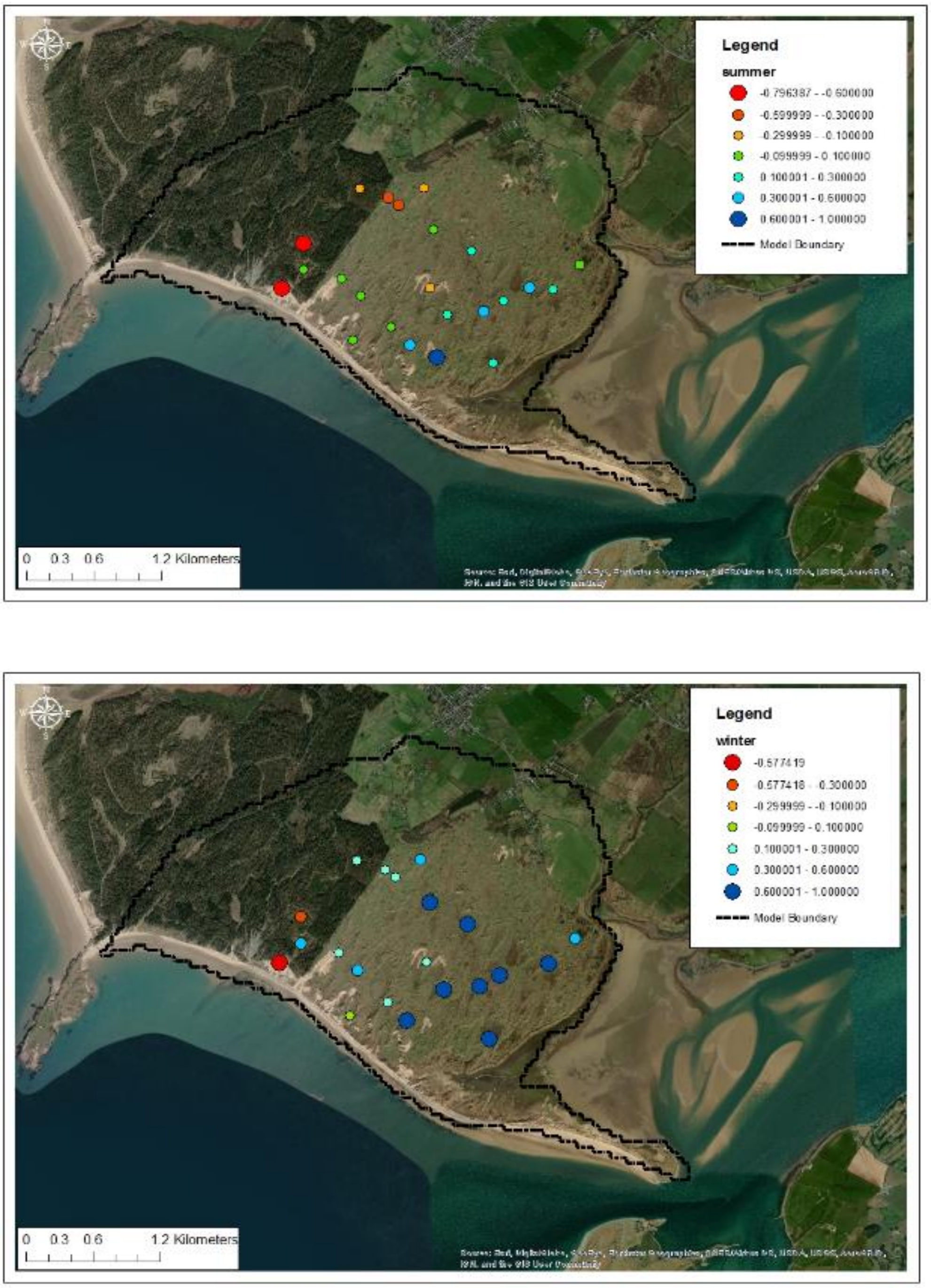

Figure 3.4 Model validation results: Groundwater level offsets (m) during summer conditions 1-7-2014 (Top figure), and during winter conditions 1-2-2015 (Bottom figure), displayed per observation well (circle locations), in which the colour indicates the model performance. The colour scale represents the offset values (m): red marks the highest underperformance (drier conditions) of the model and dark blue marks the highest overperformance of the model (wetter conditions). Offsets are calculated by the predicted groundwater levels from the standard model minus the observed groundwater levels from the observation wells.

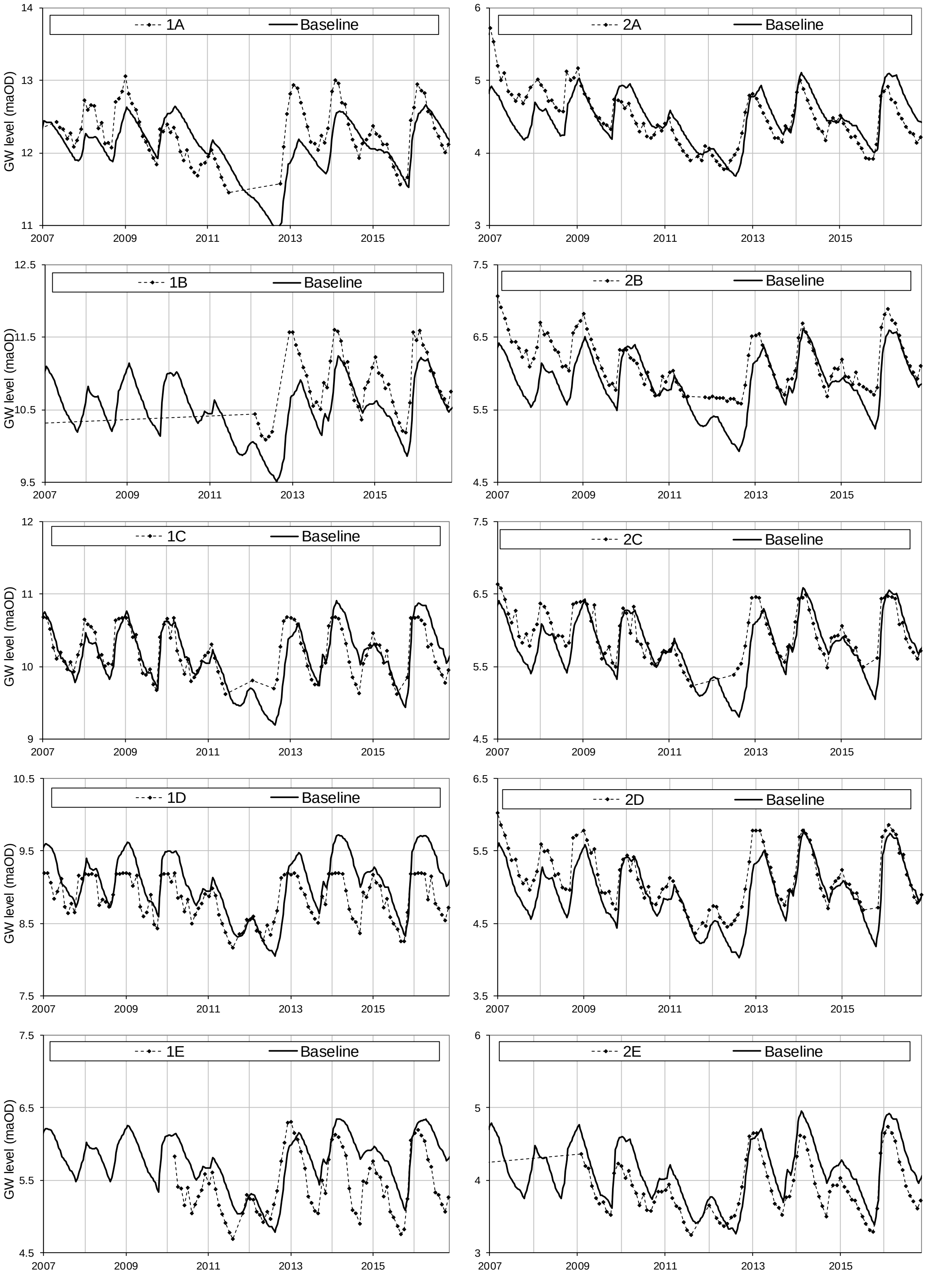

Figure 3.5 Model validation results: Predicted water levels from the baseline scenario of the model (Baseline, continuous line) and observed water levels (observation well ID, dotted line) for the transect line 1 (1A-1E) and transect line 2 (2A-2E) displayed in Figure 3.2, in meter above Ordnance Datum (maOD)).

3.3.3. Assessing management scenarios

The model output of both scenarios resulted in a change of groundwater levels compared to the baseline scenario (**Figure 3.6**). The first scenario, zero management which effectively represents the result of current management status compared with zero management, resulted in a decrease of the water level in most of the observation wells (**Table 3.2**). The highest average decrease was predicted within the forest, with an average decrease of -0.44 m in the period of 2007-2018. The effect of this scenario was also observed outside the forest, with a decrease of -0.3 m at a distance of 150 m into the dunes from the forest border, and a decrease of -0.14 m at a distance of 450 m into the dunes. At 1000 m from the forest border the decrease has been narrowed to 0.01 m (**Figure 3.6**; left panel). The second more extreme scenario, forest felling, resulted in an overall rise of the groundwater within the transect observation wells (**Table 3.3**). The rise of the groundwater level was highest within the forest with an average increase of 2.3 m (**Figure 3.6**; right panel, **Table 3.3**). The effect of the scenario was still measurable up to observation well 1E, which was 1500 m located from the forest border, with an average increase of 0.13 m (**Table 3.3**), and around 0.75 m rise at a distance of 280 m into the dunes. **Figure 3.7** shows the time series of scenario outputs and illustrates that differences in water table are broadly comparable across the seasonal pattern, despite reduced evapotranspiration effects occurring in the winter period. This suggests there are time-lags of responses of the water table to changes in inputs.

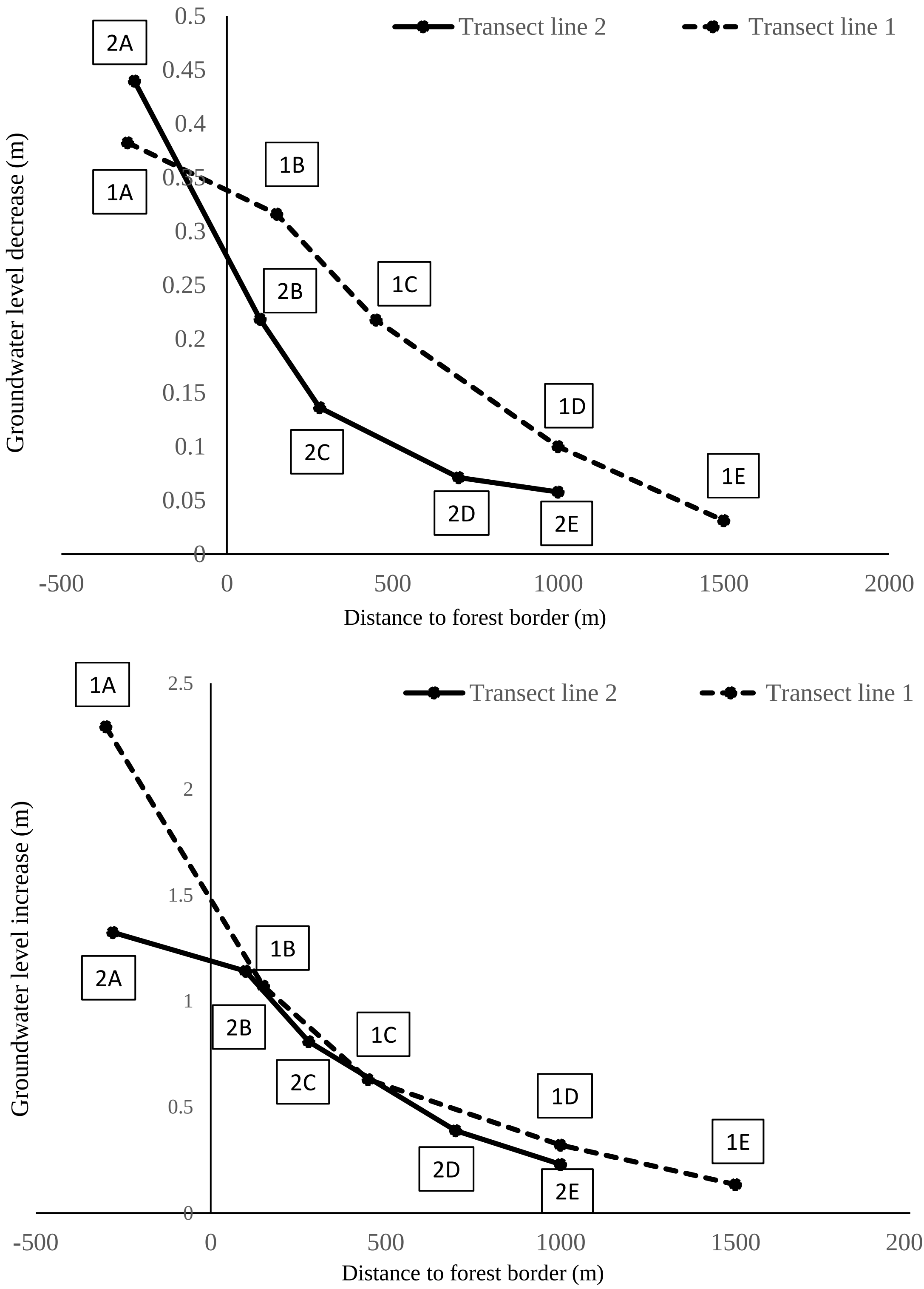

Figure 3.6 Model scenario results: zero management (left) and forest felling (right). The y axis shows the average groundwater level (m) decrease (left) or increase (right) during the period of 2007-2018, plotted against the distance of the observation wells to the forest border on the x-axis (m). The observation wells of Transect line 1 (1A-1E) and transect line 2 (2A-2E) are displayed in Figure 3.2 and the distance is reported in Table 3.2 and 3.3. *Note difference in direction of groundwater change on y axis between the two panels, reflecting the nature of the scenarios.

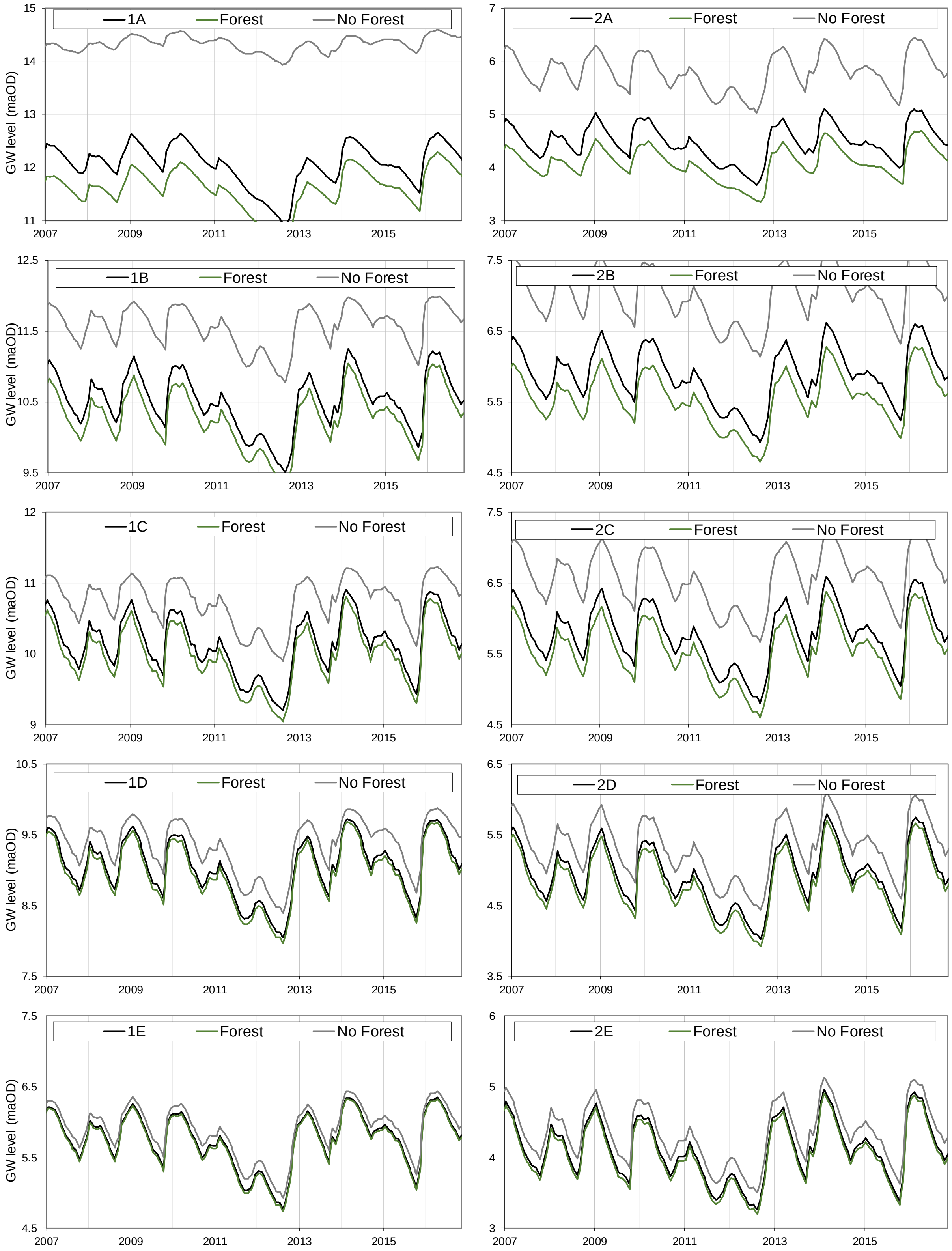

Figure 3.7 Model scenario results: Predicted water levels per observation wells of Transect 1 and Transect 2 (Figure 3.2) in meter above Ordnance Datum (maOD), from the 3 scenario of the model: zero management “Forest” (green line), forest felling “no Forest” (grey line) and normal baseline scenario “Observation ID” (black line).

Table 3.2 Model scenario results of zero management “Forest”: Predicted groundwater level decrease (average, minimal and maximal in meter (m)) of the observation wells of Transect 1 and Transect 2 (Figure 3.2) for period 2007-2018. The distance to forest border per observation well is also reported for transect line 1 (1A-1E) and transect line 2 (2A-2E) (Figure 3.2). *Note that observation well 1A and observation well 2A are located within the forest, and the other observation wells are located in the dunes along an transect line.

Observation well	1A	2A	1B	2B	1C	2C	1D	2D	1E	2E
Distance to forest border (m)	-300	-280	150	100	450	280	1000	700	1500	1000
Average decrease (m)	0.44	0.38	0.22	0.32	0.14	0.22	0.07	0.10	0.03	0.06
Min decrease (m)	0.31	0.24	0.17	0.23	0.09	0.17	0.03	0.08	0.02	0.05
Max decrease (m)	0.61	0.59	0.27	0.40	0.16	0.26	0.13	0.11	0.04	0.07

Table 3.3 Model scenario results of forest felling “no Forest”: Predicted groundwater level rise (average, minimal and maximal in meter (m)) of the observation wells of Transect 1 and Transect 2 (Figure 3.2) for period 2007-2018. The distance to forest border per observation well is also reported for transect line 1 (1A-1E) and transect line 2 (2A-2E) (Figure 3.2). *Note that observation well 1A and observation well 2A are located within the forest, and the other observation wells are located in the dunes along an transect line.

Observation well	1A	2A	1B	2B	1C	2C	1D	2D	1E	2E
Distance to forest border (m)	-300	-280	150	100	450	280	1000	700	1500	1000
Average rise (m)	2.29	1.32	1.07	1.14	0.63	0.81	0.32	0.39	0.13	0.23
Min rise (m)	1.88	1.11	0.73	1.00	0.31	0.66	0.14	0.30	0.08	0.17
Max rise (m)	3.02	1.49	1.35	1.28	0.77	0.89	0.46	0.42	0.18	0.25

3.4. Discussion

This study created a validated hydrological model using climatic data over a 10-year period, and incorporating structural variation of 27 vegetation types, at 50 m grid cell resolution. This allowed for management interventions to be modelled and predicted. The results from the felling scenarios emphasized the sensitivity of groundwater-fed dune systems to small-scale interventions (e.g., 2-ha of tree felling) right through to larger large-scale interventions such as forest felling. Therefore, there are opportunities for improving habitat quality in dune slacks as an outcome of management interventions in the forest which covers part of the site.

3.4.1. **Baseline Model**

Overall, the performance of the model over the 10-year window represented the long-time span of hydrology data obtained in the field with observation wells. This was achieved by optimization of the parameters and the availability of high quality spatial and temporal data used as inputs to the model. The high number of observation wells (30) allowed for detailed correction and intervention when needed, resulted in acceptable overall residual offsets compared with similar models (Abesser et al., 2017). There were some areas where model fit was less ideal, resulting in either high positive (wetter conditions than predicted) or negative (drier than predicted) offsets. The extreme offsets were either highly location specific, like isolated locations within the forest or in the middle of the dune site, or related to seasonality, winter or summer. Model performance can be constrained by the parameters defined in the modelling approach (Zhang & Hiscock, 2010; Abesser et al., 2017). The geological features and soil characteristics used to set the model parameters have been discussed and optimized in previous research (Betson et al., 2002; Bristow, 2003; Hollingham, 2006). Dune slack systems are often underlain by relatively simple geological features and textures (Davy et al., 2006), however the geological settings at Newborough are highly complex, and the baseline model offsets showed strong indicating for complex geological features causing localised effects, a feature also observed in some other UK sites (Jones et al., 2007).

A number of effects can alter the estimation of groundwater storage or groundwater flow. Spatial surface elements can have high impact, as the resolution of grid cells can have high impact. Our spatial resolution of 50 m x 50 m might be considered rather coarse given the dimensions of many smaller dune slacks, however compared to other models this actually can be considered to be acceptable resolution (Abesser et al., 2017). Smaller grid size models have been tested (Bradford & Acreman, 2003), however total model domain in that study was only 400 m x 400 m, to accommodate for the large site in this study would ask for high computational power. Other challenges of accurately representing geology layers or features can lead to uncertainty in the boundaries of hydraulic conductivity zones, which can affect local groundwater flow in the dune slacks. This might have been observed in the transect observation wells located in the dune slacks for example during winter, where surface flooding was observed as too high, indicating groundwater flow was either too low or groundwater storage was too high within the system for this part of the site, leading to accumulation of groundwater in the dune slacks. Locally occurring effects such as overland flow due to topography was difficult to include correctly in the model, potentially contributing to some of the discrepancies observed for high winter water tables. Another example was found within the forest, with difficulties in accurately defining bottom elevation and hydraulic conductivity. There have been indications of historical drainage, suggestions of geological faults and local springs that have all been found in parts of the forest within 100-200 m of the forest boundary. These may be contributing to some of the offsets in modelled predictions. The presence of numerous springs in the vicinity of transect 1 in the forest for example may be influencing the observations being wetter than modelled values in this location. Another reason for the mismatch in offsets can also be found within the input data, of evapotranspiration or rechange. As precipitation is a key factor for the calculation of both, there is a need for high quality climate data. Although, our weather station data quality was excellent, the location of the weather station was 10 km away and similar altitude, local differences in rainfall patterns or magnitude might affect our rainfall estimates, for example during 2012-2013. The 10-day time step has been used in other MODFLOW models (Abesser et al., 2017), but might be too slow for high hydraulic conductivity zones with complex geological features. The results do underpin the need for the combination of both optimal spatial and temporal resolution to represent the parameters used in hydrological models, to obtain accurate groundwater level predictions.

3.4.2.**Model scenario**

In this study, our scenario results were in broad agreement with previous studies using models to simulate the impact of temporal changes in groundwater regime in other dune systems (Kamps et al., 2008), or the impact of management interventions (Adane et al., 2018). The modelling output of both scenarios revealed that management interventions had a significant impact on the local hydrological system, changing recharge and groundwater levels over time. The decrease of groundwater recharge in the zero management scenario compared to the baseline model, indicated that even small-scale changes, like thinning or 2 ha felling, can lead to measurable changes in the groundwater system, with implications for the plant and animal communities dependent on groundwater within the adjacent open dune system. These findings were in line with other small scale changes in land management calculated with numerical groundwater modelling (Zhang & Hiscock, 2010; Adane et al., 2018). The study of Adane assessed for grassland to pine forest land-use conversion, resulting in a decrease of recharge of 9.58 cm in the pine plot, which are in line with our results, as we found decreases of 45 cm within and 20-30 cm close to the forest depending on distance. A groundwater level decrease of 30 cm was found as a result of afforestation in the study of Zhang (2010), was minimal compared to our results, 130 cm and 229 cm of the forest felling scenario. This can perhaps be explained by the difference in size of the forest felling and the storage ability of the sandstone aquifer in the Zhang study, which would lead to stronger decrease estimates. There also have been other reports of groundwater level changes due to pine plantations in sand dune systems (Bakker et al., 1979), in which a 60-year old pine plantation of comparable size and age resulted in a suggested drop of 30 -100 cm during the period of 1818 and 1940. In that study, possible confounding effects of climate and drainage were reported to be minimal, suggesting that the plantation of pine was the main impact on the groundwater level. Although that study was on a different dune system without metamorphic rock as a base and might be considered a rather old study, the evaporation calculations and field experiments with lysimeter measurements conducted were in line with the estimates for dune grassland, shrub and bare sand (Voortman et al., 2015; Voortman et al., 2016). The evaporation estimates used in our study were also in range with both studies and with other previously reported evaporation estimated for sand dunes (Adane et al., 2018) and pine plantations (Zhang & Hiscock, 2010). Overall, the results found in this study are consistent with other studies with some variation depending on the size of the management intervention. Both scenarios in this study show that local groundwater conditions can be influenced by management intervention, from small- to large-scale interventions were predicted to have measurable impact. Therefore, the use of hydrological modelling with management interventions can be an important tool to study the impact on wetland ecosystem and maintain optimal groundwater conditions.

3.4.3. **Recommendations and future research**

Our study confirmed the potential of using 3-D hydrological modelling to run management scenarios which may affect groundwater levels. Using future climate predictions to run our hydrological model, would be of high importance to gain better insights in future conditions for dune slack management and conservation. However, analysing future scenarios brings additional challenges in representing essential evapotranspiration processes with high accuracy in the model, as there are still many unknowns about the effect of temperature rise, or elevated CO_2 values on water use by vegetation. It is therefore important to study and analyse these effects under controlled conditions and then to incorporate these data to enable more accurate model predictions. Another way is to study these effects in separate models, either using SWAP or using species response models to analyse individual or community response (van Dam et al., 2008). Using controlled manipulations at field scale (e.g., monitoring before and after felling of well-instrumented forest blocks) will be important to validate models. In addition to the climate impact on evapotranspiration, there are also other factors which can also affect evapotranspiration which might need more recognition including plant diseases (e.g., *Dothistroma septosporum*), which causes loss of pine needles in the forest, reduction in canopy thickness and therefore evapotranspiration, or the role of invasive shrub or tree species (e.g., *Prunus serotina*) which might increase evapotranspiration within the dunes.

The hydrological modelling of groundwater level in the context of climate change can also be used to evaluate impacts on the dune slack plant communities. As dune slack vegetation is sensitive to small scale change in the groundwater level, of around 20 cm (Curreli et al., 2013), using future predictions would give insight into the future status and dynamics of these plant communities. The role of long-term hydrology data has also been emphasized in this study for calibration and validation of hydrological models, as well as for assessing impacts on vegetation. Predicted groundwater data from model outputs can also be used to generate longer time series of hydrology metrics for vegetation research (Dwyer et al., 2021a), when monitoring data is only available for short durations.

3.5. Conclusion

This study highlights the role of hydrological modelling as a tool for management, to simulate the impact of temporal changes or management interventions. Although other methods and hydrology models have been used to predict the impact of management intervention or climate on dune hydrology, this numerical model has allowed the study of sand dune forest management in greater detail, simulating events like thinning and felling while incorporating a complex array of geological and topographical features. These results are consistent with other studies and show that the level of temporal and spatial resolution has allowed for the successful prediction of the groundwater flow and seasonal dynamics such as annual flooding to be observed in the model. Thus, hydrological modelling can be an important tool in management of coastal ecosystems, especially when there is a need for long-term hydrology predictions. Future research should be focussed on adjusting evapotranspiration estimates to further improve the hydrological model, and on running scenarios of climate change projections to evaluate future management options to address this threat.

3.6. Acknowledgement

For this chapter, the initial hydrology model and model data input has been developed and set up by Adam Taylor and Rob Low. The monthly manual groundwater measurement has been conducted by Martin Hollingham for the duration of the period of 2006 -2018. Additional

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Chapter 4

Chapter 4

4. Exploring the link between dune slack habitat and the groundwater regime: hydrology metrics and intra- and inter-annual variation

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Abstract

Introduction: Dune slacks are low-lying seasonal wetlands within sand dune systems, strongly influenced by the dynamics of the local groundwater regime. The condition of dune slack habitat in the UK has been classed as ‘unfavourable and bad’ and therefore, there is a need to preserve and protect dune slack habitat. Future climate predictions indicated high impact on the hydrology of wetland ecosystems, so there is a need for a better understanding of the relationship between hydrology and dune slack vegetation.

Aim: To expand our knowledge we explored a variety of approaches to understand and reliably characterise the relationship between dune vegetation and the likely to be affected hydrological regime. We tested different calculation methods based on the mean Ellenberg indicator for soil moisture (EbF) to characterise vegetation status or response, and tested a wide selection of hydrology metrics to understand the inter- and intra- annual variation between vegetation and hydrology over multiple years. Specifically, we address these questions: I. Which hydrology metrics have the strongest affinity to dune slack vegetation mean EbF values? II. How does inter-annual variability affect the relationship? III. Which hydrological year best represents the relationship between vegetation and hydrology?

Location: Newborough Warren, North Wales, United Kingdom.

Methods: Vegetation monitoring consisted of 81 permanent plots across 17 dune slacks, set up in 2010 (Curreli et al., 2013) and repeated for six years (2012, 2013, 2015, 2017, 2018, 2019). Each dune slack had 3 to 8 plots of 1m x 1m, arranged around a co-located piezometer. Hydrology metrics (maximum, minimum, median, average, mean spring level) were composed out of monthly measured groundwater levels, and corrected for plot and piezometer elevation using surveyed DGPS data with 1 cm vertical accuracy. Statistical analysis was conducted according to the research questions.

Results: The highest correlation coefficients were found with the hydrology metrics was the unweighted 5-year average MSL. Within our study we also found that the relationship between hydrology metrics and mean EbF displayed inter-annual variation with different patterns and correlations between years. Exploring this finding within dune slacks, we found that there are strong indications that "dry" and "wet" years have different impacts on dune slacks, and might be constrained by time lags or different thresholds depending on the type of dune slack. The standard time period input for hydrology metrics runs from 1st June till 30th May, definition for a hydrological year, was found to be sufficient for future research.

Conclusions: This study re-established the presence of a strong direct relationship between hydrology and vegetation, in which hydrology metrics were linked to mean EbF response in dune slack habitat. Results indicated that dry and wet hydrology years have different impacts on dune slacks, and might be constrained by time lags or different thresholds depending on the type of dune slack. Understanding the mechanisms behind the inter-annual variation of the relationship will most likely be imperative for dune slack management against climate change. Hydrology metric MSL would be most practical to implement within manual monitoring programmes, which could be set to 3-months per year as a minimum requirement. Using longer averaging periods with short term measurements for hydrology and co-located vegetation monitoring is key to gaining an improved understanding of dune slack resilience. The ability to predict thresholds of dune slack habitat is of high importance for management and conservation of dune slack habitat.

Keywords: Vegetation, Hydrology, Metrics, Ellenberg, Plant community, Response.

4.1. Introduction

Dune slacks are seasonal wetlands within coastal sand dune systems, known for their ability as habitat to obtain high diversity, strongly influenced by the dynamics of the local groundwater regime (Grootjans et al., 2004). Dune slacks experience high inter- and intra-annual variation of the water table (Ranwell, 1959; Jones et al., 2006); although seasonal flooding occurs every few years, the annual water table range is always close to the surface. The low-lying areas are enclosed with dune ridges and can vary in shape, size and age, resulting in a variety of dune slack communities along a gradient of hydrology (Berendse et al., 1998; Grootjans et al., 1998; Sýkora et al., 2004). However, the condition of dune slack habitat in the UK has been classed as ‘unfavourable and bad’ and was still declining during the last decade (Stratford, 2014). Anthropogenic influences like eutrophication, drainage, water extraction and afforestation have contributed towards the stabilization of the dynamic habitat, reducing and degrading dune slack habitat (Bakker, 1981; van Dijk & Grootjans, 1993; Rhind et al., 2007; Provoost et al., 2011; Rhymes et al., 2014). On top of that, future climate predictions indicated high impact on dune slack habitat (Clarke & Sanitwong Na Ayutthaya, 2010). Sea water level and annual precipitation can be important controls of the phreatic water zone within a dune system, and both will irreversibly impact the timing and amount of water available in the future. Temperature rise, summer droughts and longer growing seasons will affect total evapotranspiration and soil moisture availability, which is likely to increase the dependence on phreatic water zone even more (Kamps et al., 2008; Witte et al., 2012). In order to ensure preservation and protection of dune slack habitat, there is a urgent need to expand our knowledge of the relationship between dune vegetation and the likely to be affected hydrological regime, with special focus towards variability linked to climate change predictions (Martins et al., 2018).

Dune slack habitat has been classified using hydrology metrics (Davy et al., 2010), in which the suite of dune slack plant communities can be separated by 40 cm in the 5-year average winter water table in the UK (Curreli et al., 2013). Also several studies in the Netherlands have used hydrologic metrics to describe hydrology management of dune slack plant communities, although the role of soil- and water-chemistry is highlighted within the context of hydrology (Lammerts & Grootjans, 1998; Lammerts et al., 2001; Aggenbach et al., 2002). The link between hydrology and dune slack vegetation has also recently been re-confirmed in UK field studies (Dwyer et al., 2021b; Dwyer et al., 2021a). However, despite the strong role of hydrology driving dune slack community structure, the relationship showed displayed plasticity in response to environmental conditions, like atmospheric nitrogen deposition or organic matter in the soil (Dwyer et al., 2021a). Although we have good knowledge of the long-term impacts and thresholds within the dune slack habitat, there is less known about the dynamics around those limits. To understand the impact of climate change, there is more research necessary to understand how the dynamics around hydrology and dune slack vegetation are affected in the future. Therefore, there is a need to re-analyse_the relationship of hydrology and dune slack vegetation in the context of climate-induced variation.

The impact of hydrology on dune slack vegetation has been well studied using quantitative hydrology metrics (Lammerts et al., 2001; Davy et al., 2010). Hydrology metrics are often used to summarize variability of the phreatic groundwater zone, representing a link towards environmental and climate conditions, which can be used to explain general patterns of succession (Davy et al., 2006), niche boundaries of plant species (Aggenbach et al., 2002; Kooijman et al., 2016b) or community composition (Lammerts et al., 2001; Curreli et al., 2013). The hydrological metrics used to describe or test relationships with vegetation vary in the literature. Spring water level has been used to characterize vegetation communities or has been tested in relation to Ellenberg indicators reflecting ecological tolerance (Wamelink et al., 2002; Käfer & Witte, 2004). Other hydrological metrics that have been used in research on wetland vegetation are: median water level (García-Baquero Moneo et al., 2022), average water level (Dwyer et al., 2021a), winter water level (Curreli et al., 2013) or multiple metrics (Rhymes et al., 2014). Although these metrics are to a large degree correlated (Curreli et al., 2013), few studies have systematically tested which give the strongest relationship with vegetation response. Even fewer still have tested how the hydrology-vegetation relationship changes over different time frames of hydrological summary (Bartholomeus et al., 2008). Including a broader range of temporal data will help to understand the dynamics and response of dune slack communities around hydrological thresholds. To study and understand vegetational change, Ellenberg indicators have been popular as plant and bryophyte based metrics, and been often used to quantify relationships with hydrology metrics (Schaffers & Sýkora, 2000; Diekmann, 2003). Originally designed for plant species in Central Europe and adapted for the UK, Ellenberg indicator values can be used to indicate local environmental conditions derived from species community composition, as each species has an individual indicator value assigned based on expert knowledge representing their habitat preference or ecological niche (Ellenberg et al., 1991; Hill et al., 2004). For instance, Ellenberg soil moisture (EbF) indicates ranges from dry (1) to wet (9) to very wet/submerged (10-12). Previous studies have shown that the Ellenberg indicator for soil moisture often displays a high correlation with hydrology metrics and can be used as a quantitative measure for modelling or to monitoring for management (Ertsen et al., 1998; Schaffers & Sýkora, 2000; Käfer & Witte, 2004; Brunbjerg et al., 2012; Dwyer et al., 2021a). Ellenberg indicators can also be excellent for studying community response, as they can reveal small scale changes governed by the sensitivity of the dune slack vegetation to hydrological conditions (Curreli et al., 2013; Dwyer et al., 2021b). If these small scale changes can be reflected in hydrology metrics, this can be very useful for monitoring and management, particularly in the context of detecting ecological responses to climate change.

Therefore, in this study we explored a variety of approaches to understand and reliably characterise the relationship between hydrology and dune slack vegetation. We tested different calculation methods based on the mean Ellenberg indicator for soil moisture (EbF) to characterise vegetation status or response, and tested a wide selection of hydrology metrics to understand the inter- and intra- annual variation between vegetation and hydrology over multiple years. This will increase our knowledge of climate-induced responses, and allow us to determine what the more robust hydrology metrics will be for future management. Specifically, using dune slack wetlands, we addressed these questions: I. Which hydrology metrics have the strongest affinity to explain dune slack vegetation mean EbF? II. How does inter-annual variability affect the relationship? III. Which hydrological year best represents the relationship between mean EbF and hydrology?

4.2. Methods

4.2.1. Study site

This study was conducted at Newborough Warren, a large dune system of 1295 ha, located on the Isle of Anglesey, North Wales (53°08’56”N, 4°21’38”W). The dune system is bounded by two estuaries and a rock ridge, consisting of Holocene aeolian calcareous sands that overlie glacial till deposits, resting on Palaeozoic and Precambrian basement (Bristow & Bailey, 1998). Between 1947 and 1965, the western side of the warren was afforested with Corsican pine (*Pinus nigra* ssp. *Laricio*) (Hill & Wallace, 1989). The remaining east side of the site has developed as open dune grassland with four lines of parabolic dunes containing a high number of dune slacks. The site is managed by livestock grazing with sheep, cattle and Welsh mountain ponies since 1987 (Plassmann et al., 2010). Local climate can be described as mildly oceanic with an long-term average annual rainfall of 872 mm between 2006 and 2019 (RAF Valley station; (Met Office, 2012)). The area is officially designated as a Special Area of Conservation (SAC), a National Nature Reserve (NNR) and a Site of Special Scientific Interest (SSSI) and managed by Natural Resources Wales.

4.2.2. **Vegetation survey**

To gain a better understanding of relationship between vegetation and hydrology regime, a total of 453 quadrats were surveyed across 17 dune slacks at Newborough Warren. Vegetation monitoring was set up with 81 permanent quadrats, surveyed in 2010 (Curreli et al., 2013), and repeated between 2012-2019 (**Table 4.1**). Each dune slack contained 3 to 8 permanent quadrats of 1 m × 1 m, arranged in four directions (N, W, S, E) around a co-located piezometer, unless the topographic variability would result in a location outside the margin of dune slack vegetation. Quadrats are marked with discrete corner posts to allow exact re-location. Plant and bryophyte species presence and abundance (percentage) were recorded using the nomenclature of Stace for vascular and non-vascular plant species (Stace, 2019) and the nomenclature of Atherton for bryophyte species (Atherton et al., 2010).

4.2.3. **Ellenberg indicator for soil moisture (EbF)**

The mean Ellenberg values for soil moisture (EbF) were calculated for each quadrat using the PlantATT database for vascular plants and bryophytes, which were recalibrated for the UK (Hill et al., 2004). Both presence-only and cover-weighted mean EbF quadrat values were calculated using the software R (R Core Team, 2021). Preliminary analysis showed that the optimal correlation coefficients were obtained using the plant presence-only data (Appendix,**Table 0.3**), similar to previous work on optimalization of EbF for calibration (Käfer & Witte, 2004). There is a risk of over-weighting rare and low-cover species when excluding abundance data (Schaffers & Sýkora, 2000). However rare species are often better qualified as indicator species as they have strong habitat preference and usually a relatively narrow ecological niche (Wamelink et al., 2014). As dune slack habitat is well represented with rare low cover species, we expect the presence-only data to be more sensitive to compositional change in response to hydrology. For these reasons, we selected the mean EbF values based on presence-only data for our analysis. Preliminary analysis also showed higher correlation coefficients using mean EbF dependent on vascular plants only, compared to corelation coefficients of mean EbF dependent on both bryophytes and vascular plants (Appendix, **Table 0.3**). Therefore, we used mean EbF for vascular plant species only for scope of the study.

4.2.4. **Hydrology data**

Phreatic groundwater levels were recorded at each piezometer, monthly measured from 2006 to 2019. Measurements were represented as metres above ground surface (i.e. -0.65 stands for 0.65 m below ground surface), corrected for upstand of the piezometer above ground level in meter (m). Each piezometer was located within 7 m reach of the vegetation quadrats to ensure similar groundwater conditions with acceptable variation (Curreli et al., 2013; Dwyer et al., 2021a).

Table 4.1 Monitoring list of piezometers with co-located number of quadrats for each monitoring year.

No.	Piezometer	2010	2012	2013	2015	2017	2018	2019
1	CEH8	3	3	3	3	3	3	3
2	CEH24	3	3	3	3	3	3	3
3	WMC2	3	3	3	3	3	3	3
4	CEH23	5	4	4	4	5	5	5
5	CEH26	5	4	4	4	5	5	5
6	NW3	4	3	3	3	4	4	4
7	CEH9	7	6	6	6	7	7	7
8	CEH22	7	7	7	7	7	7	7
9	NW4	8	7	7	7	8	8	8
10	T41A/B/C/D	7	7	7	7	7	7	7
11	CEH4	3				3	3	3
12	CEH5	5				5	5	5
13	NW5	4				4	4	4
14	NW6	5				5	5	5
15	CEH1	4				4	4	
16	NW2	4				4	4	
17	NW7	4				4	4	
Total	Total	81	47	47	47	81	81	69

4.2.5. **Topographical induced variation**

To ensure high accuracy of the hydrology metrics for analysis, the elevations of all piezometers and vegetation quadrats have been surveyed using a Leica 1200 RTK dGPS, with a vertical accuracy of < 10 mm (Curreli et al., 2013). This allowed us to correct for elevational differences between quadrats and piezometer to ensure accurate relationships between the hydrology and the vegetation data.

Figure 4.1 Arial map of monitoring locations indicated with number (Table 4.1) of Newborough, Wales.

4.2.6. Hydrology metrics for co-located quadrats

To test the relationship between hydrology metric and mean EbF, 80 hydrology metrics were calculated using the hydrological data from 2010-2019 (Appendix, **Table 0.2**). Each “hydrology metric” summarizes a component of the hydrology year for example the minimum (MIN), mean, median or maximum (MAX) of the groundwater level during a hydrology year (**Table 4.2**). A “hydrology year” is defined as the period of 12 months prior to the vegetation monitoring, running from 1st of June in the previous year until the 31st of May of the year of vegetation monitoring.

Table 4.2 Hydrology metrics component list.

Hydrology metric Components	Description (+ period before vegetation monitoring)
MSL	Mean spring water level (1st March to 31st May)
MIN	Minimal water level (1st June to 31st May)
MAX	Maximum water level (1st June to 31st May)
Median	Median (1st June to 31st May)
Mean	Mean (1st June to 31st May)
10% Percentile	10% Percentile water level (1st June to 31st May)
90% Percentile	90% Percentile water level (1st June to 31st May)
95% Percentile	95% Percentile water level (1st June to 31st May)
Mean Summer	Mean summer water level (30st June - 31st August)
Mean Winter	Mean winter water level (31st December- 28th February)

To calculate the muti-year hydrology metrics for this study, we averaged the hydrology metrics over a period of 1 up to 8 years. For example, the 2-year average MAX, represents the average of the 2 MAX of 2 hydrology years before vegetation monitoring. We, therefore had different combinations of components of intra-annual variation of the hydrology regime (min, max, msl, etc.) averaged over different combinations of inter-annual variation (1 to 8 years).

A second range of muti-year hydrology metrics was created defined as “weighted hydrology metrics”, in which the hydrology metric was multiplied with “weights” for each year in the calculation, before averaging (**Equation 1**). This was to emphasise the role of the most recent event in the series of inter-annual variation, resulting in the highest weight coupled with the most recent hydrology years’ hydrology metric. For example, a 3-year weighted mean would be calculated as in **Equation 2**. The full list of hydrology metrics can be found in the Appendix, **Table 0.2.**

Equation 1. The weighted hydrology metric calculation

$$\mathrm{iM_j} = \frac{\sum\left(\mathrm{i} * \mathrm{M_j} + (\mathrm{i}-1) * \mathrm{M_{j-1}} + (\mathrm{i}-2) * \mathrm{M_{j-2}} \ldots + (\mathrm{i}-\mathrm{n}) * \mathrm{M_{j-n}}\right)}{\sum(\mathrm{i} + \mathrm{i} - 1 + \mathrm{i} - 2 \ldots + \mathrm{i} - \mathrm{n})}$$

iM_j is explained as: i = the averaging period, number of years. M = hydrology metric and j = year of the metric. The metric calculation is as long as n = i, the number of years included.

Equation 2. Example of 3-year weighted mean of 2018

$$i = 3\ year, \mathrm{M} = \mathrm{Mean}_{,\mathrm{j}=2018} = \frac{\sum(3 * \mathrm{M}_{2018} + 2 * \mathrm{M}_{2017} + 1 * \mathrm{M}_{2016})}{\sum(3 + 2 + 1)}$$

4.2.7. Data analysis

We tested the relationship between dune slack vegetation and hydrology, analysing the relationship between the hydrology metrics and mean EbF. We explored a variety of approaches to understand and reliably characterise the relationship between hydrology and dune slack vegetation, using different calculation methods based on the mean EbF to characterise vegetation, and a wide selection of hydrology metrics to understand the inter- and intra- annual variation between vegetation and hydrology over multiple years. Statistical analysis was undertaken in SPSS v.27 (IBM Corp, 2020) to obtain correlation coefficients, as listed per focus of the research questions:

I. Full range analysis of mean EbF and hydrology metrics

To test for the strongest affinity between hydrology metrics and dune slack vegetation, we used Pearson's correlation test between 80 hydrology metrics (Appendix, **Table** 0.2) and the mean EbF values of the 2018 data (81 vegetation quadrats, **Table 4.1**). The year of 2018 was selected based on the longest available time period for the hydrology metrics in combination with the highest number of quadrats. There is a potential risk of pseudo replication because of spatial autocorrelation without correcting for nesting within dune slacks or to co-located piezometers.

II. Inter-annual variation

In order to determine influence of the inter-annual variation on the relationships, three years of data were selected for separate statistical analysis (2017, 2018, 2019). For each year, a subset of 69 vegetation quadrats was tested using the Pearson's correlation test between mean EbF values and selected hydrology metrics. Based on results from the first question, the two highest performing hydrological metrics were selected (MAX and MIN) and assessed for multiple hydrology years (1-7 years). To gain more perspective to understand the inter-annual variation within the dune slack habitat, another subset of 47 quadrats mean EbF were plotted against MAX, MIN and MSL, to display the full time span of the vegetation monitoring in this study (2010-2019, **Table 4.1**). Within this subset, 2 dune slacks have been selected to show inter-annual pattern of the mean EbF variation on dune slack level. As last part of this research question, we plotted one of the metrics resulting from research question I with the high affinity against the mean EbF response for 2017, 2018 and 2019 with separate lines to visualize the inter-annual effect.

III. Hydrology year

To assess the optimal monitoring year for calculating the hydrology metrics, three different periods were selected for their impact on the associations between hydrology metrics and mean EbF (Figure 4.2). These periods were: Hydrological year A (1st of March till the 28st of February), hydrological year B (1st of June till the 31st of May, which can be regarded as the standard "hydrological year" up till now) and hydrological year C (1st of September till the 31st of August). To compare the different hydrological years, the subset of 69 quadrats mean EbF data were re-analysed against the newly created hydrology metrics with Pearson's correlation test the years 2017, 2018 and 2019.

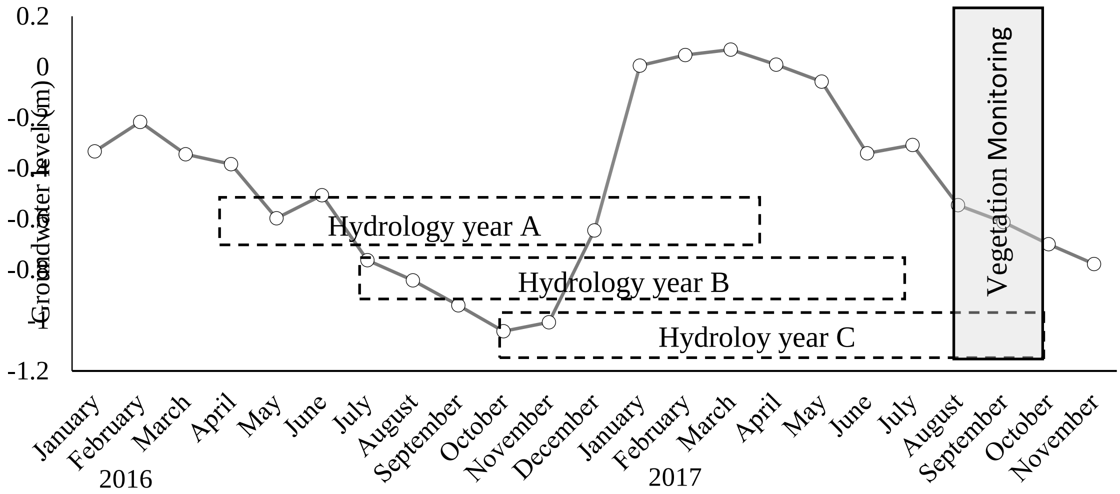


Figure 4.2 Hydrograph of the groundwater level (m) per month of a dune slack, running from January 2016 till end of the year of 2017. Illustrating the term of "hydrology year" with three different time periods: Hydrology year A, B and C which are marked by the dashed blocks. The light grey lined block marks the period of vegetation monitoring corresponding to the hydrology year. Ground surface is 0, negative values represent water levels below ground surface.

4.3. Results

4.3.1. Which hydrology metrics have the strongest affinity to dune slack vegetation mean EbF values?

The Pearson's correlations exploring the relationships between hydrology metrics and mean EbF ranged from 0.71 (moderate affinity) to 0.80 (high affinity), Appendix, **Table 0.3**, column - EbF 1a. The components of hydrology metrics with the highest affinity were the maximum water level (MAX) and spring mean water level (MSL) had the highest positive correlations (r = 0.83 - 0.86 **(Figure 4.3)**. In general, all associations with mean EbF increased when multiple hydrology years were included in the summarisation of the hydrology metrics. The weighted metrics did often not increase the strength of the correlations. Based on these findings, the non-weighted hydrology metrics with MAX and MSL were used for further analysis. Although the 90th and 95th percentile and winter maximum levels also had high correlations, for the sake of simplicity of calculation by site managers, MAX was chosen for further analysis.

4.3.2. How does inter-annual variability affect the relationship?

The influence of the inter-annual variation on the found relationships between hydrology metrics and mean EbF resulted in Pearson's correlation coefficients from 0.73 (moderate affinity) to 0.85 (high affinity), depending on vegetation monitoring year (2017-2019), hydrology years included (1-7) and hydrology metric (MAX or MSL) (**Figure 4.4**, Panel B, D and F). There was also considerable inter-annual variation shown in the hydrology metrics, with the 1-year MSL varying between -0.53 m and -0.27 m and 1-year MAX between -0.43 m and -0.20 m (Panel A, C and E, **Figure 4.4**).

The correlation coefficients of 2018 were found to be constant for both hydrology metrics MAX and MSL, varying between r = 0.78 and r = 0.82, in which the averaging period had little effect on the relationship (Panel D, **Figure 4.4**). A different pattern was observed for 2017 and 2019, where the correlations coefficient increased when averaging more seasons in the hydrology metric (Panel B and F, **Figure 4.4**). In single years, and over short-averaging periods, there was shift in the most significant metric between years (MAX or MSL). In 2017, MSL had higher positive correlations and MAX in 2019. The role of weighting the hydrology metrics almost never increased the correlations, but did show a more constant pattern when adding multiple hydrology seasons. The highest positive correlation was found between the 4 year average MAX and EbF r = 0.85 in 2017. In general, the correlation relationship stabilises around the 5-7 hydrology years average (+/- weighted) for both of the hydrology metrics.

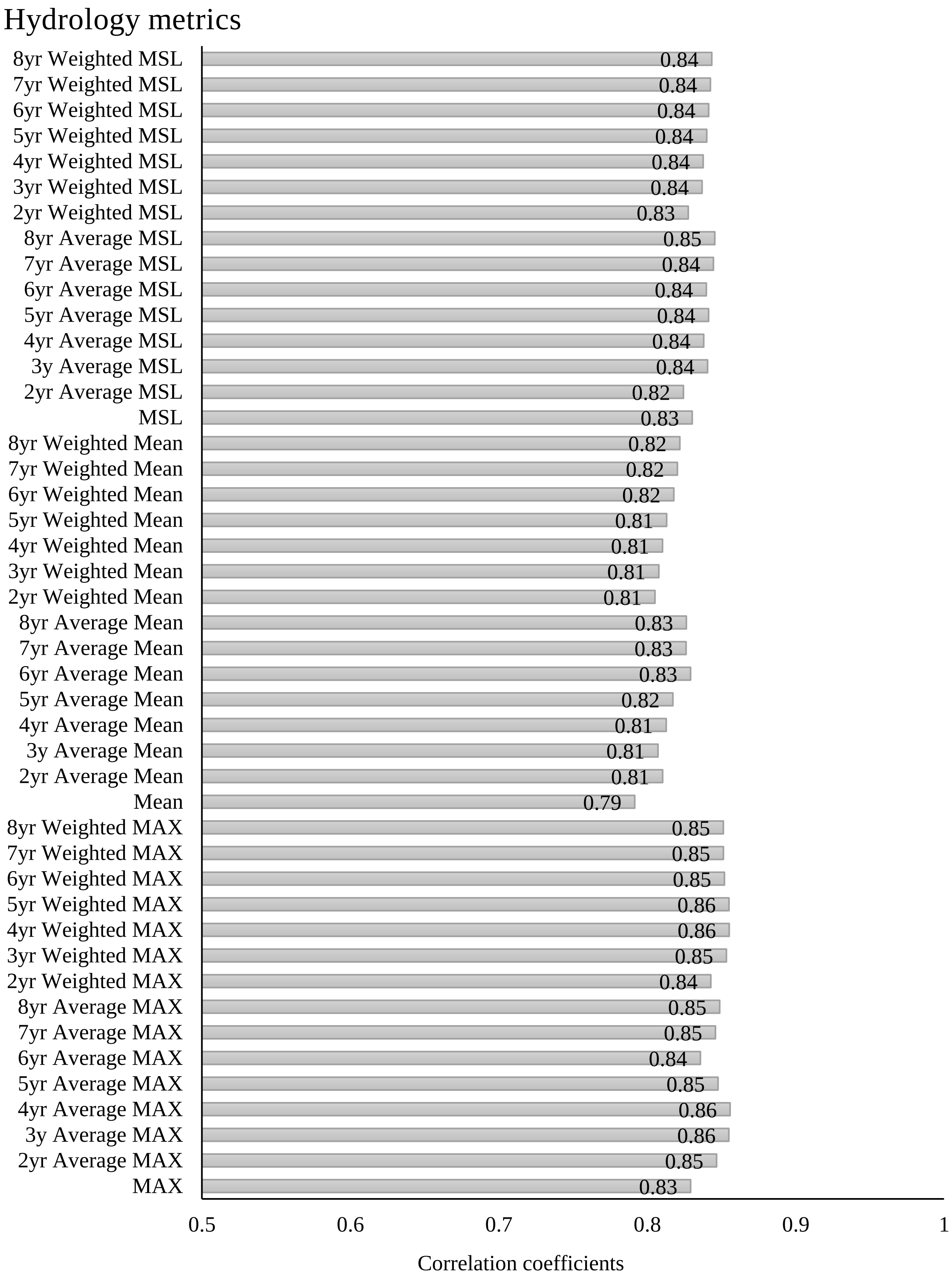


Figure 4.3 Pearson's correlation between mean Ellenberg values (EbF) and families of hydrology metrics from 81 vegetation quadrats of 2018 only. The displayed hydrology metrics contained the 1-8 hydrology year(s) average or weighted average of a hydrology metric component (mean water level, spring water level (MSL) or maximum water level (MAX)). All correlations were significant at $p < 0.05$.

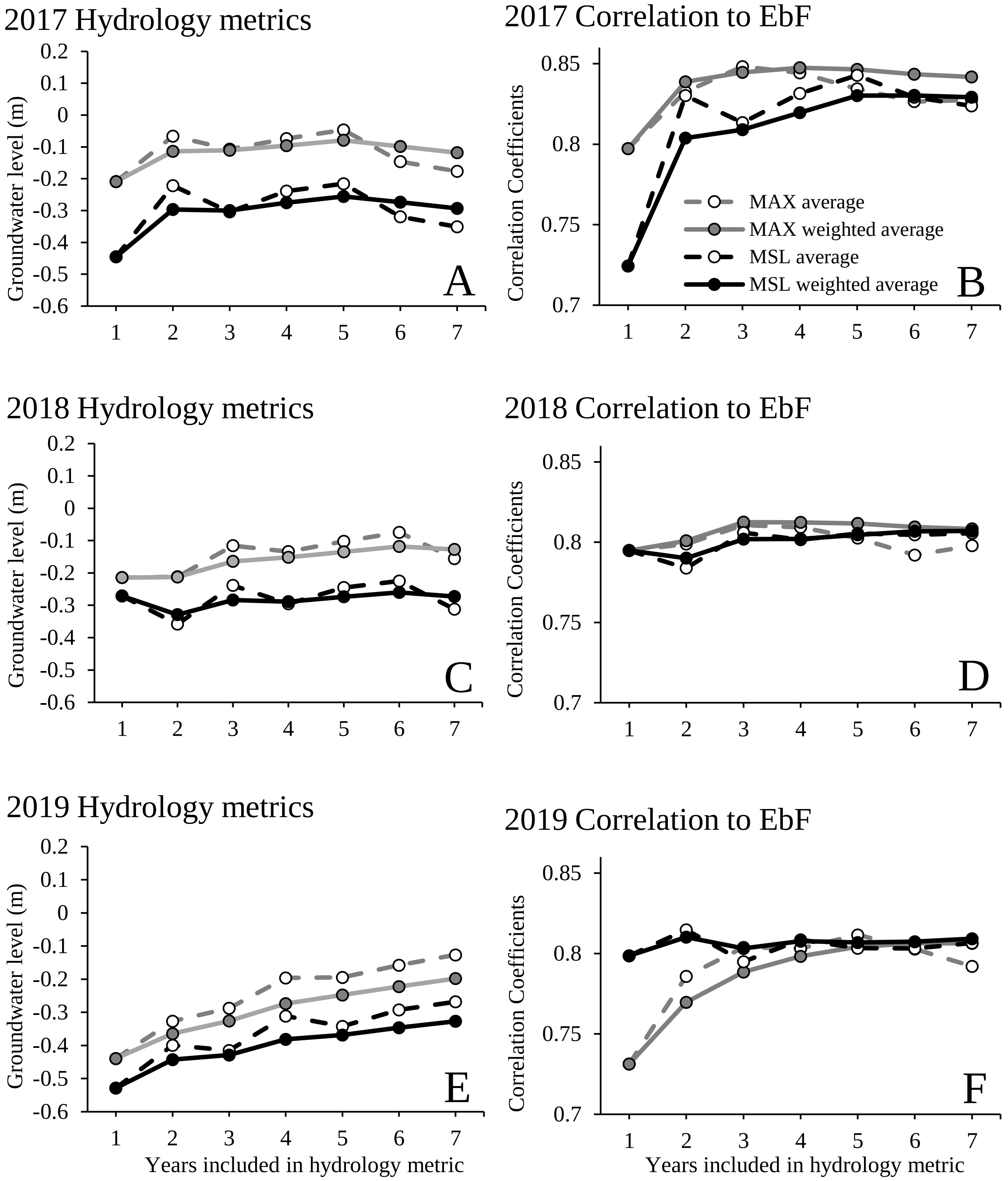
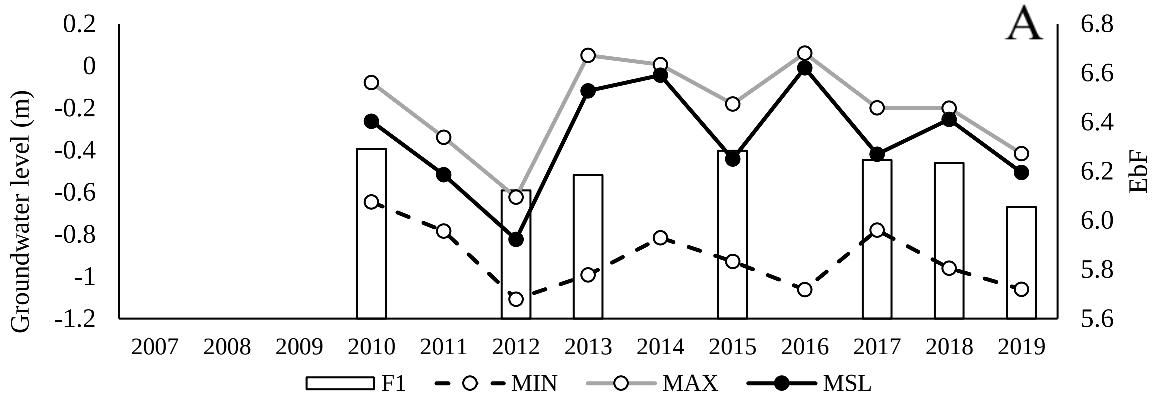
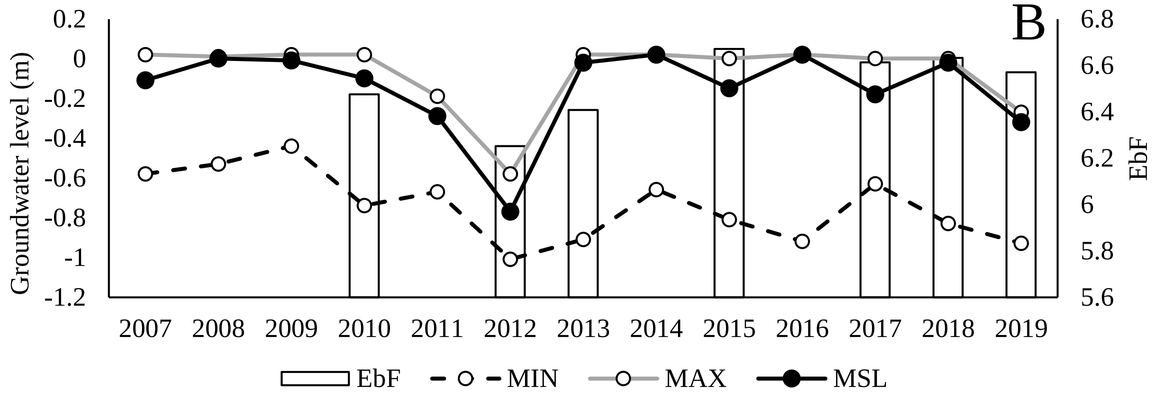


Figure 4.4 An overview of the hydrology metric values (Panel A, C and E) and Pearson's correlations coefficients with mean EbF (Panel B, D and F) of 69 vegetation plots for monitoring year 2017, 2018 and 2019. Each panel has data of 69 quadrats, the monitoring year is displayed above the left upper corner of the panels. For panel A, C and E, groundwater level (m) on the y-axis, ground surface is 0, negative values represent water levels below ground surface, and for panel B, D F the correlation coefficients are on the y-axis. All panels have the x-axis displaying the number of hydrology years (1-7) included in the (weighted) average of the hydrology metrics (MAX and MSL). The legend of the hydrology metrics for all plots is in plot B. All correlations were significant at $p < 0.05$.

Figure 4.5, Panel A summarises the annual variation for the hydrology metrics MIN, MAX and MSL of 47 quadrats with data spanning the period of 2010-2019. Hydrology metrics are calculated only for that monitoring year (i.e. no multi-year averaging). MAX and MSL display a similar patter over time, but differ from MIN, where the inter-annual variation of MIN is smaller and the pattern differs substantially from MAX and MSL in some years. The response of mean EbF to the hydrology metrics is broadly similar to that of MAX and MSL; higher values were found in response to wetter seasons 2012-2013 (+0.06 mean EbF) and lower values in drier seasons 2018-2019 (-0.18 mean EbF), corresponding with the previously found correlations. Although the general pattern is similar, the response of mean EbF is not consistent over the whole period; in 2018-2019 there is a strong decrease in mean EbF (-0.18 mean EbF) in response to a relatively small decrease in MSL and MAX (-0.21 m MSL, -0.25 m MAX). During the period 2010-2012 the decrease in mean EbF over this period is similar (-0.17 mean EbF), but the decrease in MSL and MAX is greater (-0.54 m MSL, -0.56 m MAX). In response to re-wetting, during the period of 2012-2013 MAX and MSL have increased to levels above those of 2010, mean EbF has increased (+0.06 mean EbF of the +0.16 mean EbF). Overall, the apparent non-linear response of mean EbF to the one year hydrology metrics suggests the presence of additional mechanisms governing the response of vegetation to changes in hydrology.

Figure 4.5, Panel B and C, illustrate the mean EbF response at dune slack level two individual dune slacks (Panel B: NW4, a wetter dune slack and panel C: NW3, a drier dune slack) for the period 2007-2019. The hydrology metrics MSL, MAX and MIN of dune slack NW3 had more negative values (drier conditions) compared to the dune slack NW4. The mean EbF values were also different between the dune slacks, in range (NW4 6.25-6.7, NW3 5.85-6.2), but also showing different inter-annual patterns. During the period of 2012-2013, the mean EbF of NW3 did not change much (-0.05 mean EbF), showing no direct or positive effect in response to the increase in groundwater levels, while NW4 does show an increase in mean EbF (+0.15 mean EbF). The response to decreases in the hydrology metrics resulted in a similar response between dune slacks, however the decrease in mean EbF within dune slack NW3 was more profound. For example the period 2018-2019, NW4 had a decrease of -0.6 mean EbF versus the decrease in NW3 -0.23 mean EbF, while the decrease in MSL was for both dune slack -0.3 m.


47 quadrats


Dune slack NW4

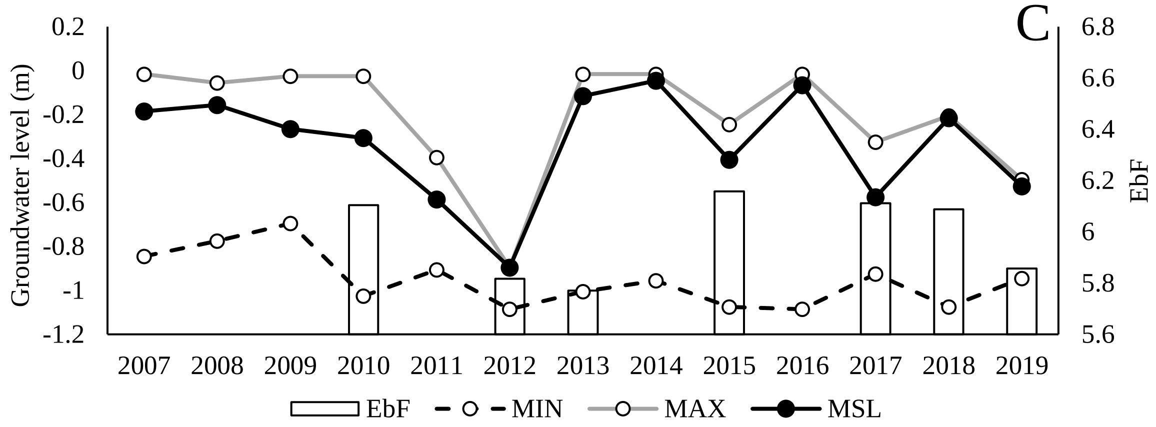

Dune slack NW3

Figure 4.5 Hydrology metrics (MAX, MSL and MIN) groundwater level value (m) and mean EbF values for: 47 quadrats (Panel A), dune slack NW4 (Panel B) and dune slack NW3 (Panel C), plotted over time (2007-2019). Hydrology metrics MIN, MAX and MSL are displayed with solid or dashed lines on the left y-axis (groundwater level, m) and mean EbF is displayed with bar plots on the right y-axis. The years 2011, 2014 and 2016 have only mean values for MSL, MAX and MIN; there was no vegetation monitoring. Hydrology data was shown 2007 onwards in Panel B and C to give the picture of the preceding years' hydrology regime of the plots. Ground surface is 0, negative values represent water levels below ground surface.

To further analyse the effect of the inter-annual variation of the relationship between mean EbF and hydrology metrics MAX and MSL, we used the multiple-year average, the 5-year average of MAX and MSL (**Figure 4.6**), as most of the correlation coefficients stabilized after including 5 hydrology years (**Figure 4.4**). All years had a similar positive linear relationship between EbF and MAX or MSL, but each year had a slight offset in slope and intercept. The year 2017 and 2018 appear comparable in relationship, for MSL almost identical, the trendlines show similar slope and mean EbF range but a different intercept. The drier year of 2019 has a steeper slope and lower intercept of the relationship, both MSL and MAX, separating itself from the other years. The steeper slope of 2019, resulted in a more positive relationship, in which lower mean EbF values were found at drier conditions of the hydrology regime, but with the increase in groundwater level leads to an increase in mean EbF at a higher rate than 2017 and 2018, almost the linear relationship of 2017 and 2018. The maximal of mean EbF values of 2019 were also lower in comparison to 2017 and 2018, but the lowest mean EbF values remain the same for all years. Overall, the results and data show the presence of considerable inter-annual variation in hydrology regime and the mean EbF response, resulting in different linear relationships, at least at dune slack level.

Table 4.3 Summary table of the Pearson's correlations between mean EbF and hydrology metrics MAX and MSL, of 69 vegetation quadrats tested per monitoring year (2017-2019). Hydrology year A, B, and C, each containing a different time period (Figure 4.2), were used to calculate for the hydrology metrics. All correlations were significant at $p < 0.05$. *The relationship of the 5-yr Average MSL and 5-yr Average MAX and mean EbF has been plotted in Figure 4.6.

Hydrology year A				**Hydrology year B**				**Hydrology year C**			
Hydrology metric	2017	2018	2019	Hydrology metric	2017	2018	2019	Hydrology metric	2017	2018	2019
MSL	0.81	0.78	0.85	MSL	0.74	0.82	0.81	MSL	0.74	0.82	0.81
2yr Average MSL	0.89	0.86	0.82	2yr Average MSL	0.88	0.81	0.83	2yr Average MSL	0.88	0.81	0.83
3y Average MSL	0.89	0.85	0.84	3y Average MSL	0.86	0.86	0.82	3y Average MSL	0.86	0.86	0.82
4yr Average MSL	0.89	0.87	0.84	4yr Average MSL	0.88	0.85	0.84	4yr Average MSL	0.88	0.85	0.84
5yr Average MSL	0.89	0.86	0.83	***5yr Average MSL**	**0.89**	**0.87**	**0.83**	5yr Average MSL	0.89	0.87	0.83
6yr Average MSL	0.88	0.87	0.83	6yr Average MSL	0.88	0.87	0.84	6yr Average MSL	0.88	0.87	0.84
7yr Average MSL	0.87	0.86	0.82	7yr Average MSL	0.87	0.87	0.84	7yr Average MSL	0.87	0.87	0.84
MAX	0.75	0.81	0.85	MAX	0.76	0.82	0.72	MAX	0.76	0.82	0.72
2yr Average MAX	0.74	0.86	0.84	2yr Average MAX	0.87	0.81	0.79	2yr Average MAX	0.87	0.81	0.79
3y Average MAX	0.77	0.84	0.84	3y Average MAX	0.86	0.86	0.80	3y Average MAX	0.86	0.86	0.80
4yr Average MAX	0.79	0.83	0.80	4yr Average MAX	0.88	0.85	0.80	4yr Average MAX	0.88	0.85	0.80
5yr Average MAX	0.79	0.82	0.77	***5yr Average MAX**	**0.88**	**0.87**	**0.81**	5yr Average MAX	0.88	0.87	0.81
6yr Average MAX	0.84	0.81	0.77	6yr Average MAX	0.86	0.87	0.81	6yr Average MAX	0.86	0.87	0.81
7yr Average MAX	0.85	0.83	0.75	7yr Average MAX	0.85	0.86	0.81	7yr Average MAX	0.85	0.86	0.81

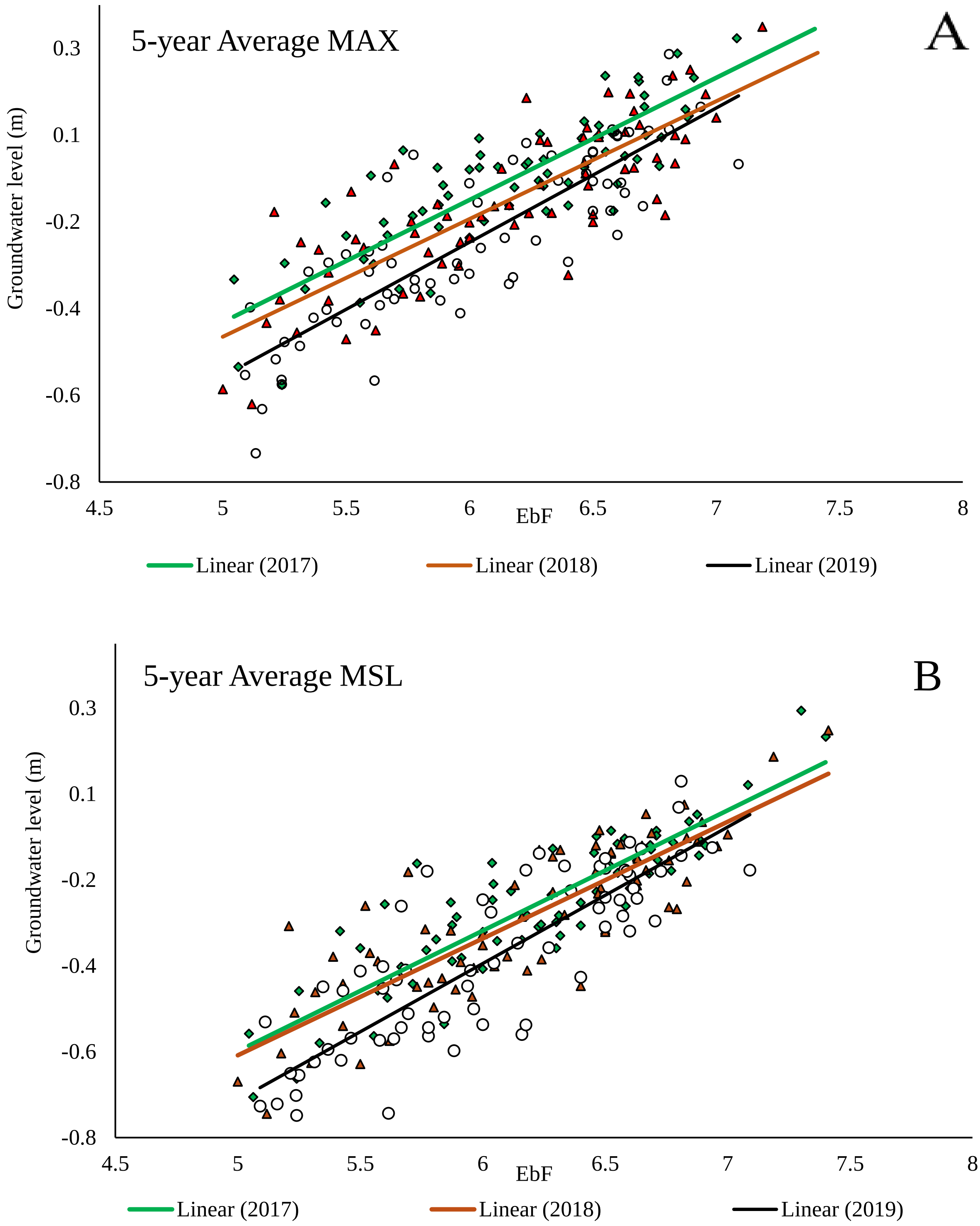


Figure 4.6 Linear correlation of 69 vegetation quadrats between mean EbF against the 5-year average of MAX (panel A) and MSL (panel B) for the year 2017 (green line, plots = green squares), 2018 (orange line, plots = orange triangles) and 2019 (black, plots = open circles). Hydrology metrics MAX and MSL measure unit is groundwater level (m) on the y-axis, ground surface is 0, negative values represent water levels below ground surface. Correlation coefficients are displayed in Table 4.3.

4.3.3. Which hydrology year best represents the relationship between vegetation and hydrology?

The Pearson's correlations between mean EbF and the hydrology metrics resulting from hydrology year A, B and C were summarised in **Table 4.3**. Across all the hydrology metrics, the highest correlation was found in hydrological year A, year 2017 with r = 0.89 for the 3-year average MSL. On average, the correlations for the hydrology metrics with MSL, were generally higher in hydrological year A, but the other hydrological years (B and C) produced also high correlations for the hydrology metrics with MSL ($0.74 > r < 0.89$) **Table 4.3**. Hydrology year B and C performed better for hydrology metrics with MAX, with the highest correlations of r = 0.88 for the 5-year average MAX. Overall, there are no outstanding differences between the hydrological years' correlations.

4.4. Discussion

This research demonstrates that there was a strong relationship between hydrology metrics and mean EbF in dune slacks, of which hydrology metrics using the MAX or MSL had the best ability to predict mean EbF response, with higher correlations gained by using longer averaging periods in the metrics. The highest correlation coefficients were found with the hydrology metrics was the unweighted 5-year average MSL. Within our study we also found that the relationship between hydrology metrics and mean EbF displayed inter-annual variation with different patterns and correlations between years. Exploring this finding within dune slacks, we found that there are strong indications that "dry" and "wet" years have different impacts on dune slacks, and might be constrained by time lags or different thresholds depending on the type of dune slack. We will discuss these findings in detail below per research question.

4.4.1. Which hydrology metrics have the strongest affinity to dune slack vegetation mean EbF values?

Previous studies have shown that there was a strong relationship between hydrology metrics and dune slack vegetation (Curreli et al., 2013; Dwyer et al., 2021a; Dwyer et al., 2021b). Within this study, most of the hydrology metrics displaying normal to high correlation coefficients, re-confirming the link of the hydrological regime as a driver of the dune slack vegetation response. Hydrology metrics MAX and MSL were found to best type of metrics to explain the vegetation response, of which MAX was in line with previous research (Curreli et al., 2013). Both metrics represent more the extreme end of the hydrological regime, which might indicates the habitat might be driven by the wettest conditions during a short period of the year. Plant communities or plant species tend to have a strong response to the more short-term extreme events compared to long-term more average conditions ((Smith, 2011). Equally, we would have expected that the MIN might have had an similar impact for the same reason as also been found before in dune slack research (Curreli et al., 2013), but did also explained less variation compared to MAX. Overall, the 5-year average MSL was found to have the highest correlations with EbF (r = 0.89), which was in line with other wetland studies using MSL in mean EbF calibrations (Schaffers & Sýkora, 2000; Käfer & Witte, 2004). This averaging period used to calculate hydrology metrics was in line with other metrics used in research before to explain EbF (Curreli et al., 2013; Dwyer et al., 2021b). Our results also showed that the "weighted" average hydrology metrics did explained more variation or leaded to higher correlation coefficients compared to the "normal" average hydrology metrics. Previous attempts to adjusting calculations of community centred means has been done before for Ellenberg indicators (Käfer & Witte, 2004), but adding weight to selected species, dominant or indicators, or abundance-related also did not lead to improvement to correlations. As dune slack habitat is highly dynamic and depended on the hydrological regime, we expected the most recent events, in the series of inter-annual variation, to have a higher impact on vegetation response, however, the results did reflect this. It might be that this calculation method did not represent this mechanisms in the best way or other mechanisms might be more important driving the vegetation response. Another explanation is that each hydrology year, up to 5 years, has an equal effect on the vegetation response. This would suggest there might be a kind of lag- or memory-effect present in the dune slack vegetation response. In general, we would recommend using the hydrology metric of MSL for monitoring, as this only required a minimum of 3-month monitoring per year. This would have a beneficial implication for dune slack conservation, as funding or resources can be limited to allocate to monitoring, but would allow for a suitable solution.

4.4.2. **How does inter-annual variability affect the relationship?**

Within the scope of this study, we found the of the relationship between hydrology and dune slack vegetation altering with inter-annual dynamics, on site- and dune-slack level. There was no clear pattern indicating what would drive the variation of the vegetation response over time, however we did found some indications that there is a difference in response between dry and wet years. The effect of drier conditions between years has also been found in *cladonia* population dynamics, where the influence of decreased rainfall during one season was also found across the following years (Martins et al., 2018). Drought sensitivity could be problematic, as future conditions often describe changes in precipitation and more summer drought periods, which then could lead to critical conditions in the future for the wetland ecosystem response (Kløve et al., 2014). In our study, the more drier dune slacks appeared to be more affected, displaying slower recovery compared to the more wetter dune slacks. This might be related to niche limitations for different types of dune slacks, as the hydrological regime is the main driver of dune slack vegetation (Dwyer et al., 2022). For example, capillary pressure can compensate for drought if the groundwater level is within reach of the ground surface, however, this mechanism is out of reach for drier dune slacks, as their groundwater level niche is often considerably lower in comparison to the wetter dune slacks (Curreli et al., 2013). It is also likely that other hydrology related mechanisms influence the inter-annual response, like soil organic matter (Dwyer et al., 2021a), which is known to vary between communities (Sýkora et al., 2004; Grootjans et al., 2017). Soil organic matter allows for a higher moisture content, leading to different soil moisture capacity to endure drought (Schaffers & Sýkora, 2000). Another explanation for the inter-annual variation in response between dry and wet dune slacks, is that the impact of (multiple) dry years had stronger effect on drier dune slacks, resulting in a time-lag in the vegetation response, compared to wetter dune slacks, who seemed to recovered more quickly. This time lag effect would support the mechanism we described before during the first research question, in which the normal averaging of multiple hydrological years (up to 5 years) results with each year having a similar impact, rather than "weighting" the most recent events in the calculation of hydrology metrics. This might also explain and emphasize the role of using multiple years for summarisation in the hydrology metrics, and why they lead to higher correlations compared to 1/3-year metrics, but would also be likely to give an better presentation of the inter-annual dynamics present in the vegetation response. Thus, understanding the mechanism behind the inter-annual variation of the relationship will likely also lead to more knowledge about resilience and recovery dune slack habitat.

4.4.3. Which hydrology year best represents the relationship between vegetation and hydrology?

There has been limited research into the best way to calculate hydrology metrics to explain vegetation response, partly because many UK sites have lacked co-located vegetation and hydrology data for dune slacks. Within the field of hydrology, the term "hydrological year" is often used to describe either the full year or another period of 12 months to include calculate total rainfall or to include most of the seasonal dynamics (min, max) of the ecosystem. Timing also depends on the location within the hemisphere (northern or southern) or climatic dynamics (seasonality, or seasons). Our results showed that for dune slack vegetation, the three selected periods for the “hydrological year”, lead to similar correlation results between the hydrology metrics and mean EbF. The small differences between hydrological year A, B and C can be explained by the small variation in period selection, with each period included 6 months of overlapping data, which might have been the most important period driving the relationship (September – March). As we tested hydrology metrics MAX and MSL, this was not surprising, as both hydrology metrics depend on the dynamics of the winter to provide as the “recharge” season of the year. However, it might be good to keep in mind that using other hydrology metrics will lead to different correlations and links to different periods for the hydrological year. Overall, the results showed that the standard hydrological year B would be sufficient, running from 1st of June till the 31st of May, as it matches a conceptual understanding of a logical divide of the hydrological year to neatly contain the maximum and minimum water levels within a single year while accounting for inherent variability in their periods. The hydrological year will be sufficient for further dune slack research related to hydrology metrics with MSL and MAX, but other periods could be considered if needed when looking at different (hydrology) metrics.

4.4.4. **Recommendations and future research**

The relationship found with mean EbF and the hydrology metrics would be considered optimal if the gradient present in the metrics data would be moderate long (Diekmann, 2003). As this study is focussed on a single site, the hydrology gradient of dune slack habitat might not be fully represented, however recent dune slack research had a comparable mean EbF range surveyed on a national scale with multiple sites (Dwyer et al., 2021a). Therefore, we do conclude that there was sufficient hydrology gradient present within our study to analyse hydrology metrics in relation to vegetation response. However, it is important to understand the implication of scale in research when studying vegetation response. For further analysis with focus on vegetation response, we do recommend incorporating the nested design of the research in analysis to account for spatial autocorrelation or other random variation. To further explore the inter-annual dynamics, we suggest using species assemblages as a factor, as the dune slack vegetation can be classed accordingly to hydrology limits and vegetation communities (Davy et al., 2006; Curreli et al., 2013), this might help to further entangle the potential lag- or memory-effect. The vegetation communities can be separated by a 20 cm difference in hydrological regime and are likely to have a different response to the inter-annual variation over time, as each community has different species combinations and preferences.

4.5. Conclusion

Dune slack habitat is highly depended on the hydrology regime, and is highly vulnerable to future climate change. This study re-establishes that there is a strong direct relationship between hydrology and vegetation, using mean Ellenberg soil moisture indicator values as a proxy for vegetation responses to hydrological change. Through extensive testing of a suite of vegetation and hydrological indicators, this study has shown that a 5-year average based on Mean Spring Level (MSL) is a robust metric that summarises the main hydrological influences on dune slack vegetation. Although some other metrics (such as MAX water level), perform similarly, the selection of un-weighted MSL as a metric allows site managers to more easily obtain data from their site. For example, when under pressure of limited time and resources, the site manager can get by with just measuring the water table in three months of the year. Our study highlights the role of long term monitoring for both hydrology and vegetation studies to better understand these complex ecological systems. Using longer averaging periods with short term measurements for hydrology and co-located vegetation monitoring is key to gaining an improved understanding of dune slack resilience. The ability to predict thresholds of dune slack habitat is of high importance for management and conservation of dune slack habitat. The inter-annual variation within the relationship between the hydrology and vegetation indicated differences in dune slack resilience and recovery depending on the dune slack type or a similar classification. Further research to determine the mechanisms behind this response is an important next step for dune slack management to respond to climate change.

4.6. Acknowledgements

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Ellenberg calculations done by Lisanne van Willegen and Ciara Dwyer. Analysis and writing the main paper done by Lisanne van Willegen assisted and reviewed by Laurence Jones, Ciara Dwyer, Hillary Wallace, John Ratcliffe, Graham Williams and Davey Jones. Lisanne van Willegen was supported through a KESS 2 scholarship. Knowledge Economy Skills Scholarships (KESS 2) is a pan-Wales higher level skills initiative led by Bangor University on behalf of the HE sectors in Wales. It is part funded by the Welsh Government's European Social Fund (ESF) convergence programme for West Wales and the Valleys. The KESS 2 project collaborated with the Natural Resources Wales (NRW) as company partner in this project.

Chapter 5

Chapter 5

5. Plant community and soil conditions moderate vegetation responses to hydrology in dune slack wetlands

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Abstract

Introduction: Within Europe, climate change is expected to have a major negative impact on wetland ecosystem functioning and the subsequent delivery of key ecosystem services. To promote the future survival of coastal wetlands, we need a better fundamental understanding of how and when dune slack habitat will respond to climate change and what factors govern sensitivity to changing hydrological conditions.

Aim: To determine the importance of soil and plant community characteristics in modifying vegetation responses to hydrological regime. To do so, we focused on the dynamics of the hydrological regime over time, using repeated measurements of co-located groundwater and vegetation monitoring. Specifically, this study addresses the following questions: I. What are the differences in plant community response related to species assemblages to the hydrology regime? II. Which hydrology metrics or other variables influence the plant communities' responses? III. How are the inter-annual responses within and between the plant communities related to species assemblages? IV. How do bryophytes species alter the interpretation of key hydrological relationships? And do they display similar relationships and inter-annual patterns as shown in plant communities?

Location: Newborough, Anglesey, United Kingdom.

Methods: We focus on the dynamics of the dune slack vegetation over time, using repeated measurements of co-located groundwater and vegetation monitoring. A total of 69 quadrats in 14 dune slacks were monitored for plant and bryophyte species composition with co-located groundwater level monitoring over 3 years (2017-2019). Quadrats were assigned to a UK National Vegetation Classification (NVC) community type, based on species composition, and hydrology metrics were calculated for each quadrat, covering min, max, mean and median annual water table, each averaged over multiple years. Linear mixed models (LMM) were used to analyse the link between the mean Ellenberg soil moisture (EbF) as a proxy for vegetation responses to hydrology, and possible explanatory variables: hydrology metrics, soil pH and soil organic matter, NVC community type. Vascular plant and bryophyte community responses were analysed separately.

Results: The LMM analysis revealed a significant effect of species composition on the mean EbF response in both vascular plant and bryophyte species. The vascular plant communities resulted in 3 different groups of mean EbF responses: wet, intermediate and dry dune slack communities. The intermediate and wetter dune slack communities were sensitive to inter-annual variation of the hydrological regime during this study, particularly in the vascular plant communities. Overall, our results shown that the mean EbF response of dune slack communities, resulting from plant or bryophyte compositions, can be predicted by hydrology and soil metrics.

Main conclusion: Our study highlights the role of vegetation species composition (NVC community types) in moderating the plant and bryophyte community response to hydrological regime. It shows that species composition is relevant in niche partitioning, where collective traits or features within species assemblages are likely to result in differential responses to the hydrology regime, as shown within the timeframe of this study. This is important, as resilience to drought might be related to diversity within and between communities. Based on all our evidence, we conclude that wet and intermediate dune slack plant communities are sensitive to hydrological regime making them highly vulnerable in the face of climate change.

Keywords: Vegetation, hydrology, plant communities, Ellenberg, drivers, soil attributes, bryophytes.

5.1. Introduction

Dune slacks are seasonal coastal wetlands, representing important habitats due to their high inherent biodiversity, which are strongly influenced by the temporal dynamics of the local groundwater regime (Ranwell, 1959; Grootjans et al., 1998). Dune slacks have a global distribution but face increasing threats worldwide. Within Europe, climate change is expected to have a major negative impact on wetland ecosystem functioning and the subsequent delivery of key ecosystem services (Čížková et al., 2013; Pörtner et al., 2022). There is therefore a critical need to protect these ecosystems against further degradation. Currently, the Atlantic-region countries hold 66% of the humid dune slack habitats in Europe (France and Portugal excluded, ~112 km²) with none classed as being of favourable status according to Article 17 under the Habitats Directive assessment of 2013-2018 (https://nature-art17.eionet.europa.eu/). Furthermore, the future prospects for these habitats were ranked as being either bad or poor. The condition of dune slack habitat in the UK has also been classed as ‘unfavourable and bad’ and has been progressively declining over the last few decades (Stratford, 2014). Future climate conditions are expected to change groundwater dynamics and are likely to have a major impact on dune slack functioning in North-West Europe (Saye & Pye, 2007; Kløve et al., 2014). Based on modelled’ future groundwater level predictions, studies have indicated the possibility for a general climate change-induced shift towards grassland communities in these habitats by the end of 2080 (Clarke & Sanitwong Na Ayutthaya, 2010; Curreli et al., 2013). To promote the future survival of coastal wetlands, we need a better fundamental understanding of how and when dune slack habitat will respond to climate change and what factors govern sensitivity to changing hydrological conditions (Stratford et al., 2013).

Dune slack habitat can be considered as lacustrine wetland, in which seasonality drives a major fluctuation of groundwater levels. This is often associated with periods of partial or complete submergence, leading to the creation of distinct edaphic conditions which drives plant community selection. Hydrology is one of the main drivers within the dune slack niche (Dwyer et al., 2021b; Dwyer et al., 2021a) and each dune slack plant community consists of a set of vascular and bryophyte species adapted for a certain range or dynamic of groundwater hydrological regime, an example of niche partitioning (Grootjans et al., 2004; Curreli et al., 2013). Although the general concept of hydrology drivers and limits within the dune slack habitat has been established (Davy et al., 2010), little work has been undertaken to understand how plant and bryophyte communities respond to short-term dynamics of the hydrological regimes. Most plant community research has been focused on long-term dynamics, using chronosequence or population studies. Fen orchid *Liparis loeselii* (Kooijman et al., 2016b; Grootjans et al., 2017; Waud et al., 2017) and petalwort *Petalophyllum ralfsi* (Callaghan et al., 2021) have gained some attention for their role as key indicator species within dune slack plant communities (Rodwell, 2000), where soil conditions, like bulk density and chemistry play an important role in their distribution. Other soil attributes known to influence plant communities are soil organic matter (SOM) and soil pH (Berendse et al., 1998; Sýkora et al., 2004). Other soil attributes known to influence plant communities are soil organic matter (SOM) and soil pH (Berendse et al., 1998; Sýkora et al., 2004). Typically, the effect of both are correlated, as soil buffering capacity with $CaCO_3$ is closely linked with the ability to maintain low available nutrient status to prevent succession within dune slack habitat (Lammerts & Grootjans, 1997; Sival et al., 1998). Most soil attributes are indirectly controlled by hydrological regime as soil chemistry is often highly dependent on groundwater flow or anoxic flooding conditions in the soil (Stuyfzand, 1999; Adema & Grootjans, 2003). Even the location of groundwater infiltration or exfiltration can have a large impact on soil chemistry and therefore, plant community distribution (Adema et al., 2003). However, soil attributes, like SOM, can increase soil water holding capacity in mineral soils (Libohova et al., 2018; Wösten & Groenendijk, 2019), which can be an important mechanism for water retention during summer drought. Plant communities growing with lower OM content will likely be more dependent on the local groundwater level for hydrology conditions, compared to plant communities adapted to high OM content. Therefore, it is likely that more diverse communities have higher dependency on groundwater regime, as their niche is often indirectly limited to nutrient-poor conditions with buffering capacity or high soil pH.

Bryophytes can be an important component of dune slack plant assemblages, as well as being key indicator species within dune slack communities (SD13 and SD14b; (Rodwell, 2000)). Bryophytes have the ability to function as a barrier between the soil and atmosphere, as they can have the ability to maintain a moisture supply during dry conditions using low hydraulic conductivity, which allows for higher evapotranspiration rates compared to open mineral soils (Voortman et al., 2014). They can also function as an important epiphytes for vascular plant species, offering moisture and anchorage (Jacquemyn et al., 2023). However, the combination of vascular plant and bryophyte species and their numerous adaptations makes it hard to predict how they will respond to environmental change. Additionally, vascular plant species can have different environmental requirements to bryophytes, as the timing of the growing season can be months apart. Therefore, bryophytes might have a different relationship with the hydrological regime resulting in different responses or temporal dynamics. Overall, these different drivers and mechanisms are likely to make it difficult to generalise plant community changes from individual indicator species, therefore, it would be beneficial to have different predictors between dune slack communities.

A recent study on dune slacks have emphasized the importance of spatial-scale dependence of plant community drivers (Dwyer et al., 2022). Although alpha- and beta-diversity are indicators of habitat quality, there can be different environmental drivers dependent on the spatial level, between and within dune sites, dune slacks and quadrats. To determine short-term dynamics of drivers of dune slack habitat, we need to consider how plant community drivers can be observed best within those spatial levels (Felton & Smith, 2017). Another important element in studying environmental drivers of dune slack vegetation, is the dynamic nature of the habitat or ecosystem (Alkemade et al., 1996). As small-scale hydrology changes are found to be of direct impact on dune slack plant communities, it is important to consider the temporal state of monitoring (Ertsen et al., 1998). Previous research has tended to focus on short time frames to determine patterns or drivers, however, they only provide a snapshot view and can lead to misrepresentation. Repeated measurements and long-term inter-annual studies are therefore essential to study environmental change, especially when considering the temporal dynamics of plant communities (Del Vecchio et al., 2022). By allowing environmental variation to drive compositional change over time, drivers of community change can be observed together, which is difficult to find within one season of experimental settings. Systematic monitoring also increases the power of analysis of small-scale levels to understand the biodiversity changes at the appropriate level (McGill, 2011; Dwyer et al., 2021b).

In this study, we aim to gain a better understanding of dune slack habitat, specifically the mechanisms which govern differences in responses of plant communities to hydrological regime, and the factors which govern that. To do so, we focused on the dynamics of the hydrological regime over time, using repeated measurements of co-located groundwater and vegetation monitoring. We assessed the relationship between dune slack vegetation, hydrology and the species compositional characteristics by adding NVC community types as a categorical factor (i.e., SD13-SD17), using a linear mixed modelling (LMM) approach. Each sand dune (SD) community occupies a niche with varied species; therefore, we expect contrasting responses between NVC communities, or at least distinct groups of NVC communities, based on the abilities of the species' assemblages. This will allow us to determine to role of drivers within and between dune slack communities and ultimately, give a better view on resilience of thresholds to climate in future research. As a result, we will be able to utilise hydrology indicators for more effective management of these habitats, building a predictive model with the ability to quantify dune slack community response.

Specifically, this study addresses the following questions: I. What are the differences in plant community response related to species assemblages to the hydrology regime? II. Which hydrology metrics or other variables influence the plant communities' responses? III. How is the inter-annual responses within and between the plant communities related to species assemblages? IV. How do bryophytes species alter the interpretation of key hydrological relationships? And do they display similar relationships and inter-annual patterns as shown in plant communities?

5.2. Methods

5.2.1.**Study site**

This study was conducted at Newborough Warren, a large dune system of 1295 ha, located on the Isle of Anglesey, Wales (53°08'56"N, 04°21'38"W; **Figure 5.1**).The dune system is bounded by two estuaries and a rock ridge, consisting of Holocene aeolian calcareous sands that overlie glacial till deposits, resting on Palaeozoic and Precambrian basement (Bristow & Bailey, 1998). Between 1947 and 1965, the western side of the warren was afforested with Corsican pine (*Pinus nigra* ssp. *Laricio*) (Hill & Wallace, 1989). The remaining east side of the site has developed as open dune grassland with four lines of parabolic dunes containing a high number of dune slacks. The site is managed by livestock grazing with sheep, cattle and Welsh mountain ponies since 1987 (Plassmann et al., 2010). Local climate can be described as mildly oceanic with an long-term average annual rainfall of 872 mm between 2006 and 2019 (RAF Valley station; (Met Office, 2012)). The area is officially designated as a Special Area of Conservation (SAC), a National Nature Reserve (NNR) and a Site of Special Scientific Interest (SSSI) and managed by Natural Resources Wales.

5.2.2.**Vegetation survey**

To gain an improved understanding of the relationship between vegetation and hydrological regime, a total of 207 quadrats were surveyed across 14 dune slacks at Newborough Warren. Vegetation monitoring was set up with 69 permanent quadrats in 2010 (Curreli et al., 2013) and re-recorded in 2017, 2018 and 2019 (**Table 5.1**). Each dune slack contained 3 to 8 permanent quadrats of 1 m × 1 m, arranged in four directions (N, W, S, E) around a co-located piezometer, unless the topographic variability would result in a location outside the margin of dune slack vegetation. Quadrats are marked with discrete corner posts to allow exact re-location. Plant and bryophyte species presence were recorded using nomenclature; vascular plants (Stace, 2019) and bryophytes (Atherton et al., 2010).

5.2.3. **LOI and Soil pH**

Soil samples were measured in 2010, when setting up the permanent quadrat locations (Curreli et al., 2013). Soil cores consisted of 15 cm depth and 5 cm diameter. Moisture content was determined on homogenised soil (10 g) by oven drying (105 °C, 16 h). Loss-on-ignition (LOI) was calculated by measuring mass loss from dry soil after heating at 375 °C for 16 h. Soil pH was measured after 30 min equilibration of 10 g dry soil stirred in 25 ml deionised water, with pH electrode calibrated with standard solutions. Although not from the same year as vegetation measurements, relative differences in soil parameters across sampling locations are assumed to be maintained (Jones et al., 2010).

Figure 5.1 Aerial map of dune system of Newborough, Wales, United Kingdom. Dune slack locations are marked with a black dot (Table 1).

Table 5.1 Overview of vegetation survey during 2017-2019, with number of quadrats assigned per co-located piezometer per year.

No.	Piezometer	2017	2018	2019
1	CEH8	3	3	3
2	CEH24	3	3	3
3	WMC2	3	3	3
4	CEH23	5	5	5
5	CEH26	5	5	5
6	NW3	4	4	4
7	CEH9	7	7	7
8	CEH22	7	7	7
9	NW4	8	8	8
10	T41A/B/C/D	7	7	7
11	CEH4	3	3	3
12	CEH5	5	5	5
13	NW5	4	4	4
14	NW6	5	5	5
	Total	69	69	69

5.2.4. **Ellenberg indicator for soil moisture (EbF)**

The mean Ellenberg values for soil moisture (EbF) were calculated for each quadrat using the PlantATT database for vascular plants and bryophytes, which were recalibrated for the UK (Hill et al., 2004). Mean EbF values were calculated based on vascular plant and bryophyte species presence data using the software R (R Core Team, 2021).

5.2.5. **Dune slack communities**

To classify dune slack communities from quadrat plant and bryophyte species data, we used the software MATCH (Malloch, 1998) to assign dune slack NVC communities types (SD13 – SD17). Match community analysis used presence and abundance data per quadrat to assign a dune slack NVC community type according to the classification of Rodwell (2000). The main and sub communities used in this study are described in **Table 5.2**.

5.2.6. **Hydrology data**

Phreatic groundwater levels were recorded at each piezometer, monthly measured from 2006 to 2019. Measurements were represented as metres above ground surface (i.e., -0.65 stands for 0.65 m below ground surface), corrected for upstand of the piezometer above ground level in meter (m). Each piezometer was located within 7 m reach of the vegetation quadrats to ensure similar groundwater conditions with acceptable variation (Curreli et al., 2013; Dwyer et al., 2021a).

5.2.7. **Correction for ground surface elevation**

To ensure high accuracy of the hydrology metrics for analysis, the elevations of all piezometers and vegetation quadrats have been surveyed using a Leica 1200 RTK dGPS, with a vertical accuracy of < 10 mm (Curreli et al., 2013). This allowed us to correct for elevational differences between quadrats and piezometer to ensure accurate relationships between the hydrology and the vegetation data.

5.2.8. **Hydrology metrics for co-located quadrats**

In this study, the hydrology metrics were selected based on those identified in previous research (Chapter 3, van Willegen) as the best predictors of vegetation response. Hydrology metrics are calculated using the hydrology data per quadrat. To account for the period of vegetation monitoring, we used “hydrology year” which are defined as the period of 12 months before vegetation monitoring, running from 1st of June to the 31st of May. The hydrology metrics used in the linear mixed models are listed in **Table 5.3**, in which all basic metrics (MIN, MAX, MSL, MWL, median and mean) are described, with variants of each one calculated as averages over the 1 to 8 years of preceding data.

Table 5.2 Summary of dune slack communities NVC types within the UK (adapted from Rodwell et al. (2000) and Curreli et al. (2013)), describing key indicator species and affinity with other communities.

NVC type	Dune slack community (Rodwell 2000)	Natura 2000 Habitat type	Description
SD13	Main community SD13 *Sagina nodosa-Bryum pseudotriquetrum* Subcommunity: SD13b *Sagina nodosa-Bryum pseudotriquetrum*	H2190-Humid dune slacks	Early successional stage, rich in bryophytes and liverworts. Usually with bare sand. Fairly drought tolerant.
SD14	Main community SD14 *Salix repens–Campylium stellatum* Subcommunities: SD14b *Rubus caesius–Galium palustre* SD14c *Bryum pseudotriquetrum–Aneura pinguis* SD14d *Festuca rubra*	H2190-Humid dune slacks	SD14b Frequently species rich and associated with persistently humid soils and base-rich groundwater. Several rare species occur in this vegetation. Some of its constant species (*Ranunculus flammula*, *Carex nigra*) can indicate tolerance to very wet periods. SD14c Young successional stage, mosses have sparse cover, heliophilous and pioneer species can be present. SD14d Characteristic of drier substrates, it can be an intermediate stage towards grass encroachment.
SD15	Main community SD15 *Salix repens–Calliergon cuspidatum* Subcommunities: SD15b *Equisetum variegatum* subcommunity	H2190-Humid dune slacks	Late successional stage, generally species poor. Less dependent on base-richness of water, but strongly related with flooding.
SD16	Main community SD16 *Salix repens-Holcus lanatus* Subcommunities: SD16a SD16b SD16c SD16d	H2190-Humid dune slacks H2170-Dunes with creeping willow	Late successional stage in dry slacks. Dominated by fescue and other grasses, forbs are still indicative of calcicolous substrate.
SD17	Main community SD17 *Potentilla anserina-Carex nigra*	H2190-Humid dune slacks	Species composition reflects damp habitat, recalling fen meadows. Forbs-rich, with a sparse shrub cover.

Table 5.3 Hydrology basic metrics list.

Hydrology metric	Description (+ period before vegetation monitoring)
MSL	Mean spring water level (1st March to 31st May)
MIN	Minimal water level (1st June to 31st May)
MAX	Maximum water level (1st June to 31st May)
Median	Median (1st June to 31st May)
Mean	Mean (1st June to 31st May)
MWL	Mean winter water level (1st December to 28th February)
Example of multiple season:	
5-year Average MSL	Average MSL of 5 hydrology seasons

5.2.9. **Data analysis**

We assessed the relationship between dune slack vegetation, hydrology and the species compositional characteristics by adding NVC community types as a categorical factor (i.e., SD13-SD17), using a linear mixed modelling (LMM) approach (LMM, SPSS, (IBM Corp, 2020)). The full dataset of 207 data points was used (69 quadrats in 14 dune slacks and 3 years of monitoring for each), in which quadrats are nested within dune slacks.

5.2.9.1. LMM model analysis

The dependent variable, the mean Ellenberg soil moisture (mean EbF), was assessed with LMM approach with repeated measures to account for time, by adding factors (categorical or continuous), as described per research question. For each research question, we set out to analyse multiple LLM, containing several factors, to obtain the most parsimonious model for monitoring and management. Evaluation and comparison of LLM was based on the Akaike Information Criterion (AIC). The statistical analysis was focussed on different components, listed per research question:

I. NVC Parameters (Categorical factors with levels; containing single or groups of dune slack communities, **Table 5.4**)
II. Soil organic matter (loss-on-ignition) and soil pH
III. Inter-annual variation (year), fixing the NVC community assessment results of MATCH of 2017 as a treatment factor for each plot in 2018 and 2019.
IV. Bryophytes mean EbF response.

5.2.9.2. LMM model structure

The first linear mixed model (Model 1, Appendix, **Table 0.4**) was built using forward selection with maximum likelihood estimation (ML), testing the random effect levels of the nested design (Baayen et al., 2008). The random effect levels were tested up to the maximum random-effect structure, including all levels (dune slack, quadrat) to evaluate model structure (Barr, 2013). Model 1 included the random intercepts for dune slack ID (intraclass coefficient (ICC) > 0.10), Appendix **Table 0.4**), but not the random intercepts of dune slack(quadrat) ID (ICC < 0.10). This random intercept had also been confounding with the hydrology metric and lead to convergence failures expending the model (Bates et al., 2015) and both the dune slack and quadrat location contained similar variance with some of the covariate hydrology metrics, i.e. have an exogenous relationship, which could lead to violating model assumptions (Schielzeth et al., 2020). Model covariate structure was evaluated with the -2 $\log_{10}$ likelihood using maximum likelihood estimation (ML), using a chi-square test and Akaike Information Criterion (AIC). The model covariance structure for the models was an autoregressive covariance structure with heterogeneous variances (Ar1-H), however other structures like ARMA-1 were also adequate for the model.

5.2.9.3. LMM model - hydrology metrics and soil attributes

Hydrology metrics were pre-selected based on previous research (Chapter 4, van Willegen et al) and using Automatic Linear Modelling in SPSS, using forward selection of metrics based on adjusted R-square and AICC scores (Yang, 2013). Predictors (continuous factors; hydrology metrics and soil attributes) were not transformed or centred, as the focus of this research is the application of the hydrology metrics for prediction of plant community response for management purposes.

5.2.9.4. LMM final models

The final model coefficients were estimated using restricted maximum likelihood (REML) with Satterthwaite approximation to obtain the most unbiased predictors with relatively small sample size. Model residuals were visually inspected to check for normality, overdispersion and heteroscedasticity if relevant. Outliers with higher standardized residuals >2 were inspected and evaluated with model fit and estimate influence.

Table 5.4 Parameter NVC (categorical factors) description, with levels of single or groups of NVC dune slack community types (described in Table 5.2). Dune slack communities using "/" were combined into 1 level. All NVC Parameters were assessed in the Linear Mixed Models (LMM) of Appendix, Table 0.4.

Parameter name	Levels (NVC dune slacks community ID)
NVC1	10 levels (SD13, SD14b, SD14c, SD14d, SD15, SD16a, SD16b, SD16c, SD16d, SD17)
NVC2	8 levels (SD13, SD14b, SD14c, SD14d, SD15/SD17, SD16a, SD16b/c, SD16d)
NVC3	7 levels (SD13, SD14b, SD14c, SD14d, SD15/SD17, SD16a/b/c, SD16d)
NVC4	6 levels (SD13, SD14b, SD14c, SD14d, SD15/SD17, SD16a/b/c/d)
NVC5	3 levels: Group 1 – Wet dune slack communities (SD14b, SD15, SD17) Group 2 – Intermediate dune slack communities (SD14c, SD14d, SD16d) Group 3 – Dry dune slack communities (SD13, SD16a, SD16b, SD16c)
NVC6	2 levels: Group 1 – Wet dune slack communities (SD14b, SD15, SD17) Group 2 – Intermediate/ dry dune slack communities (SD13, SD14c, SD14d. SD16a, SD16b, SD16c, SD16d)
NCV7	7 levels (SD13, SD14b, SD14c, SD14d, SD15/SD17, SD16a, SD16b/c/d)
NCV8	3 levels: Group 1 – Wet dune slack communities (SD14b, SD15, SD17) Group 2 – Intermediate dune slack communities (SD14c, Sd14d, SD16b, SD16c, SD16d) Group 3 – Dry dune slack communities (SD13, SD16a)

5.3. Results

Statistical analysis resulted in a total of 37 linear mixed models (LMM) (Appendix, **Table 0.4** and **Table 0.7**), each exploring different components of the research questions. Based on previous analysis (Chapter 3), our starting hydrological metric to describe the vegetation community response to water levels was 5-year average MSL, describing a linear relationship with mean EbF (**Figure 5.2**, $p < 0.001$ Model 1 Appendix **Table 0.4**). The hydrology metric had a significant effect on mean EbF in each model $p < 0.001$, Model 1-11, 21-29, Appendix **Table 0.4**.

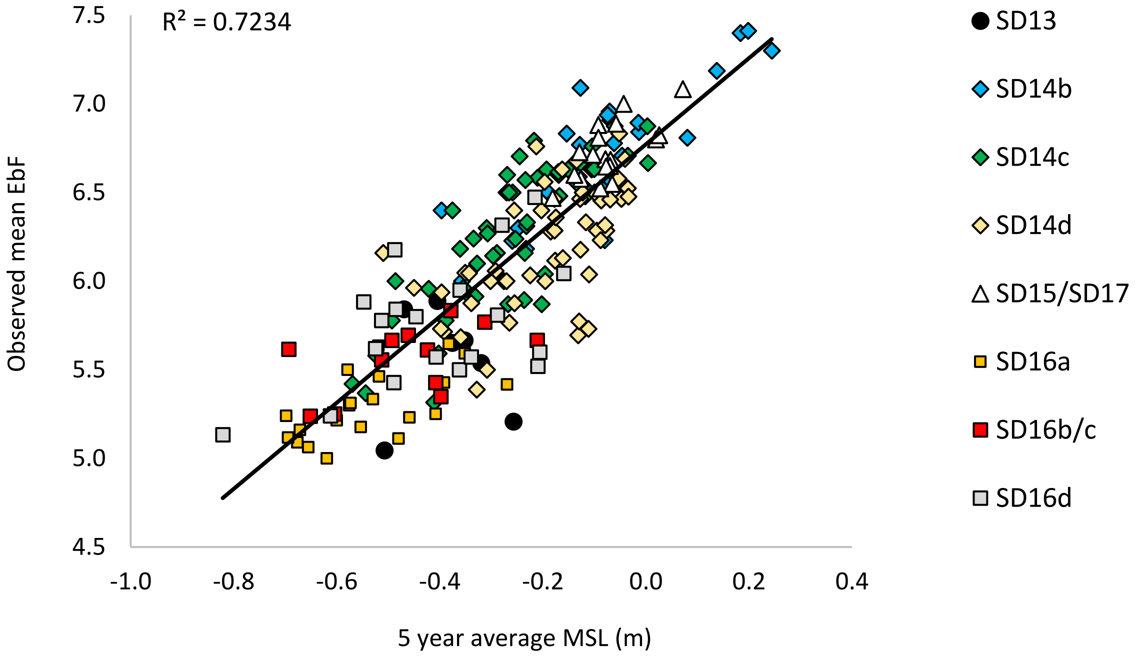


Figure 5.2 Relationship between the observed mean EbF against 5-year average MSL (m) fitted with a trendline with the R-square. Each symbol stands for a NVC community, described in the legend. On the x axis, ground surface is 0, negative MSL values represent water levels below ground surface.

5.3.1. What are the differences in plant community response related to species assemblages to the hydrology regime?

A total of 8 NVC parameters (categorical factors, **Table 5.4**.) were created, testing the effect of the species composition with levels of single or groups of NVC dune slack communities (**Table 5.2**). All the NVC parameters had a significant effect on the mean EbF response, of which model 11 (including parameter NVC8), had the best fit based on AIC scores (F (2, 176.9) = 13.4, p <0.001 (Appendix **Table 0.4**). Parameter NVC8 consisted of 3 levels with 3 groups of NVC communities, in which the groups were divided into '1. Wet-', '2. Intermediate-' and '3. Dry-' dune slacks' communities' (**Table 5.5**). With the use of LMM coefficient estimates of each level, mean EbF was calculated using the formulae in **Table 5.5**. Random variation as a result of dune slack ID were included in each model ($p < 0.05$, Appendix **Table 0.4**), with the standard error of 0.033/0.059 mean EbF for year and -0.4/-0.2 mean EbF depending on dune slack ID (Appendix, **Table 0.6**).

Table 5.5 Model parameter NVC8 level description (3 levels: groups of dune slack communities) and model coefficients to predict mean EbF (Model 11, Appendix Table 0.5).

NVC 8 level (group)	**Description**	**Dune slack communities types**
1	Wet dune slack communities	SD14b, SD15, SD17
	Mean EbF ~ 6.75 + 1.64 * 5-year average MSL	
2	Intermediate dune slack communities	SD14c, SD14d, SD16b/c, SD16d
	Mean EbF ~ 6.54 + 1.64 * 5-year average MSL	
3	Dry dune slack communities	SD13, SD16a
	Mean EbF ~ 6.37 + 1.64 * 5-year average MSL	

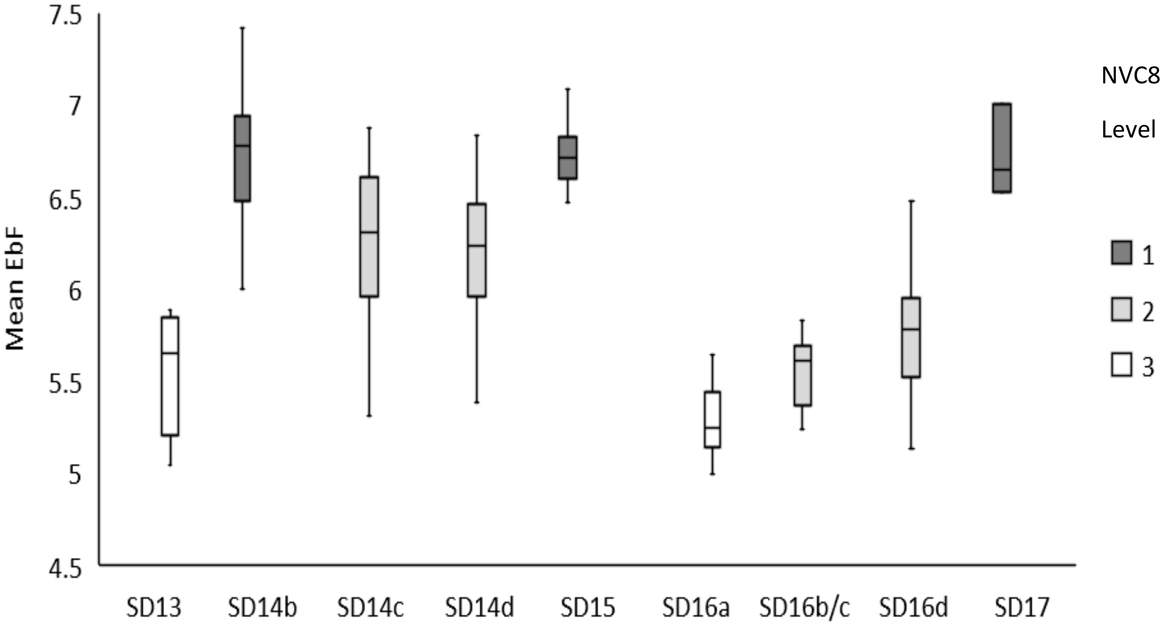


Figure 5.3 Boxplot with mean observed EbF per NVC community type. Each NCV8 level is represented with a colour (1 (white) = wet, 2 (grey) =intermediate, 3 (black) = dry dune slack communities), F (2, 176.9) = 13.4, *p* < 0.001.

5.3.2. Which hydrology metrics or other variables influence the plant communities' responses?

Comparing the 8 levels of parameter NVC2, there was no clear effect of SOM (loss-on-ignition (LOI)) or soil pH on mean EbF as shown in **Figure 5.4**. Although there appeared to be a slight positive relationship for LOI and mean EbF in panel (c), the 8 levels of parameter NVC2 in panel (a) indicate that the effect is driven by LOI variance present in the 2 levels of SD14d and SD15/SD17. Panel (b) displays that there is variance in soil pH between the 8 levels of NVC2, in which most dune slack communities centre around a high soil pH mean. There appears not to be an effect between soil pH and mean EbF in panel (d).

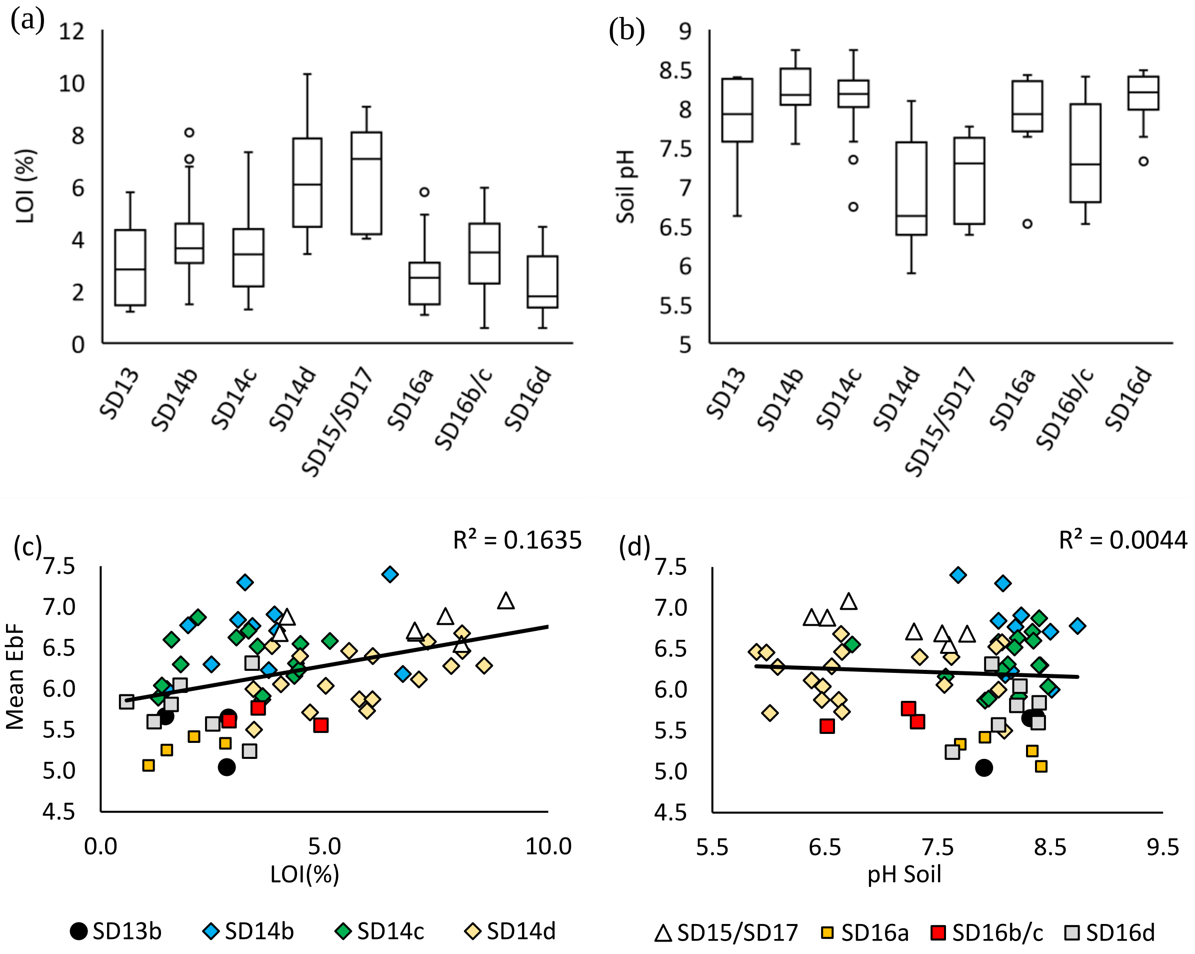


Figure 5.4 Panel (a): Soil organic matter (loss-on-ignition %) for each level of parameter NVC 2 (8 levels of dune slack community types). Panel (b): Soil pH for each level of NVC 2 (8 levels of dune slack communities. Panel (c) and Panel (d): Mean observed EbF values of 2017 plotted against the soil organic matter (loss-on-ignition, LOI %, Panel (c)) and soil pH (panel (d)) for each level of NVC 2 (each level is represented with a symbol).

These general patterns were also supported in the model results, both SOM (LOI; Model 12 and Model 13, Appendix **Table 0.4**) and soil pH (Model 17 and 18, Appendix **Table 0.4**) had no overall effect on the mean EbF response in models with either parameter NVC2 or NVC8. However, there was a significant interaction effect between the SOM (LOI) and the levels of parameter NVC8 in model 16 F (2, 174.5) = 4.0, $p < 0.05$ (Appendix, **Table 0.4**).

To understand the interaction of SOM (LOI) and NVC8, in combination with other hydrology metrics, new relationships were assessed and displayed in **Table 5.6** for the 3 levels of parameter NVC8. Group 1, the wet dune slack communities (SD14b, SD15b/SD17), showed the best fit using the 5-year average MSL without any other metrics. For group 2 (SD14c, SD14d, SD16b/c, SD16d), a combination of 2 hydrology metrics and the NVC2 parameter explained the most variation: 4-year average MSL and 4-year MIN. Group 3 (SD13 and SD16a) was best matched with the 8-year average minimal water level (MIN) and SOM (LOI %). The model accuracy of group 3 was without LOI low (from 68.3% to 11.5%), indicating high influence of the SOM (LOI) in the level of group 3 likely driving the interaction effect in model 16.

There was no significant interaction found with soil pH in the models with parameter NVC8 (F (3,153.5) = 2.7, $p < 0.06$ Model 20, Appendix **Table 0.4**), but the AIC-score indicated a better model fit including the non-significant variables (-56.3, Appendix **Table 0.4**). The effect of soil pH was also further analysed including other hydrology metrics for the levels of parameter NVC2, the results displayed in **Table 5.7**. Dune slack communities SD15/SD17 was the only level of parameter NVC 2 that showed a significant effect of soil pH on the mean EbF response, however, model accuracy was only 55.6%. The other levels of parameter NVC2 did had combinations with other significant hydrology metrics, and in line with our previous analysis of the levels of parameter NVC8, the drier dune slack communities also had significant effects of SOM (LOI) on the mean EbF response. The hydrology metrics found with the levels of parameter NVC2 were the maximum water level (MAX) for the drier communities of SD16 (a/b/c/d), while the more intermediate dune slack communities SD14c and SD14d and drier dune slack community of SD13 were driven by the minimum water level (MIN). The level of SD14c was found with hydrology metrics including the mean spring level (MSL), like the wet dune slack communities SD15/SD17. Overall, a range of timescales (1-year to 8-year averages) and type of hydrology metrics (MIN, MAX, MSL, Median, Mean) were found to drive mean EbF response between the levels of parameter NVC 2 (dune slack communities) aside from SOM (LOI) and soil pH.

Table 5.6 Automatic linear model results for each level of parameter NVC8 (3 levels: groups) to select hydrology metrics using forward selection based on adjusted R^2 scores (model accuracy per group). For each NVC8 level the selected hydrology metric has been plotted against the observed mean EbF plot scores within that level (red dashed line). Each dune slack community has also been plotted with a separate line (grey, black).

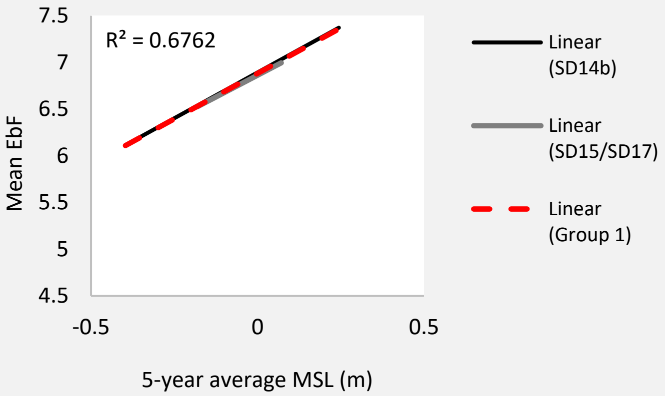
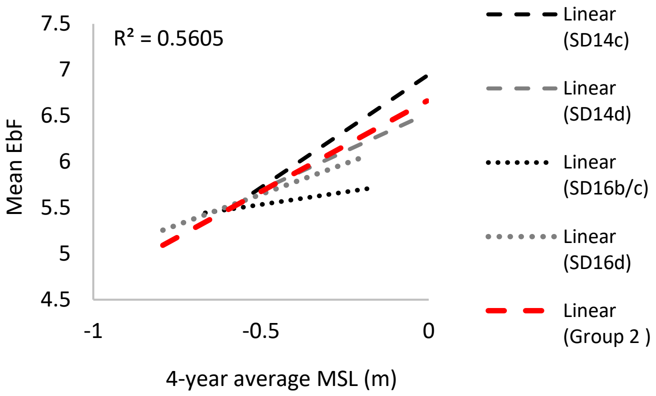
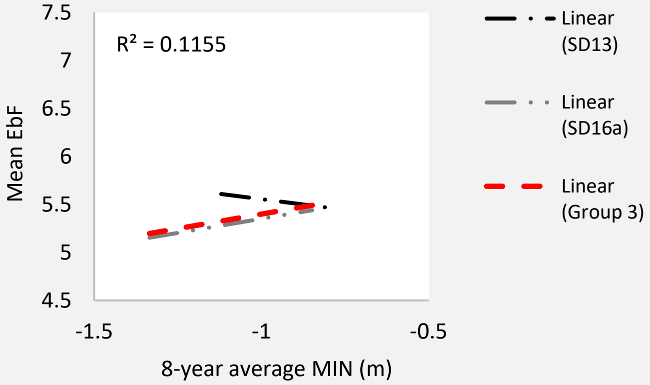
Parameter NVC8 (3 levels)	Parameters	*p* *	Adj. R^2
Group 1: Wet dune slacks (SD14b, SD15/SD17)  	5-year average MSL	<0.001	66.90%
Group 2: Intermediate dune slacks (SD14c, SD14d, SD16b/c, SD16d)  	4-year average MSL 4-year average MIN NVC2	<0.001 0.003 <0.001	65.6%
Group 3: Dry dune slacks (SD13, SD16a)  	8-year average MIN LOI (%)	<0.001 <0.001	68.3%

Table 5.7 Automatic linear model results for each level of parameter NVC2 (8 levels) to select hydrology metrics using forward selection based on adjusted R-square scores. Each level holds a separate model analysis. * Level has multiple dune slack communities.

Parameter NVC2 (8 levels)	Covariate(s)	p	Model Adj. R^2
SD13	LOI (%)	0.006	84.3%
	7-year average MIN	0.007	
SD14b	5-year average Mean	0.001	70.6%
SD14c	4-year average MSL	<0.001	76.7%
	4-year average MIN	0.030	
SD14d	5-year average MIN	<0.001	42.8%
SD15/SD17*	5-year average MSL	<0.001	56.0%
	Soil pH	<0.001	
SD16a	LOI (%)	0.003	66.6%
	6-year average MAX	0.040	
SD16b/c*	3-year average MAX	0.050	20.7%
SD16d	7-year average MAX	0.001	56.0%
	1-year MWL	0.040	

5.3.3. How are the inter-annual responses within and between the plant communities related to species assemblages?

During the scope of this research, there was a sequence of wetter (i.e., 2017) to drier years (i.e., 2019), in which we studied the plant community response over time. We found an overall effect of the inter-annual variation on the mean EbF response in model 21 with parameter NCV8 F (2, 102.0) = 19.9 $p < 0.001$ and in model 22 with parameter NCV2 F (2, 98.5) = 20.1 $p < 0.001$ (Appendix **Table 0.4**). The negative trends showed a decrease of 0.04 mean EbF in 2018 and another 0.15 mean EbF in 2019 for all dune slack communities. We also found significant interactions (model 23 and 24, Appendix **Table 0.4**), revealing different responses between years and the levels of the parameters of NVC8 and NVC2 (**Figure 5.5**, panel (a) NVC8 F (6,113) = 7.1, $p < 0.001$ and panel (b) NVC2 F (16,107.4) = 3.7, $p < 0.001$). The mean EbF response of parameter NVC8 was significant lower in 2019 for group 1 and group 2 in panel (a), compared to group 3, which displayed no inter-annual response. The model with parameter NVC2 showed similar trends in the dune slack community levels, in which SD13, SD16b/c and SD16a showed no-inter annual differences. Interestingly, the rest of dune slack communities either had a decreasing trend in mean EbF for 2018 and 2019 (SD15/SD17 and SD16d) or only a significant decrease in 2019 (SD14c and SD14d), in line with the results of parameter NVC8.

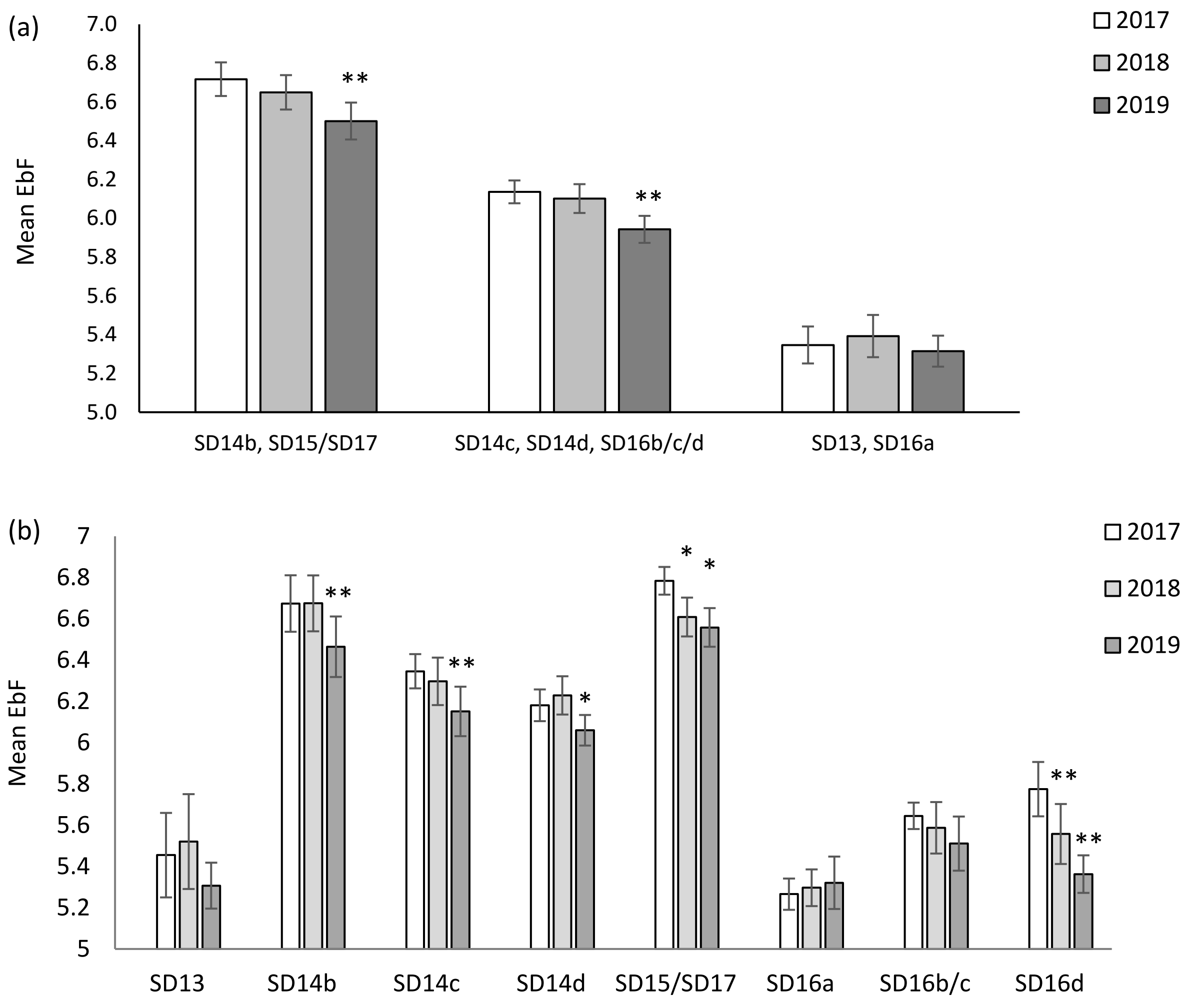


Figure 5.5 Panel (a): Observed mean EbF quadrat values with SE for each level of parameter NVC8 (panel (a): 3 levels with groups of dune slack communities) and parameter NVC2 (panel (b): 8 levels of dune slack communities) for monitoring year 2017, 2018 and 2019. NVC communities were assigned and fixed in 2017 as a treatment factor and were assessed for interaction with year ($p < 0.001$, Appendix Table 0.4). The significant interactions within dune slack communities were marked with * $p < 0.05$ and ** $p < 0.01$ (Appendix Table 0.4).

5.3.4. How do bryophytes species alter the interpretation of key hydrological relationships? And do they display similar relationships and inter-annual patterns as shown in plant communities?

The hydrology metric of the 8-year average MSL had the best model fit with NVC2 based on AIC scores F (1, 86.3) = 54.7, $p < 0.001$ (Model 31, Appendix, **Table 0.7**). The model including the 5-year MSL had also a significant effect on the mean EbF response F (7,166.7) = 8.9, $p < 0.001$ (**Figure 5.6**). The levels of parameter NVC8 did not have a significant effect on the mean EbF response indicating there might be a different community structure better suited to explain the mean EbF response. The pairwise comparison of NVC2 did reveal some group structure for new parameter levels (Model 33, Appendix, **Table 17**: group 1 – ‘SD13, SD14b, SD14c, SD16d’ and group 2 – ‘SD14d, SD15/SD17, SD16a, SD16b/c’, although most dune slack communities of group 3 also paired with SD16d. Dune slack community SD16a could be a separate level as the model estimate coefficient was significantly different ($p < 0.001$), however the standard error (SE) of the NVC2 dune slack communities was between 0.2 – 0.3 mean EbF which lead to the classification of SD16a to group 2.

The inter-annual mean EbF response between plant and bryophyte communities was also different in pattern and trend (**Figure 5.7**, panel (a): bryophyte response; and panel (b): vascular plant response). The bryophyte mean EbF response had no inter-annual effect with parameter NVC8 or NVC2, neither was the interaction found to be significant. The comparison between panel (a) and panel (b) of **Figure 5.7** showed differences in range and variance of mean EbF per dune slack community, in which the m confidence interval (CI) of the bryophytes was often wider compared to the plant community range (SD13, SD16d). The mean EbF CI of bryophytes was also higher. For example, with SD14b and SD14c the bryophyte niche was higher (CI 95%: 6.7 - 8.2 mean EbF) compared to the corresponding plant niche (CI 95%: 5.6 - 7.0 mean EbF). There was a strong niche separation in mean EbF response within the SD16(a/b/c/d) for the bryophyte community; in which SD16a was also the driest bryophyte community which was considerably lower in mean EbF range (CI 95%, 3.3 – 5.2) than the plant community mean EbF response (CI 95%, 5.1 – 5.6).

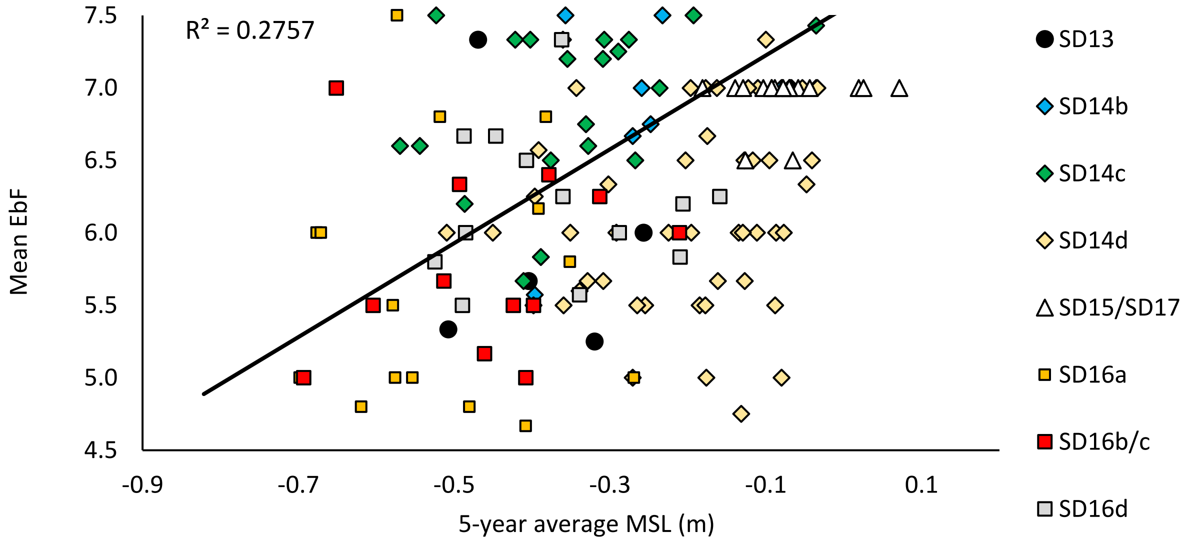


Figure 5.6 Relationship between the observed mean EbF (bryophyte) against 5-year average MSL (m) fitted with a trendline with the R-square. Each symbol stands for a NVC community, described in the legend. On the x axis, ground surface is 0, negative MSL values represent water levels below ground surface.

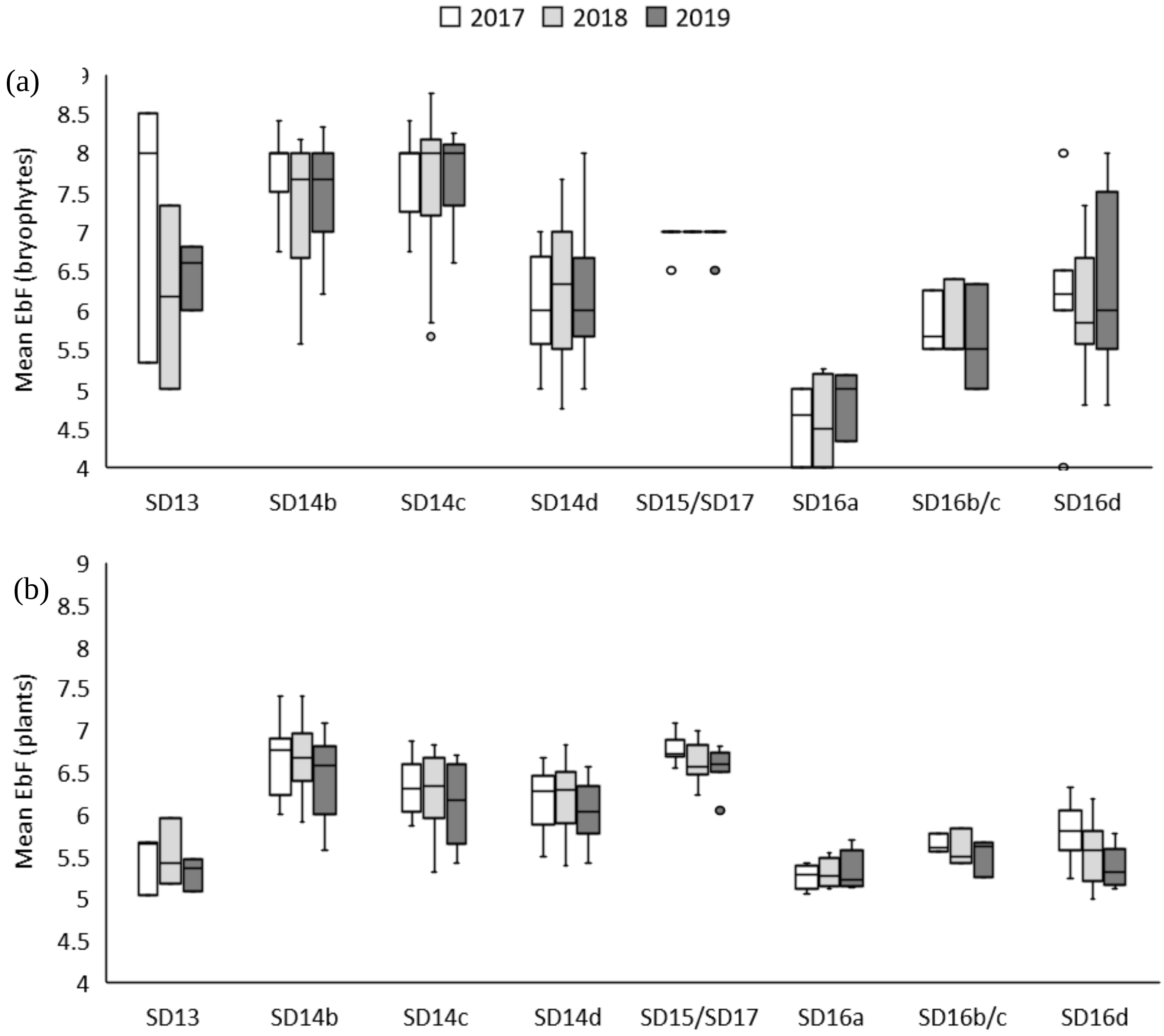


Figure 5.7 Mean observed EbF each level of parameter NVC2 (8 levels of dune slack communities) for per year. Panel (a) Mean observed EbF averaged on bryophytes species only. Panel (b): Mean EbF averaged on plant species only.

5.4. Discussion

Our mixed model analysis showed that the mean EbF response of the dune slack vegetation was moderated by levels of species assemblages, both for vascular plant and bryophyte communities. On top of that, we showed that levels of species assemblages of vascular plants can be grouped according to their effect on the mean EbF response, indicating there might be different diver mechanisms between the levels of dune slack communities. The inter-annual patterns within the scope of our study also confirm the possibility of different driver mechanism between at least two groups of dune slack community’s type. We will discuss our findings according to research questions in more detail further below.

5.4.1. What are the differences in plant community response related to species assemblages to the hydrology regime?

Our results showed the importance of species assemblages in the analysis of ecohydrology vegetation responses. By including levels of single or grouped plant community types in the analysis, we were able to obtain more accurate community responses to the hydrology regime. Studies on the level of individual plant communities have been limited, but using weighted plant community indicators like Ellenberg have been popular in niche studies (Diekmann, 2003; Jarvis et al., 2016; Hedwall et al., 2019; Dwyer et al., 2021a), despite the strong recommendation to maintain analysis within the same vegetation type (Wamelink et al., 2002; Smart & Scott, 2004), this advice has not been tested frequently. Other examples of plant community research often focus on biodiversity patterns and drivers, but also without including actual levels of plant community types in the analysis (Connor et al., 2021). Regional metrics like slack age or area were found to be of higher influence than abiotic variables on plant community diversity, based on three sites analysis. The study of Dwyer et al. (2022) revealed the importance of the spatial level (sites, dune slacks, plots) and spatial dimensions in metrics when looking at biodiversity patterns, indicating this could lead to the misrepresentation of key environmental or management drivers. Regional metrics might explain some of the variation driving the plant community patterns as a (spatially structured) proxy, but abiotic divers will ultimately control niche partitioning of the plant communities and therefore, biodiversity patterns. To understand the response of plant communities to drivers, especially climatic-variation, research needs to be within site level or account for the heterogeneity between sites or this will likely reflect most dominant drivers of the highest level. Including the level of species assemblages will help to accommodate the spatial heterogeneity between sites and gain a far better understanding of plant community responses to environmental drivers.

5.4.2. Which hydrology metrics or other variables influence the plant communities' responses?

Research has often been focused on including one hydrology metric predicting all communities within vegetation types (Käfer & Witte, 2004; Jamil et al., 2013; Punalekar et al., 2016; Dwyer et al., 2021a). However, our study showed that each species assemblage has their own hydrology and mean EbF response niche, of which some overlap, resulting in 3 main groups which can be used for research or monitoring (wet, intermediate, and dry dune slack communities). Dune slack niche segregation has been found before (Lammerts & Grootjans, 1998; Curreli et al., 2013; Dwyer et al., 2021b), and in line with our results, local hydrology was one of the main drivers behind the partitioning. The distinct levels of plant community response are likely the results of abilities contained in the vascular plants species, which can be reflected in the combinations of hydrology and soil metrics moderating the hydrology response found in this study. The difference in plant community response might also be explained by the presence of hydrology-related mechanisms because of those abilities, like drought tolerance or soil chemistry, where different averaging periods and type of metrics indicate what is most important to the level of plant communities.

One of the mechanisms is likely to depend on soil organic matter (SOM), which only had a significant effect for the dry plant communities' level in our results. The significant role of SOM has been described before (Berendse et al., 1998; Sýkora et al., 2004), often in context of the trade-off in accumulation rates between low productive species and high productive species present in different plant communities (Rohani et al., 2014). The trade-off supports the idea of a SOM-dependent mechanism for the drier communities, versus wet and intermediate levels of plant communities, which thrive on low SOM conditions and inter-annual flooding (Lammerts & Grootjans, 1997; Sýkora et al., 2004). Our results confirm this, in which the wet and intermediate plant community' level response was best predicted by shorter averaging period and spring conditions versus the highly significant effect of SOM driving the dry plant community response. Other studies also confirmed the presence of SOM-dependent mechanisms between plant communities, with different hydrology responses between types of textural soil (peat, sand and clay) (Ertsen et al., 1998) and different SOM-content development with soil age depending on dry or wet dune communities (Jones et al., 2010). The study of Dwyer et al. (2021), also found a similar effect of SOM (LOI) on the mean EbF response, including all dune slack plant communities. The study was similar to our analysis, but with many more sites included, which could result in a stronger link because of the spatial level differences (Dwyer et al., 2022).

Although the effect and importance of soil pH on dune slack plant communities is well studied (Lammerts & Grootjans, 1998; Grootjans et al., 2017), we found no direct significance effect of soil pH on the hydrology response. However, this relationship is likely indirectly reflected by the stronger link of the 5-year average MSL in our analysis. Buffering conditions can be supported by annual flooding, and therefore, represent the effect of soil pH within the hydrology metric. Our results showed that soil pH might have a significant effect on the hydrology response of plant community SD15-SD17, nevertheless, the effect was not significant on the level of the wet plant communities as a group, confirming that the hydrology metric explains the effect of both on group level. This was also found in the form of co-linearity of soil pH in a similar analysis, which was removed from the analysis in favour of the hydrology metric (Dwyer et al., 2021a). Another reason might be that, within the scope of our study, soil pH was considerable high, as this dune site has excellent buffering conditions. This could also explain the weaker relationship in analysis, while including more (acidic) sites would lead to a higher spectrum of soil pH and potentially a stronger relationship.

5.4.3. How are the inter-annual responses within and between the plant communities related to species assemblages?

As this study was conducted, there were inter-annual differences due to rainfall and drought, which was reflected in the hydrology metrics. Our results showed clear interaction between years and the levels of dune slack communities, where the wet- and intermediate dune slack communities showed dynamic behaviour because of the inter-annual variation. However, the level of dry communities displayed no response to the inter-annual variation, indicating the possibility of high drought tolerance. Drought tolerance can be based on the difference vascular characteristics, like with woody plants, drought tolerance can dependent on their strategy based on hydrology margins within their vascular network (McDowell et al., 2008). Although dune slack habitat is often without trees, shrubs like *Salix* are important for dune slack habitat, which can reach high dominance in the drier communities. Drought tolerance can also be affected by diversity of plant communities, as resilience of plant communities, expressed as production, can be more stable and lead to quicker recovery in response to climate extremes (Isbell et al., 2015). We did not observed an inter-annual response for drier dune slack communities, however, this still might apply to the range of wet and intermediate plant communities inter-annual response. For example, species assemblages of the wet communities can reach high diversity, and some of those plant species, like orchids, are dependent on fungal symbionts (Wang et al., 2023). Fungal symbionts also have a high dependence on soil pH and soil moisture (Waud et al., 2017), so the effect of drought can lead to strong impacts within those plant communities. This kind of negative feedback not only lowers within plant community diversity, bus also decrease resilience, leading to even stronger effects.

In the study of Dwyer et al. (2021), hydrology sensitivity was discussed in relation to SOM, where increased hydrology sensitivity was found with thicker organic matter layers. This finding was in contrast with the results in this study, as there was no effect of SOM for the level of wet- and intermediate dune slack communities. However, we did find a significant effect of SOM for the drier dune slacks. Another reason might be that the SOM content measured in this study was potentially too low to observe this effect for the wet- and intermediate dune slack communities. It would, though, support the previously discussed hydrology-mechanism for the level of wet and intermediate plant communities and their hydrology sensitivity. Dune slack plant community SD14d and SD15/SD17 have higher SOM content, and possibly can be more susceptible to drought with increased SOM content. This would be caused by the shift or decrease in species in relation to the increase of SOM, potentially indicate that diversity within the level of plant communities is related to drought resilience as well.

5.4.4. How do bryophytes species alter the interpretation of key hydrological relationships? And do they display similar relationships and inter-annual patterns as shown in plant communities?

Bryophytes are ectohydric and have been known to have different requirements compared to vascular plants, with different seasonal timings, recovery abilities and rainfall dependence (Bartholomeus et al., 2012b). This was in line with our results, as we found different ranges of mean EbF response between and within of the dune slack communities, comparing vascular plant and bryophyte compositions, indicating that for some levels of dune slack communities' different hydrology dynamics or hydrology seasons drive the mean EbF response. There was no inter-annual effect on the bryophyte communities, nor was there an interaction between any of the levels of bryophyte communities. This was surprising, as bryophytes have been found to be sensitive to other environmental triggers, like elevated temperature (He et al., 2016).

Bryophytes abundance has been found to depend on water availability, similar to our observations between the levels of plant communities. Indications SOM-related mechanisms in bryophytes have been reported previously in dune slacks (Callaghan et al., 2021), where species presence was related to either annually flooded locations or drier SOM-rich locations, indicating the dependence on water availability by the use of SOM soil content rather than soil chemistry. This could partially explain why there was no inter-annual response observed within our study, as bryophytes communities might depend more on SOM content. Bryophyte species can also increase the water capacity of the community (Lett et al., 2022), nonetheless, they are still highly dependent on external water sources (He et al., 2016). Although they withstand drought by adjusting their hydraulic conductivity (Voortman et al., 2014), they often have good abilities to regain physiological function after dehydration (Proctor et al., 2007). This might explain the lack of inter-annual response, as recovery can be as quick as the period of extreme conditions. Another explanation would be that despite the variation between the years during the monitoring period, intra-annual cycle dynamics were still in order, and as long as the minimum requirement was reached, the bryophytes species were able to grow. Our results support this, selecting the 8-year average MIN, which was compromises a longer averaging period compared to the vascular plant model. Previous analysis also supports this, in which the bryophyte response had little influence on the overall mean EbF hydrology response, bryophytes and vascular plants scores, within the dune slack vegetation (Chapter 4, van Willegen). This could also indicate that seed bank dynamics might be involved in this mechanism, in which resprouting is dependent on high seed viability within a period of at least 8 years. The quality of diaspore bank was found to be extremely high in the upper 0-5 cm of the soil (97%), which would make such a suggestion plausible (Callaghan et al., 2020). Overall, it is still unclear what is driving the bryophytes species response, high tolerance to drought or short-term population dynamics? The results emphasize this mechanism is still poorly understood and there is need for more research on bryophytes response.

5.4.5.**Recommendations and future research**

The results in this study have revealed insights into hydrology responses within dune slack plant communities, though, there have been limitations. To fully understand the plant response on community level, we need to increase sample size per species assemblage, especially towards the plant communities that are becoming rarer and more endangered. As there are differences in species assemblages depending on regionality within Europe, or even beyond, attention needs to be paid to include the full range of dune slack plant communities as possible. This is also to ensure that we understand the full range of the relationship between the dune slack plant communities and hydrology, including the non-linearity at the end of the hydrology gradient, as there is little known on the transition at the end of the gradient. This could be done using a GAMMS model or using GLMM, as they would consent for non-linearity and allow for scaling of the variables as well. Using scaled and community-centred variables acknowledges for a more accurate analysis per level of plant communities. To obtain a higher number of samples more sites can be included in the research, this will also help to determine how the relationship holds with more environmental variation, as long as we keep the scaling problems in mind (Felton & Smith, 2017; Dwyer et al., 2022).

Acidic and enriched dune slack environments can affect species composition, which often leads to a lower diversity within plant communities (Rhymes et al., 2014). Using plant community types will not address those diversity patterns directly, but incorporating a quality indicator of plant community type could address diversity patterns within plant communities.

As resilience to climate change is likely to be linked to biodiversity (Isbell et al., 2015), this might lead to better insights on different scales. Longer time-series data will also increase knowledge of mechanisms on resilience and especially tipping points. This study has shown the differences in responses to dry years; however, this was rather a short timeframe without any re-wetting occurring during the study. To gain more knowledge on the potential for the habitat in the future, we need more longitudinal time-series data, to really understand tipping points for compositional change on between and within plant community level. Long term comparisons can often only reveal the most dominant drivers and are more difficult to analyse and to understand. In regard, short-term repeated data is still a necessity for inter-annual dynamics.

Research on the role of bryophytes within dune slack communities has been limited, often constrained by the small number of species and difficult identification within vegetation quadrats. It might be that mean EbF as an indicator for bryophytes has not been recommend due to the difficult interpretation and calculation legacy (Pakeman et al., 2019). However, using repeated measurements in mixed model analysis increases power and limits the standard error. We might need to re-think using Ellenberg indicators for bryophyte research, though, our results did give some insight in the bryophyte response. Although we did not find inter-annual responses, we did observe inter-annual change in species and abundance in the field. Another way is to re-do the analysis using hydrology metrics who focus on the different timings of the bryophyte growing season, like autumn and winter. More research could focus on this, as there is still much unknown about bryophyte species and community response and driving mechanisms.

5.5. Conclusion

Our study highlights the role of vegetation species composition in moderating the plant and bryophyte community response to hydrological regime. We show that species composition is relevant in the hydrology niche partitioning, where traits or features of assemblages of vascular plants and bryophytes likely drive adaptation to different hydrology niches, as environmental influences and conditions are directly linked to the hydrology regime. This is important to understand, as our study indicates that resilience to drought might be related to biodiversity within and between plant communities and needs to be considered for habitat conservation. We provide the warning that wet and intermediate dune slack plant communities can be highly responsive and sensitive to variation of the hydrology regime as shown within our study. More research is necessary to understand resilience and the ability to recover before making assumptions of long-term effects to climate change. Studies with repeated measurements will help to analyse trends and resilience in dune slacks towards climate change. This study emphasises the dynamic character of natural sides like dune slack habitats in response to the inter-annual variation.

5.6. Acknowledgements

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Chapter 6

Chapter 6

6. Discussion

6.1. Overview

The primary aim of this thesis was to explore the spatial and temporal dynamics of the hydrology regime and the associated vegetation communities at Newborough Warren in an effort to improve our fundamental understanding of dune ecosystem functioning and to contribute to the formulation of improved dune slack management and conservation practices. To safeguard dune wetlands and to provide sustainable management practices into the future, there is a critical need to increase our knowledge on the factors which regulate dune slack plant communities, and to design science-led interventions to protect these high conservation habitats from current and emerging threats. By integrating field monitoring, statistical analysis and numerical modelling, this thesis set out to gain a better understanding of the relationship between dune slack vegetation and underlying hydrological regime.

As outlined in Chapter 1, the research objectives of this thesis were:

- To develop a representative 3-D hydrological model of the dune water table at Newborough Warren, using existing long-running hydrological monitoring data, hourly climate data, topography and previous studies and published literature. The validated model can be used to test the influence of different forest management scenarios on groundwater regime.

- To assess and explore the influence of climate induced intra- and inter- annual variation of the hydrological regime as a driver of dune slack vegetation assemblages.

- To identify the role of vascular plant and bryophyte community species composition in the vegetation response to hydrological regime.

- To utilise hydrology metrics to predict the vegetation response of dune slack vegetation, which is of high importance for the future design of better management and conservation practices.

This chapter will provide a general discussion of the thesis, bringing together the findings within the wider context of existing knowledge, provide recommendations for management, identifying avenues for future research, and ending with some final concluding remarks.

6.2. Relationship between hydrology and dune slack habitat

6.2.1.**Hydrological modelling, a vital tool for future dune management planning**

The validity of the hydrological model in chapter 3 was supported by meteorological data-series collected over a 10-year period, using rainfall and evapotranspiration, alongside structural variation of the 27 vegetation types. This allowed for management interventions to be modelled and predicted. The results from the management scenarios emphasized the sensitivity of groundwater-fed dune systems to small-scale interventions (e.g. 2 ha of tree felling) that were removed from the zero management scenario, right through to larger large-scale interventions as in the full forest removal management scenario. Therefore, there are opportunities for improving habitat quality as an outcome of management interventions. Our results were in broad agreement with previous studies using models to simulate the impact of temporal changes in groundwater regime in other dune systems (Kamps et al., 2008), or the impact of management interventions (Adane et al., 2018). Although other methods and hydrology models have been used to predict the impact of management intervention or climate on dune hydrology, our numerical model allowed us to study sand dune management in greater detail, simulating events like thinning and felling while incorporating a complex array of geological and topographical features. The level of temporal and spatial resolution, allowed for the successful prediction of the groundwater flow and seasonal dynamics such as annual flooding to be observed in the model. Overall, the performance of the model over the 10-year window did resemble the long time span of hydrology data obtained in the field with piezometers. The predictions of management interventions, therefore, shows how model and field monitoring can be combined to help improve our ability to predict the impact of current and future management interventions. For future research, but also highly important for dune slack management, will be the ability to run future climate scenario’s with numerical hydrology models. Allowing to test different scenario of global warming and changing precipitation patterns will be vital to understand how dune slack habitat will respond. As climate change is highly expected to have high impact on wetland hydrology regimes (Salimi et al., 2021), hydrology modelling will offer opportunity to test moderate, but also extreme scenario’s and adapt accordingly. For example, it would be a good opportunity for the site dune management of Newborough, to use this spatial hydrology model for future predictions, but it could also provide information where it is essential to implicate management interventions in the future. This can be used to adapt the dynamics in the forest, with felling and thinning, or replanting with other species to change evapotranspiration on site. But it can also be a used to adjusted the hydrology regime with other options, like reducing drainage, restoring erosion, scraping of dune slacks or other management implications. Above all, it can help to determine where the areas are that might be most sensitive to drought or high precipitation evens, which could help to improve future monitoring and select area’s for research.

6.2.2. **Hydrology metrics as explanatory drivers of dune slack communities**

Hydrology has been recognized as the main driver of dune slack communities by many studies, and at many different spatial scales; from dune slack (Dwyer et al., 2021b), to site (Curreli et al., 2013; Grootjans et al., 2017), to the national level (Grootjans et al., 1991; Dwyer et al., 2022). This link between vegetation and hydrology has often been expressed in the form of hydrology metrics, ranging from single-year metrics, to averages of 4-years (Dwyer et al., 2021b; Dwyer et al., 2022), often representing spring conditions (Bartholomeus et al., 2012a), but also minimum water level (Curreli et al., 2013) and mean water table (Dwyer et al., 2021a; Dwyer et al., 2021b). Within this study (chapter 4 and 5), we found the 5-year mean spring level (MSL) to be the metric which best explained and predicted overall dune slack vegetation responses to hydrological regime. For dune slack management this 5-year metric would work well in management planning and evaluation, as most sites with protected status, like Natura 2000 (European) SAC or SSSI (United kingdom) status are obligated to survey and report 6 year periods by the Habitats and Wild Birds Directives (Sundseth, 2015). Using the 5-year MSL metrics as an indicator of site conditions in direct relation to the (moisture-)status of the plant communities would provide managers with an additional tool to validate monitoring results (observations and analysis) and maybe even more important, evaluation of site status. As the result in this study emphasize, especially the wet- and intermediate plant communities are vulnerable to the inter-annual variation of the hydrology regime and will have good potential for evaluation with hydrology metrics. Therefore, it should be noted that this metric is likely to have the highest predictive power for dune site with calcareous dune slacks and carbonite-rich seepage, as other variation in environmental variables are likely to be driven by the same hydrology regime. Although the best model predictions resulted from the relationship with the 5-year MSL, shorter averaging periods also might also be suitable when monitoring data is limited. The hydrology metric MSL presented the best relationship with the shape of dune slack plant communities, however, this does not mean we should not explore other metrics when we look into plant species or community responses. Statistical analysis using mixed model techniques allowed us to understand parts of the complex interactions between the hydrology regime and the other environmental variables, and needs further analysis, especially with dry plant communities. Overall, we conclude that vascular plant dune slack community responses can be predicted with a range of hydrology metrics and that these can provide a valuable management tool enabling more accurate predictions of how these communities will respond to management interventions and climate change.

6.2.3. **Species assemblages, an unexplored role of moderation within the vegetation response**

This thesis examined the role of species assemblages in the response of dune slack communities to hydrological regimes in Chapter 5. The addition of species assemblages as an explanatory factor in the model allowed for differentiating responses within the overarching dune slack vegetation community. This finding highlights that dune slack vegetation cannot be treated as a homogeneous entity in terms of hydrological responses. Rather, species composition imparts meaningful differences in hydrological relationships across moisture gradient zones (Isermann, 2011; Dwyer et al., 2021b). Accounting for species assemblages enables a more refined understanding of variations in dune slack hydrology-vegetation linkages. This moderating effect was evident for both vascular plant and bryophyte communities, highlighting the importance of accounting for species assemblages in statistical analyses of vegetation response in dune wetlands. The influence of separating plant community types on vegetation response has been discussed previously in relation to Ellenberg indicators (Wamelink et al., 2002; Witte et al., 2007), but has seldom been incorporated as a moderating variable. This study demonstrates that species assemblages can have a major impact on modelled vegetation-hydrology relationships, underscoring the need to consider species composition as a potential effect modifier in dune ecosystems and likely other wetland types (García-Baquero Moneo et al., 2022).

As analysing different spatial levels of community diversity can result in different drivers (Dwyer et al., 2022; Del Vecchio et al., 2022), adding the level of vegetation community types might offer some clarity into the mechanisms underpinning those dynamics (see section 6.2.5). The results in this study might be limited to plant communities in Wales with classification of Rodwell (Rodwell, 2000), but the plant community groups and successional pathways will likely have similarities with other European classifications (Davy et al., 2006).

The principle of plant assemblages shaped by environmental variables, biotic interactions and adaptations of evolution or plasticity has been studied widely, there is need to explore the interactions that shape plant communities in a multi-disciplinary way to understand responses to climate change (HilleRisLambers et al., 2012). Although plant communities in Wales might show differences due to geographical distance or climatic region, the application of plant community ID as a moderating factor in data analysis will provide a potential to study mechanisms and drivers, serving as a categorical proxy of shaping dynamics not included in the analysis. Although environmental factors play an important role as drivers, it might be more difficult to account for the role of evolutionary dynamics in other ways. Overall, this might lead to better insights in the successional dynamics of dune slacks, across many regions, and a tool that might also allow comparisons between sites on different levels.

6.2.4. Inter-annual dynamics within dune slack habitat

The findings in this thesis revealed the presence of significant inter-annual variation within the vegetation response, which had a large impact on the relationship between hydrology and dune slack vegetation. Both chapter 4 and 5 showed how the relationship between hydrological regime and dune slack vegetation altered between years, from dune slack to site level. In the context of the level of species assemblages' moderation noted previously, we found that especially wet and intermediate dune slack communities of vascular plant displayed variation in their hydrology response over time. This is an important finding, as most previous studies have often been limited by short monitoring periods, or analysing multiple years together as one relationship. Further, although long-term and multi-site comparisons, like chronosequences, have been useful to determine thresholds and vegetational community change over time (Jones et al., 2010; Plassmann et al., 2010; Isermann, 2011; Aggenbach et al., 2017), they only tend to reveal the most dominant driver over that period. However, we need more knowledge on short-term behaviour explaining inter-annual dynamics, as this will bring us closer to understanding dune slack resilience. Therefore, the findings in this study conclude that long-term monitoring is necessary, especially with repeated measures, to determine the short-term dynamics and how they affect vegetation response around hydrology thresholds in the future.

6.2.5. Drought sensitivity and hydrology mechanisms

Incorporating species assemblages as a moderating variable revealed further nuances in dune slack vegetation responses. As discussed in the previous sections, the analysis uncovered a clear delineation between dry dune slack communities and intermediate/wet dune slack communities in their vegetation responses to inter-annual hydrological variation. The question remained, how far this differentiation would impact the dune slack response, and if this might be related to the main driver behind niche partitioning in dune slack habitat. Within our results, we found a difference in their dependence on hydrology, with dry dune slack communities likely to depend on soil organic matter (SOM) levels while wet and intermediate dune slack communities had a closer relationship with the seasonal flooding dynamics (Dwyer et al., 2021a). This mechanism brings together most of our findings, as the hydrology metrics per group supported this finding, as was the relationship with SOM only relevant for the drier dune slack communities. The wet and intermediate plant communities were highly responsive within our study, and are also likely to be vulnerable to drier hydrology conditions during drier years. Similar separation of the dry and wetter dune slack communities have been described before, with different drivers or mechanisms, but ultimately relying on the same principle. Soil pH is often cited as an influential driver of vegetation communities, yet its impact frequently stems from maintaining stable soil conditions, restricting nutrient availability, or enabling processes like enhanced nitrogen loss or altered nitrogen and carbon cycling (Adema et al., 2005; Rhymes et al., 2014). As a result, it is likely there is a mechanism based on soil pH, which is facilitated by the hydrological regime, specifically by annual flooding. Dry slack communities have been described to increase nutrient uptake to reach the opposite state, nutrient-rich conditions, to maintain their species assemblages. Even so, with drier conditions (e.g., lowering of the water table by 5 cm) the hydrology dynamics can fundamentally change denitrification processes, leading to even higher nutrient loads, describing a positive feedback for dry dune slack communities (Rhymes et al., 2016). This would be a reasonable explanation for the dry dune slacks community response to inter-annual variation, especially since we found a high dependence on SOM for dry dune slack communities supporting the theory of niche partitioning. It could be that high SOM content reduces the drought sensitivity to hydrological change, because SOM content is able to keep soil moisture within normal levels, along with maintaining high nutrient levels. Overall, we conclude that these community mechanisms are closely linked to soil pH and SOM, and that these are highly important in maintaining this type of dune slack community, with both soil quality indicators being dependent on hydrological regime.

6.2.6. **Role of bryophytes in shaping dune communities**

Only a handful of studies have looked at the implications and role of bryophytes in dune ecosystem functioning (Callaghan et al., 2020; Callaghan et al., 2021; Lett et al., 2022). Bryophytes play an important role as key indicators within dune slack communities. Within our results, we found that bryophyte communities were best predicted by the 8-year average MSL, a different metric to the relationships established between vascular plant communities and hydrological regime. However, the prediction model showed that the relationship could be improved and the inter-annual dynamics were not reflected in our results. Despite that the role of bryophytes within dune slack communities is not completely clear, there are enough indications that bryophytes can serve as important epiphytes for orchids and facilitate the presence of more species within dune slack habitat. As epiphytes, they offer protection against drought, but also serve as an anchor, allowing for roots to take up oxygen rather than being submerged and potentially hypoxic (Jacquemyn et al., 2023). Bryophytes can also serve as bio-indicators, as they are highly sensitive to environmental change (Printarakul & Meeinkuirt, 2022). Overall, bryophytes might play a vital role within dune slack communities, and potentially have strong inter-annual variation as observed during the study period, but our results could not capture or translate the dynamics of the bryophyte communities that reflected this observation based on diversity numbers alone. Therefore, more research is needed on bryophyte communities and dynamics.

6.3. Wider implications for management and conservation

6.3.1. **Monitoring guidelines: The 5-year average MSL**

Within our study, we analysed the role of hydrology metrics, with the intention to optimize the understanding and use of hydrology metrics for management practice and conservation. As a result, we will be able to utilise hydrology indicators for more effective management of these habitats, building a predictive model with the ability to quantify dune slack community response. The analysis in Chapter 4 has resulted in the advice to use the mean spring level (MSL) as a hydrology metric. This is based on the groundwater level monitoring of 3 months of the year, February to April, to be averaged as a mean of spring conditions. Chapter 5 resulted in the final advice to use the 5-year average MSL, as the best metric to describe the response of the overall dune slack plant communities to hydrological regime. From the results of this study, we calculated the mean 5-year MSL values for each community, displayed in **Table 6.1**, and from which we identified 3 groups based on NVC dune slack community type in **Table 6.2.**

Table 6.1 The average 1-year MSL and 5-year MSL values for each NVC community type (Rodwell, 2000) during the monitoring period of 2017-2019.

NVC type	Mean spring level (m)	5-year average MSL (m)
SD13b	-0.56	-0.38
SD14b	-0.21	-0.09
SD14c	-0.41	-0.26
SD14d	-0.29	-0.20
SD15b	-0.22	-0.07
SD16a	-0.72	-0.53
SD16b	-0.90	-0.65
SD16c	-0.67	-0.43
SD16d	-0.63	-0.41
SD17	-0.08	-0.07

Table 6.2. Equations linking Mean Ellenberg F and hydrological characteristics (5-year MSL), for: wet (group 1), intermediate (group 2) and dry (group 3) dune slack communities.

Group	Description	Dune slack communities
1	Wet dune slack communities	SD14b, SD15, SD17
	Mean EbF = 6.75 + 1.64 * 5-year average MSL	
2	Intermediate dune slack communities	SD14c, SD14d, SD16b/c, SD16d
	Mean EbF = 6.54 + 1.64 * 5-year average MSL	
3	Dry dune slack communities	SD13, SD16a
	Mean EbF = 6.37 + 1.64 * 5-year average MSL	

The values of each dune slack community can be used as guidelines for monitoring at Newborough and at other sites that are comparable. As discussed in 6.2.2, the hydrology metrics and model will assist dune managers in the evaluation of plant community status, and can be of high importance to optimize monitoring and dune slack management. More research will be needed to verify our predictive models with systems of different geological origin, environmental range and longer time periods to verify the impact of other climatic variation.

6.3.2. **Future management opportunities at Newborough**

Within the scope of this thesis and the site of Newborough, we provide the warning that wet and intermediate dune slack plant communities can be highly responsive and sensitive to variation in hydrological regime. These warnings need to be considered within the boundaries of our study, as more research is still needed to fully understand the implications of climate change, but also the effect of the management regime on dune slack resilience.

For example, if the small-scale felling of parts of the forest had not happened over time, then the dune slacks which are currently NVC SD14 community within 280 m of the forest edge would likely be 15 to 28 cm drier and the communities would have changed to a SD16 community. It is therefore important to prepare a programme of management that is informed by science, and to undertake the routine monitoring and associated research that should accompany any management intervention. Monitoring of conditions should take place both before any intervention and for a minimum of five years afterwards, and ideally longer to fully understand the observed changes, and learn lessons to apply to other restoration cases. The restoration of older dune slacks, by scraping or sod-cutting, are examples of management interventions which can be used for monitoring plant community dynamics. The restoration projects also offer opportunity to study seedbank dynamics or founding effects in pioneer dune slack communities (Plassmann et al., 2009; Callaghan et al., 2020), as knowledge of pioneer communities needs more attention.

Other ways to improve management can be found using the predictive ability of a numerical hydrology model as discussed in 6.2.1, and the models that resulted from this study from Chapter 4 and 5. The combination of the models can provide an opportunity to predict and evaluate plant community status and response at Newborough in the future. With the use of the dune slack plant community prediction models in Table 6.2, we can extrapolate the results of the hydrology model running future climate predictions into hydrology metrics of the 5-year MSL, and calculate possible future mean EbF responses. This would help dune management at Newborough to understand which plant communities are likely to expect in the future, and if this corresponds with our actual findings and research (Curreli et al., 2013). Overall, this combined use of all three findings, would be a way to study the impact of climate change and management interventions, providing a vital tool for wetland management and conservation.

6.4. Future research

To contribute to future management and dune slack conservation, more research is clearly needed to better understand the resilience and recovery response of dune communities to climate change. I will discuss how my research results and insights have led to improvements in understanding, identified new avenues for future work and highlight challenges for further research.

6.4.1. Impact of climate change

Climate conditions are expected to become more erratic in the near future based on current IPCC predictions (Pörtner et al., 2022). These include a number of changes related to hydrology, such as increases in summer drought or changing precipitation patterns. These are expected to have a major impact on wetland ecosystems (Kløve et al., 2014; Salimi et al., 2021). Our study confirmed the potential of using hydrological modelling to run scenarios which may affect groundwater levels. As discussed in section 6.3.1 and 6.3.2, using future climate predictions to run our groundwater model, in combination with our selected hydrology metrics and model descriptions resulting from chapter 4 and 5, we would be able to use predicted groundwater levels to predict future' vegetation community response. These tools would be of high importance to gain better insights in future conditions for dune slack management and conservation. However, using future climate data is not only about data input; it will also be a challenge to represent essential evapotranspiration processes with high accuracy in the model, as there are still many unknowns about the true effect of temperature rise, or elevated CO_2 values on vegetation performance. It is therefore important to study and analyse these effects under controlled conditions, or controlled field-scale manipulations, and then to incorporate these data to enable more accurate model predictions. Another way is to study these effects in separate models, either using SWAP or using species response models to analyse individual or community response (van Dam et al., 2008). Using experimental settings will be important to validate models. In addition to the climate impact on evapotranspiration, there are also other factors which can also affect evapotranspiration which might need more recognition including diseases (e.g., *Dothistroma septosporum*) or the role of invasive species (e.g., *Prunus serotina*), which will affect evapotranspiration and therefore recharge to the groundwater, in different ways.

6.4.2. Resilience and tipping points

To gain a better understanding of the inter-annual dynamics and species assemblages' responses found in this study, we need to ensure we understand the underlying dynamics and mechanisms that translate into metrics predicting resilience and tipping points. Although we have an excellent knowledge of thresholds on a national (UKCEH & Dunescapes, 2021) and European level (Houston, 2008), we lack the understanding of how to feed short-term dynamics into those long-term models. In other words, how resilient plant communities are to climatic variation and how is that ability influenced by environmental, spatial or temporal factors? To get a more complete understanding of the dynamics around tipping points on different levels, we do need to incorporate the full range of dune slack communities, in excellent- or poor-conditions, to understand the full extent of resilience. This can be done by including more sites, nationally or internationally, data on a wider hydrological gradient beyond that which defines dune slacks, from fully dry grassland through to permanently flooded dune wetlands, and most importantly long combined time series of both vegetation monitoring and hydrology. Resilience has been found to alter with plant community diversity (Isbell et al., 2015; Wright et al., 2021), and as diversity can be linked to spatial heterogeneity and spatial levels (Dwyer et al., 2021b; Dwyer et al., 2022), it is important to incorporate multiple sites, preferable national or international level of research. A way to study the long-term dynamics in a new light, would be by the combined role of hydrology metrics and the hydrological model in Chapter 3, which has the ability of predicting long term groundwater level data. Using periods of long-term climate data would allow to produce longer data-series of groundwater data, which enables for long-term (multiple-year) hydrology metrics to be calculated. Up until now it has been difficult to produce hydrology metrics including 10-year or longer groundwater level data, but with the prediction ability of hydrological models, this can be done in an accurate way. The combination of both hydrological model and hydrology metrics with long-term vegetation monitoring would then allow to perform a novel way of studying long-term hydrology dynamics on coastal wetlands or other wetland ecosystems.

6.4.3. Biodiversity patterns might be driven by hydrology-mechanisms

Acidic and enriched environments create different species composition, often less diverse, and are likely to have different mechanisms related to hydrology. Using plant community types will not address those diversity patterns directly, but incorporating a quality indicator of plant community type could address diversity patterns within plant communities. As resilience to climate change might be linked to biodiversity, this might lead to better insights to the diversity patterns on different scales (Dwyer et al., 2022).

6.4.4. **Bryophytes, key indicators**

Bryophytes are ectohydric and have been known to have different requirements compared to vascular plants, with different seasonal timings, recovery abilities and rainfall dependence (Bartholomeus et al., 2012b). We need more studies to clarify the relationship between hydrological regime and bryophytes, using different season hydrology metrics, like winter and autumn. It might also be good to re-think the use of Ellenberg indicators or other indicators, or devise a way to re-calibrate the values of Ellenberg, as they might be more generalized and create therefore a legacy effect in the community-mean values. Soil conditions, like SOM and bulk density can also have high impact on bryophytes species, or potential symbiotic relationships with fungal species or cyanobacteria such as *Nostoc* (Callaghan et al., 2021). But most important, we might expect that the seed bank dynamics have a role in bryophyte population dynamics, potentially as an adaptation to hydrology. As water availability is highly important for bryophytes, there might be mechanisms linked to both; why is seed bank vitality limited to the topsoil layer? We need to know more, as restoration of pioneer habitat often required topsoil removal of more than 5 cm and could potentially lead to problems.

Our results also suggest that long term monitoring is needed to understand the impact of groundwater level dynamics on bryophytes. During the monitoring period, we have observed high annual turnover, where complete bryophyte communities can change over winter. We also noted the impact of frost on flooded dune slacks during the winter period, as this seemed to have high impact in shaping bryophyte communities in the following spring. Another point of interest would be the grazing pressure, as the “normal” disturbance can be high, resulting in soil bulk density which can be positive (Callaghan et al., 2021), but the effect of grazing might be negative when the disturbance is during frozen winter conditions. Although the impact of grazing has been studied previously, long term comparisons were not able to find any change in bryophyte species over time (Plassmann et al., 2010). This again, confirms that bryophyte communities do not display change over time, the question remains however, if this is resilience or simply a case of the wrong type of analysis to study bryophyte communities.

6.4.5. **Experimental approach**

Dune slack community dynamics can also be studied using a more experimental approach. The results of Chapter 5 indicated that bryophyte community dynamics are poorly understood, however, bryophytes are often notoriously difficult to identify. DNA genotyping has gained a vital role in population ecology, however, has not been used much in ecohydrology studies. However, to overcome issues of identification, DNA sequencing would be a good solution, potentially becoming a new method to identify key indicators among bryophytes species.

Other experiments that would be suitable to conduct are inoculation experiments or controlled flooding experiments, which can actually be done *in vitro*, but also *in situ*. Inoculation experiments can play an important role to determine dispersion or seedbank vitality (Callaghan et al., 2020), which would also be interesting not only for bryophytes, but also the recently gained role of fungal activity in relation to orchids and other plant/bryophyte species, might be part of an important symbiosis, like found for *Neottia ovata* (Wang et al., 2023). Controlled drought resilience or flooding experiments are common on single or groups of plant species in vitro but rarely reflect plant communities *in situ*.

6.5. Concluding remarks

Our study highlights the role of hydrology to understand mechanisms and drivers of dune slack vegetation. The thesis addresses important questions regarding dune slack vegetation response, hydrology metrics and the effect of the inter-annual dynamics. As a result, we now have a better understanding of the short- and long-term dynamics behind the drivers of the hydrological relationship within and between dune slack communities. This is expected to play a vital role in the prediction of vegetation response to climate conditions and site management, improving guidance and leading to better future prospects for dune slack conservation.

As a final step, we can now conclude:

- Long term monitoring is costly and labour-intensive, but this study emphasizes the role of repeated measurements on an annual basis, maybe even bi-annual (bryophytes), to understand short- and long-term dynamics. Once this monitoring has characterised a site, the results also show that it is possible to conduct a reduced hydrological monitoring programme targeted on particular key metrics (e.g. MSL).

- The 5-year mean spring level (MSL) was the best metric to explain and predict dune slack vegetation response overall to the hydrological regime, but there is variation in responses among communities (see next point).

- We found that species composition moderates the plant and bryophyte community response to hydrological regime. Each species assemblage has their own hydrology and mean EbF response niche, of which some overlap, resulting in 3 main groups within the dune slack types, which can be used for research or monitoring (wet, intermediate, and dry dune slack communities).

- We show that one of the key mechanisms driving niche partitioning is likely to depend on the interaction between soil organic matter (SOM) and hydrology regime and that this has a significant effect in regulating dry plant communities. As a result, dry plant communities with high SOM were likely to be less drought sensitive, displaying no significant mean EbF responses during this study.

- The inter-annual dynamics found within our study revealed that wet and intermediate dune slack plant communities were highly responsive and sensitive to variation of the hydrological regime.

- Hydrological modelling can be an important tool for the predictions of small- and large-scale management interventions. Our study confirmed the impact of past management interventions had an impact on the local groundwater levels close to the forest, preventing a likely change of dune slack plant communities in the affected areas.

Appendix

Chapter 3

Table 0.1 List of vegetation zones descriptions incorporated in the hydrology model.

Vegetation zone	Description
1	Semi-fixed dune grassland SD7
2	Bare sand 1
3	Grazed fixed dune grassland SD8/11
4	Salix repens on dunes
5	Embryonic shifting dune sand
6	Fixed dunes
7	Humid dune slacks
8	Mosaics of selected Annex 1 habitats
9	Non-SAC habitat 1
10	Deciduous Forest
11	Shifting dunes
12	Forest zones 1
13	Forest zones 2
14	Forest zones 3
15	Forest zones 4
16	Forest zones 5
17	Forest zones 6
18	Forest zones 7
19	Forest zones 8
20	Forest zones 9
21	Forest zone 10
22	Forest zone 11
23	Forest zone 12
24	Forest zone 13
25	Forest zone 14
26	Bare sand 2
27	Non-SAC habitat 2

28	Forest zone 15
29	SD9 Ungrazed fixed dune grassland

Chapter 4

Table 0.2 List of hydrology metrics, with description. The calculation process of the metrics and the definition of hydrology year was described in the methods.

No.	Hydrology metric	Description
1	10% Percentile	10% Percentile water level of 1 hydrology year
2	90% Percentile	90% Percentile water level of 1 hydrology year
3	95% Percentile	95% Percentile water level of 1 hydrology year
4	Mean Summer	Mean summer water level (June-August)
5	Mean Winter	Mean winter water level (December-February)
6	MIN	Minimum water level of 1 hydrology year
7	2yr Average MIN	Average minimum water level of 2 hydrology years
8	3y Average MIN	Average minimum water level of 3 hydrology years
9	4yr Average MIN	Average minimum water level of 4 hydrology years
10	5yr Average MIN	Average minimum water level of 5 hydrology years
11	6yr Average MIN	Average minimum water level of 6 hydrology years
12	7yr Average MIN	Average minimum water level of 7 hydrology years
13	8yr Average MIN	Average minimum water level of 8 hydrology years
14	2yr Weighted MIN	Weighted average minimum water level of 2 hydrology years
15	3yr Weighted MIN	Weighted average minimum water level of 3 hydrology years
16	4yr Weighted MIN	Weighted average minimum water level of 4 hydrology years
17	5yr Weighted MIN	Weighted average minimum water level of 5 hydrology years
18	6yr Weighted MIN	Weighted average minimum water level of 6 hydrology years

19	7yr Weighted MIN	Weighted average minimum water level of 7 hydrology years
20	8yr Weighted MIN	Weighted average minimum water level of 8 hydrology years
21	MAX	Maximum water level of 1 hydrology year
22	2yr Average MAX	Average maximum water level of 2 hydrology years
23	3y Average MAX	Average maximum water level of 3 hydrology years
24	4yr Average MAX	Average maximum water level of 4 hydrology years
25	5yr Average MAX	Average maximum water level of 5 hydrology years
26	6yr Average MAX	Average maximum water level of 6 hydrology years
27	7yr Average MAX	Average maximum water level of 7 hydrology years
28	8yr Average MAX	Average maximum water level of 8 hydrology years
29	2yr Weighted MAX	Weighted average maximum water level of 2 hydrology years
30	3yr Weighted MAX	Weighted average maximum water level of 3 hydrology years
31	4yr Weighted MAX	Weighted average maximum water level of 4 hydrology years
32	5yr Weighted MAX	Weighted average maximum water level of 5 hydrology years
33	6yr Weighted MAX	Weighted average maximum water level of 6 hydrology years
34	7yr Weighted MAX	Weighted average maximum water level of 7 hydrology years
35	8yr Weighted MAX	Weighted average maximum water level of 8 hydrology years
36	Median	Median water level of 1 hydrology year
37	2yr Average Median	Average median water level of 2 hydrology years
38	3y Average Median	Average median water level of 3 hydrology years
39	4yr Average Median	Average median water level of 4 hydrology years
40	5yr Average Median	Average median water level of 5 hydrology years
41	6yr Average Median	Average median water level of 6 hydrology years
42	7yr Average Median	Average median water level of 7 hydrology years
43	8yr Average Median	Average median water level of 8 hydrology years
44	2yr Weighted Median	Weighted average median water level of 2 hydrology years

45	3yr Weighted Median	Weighted average median water level of 3 hydrology years
46	4yr Weighted Median	Weighted average median water level of 4 hydrology years
47	5yr Weighted Median	Weighted average median water level of 5 hydrology years
48	6yr Weighted Median	Weighted average median water level of 6 hydrology years
49	7yr Weighted Median	Weighted average median water level of 7 hydrology years
50	8yr Weighted Median	Weighted average median water level of 8 hydrology years
51	Mean	Mean water level of 1 hydrology year
52	2yr Average Mean	Average mean water level of 2 hydrology years
53	3y Average Mean	Average mean water level of 3 hydrology years
54	4yr Average Mean	Average mean water level of 4 hydrology years
55	5yr Average Mean	Average mean water level of 5 hydrology years
56	6yr Average Mean	Average mean water level of 6 hydrology years
57	7yr Average Mean	Average mean water level of 7 hydrology years
58	8yr Average Mean	Average mean water level of 8 hydrology years
59	2yr Weighted Mean	Weighted average mean water level of 2 hydrology years
60	3yr Weighted Mean	Weighted average mean water level of 3 hydrology years
61	4yr Weighted Mean	Weighted average mean water level of 4 hydrology years
62	5yr Weighted Mean	Weighted average mean water level of 5 hydrology years
63	6yr Weighted Mean	Weighted average mean water level of 6 hydrology years
64	7yr Weighted Mean	Weighted average mean water level of 7 hydrology years
65	8yr Weighted Mean	Weighted average mean water level of 8 hydrology years
66	MSL	Mean spring water level of 1 hydrology year (March-May)
67	2yr Average MSL	Average mean spring water level of 2 hydrology years
68	3y Average MSL	Average mean spring water level of 3 hydrology years
69	4yr Average MSL	Average mean spring water level of 4 hydrology years
70	5yr Average MSL	Average mean spring water level of 5 hydrology years

71	6yr Average MSL	Average mean spring water level of 6 hydrology years
72	7yr Average MSL	Average mean spring water level of 7 hydrology years
73	8yr Average MSL	Average mean spring water level of 8 hydrology years
74	2yr Weighted MSL	Weighted average mean spring water level of 2 hydrology years
75	3yr Weighted MSL	Weighted average mean spring water level of 3 hydrology years
76	4yr Weighted MSL	Weighted average mean spring water level of 4 hydrology years
77	5yr Weighted MSL	Weighted average mean spring water level of 5 hydrology years
78	6yr Weighted MSL	Weighted average mean spring water level of 6 hydrology years
79	7yr Weighted MSL	Weighted average mean spring water level of 7 hydrology years
80	8yr Weighted MSL	Weighted average mean spring water level of 8 hydrology years

Table 0.3 Pearson’s correlation results between hydrology metrics and mean EbF values of 81 quadrats, from 2018. The four calculated mean EbF values were based on: EbF 1a. Presence weighted plant only values, EbF 1b. Presence weighted plant and bryophyte values, EbF 2a. Abundance weighted plant only values and EbF 2b.Abundance weighted plant and bryophyte values. All correlations were significant at $p < 0.05$.

Hydrology metric	EbF 1a	EbF 1b	EbF 2a	EbF 2b
10% Percentile	0.73	0.69	0.63	0.64
90% Percentile	0.82	0.79	0.69	0.71
95% Percentile	0.83	0.80	0.69	0.72
Mean Summer	0.77	0.74	0.66	0.68
Mean Winter	0.80	0.77	0.68	0.70
Min	0.71	0.67	0.62	0.62
2yr Average MIN	0.76	0.73	0.65	0.66
3y Average MIN	0.74	0.71	0.64	0.64
4yr Average MIN	0.75	0.72	0.64	0.65
5yr Average MIN	0.76	0.73	0.64	0.65
6yr Average MIN	0.78	0.74	0.67	0.68
7yr Average MIN	0.77	0.74	0.67	0.67
8yr Average MIN	0.77	0.74	0.67	0.67

2yr Weighted MIN	0.74	0.71	0.64	0.65
3yr Weighted MIN	0.74	0.71	0.64	0.65
4yr Weighted MIN	0.75	0.71	0.64	0.65
5yr Weighted MIN	0.75	0.72	0.64	0.65
6yr Weighted MIN	0.76	0.73	0.65	0.66
7yr Weighted MIN	0.76	0.73	0.65	0.66
8yr Weighted MIN	0.76	0.73	0.66	0.66
MAX	0.83	0.80	0.69	0.72
2yr Average MAX	0.85	0.82	0.72	0.74
3y Average MAX	0.86	0.82	0.74	0.76
4yr Average MAX	0.86	0.83	0.74	0.76
5yr Average MAX	0.85	0.82	0.74	0.76
6yr Average MAX	0.84	0.80	0.72	0.75
7yr Average MAX	0.85	0.81	0.74	0.76
8yr Average MAX	0.85	0.81	0.74	0.76
2yr Weighted MAX	0.84	0.82	0.72	0.74
3yr Weighted MAX	0.85	0.82	0.73	0.75
4yr Weighted MAX	0.86	0.83	0.74	0.76
5yr Weighted MAX	0.86	0.83	0.74	0.76
6yr Weighted MAX	0.85	0.82	0.74	0.76
7yr Weighted MAX	0.85	0.82	0.74	0.76
8yr Weighted MAX	0.85	0.82	0.74	0.76
Median	0.73	0.68	0.63	0.64
2yr Average Median	0.78	0.74	0.67	0.68
3y Average Median	0.72	0.67	0.63	0.63
4yr Average Median	0.76	0.71	0.66	0.66
5yr Average Median	0.78	0.74	0.67	0.67
6yr Average Median	0.80	0.76	0.69	0.69
7yr Average Median	0.80	0.76	0.69	0.70
8yr Average Median	0.80	0.76	0.69	0.70

2yr Weighted Median	0.76	0.72	0.66	0.67
3yr Weighted Median	0.75	0.70	0.65	0.65
4yr Weighted Median	0.75	0.71	0.65	0.66
5yr Weighted Median	0.76	0.72	0.66	0.66
6yr Weighted Median	0.77	0.73	0.67	0.67
7yr Weighted Median	0.78	0.74	0.67	0.68
8yr Weighted Median	0.78	0.74	0.68	0.68
Mean	0.79	0.75	0.68	0.69
2yr Average Mean	0.81	0.78	0.69	0.70
3y Average Mean	0.81	0.77	0.69	0.70
4yr Average Mean	0.81	0.78	0.69	0.71
5yr Average Mean	0.82	0.78	0.70	0.71
6yr Average Mean	0.83	0.80	0.71	0.73
7yr Average Mean	0.83	0.79	0.71	0.73
8yr Average Mean	0.83	0.79	0.71	0.73
2yr Weighted Mean	0.81	0.77	0.68	0.70
3yr Weighted Mean	0.81	0.77	0.69	0.70
4yr Weighted Mean	0.81	0.78	0.69	0.71
5yr Weighted Mean	0.81	0.78	0.69	0.71
6yr Weighted Mean	0.82	0.78	0.70	0.71
7yr Weighted Mean	0.82	0.79	0.70	0.72
8yr Weighted Mean	0.82	0.79	0.70	0.72
MSL	0.83	0.81	0.69	0.72
2yr Average MSL	0.82	0.80	0.69	0.71
3y Average MSL	0.84	0.81	0.71	0.73
4yr Average MSL	0.84	0.81	0.71	0.73
5yr Average MSL	0.84	0.81	0.71	0.74
6yr Average MSL	0.84	0.81	0.71	0.74
7yr Average MSL	0.84	0.81	0.72	0.74
8yr Average MSL	0.85	0.81	0.72	0.74

2yr Weighted MSL	0.83	0.80	0.69	0.71
3yr Weighted MSL	0.84	0.81	0.70	0.73
4yr Weighted MSL	0.84	0.81	0.70	0.73
5yr Weighted MSL	0.84	0.81	0.71	0.73
6yr Weighted MSL	0.84	0.81	0.71	0.73
7yr Weighted MSL	0.84	0.81	0.71	0.74
8yr Weighted MSL	0.84	0.81	0.72	0.74

Chapter 5

Table 0.4 Linear Mixed model result with descriptions, each model corresponding to a number in the first column (1). All models predict mean EbF response (vascular plants) with the effect of added covariates, fixed factors and random factors listed in respectively column 2, 4 and 6. Fixed factors levels have been specified in Table 5.4. All models have random intercept(s) without fixed slopes, inter class correlation (ICC) of each random factor has been specified in column 7. Model significance of covariates (column 3) and fixed factors (column 5) was coded with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ or n.s. $p > 0.05$. Model comparison scores have been listed in column 9 and column 10, see methods section for selection procedure.

1.	**2.**	**3.**	**4.**	**5.**	**6.**	**7.**	**8.**	**9.**	**10.**
Model	**Covariates**	***P***	**Fixed factors**	***p***	**Random factors**	**ICC**	**df**	**-2 Log LL**	**AIC**
1	5-year average MSL	***	-	-	Dune slack	0.26	7	-48.1	-34.1
2	5-year average MSL	***	-	-	Dune slack	0.30	8	-50.2	-34.2
					Dune slack (Plot)	0.09			
3	5-year average MSL	***	Year	n.s.	Dune slack	0.23	9	-52.7	-34.7
4	5-year average MSL	***	NVC1	***	Dune slack	0.17	16	-80.8	-48.8
5	5-year average MSL	***	NVC2	***	Dune slack	0.18	14	-79.3	-51.3
6	5-year average MSL	***	NVC3	***	Dune slack	0.18	13	-76.2	-50.2
7	5-year average MSL	***	NVC4	***	Dune slack	0.19	12	-70.9	-46.9

8	5-year average MSL	***	NVC5	***	Dune slack	0.19	9	-69.6	-51.6
9	5-year average MSL	***	NVC6	***	Dune slack	0.22	8	-62.0	-46.0
10	5-year average MSL	***	NVC7	***	Dune slack	0.18	13	-78.8	-52.8
11	5-year average MSL	***	NVC8	***	Dune slack	0.2	9	-73.3	-55.3
12	5-year average MSL LOI	*** n.s.	NVC8	***	Dune slack	0.19	10	-73.3	-53.3
13	5-year average MSL LOI	*** n.s.	NVC2	***	Dune slack	0.17	15	-79.3	-49.3
14	5-year average MSL LOI	*** n.s.	NVC2 NVC2: LOI	*** n.s.	Dune slack	0.17	22	-85.2	-41.2
15	5-year average MSL LOI	*** n.s.	NVC8 NVC8: LOI	*** n.s.	Dune slack	0.19	12	-76.1	-52.1
16	5-year average MSL LOI	*** **	NVC8 NVC8: LOI	*** *	Dune slack (Plot)	0.29	12	-66.6	-42.6
17	5-year average MSL pH	*** n.s.	NVC8	***	Dune slack	0.23	10	-75.0	-55.0
18	5-year average MSL pH	*** n.s.	NVC2	***	Dune slack	0.20	15	-80.0	-50.0
19	5-year average MSL pH	*** n.s.	NVC8	***	Dune slack (Plot)	0.23	10	-57.0	-37.0
20	5-year average MSL pH	*** n.s.	NVC8 NVC8: pH	* n.s.	Dune slack	0.23	12	-80.3	-56.3
21	No covariate	-	NVC8 Year	*** ***	Dune slack	0.23	15	-14.6	15.4
22	No covariate	-	NVC2 Year	*** ***	Dune slack	0.26	10	7.6	27.6
23	No covariate	-	NCV8 Year NVC8: Year	*** n.s. ***	Dune slack	0.26	14	4.6	32.6
24	No covariate	-	NVC2 Year: NVC2: Year	*** n.s. ***	Dune slack	0.24	29	-33.7	24.3
25	Rainfall total	***	NVC8	***	Dune slack	0.25	9	10.1	28.1
26	Rainfall total	***	NVC2	***	Dune slack	0.23	14	-12.0	16.0
27	Rainfall 6 months	***	NVC2	***	Dune slack	0.22	14	12.0	40.0
28	Rainfall 3 months	***	NVC2	***	Dune slack	0.22	14	-0.0	28.0
29	Rainfall total	**	NVC2	n.s. ***	Dune slack	0.23	21	-12.5	15.5

	NVC2: rainfall	

Table 0.5 Results of the linear mixed model 11, including pairwise comparison. Model significance of covariates and fixed factors was coded with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ or n.s. $p > 0.05$.

Model 11 (including factor NVC8)

Type III Tests of Fixed Effects

Effect	Num df	Den df	F	*p*
Intercept	1	26.9	10236.4	***
5-year average MSL	1	148.9	137.9	***
NVC 8	2	180.2	13.4	***

Parameter estimates

Parameter	Estimates with ± SE	df	t-value	*p*	95% CI	
					LB	UB
Intercept	6.37 ± 0.08	68.6	76.1	***	6.20	6.54
5-year average MSL	1.64 ± 0.14	149.0	11.7	***	1.36	1.91
[NVC8 = Group 1]	0.38 ± 0.07	181.9	5.2	***	0.23	0.52
[NVC8 = Group 2]	0.17 ± 0.05	168.1	3.4	***	0.07	0.27
[NVC8 = Group 3]	0.00 ± 0.00					

Pairwise Comparisons - Least Significant Difference

F (2,176.9) = 13.4 ***

Marginal means based on 5-year average MSL = -0.262 m

(I)NVC adjusted	(J)NVC adjusted	Marginal mean Difference (I-J) ± SE	df	*p*
NVC8 = Group 1	NCV8 = Group 2	0.20 ± 0.05	155.0	***
	NVC8 = Group 3	0.37 ± 0.07	181.9	***
NVC8 = Group 2	NVC8 = Group 3	0.17 ± 0.05	168.1	***

Table 0.6 Model 11: Dune slack ID Empirical Best Linear Unbiased Predictions. LB = lower bound, UB = upper bound of the confidence interval (CI).

Dune slack ID	Parameter intercept with ± SE	df	*p*	95% CI	
				LB	UB
CEH22	-0.16 ± 0.08	37.8	*	-0.32	-0.01
CEH23	0.02 ± 0.08	41.7	n.s.	-0.15	0.18
CEH24	0.12 ± 0.10	41.4	n.s.	-0.08	0.33
CEH26	0.07 ± 0.09	43.3	n.s.	-0.11	0.24
CEH4	-0.17 ± 0.10	42.0	n.s.	-0.37	0.03
CEH5	0.06 ± 0.09	42.3	n.s.	-0.11	0.24
CEH8	0.04 ± 0.09	43.0	n.s.	-0.15	0.23
CEH9	-0.05 ± 0.07	37.3	n.s.	-0.20	0.10
NW3	0.07 ± 0.09	43.5	n.s.	-0.11	0.24
NW4	0.19 ± 0.07	36.6	**	0.05	0.34
NW5	0.05 ± 0.09	43.3	n.s.	-0.12	0.23
NW6	-0.31 ± 0.09	44.3	***	-0.49	-0.14
T41A	0.11 ± 0.12	30.9	n.s.	-0.14	0.37
T41B	0.07 ± 0.09	44.0	n.s.	-0.11	0.26
T41C	0.17 ± 0.12	31.2	n.s.	-0.08	0.42
T41D	-0.37 ± 0.10	41.4	***	-0.58	-0.17
WMC2	0.09 ± 0.09	43.1	n.s.	-0.10	0.27

Table 0.7 Linear mixed model result with descriptions with each model corresponding to a number in the first column (1). All models predict mean EbF response (bryophytes) with the effect of added covariates, fixed factors and random factors listed in respectively column 2, 4 and 6. Fixed factors levels have been specified in Table 5.4. All models have random intercept(s) without fixed slopes, inter class correlation (ICC) of each random factor has been specified in column 7. Model significance of covariates (column 3) and fixed factors (column 5) was coded with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ or n.s. $p > 0.05$. Model comparison scores have been listed in column 9 and column 10, see methods section for selection procedure.

1.	**2.**	**3.**	**4.**	**5.**	**6.**	**7.**	**8.**	**9.**	**10.**
Model	**Covariates**	***p***	**Fixed factor**	***p***	**Random factors**	**ICC**	**df**	**-2 Log LL**	**AIC**
30	5-year average MSL	***	-	-	Dune slack	0.15	7	468.4	482.4
31	5-year average MSL	***	-	-	Dune slack (plot)	0.49	7	473.0	487.0
32	5-year average MSL	***	NVC2	***	Dune slack	0.11	14	404.9	432.9
33	8-year average MSL	***	NVC2	***	Dune slack	0.17	14	382.4	410.4

34	8-year average MSL	***	NVC8	n.s.	Dune slack	0.28	9	427.1	445.1
35	No covariate	-	NVC2 year	*** n.s.	Dune slack	0.04	15	393.7	423.7
36	No covariate	-	NVC2 NVC2: year	*** n.s.	Dune slack	0.04	29	379.4	437.4
37	No covariate	-	NVC2 NVC2: year	*** n.s.	Dune slack (plot)	0.18	29	380.0	437.7

Table 0.8 Linear mixed model 33 results with pairwise comparison results. Model significance of covariates and fixed factors was coded with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ or n.s. $p > 0.05$.

Linear model 33 (including factor NVC2)

Type III Tests of Fixed Effects

Effect	Num df	Den df	F	*p*
Intercept	1	50.8	1115.8	***
8-year average MSL	1	86.4	54.7	***
NVC2	7	180.8	8.9	***

Parameter estimates

Parameter	Estimates ± SE	df	t-value	*p*	95% CI	
					LB	UB
Intercept	8.2 ± 0.3	94.3	27.4	***	7.6	8.8
8-year average MSL	4.1 ± 0.6	86.3	7.4	***	3.0	5.2
[NVC2 = SD13]	0.4 ± 0.3	155.6	1.7	n.s.	-0.1	1.0
[NVC2 = SD14b]	0.2 ± 0.2	177.6	0.7	n.s.	-0.3	0.6
[NVC2 = SD14c]	0.4 ± 0.2	181.0	2.2	***	0.0	0.8
[NVC2 = SD14d]	-0.7 ± 0.2	165.0	-3.0	***	-1.1	-0.2
[NVC2 = SD15/SD17]	-0.4 ± 0.3	172.7	-1.6	n.s.	-1.0	0.1
[NVC2 = SD16a]	-0.5 ± 0.2	183.2	-2.5	***	-1.0	-0.1
[NVC2 = SD16b/c]	-0.2 ± 0.2	161.6	-0.8	n.s.	-0.7	0.3
[NVC2 = SD16d]	0.0 ± 0.0					

Pairwise Comparisons - Least Significant Difference

F (7,166.7) = 8.9 ***

Marginal means based on 8-year average MSL = -0.331 m

(I)NVC adjusted	(J)NVC adjusted	Marginal mean difference (I-J) ± SE	df	*p*
SD13	SD14b	0.27 ± 0.30	171.8	n.s.
	SD14c	0.02 ± 0.25	168.5	n.s.

	SD14d	1.11 ± 0.28	182.2	***
	SD15b-17	0.88 ± 0.33	183.7	**
	SD16a	0.98 ± 0.25	155.4	***
	SD16b/c	0.63 ± 0.28	165.0	*
	SD16d	0.44 ± 0.26	155.6	n.s.
SD14b	SD14c	-0.25 ± 0.18	164.4	n.s.
	SD14d	0.84 ± 0.21	141.1	***
	SD15/SD17	0.61 ± 0.21	168.5	***
	SD16a	0.70 ± 0.27	184.5	**
	SD16b/c	0.35 ±0.26	185.0	n.s.
	SD16d	0.16 ± 0.24	177.6	n.s.
SD14c	SD14d	1.09 ± 0.17	118.1	***
	SD15/SD17	0.86 ± 0.23	159.4	***
	SD16a	0.96 ± 0.22	166.4	***
	SD16b/c	0.61 ± 0.24	170.5	**
	SD16d	0.42 ± 0.19	181.0	*
SD14d	SD15/SD17	-0.23 ± 0.23	140.7	n.s.
	SD16a	-0.13 ± 0.25	162.6	n.s.
	SD16b/c	-0.48 ± 0.26	166.4	n.s.
	SD16d	-0.67 ± 0.22	165.1	***
SD15-17	SD16a	0.09 ± 0.31	172.2	n.s.
	SD16b/c	-0.26 ± 0.31	178.7	n.s.
	SD16d	-0.45 ± 0.28	172.7	n.s.
SD16a	SD16b/c	-0.35 ± 0.24	143.4	n.s.
	SD16d	-0.54 ± 0.21	183.2	**
SD16b/c	SD16d	-0.19 ± 0.24	161.6	n.s.

References

Abesser, C., Clarke, D., Hughes, A.G. & Robins, N.S. 2017. Modelling small groundwater systems: experiences from the Braunton Burrows and Ainsdale coastal dune systems, UK. *Journal of Coastal Conservation* 21 (5), pp.595–614. Available at: http://dx.doi.org/10.1007/s11852-017-0525-5.

Adane, Z.A., Nasta, P., Zlotnik, V. & Wedin, D. 2018. Journal of Hydrology : Regional Studies Impact of grassland conversion to forest on groundwater recharge in the Nebraska Sand Hills. *Journal of Hydrology: Regional Studies* 15 (2018), pp.171–183. Available at: http://dx.doi.org/10.1016/j.ejrh.2018.01.001.

Adema, E.B., van Gemerden, H. & Grootjans, A.P. 2003. Is succession in wet calcareous dune slacks affected by free sulfide?. *Journal of Vegetation Science* 14 (2), pp.153–162. Available at: http://dx.doi.org/10.1111/j.1654-1103.2003.tb02140.x.

Adema, E.B. & Grootjans, A.P. 2003. Possible positive-feedback mechanisms: Plants change abiotic soil parameters in wet calcareous dune slacks. *Plant Ecology* 167 (1), pp.141–149. Available at: http://dx.doi.org/10.1023/A:1023947411605.

Adema, E.B., van de Koppel, J., Meijer, H.A.J. & Grootjans, A.P. 2005. Enhanced nitrogen loss may explain alternative stable states in dune slack succession. *Oikos* 109 (2), pp.374–386. Available at: http://dx.doi.org/10.1111/j.0030-1299.2005.13339.x.

Aggenbach, C.J.S., Grijpstra, J., Jalink, M.H. & Nooren, M.J. 2002. *Deel 7: Duinvalleien, kalkrijke duinen. Indicatorsoorten voor verdroging, verzuring en eutrofiering van plantgemeenschappen in duinvalleien van het Renoduaal district.* 1e ed. Driebergen: Staatsbosbeheer Driebergen.

Aggenbach, C.J.S., Kooijman, A.M., Fujita, Y., van der Hagen, H., van Til, M., Cooper, D. & Jones, L. 2017. Does atmospheric nitrogen deposition lead to greater nitrogen and carbon accumulation in coastal sand dunes?. *Biological Conservation* 212 , pp.416–422. Available at: http://dx.doi.org/10.1016/j.biocon.2016.12.007.

Alkemade, J.R.M., Wiertz, J. & Latour, J.B. 1996. *Kalibratie van Ellenbergs milieu-indicatiegetallen aan werkelijk gemeten bodemfactoren*. Bilthoven: Rijksinstituut voor Volksgezondheid en Milieu.

von Asmuth, J.R. et al. 2012. Software for hydrogeologic time series analysis, interfacing data with physical insight. *Environmental Modelling and Software* 38 , pp.178–190. Available at: http://dx.doi.org/10.1016/j.envsoft.2012.06.003.

Atherton, I., Bosanquet, S. & Lawley, M. 2010. *Mosses and Liverworts of Britain and Ireland: A Field Guide*. Plymouth: British Bryological Society.

Baayen, R.H., Davidson, D.J. & Bates, D.M. 2008. Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language* 59 (4), pp.390–412. Available at: http://dx.doi.org/10.1016/j.jml.2007.12.005.

Bakker, C., Rodenburg, J. & van Bodegom, P.M. 2005. Effects of Ca- and Fe-rich seepage on P availability and plant performance in calcareous dune soils. *Plant and Soil* 275 (1–2), pp.111–122. Available at: http://dx.doi.org/10.1007/s11104-005-0438-1.

Bakker, T.W.M. 1981. *Nederlandse Kunstduinen; Geohydrologie.* Wageningen Universiteit.

Bakker, T.W.M., Klijn, J.A. & van Zadelhoff, F.J. 1979. *Duinen en duinvalleien.* Wageningen: PUDOC, Centrum voor Landbouwpublikaties en Landbouwdocumentatie.

Barnaby, J.Y. & Ziska, L.H. 2012. Plant Responses to Elevated CO 2. *eLS* (July), pp.1–10. Available at: http://dx.doi.org/10.1002/9780470015902.a0023718.

Barr, D.J. 2013. Random effects structure for testing interactions in linear mixed-effects models. *Frontiers in Psychology* 4 (June), pp.3–4. Available at: http://dx.doi.org/10.3389/fpsyg.2013.00328.

Bartholomeus, R.P., Stagge, J.H., Tallaksen, L.M. & Witte, J.P.M. 2015. Sensitivity of potential evaporation estimates to 100 years of climate variability. *Hydrology and Earth System Sciences* 19 (2), pp.997–1014. Available at: http://dx.doi.org/10.5194/hess-19-997-2015.

Bartholomeus, R.P., Witte, J.P.M., Van Bodegom, P.M. & Aerts, R. 2008. The need of data harmonization to derive robust empirical relationships between soil conditions and vegetation. *Journal of Vegetation Science* 19 (6), pp.799–808. Available at: http://dx.doi.org/10.3170/2008-8-18450.

Bartholomeus, R.P., Witte, J.P.M., van Bodegom, P.M., van Dam, J.C., de Becker, P. & Aerts, R. 2012a. Process-based proxy of oxygen stress surpasses indirect ones in predicting vegetation characteristics. *Ecohydrology* 5 (6), pp.746–758. Available at: http://dx.doi.org/10.1002/eco.261.

Bartholomeus, R.P., Witte, J.P.M. & Runhaar, J. 2012b. Drought stress and vegetation characteristics on sites with different slopes and orientations. *Ecohydrology* 5 , pp.808–818. Available at: http://dx.doi.org/10.1002/eco.271.

Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67 (1). Available at: http://dx.doi.org/10.18637/jss.v067.i01.

Berendse, F., Lammerts, E.J. & Olff, H. 1998. Soil Organic Matter Accumulation and Its Implications for Nitrogen Mineralization and Plant Species Composition during Succession in Coastal Dune Slacks. *Plant Ecology* 137 , pp.71–78. Available at: http://dx.doi.org/10.1023/A:1008051931963.

Betson, M., Connell, M. & Bristow, C. 2002. *Groundwater modelling of Newborough Warren: A report for the Countryside Council for Wales, Volume 5, Hydrogeology. The impact of Forestry on Coastal Geomorphology at Newborough Warren/Ynys Llanddwyn NNR, SSSI, pSAC.* Bangor: Countryside Council for Wales.

Bindoff, N.L. et al. 2022. IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. In: Pörtner, H.-O. et al. (eds.) *The Ocean and Cryosphere in a Changing Climate*. doi: 10.1017/9781009157964.013.

Bradford, R.B. & Acreman, M.C. 2003. Applying MODFLOW to wet grassland in-field habitats: A case study from the Pevensey Levels, UK. *Hydrology and Earth System Sciences* 7 (1), pp.43–55. Available at: http://dx.doi.org/10.5194/hess-7-43-2003.

Bristow, C. 2003. *The Impact of Forestry on Coastal Geomorphology at Newborough Warren / Yn ys Llanddwyn NNR, SSSI, pSAC.* Bangor: Countryside Council for Wales.

Bristow, C.S. & Bailey, S.D. 1998. *Ground penetrating radar survey of the dunes at Newborough Warren.* London: Birkbeck College, University of London.

Brunbjerg, A.K., Ejrnæs, R. & Svenning, J.C. 2012. Species sorting dominates plant metacommunity structure in coastal dunes. *Acta Oecologica* 39 , pp.33–42. Available at: http://dx.doi.org/10.1016/j.actao.2011.11.002.

Callaghan, D.A., During, H.J., Forrest, L.L. & Wilkinson, K. 2020. Neglected and at risk: bryophyte diaspore banks of coastal dune systems. *Journal of Bryology* 42 (3), pp.223–234. Available at: http://dx.doi.org/10.1080/03736687.2020.1743561.

Callaghan, D.A., van Willegen, L., Williams, G., Hollingham, M. & Jones, L. 2021. Pony trails, hydrology and habitat restoration: aspects of the ecology of Petalophyllum ralfsii in a Welsh oceanic dune system. *Journal of Bryology* 43 (2), pp.150–161. Available at: http://dx.doi.org/10.1080/03736687.2020.1819719.

Čížková, H., Květ, J., Comín, F.A., Laiho, R., Pokorný, J. & Pithart, D. 2013. Actual state of European wetlands and their possible future in the context of global climate change. *Aquatic Sciences* 75 (1), pp.3–26. Available at: http://dx.doi.org/10.1007/s00027-011-0233-4.

Clarke, D. & Sanitwong Na Ayutthaya, S. 2010. Predicted effects of climate change, vegetation and tree cover on dune slack habitats at Ainsdale on the Sefton Coast, UK. *Journal of Coastal*

Conservation 14 (2), pp.115–125. Available at: http://dx.doi.org/10.1007/s11852-009-0066-7.

Colman, T.B. & Peart, R.J. 1993. *Mineral Reconnaissance Programme | The metalliferous mineral potential of the basic rocks of the Penmynydd Zone, south–east Anglesey*. Nottingham: Keyworth.

Connor, M.A., Tarvin, S., Quail, M. & Batke, S.P. 2021. Plant diversity and community composition in managed humid coastal dune slacks in NW England. *PLoS ONE* 16 (8 August), pp.1–10. Available at: http://dx.doi.org/10.1371/journal.pone.0256215.

Curreli, A., Wallace, H., Freeman, C., Hollingham, M., Stratford, C., Johnson, H. & Jones, L. 2013. Eco-hydrological requirements of dune slack vegetation and the implications of climate change. *Science of the Total Environment* 443 , pp.910–919. Available at: http://dx.doi.org/10.1016/j.scitotenv.2012.11.035.

van Dam, J.C., Groenendijk, P., Hendriks, R.F.A. & Kroes, J.G. 2008. Advances of Modeling Water Flow in Variably Saturated Soils with SWAP. *Vadose Zone Journal* 7 (2), pp.640–653. Available at: http://dx.doi.org/https://doi.org/10.2136/vzj2007.0060.

Davy, A.J., Grootjans, A.P., Hiscock, K. & Peterson, J. 2006. *Development of eco-hydrological guidelines for dune habitats – Phase 1*. Bangor: Countryside Council for Wales.

Davy, A.J., Hiscock, K.M., Jones, M.L.M., Low, R., Robins, N.S. & Stratford, C. 2010. *Protecting the plant communities and rare species of dune wetland systems: Ecohydrological guidelines for wet dune habitats - Wet dunes phase 2*. Bristol: Environment Agency.

Diekmann, M. 2003. Species indicator values as an important tool in applied plant ecology - A review. *Basic and Applied Ecology* 4 (6), pp.493–506. Available at: http://dx.doi.org/10.1078/1439-1791-00185.

van Dijk, H.W.J. & Grootjans, A.P. 1993. Wet dune slacks: decline and new opportunities. *Hydrobiologia* 265 (1–3), pp.281–304. Available at: http://dx.doi.org/10.1007/BF00007273.

Drenkhan, R. et al. 2016. Global geographic distribution and host range of Dothistroma species: a comprehensive review. *Forest Pathology* 46 (5), pp.408–442. Available at: http://dx.doi.org/10.1111/efp.12290.

Dwyer, C., Millett, J., Jones, L., Bartholomeus, R.P., van Willegen, L., Chavasse, A. & Pakeman, R.J. 2022. Patterns of variation in plant diversity vary over different spatial levels in seasonal coastal wetlands. *Diversity and Distributions* 28 (9), pp.1875–1890. Available at: http://dx.doi.org/10.1111/ddi.13589.

Dwyer, C., Millett, J., Pakeman, R.J. & Jones, L. 2021a. Environmental modifiers of the relationship between water table depth and Ellenberg’s indicator of soil moisture. *Ecological*

Indicators 132 (108320), p.9. Available at: http://dx.doi.org/10.1016/j.ecolind.2021.108320.

Dwyer, C., Pakeman, R.J., Jones, L., van Willegen, L., Hunt, N. & Millett, J. 2021b. Fine-scale hydrological niche segregation in coastal dune slacks. *Journal of Vegetation Science* 32 (5), pp.1–13. Available at: http://dx.doi.org/10.1111/jvs.13085.

Ellenberg, H., Weber, H., Düll, R., Wirth, V., Werner, W. & Paulissen, D. 1991. Indicator values of plants in central Europe-Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18 , pp.1–148.

Ertsen, A.C.D., Alkemade, J.R.M. & Wassen, M.J. 1998. Calibrating Ellenberg indicator values for moisture, acidity, nutrient availability and salinity in the Netherlands. *Plant Ecology* 135 (1), pp.113–124. Available at: http://dx.doi.org/10.1023/A:1009765529310.

Felton, A.J. & Smith, M.D. 2017. Integrating plant ecological responses to climate extremes from individual to ecosystem levels. *Philosophical Transactions of the Royal Society Biology* 372 (20160142). Available at: http://dx.doi.org/10.1098/rstb.2016.0142.

García-Baquero Moneo, G., Gowing, D.J.G. & Wallace, H. 2022. The contribution of the spatial hydrological niche to species diversity in rare plant communities of English floodplain meadows. *Plant Ecology* 223 (6), pp.599–612. Available at: http://dx.doi.org/10.1007/s11258-022-01234-9.

Geelen, L., de Groen, N., van der Spek, V., van Til, M. & van der Voet, A. 2020. Amsterdamse Waterleidingduinen Natuuronderzoek. *Amsterdamse Waterleidingduinen* 29 (1), pp.1–20.

Geelen, L.H.W.T., Kamps, P.T.W.J. & Olsthoorn, T.N. 2017. From overexploitation to sustainable use, an overview of 160 years of water extraction in the Amsterdam dunes, the Netherlands. *Journal of Coastal Conservation* 21 , pp.657–668. Available at: http://dx.doi.org/10.1007/s11852-016-0452-x.

Grootjans, A.P. et al. 2017. Window of opportunity of Liparis loeselii populations during vegetation succession on the Wadden Sea islands. *Journal of Coastal Conservation* 21 , pp.631–641. Available at: http://dx.doi.org/10.1007/s11852-016-0448-6.

Grootjans, A.P., Adema, E.B., Bekker, R.M. & Lammerts, E.J. 2004. Why Coastal Dune Slacks Sustain a High Biodiversity. In: Martínez, M. L. and Psuty, N. P. (eds.) *Ecological Studies*. 171st ed. Berlin, Heidelberg: Springer-Verlag.

Grootjans, A.P., Ernst, W.H.O. & Stuyfzand, P.J. 1998. European dune slacks: strong interactions of biology, pedogenesis and hydrology. *Tree* 13 (3), p.4. Available at: http://dx.doi.org/10.1016/0273-1223(95)00356-R.

Grootjans, A.P., Hartog, P.S., Fresco, L.F.M. & Esselink, H. 1991. Succession and Fluctuation in a Wet Dune Slack in Relation to Hydrological Changes. *Source Journal of Vegetation Science* 2 (4), pp.545–554.

Haddad, N.M. et al. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances* 1 (2), pp.1–10. Available at: http://dx.doi.org/10.1126/sciadv.1500052.

Harbaugh, A.W. 2005. MODFLOW-2005 , The U.S. Geological Survey Modular Ground-Water Model — the Ground-Water Flow Process. In: *Book 6. Modelinng techniques, Section A. Ground water*. Virginia: U.S. Geological Survey Techniques and Methods 6-A16.

He, X., He, K.S. & Hyvönen, J. 2016. Will bryophytes survive in a warming world?. *Perspectives in Plant Ecology, Evolution and Systematics* 19 , pp.49–60. Available at: http://dx.doi.org/10.1016/j.ppees.2016.02.005.

Hedwall, P.O., Brunet, J. & Diekmann, M. 2019. With Ellenberg indicator values towards the north: Does the indicative power decrease with distance from Central Europe?. *Journal of Biogeography* 46 (5), pp.1041–1053. Available at: http://dx.doi.org/10.1111/jbi.13565.

Hewett, D.G. 1985. Grazing and mowing as management tools on dunes. *Vegetatio*. Available at: http://dx.doi.org/10.1007/BF00044772.

Hill, M.O., Preston, C.D. & Roy, D.B. 2004. *PLANTATT - attributes of British and Irish plants: status, size, life history, geography and habitats.* Cambridgeshire: Centre for Ecology & Hydrology.

Hill, M.O. & Wallace, H.L. 1989. Vegetation and environment in afforested sand dunes at newborough, anglesey. *Forestry* 62 (3), pp.249–267. Available at: http://dx.doi.org/10.1093/forestry/62.3.249.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. 2012. Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* 43 , pp.227–248. Available at: http://dx.doi.org/10.1146/annurev-ecolsys-110411-160411.

Hollingham, M. 2006. *The water balance, water levels, apparent specific yield and relative recharge at Newborough Forest and Warren*. Bangor: CAZS Natural resources, Univeristy of Wales.

Houston, J.A. 2008. *Management of Nature 2000 Habitat. 2190 Humid dune slacks*. Europreran Commission.

Hurrell, J.W. 1995. Decadal trends in the North Atlantic oscillation: Regional temperatures and precipitation. *Science* 269 (5224), pp.676–679. Available at: http://dx.doi.org/10.1126/science.269.5224.676.

IBM Corp. 2020. IBM SPSS Statistics for Windows.

Isbell, F. et al. 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526 (7574), pp.574–577. Available at: http://dx.doi.org/10.1038/nature15374.

Isermann, M. 2011. Patterns in species diversity during succession of coastal dunes. *Journal of Coastal Research* 27 (4), pp.661–671. Available at: http://dx.doi.org/10.2112/JCOASTRES-D-09-00040.1.

Jacquemyn, H., Pankhurst, T., Jones, P.S., Brys, R. & Hutchings, M.J. 2023. Biological Flora of Britain and Ireland: Liparis loeselii: No. 304. *Journal of Ecology* 111 (4), pp.943–966. Available at: http://dx.doi.org/10.1111/1365-2745.14086.

Jamil, T., Ozinga, W.A., Kleyer, M. & Ter Braak, C.J.F. 2013. Selecting traits that explain species-environment relationships: A generalized linear mixed model approach. *Journal of Vegetation Science* 24 (6), pp.988–1000. Available at: http://dx.doi.org/10.1111/j.1654-1103.2012.12036.x.

Jarvis, S.G., Rowe, E.C., Henrys, P.A., Smart, S.M., Jones, M.L.M. & Garbutt, A. 2016. Empirical realised niche models for British coastal plant species. *Journal of Coastal Conservation* 20 , pp.107–116. Available at: http://dx.doi.org/10.1007/s11852-016-0422-3.

Jenkins, G.J., Perry, M.C. & Prior, M.J. 2008. *The climate of the UK and recent trends*. Exeter, UK: Met Office Hadley Centre.

Jones, M.L.M., Reynolds, B., Brittain, S.A., Norris, D.A., Rhind, P.M. & Jones, R.E. 2006. Complex hydrological controls on wet dune slacks: The importance of local variability. *Science of the Total Environment* 372 , pp.266–277. Available at: http://dx.doi.org/10.1016/j.scitotenv.2006.08.040.

Jones, M.L.M., Sowerby, A. & Rhind, P.M. 2010. Factors affecting vegetation establishment and development in a sand dune chronosequence at Newborough Warren, North Wales. *Journal of Coastal Conservation* 14 (2), pp.127–137. Available at: http://dx.doi.org/10.1007/s11852-009-0071-x.

Jones, M.L.M., Sowerby, A. & Wallace, H. 2007. *Better Understanding of Soil Resources – Dune Stabilisation and Rates of Soil Development on Welsh Dune Systems*. Bangor: Centre for Ecology & Hydrology.

Jones, M.L.M., Sowerby, A., Williams, D.L. & Jones, R.E. 2008. Factors controlling soil development in sand dunes: Evidence from a coastal dune soil chronosequence. *Plant and Soil* 307 (1–2), pp.219–234. Available at: http://dx.doi.org/10.1007/s11104-008-9601-9.

Käfer, J. & Witte, J.P.M. 2004. Cover-weighted averaging of indicator values in vegetation analyses. *Journal of Vegetation Science* 15 (5), pp.647–652. Available at: http://dx.doi.org/10.1111/j.1654-1103.2004.tb02306.x.

Kamps, P., Nienhuis, P. & Witte, J.P.M.P.M. 2008. Effects of climate change on the water table in the coastal dunes of the Amsterdam Water Supply. In: *Proceedings MODFLOW, 2008*.

Kløve, B. et al. 2014. Climate change impacts on groundwater and dependent ecosystems. *Journal of Hydrology* 518 , pp.250–266. Available at: http://dx.doi.org/10.1016/j.jhydrol.2013.06.037.

Kooijman, A.M. et al. 2016a. Nitrogen deposition and grass encroachment in calcareous and acidic Grey dunes (H2130) in NW-Europe. *Biological Conservation* 212 , pp.406–415. Available at: http://dx.doi.org/10.1016/j.biocon.2016.08.009.

Kooijman, A.M., Bruin, C.J.W., van de Craats, A., Grootjans, A.P., Oostermeijer, J.G.B., Scholten, R. & Sharudin, R. 2016b. Past and future of the EU-habitat directive species Liparis loeselii in relation to landscape and habitat dynamics in SW-Texel, the Netherlands. *Science of the Total Environment* 568 , pp.107–117. Available at: http://dx.doi.org/10.1016/j.scitotenv.2016.05.086.

Lammerts, E.J. & Grootjans, A.P. 1997. Nutrient deficiency in dune slack pioneer vegetation: A review. *Journal of Coastal Conservation* 3 , pp.87–94. Available at: http://dx.doi.org/10.1007/BF02908183.

Lammerts, E.J. & Grootjans, A.P. 1998. Key environmental variables determining the life span of basiphilous dune slack vegetation. *Act.Bot.* 47 , pp.369–392.

Lammerts, E.J., Maas, C. & Grootjans, A.P. 2001. Groundwater variables and vegetation in dune slacks. *Ecological Engineering* 17 , pp.33–47. Available at: http://dx.doi.org/10.1016/S0925-8574(00)00130-0.

Lett, S. et al. 2022. Can bryophyte groups increase functional resolution in tundra ecosystems?. *Arctic Science* 8 (3), pp.609–637. Available at: http://dx.doi.org/10.1139/as-2020-0057.

Libohova, Z. et al. 2018. Reevaluating the effects of soil organic matter and other properties on available water-holding capacity using the National Cooperative Soil Survey Characterization Database. *Journal of Soil and Water Conservation* 73 (4), pp.411–421. Available at: http://dx.doi.org/10.2489/jswc.73.4.411.

Malloch, A.J.C. 1998. MATCH (version 1.3): computer program to aid the assignment of vegetation data to the communities and subcommunities of the National Vegetation Classification.

Martins, S.V., Burningham, H. & Pinto-cruz, C. 2018. Climate variability impacts on coastal dune slack ecohydrology. *Irish Geography* (51), pp.261–284. Available at: http://dx.doi.org/10.2014/igj.v51i2.1374.

McDowell, N.G. et al. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought?. *New Phytologist* 178 (4), pp.719–739. Available at: http://dx.doi.org/10.1111/j.1469-8137.2008.02436.x.

McGill, B.J. 2011. Linking biodiversity patterns by autocorrelated random sampling. *American Journal of Botany* 98 (3), pp.481–502. Available at: http://dx.doi.org/10.3732/ajb.1000509.

Met Office. 2012. *Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (1853-current) 25-10-2022*. NCAS British Atmospheric Data Centre.

Millett, J. & Edmondson, S. 2015. The impact of 36 years of grazing management on soil nitrogen (N) supply rate and Salix repens N status and internal cycling in dune slacks. *Plant and Soil* 396 (1–2), pp.411–420. Available at: http://dx.doi.org/10.1007/s11104-015-2628-9.

Oliver, T.H., Marshall, H.H., Morecroft, M.D., Brereton, T., Prudhomme, C. & Huntingford, C. 2015. Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change* 5 (10), pp.941–946. Available at: http://dx.doi.org/10.1038/nclimate2746.

Onyekwelu, S.S.C. 1972. The Vegetation of Dune Slacks at Newborough Warren : II. Pattern of Carex Serotina , Leontodon Taraxacoides and Salix Repens. *Journal of Ecology* 60 (3), pp.899–905.

Oppenheimer, M. et al. 2019. Sea Level Rise and Implications for Low-Lying Islands, Coasts and Communities Supplementary Material. In: Pörtner, H.-O. et al. (eds.) *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*.

Oude Essink, G.H.P. 2001. Improving fresh groundwater supply—problems and solutions. *Ocean & Coastal Management* 44 (5), pp.429–449. Available at: http://dx.doi.org/10.1016/S0964-5691(01)00057-6.

Pakeman, R.J., Brooker, R.W., O’Brien, D. & Genney, D. 2019. Using species records and ecological attributes of bryophytes to develop an ecosystem health indicator. *Ecological Indicators* 104 (October 2018), pp.127–136. Available at: http://dx.doi.org/10.1016/j.ecolind.2019.04.084.

Pakeman, R.J., Hewison, R.L. & Lewis, R.J. 2017. Linking functional traits and species preferences to species’ abundance and occupancy trends through time to identify habitat changes in coastal ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics* 27

(December 2016), pp.35–44. Available at: http://dx.doi.org/10.1016/j.ppees.2017.06.002.

Palter, J.B. 2015. The role of the gulf stream in European climate. *Annual Review of Marine Science* 7 , pp.113–137. Available at: http://dx.doi.org/10.1146/annurev-marine-010814-015656.

Plassmann, K., Brown, N., Jones, M.L.M. & Edwards-Jones, G. 2009. Can soil seed banks contribute to the restoration of dune slacks under conservation management?. *Applied Vegetation Science* 12 , pp.199–210. Available at: http://dx.doi.org/10.1111/j.1654-109X.2009.01014.x.

Plassmann, K., Laurence M Jones, M., Edwards-Jones, G., Jones, M.L.M. & Edwards-Jones, G. 2010. Effects of long-term grazing management on sand dune vegetation of high conservation interest. *Applied Vegetation Science* 13 (1), pp.100–112. Available at: http://dx.doi.org/10.1111/j.1654-109X.2009.01052.x.

Pörtner, H. et al. 2022. *IPCC, 2022: Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY, USA: Cambridge University Press.

Printarakul, N. & Meeinkuirt, W. 2022. The bryophyte community as bioindicator of heavy metals in a waterfall outflow. *Scientific Reports* 12 (1), pp.1–12. Available at: http://dx.doi.org/10.1038/s41598-022-10980-9.

Proctor, M.C.F. et al. 2007. Desiccation-Tolerance in Bryophytes : A Review. *The Bryologist* 110 (4), pp.595–621.

Provoost, S., Jones, M.L.M. & Edmondson, S.E. 2011. Changes in landscape and vegetation of coastal dunes in northwest Europe: A review. *Journal of Coastal Conservation* 15 (1), pp.207–226. Available at: http://dx.doi.org/10.1007/s11852-009-0068-5.

Punalekar, S. et al. 2016. Characterization of a highly biodiverse floodplain meadow using hyperspectral remote sensing within a plant functional trait framework. *Remote Sensing* 8 (2), pp.1–22. Available at: http://dx.doi.org/10.3390/rs8020112.

Pye, K., Blott, S.J. & Howe, M.A. 2014. Coastal dune stabilization in Wales and requirements for rejuvenation. *Journal of Coastal Conservation* (18), pp.27–54. Available at: http://dx.doi.org/10.1007/s11852-013-0294-8.

R Core Team. 2021. R: A language and environment for statistical computing.

Ranwell, D. 1958. Movement of Vegetated Sand Dunes at Newborough Warren, Anglesey. *Journal of Ecology* 46 (1), pp.83–100.

Ranwell, D. 1959. Newborough Warren, Anglesey: I. The Dune System and Dune Slack Habitat. *Journal of Ecology* 47 (3), pp.571–601.

Ranwell, D. 1960. Newborough Warren, Anglesey: II. Plant Associes and Succession Cycles of the Sand Dune and Dune Slack Vegetation. *Source Journal of Ecology* 48 (1), pp.117–141.

Rhind, P.M. & Jones, P.S. 1999. The floristics and conservation status of sand-dune communities in Wales. *Journal of Coastal Conservation* 5 (1), pp.31–42. Available at: http://dx.doi.org/10.1007/BF02802737.

Rhind, P.M., Jones, R.E. & Jones, M.L.M. 2007. *The impact of dune stabilization and soil development on the conservation status of sand dune systems in Wales*. Martínez, M., Gallego-Fernández, J., and Hesp, P. (eds.). Berlin, Heidelberg: Springer.

Rhymes, J., Jones, L., Wallace, H., Jones, T.G., Dunn, C. & Fenner, N. 2016. Small changes in water levels and groundwater nutrients alter nitrogen and carbon processing in dune slack soils. *Soil Biology and Biochemistry* 99 , pp.28–35. Available at: http://dx.doi.org/10.1016/j.soilbio.2016.04.018.

Rhymes, J., Wallace, H.L., Fenner, N. & Jones, M.L.M. 2014. Evidence for sensitivity of dune wetlands to groundwater nutrients. *Science of the Total Environment* 490 , pp.106–113. Available at: http://dx.doi.org/10.1016/j.scitotenv.2014.04.029.

Rodwell, J.. 2000. *British Plant Communities Volume 5: Marine communities and vegetation of open habitats.* Cambridge: Cambridge University Press.

Rohani, S., Dullo, B., Woudwijk, W., de Hoop, P., Kooijman, A.M. & Grootjans, A.P. 2014. Accumulation rates of soil organic matter in wet dune slacks on the Dutch Wadden Sea islands. *Plant and Soil* 380 (1), pp.181–191. Available at: http://dx.doi.org/10.1007/s11104-014-2078-9.

Salimi, S., Almuktar, S.A.A.A.N. & Scholz, M. 2021. Impact of climate change on wetland ecosystems: A critical review of experimental wetlands. *Journal of Environmental Management* 286 (112160), p.15. Available at: http://dx.doi.org/10.1016/j.jenvman.2021.112160.

Saye, S.E. & Pye, K. 2007. Implications of sea level rise for coastal dune habitat conservation in. *Journal of Coastal Conservation* 11 (1), pp.31–52. Available at: http://dx.doi.org/10.1007/sll852-007-0004-5.

Schaffers, A.P. & Sýkora, K. V. 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science* 11 (2), pp.225–244. Available at: http://dx.doi.org/10.2307/3236802.

Schielzeth, H. et al. 2020. Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods in Ecology and Evolution* 11 (9), pp.1141–1152. Available at: http://dx.doi.org/10.1111/2041-210X.13434.

Sexton, D.M.H. & Murphy, J. 2010. *UKCP09: Probabilistic Projections of Wind Speed*. Exeter, UK: Met Office Hadley Centre.

Sival, F.P. & Grootjans, A.P. 1996. Dynamics of seasonal bicarbonate supply in a dune slack: Effects on organic matter, nitrogen pool and vegetation succession. *Vegetatio* 126 (1), pp.39–50. Available at: http://dx.doi.org/10.1007/bf00047760.

Sival, F.P., Mücher, H.J. & Delft, S.P.J. 1998. Management of basiphilous dune slack communities in relation to carbonate accumulation and hydrological conditions. *Journal of Coastal Conservation* 4 (1), pp.91–100. Available at: http://dx.doi.org/10.1007/BF02806495.

Sival, F.P. & Strijkstra-Kalk, M. 1999. Atmospheric deposition of acidifying and eutrophicating substances in Dune slacks. *Water, Air, and Soil Pollution* 116 (3–4), pp.461–477. Available at: http://dx.doi.org/10.1023/A:1005172221338.

Smart, S.M. & Scott, W.A. 2004. Bias in Ellenberg indicator values - Problems with detection of the effect of vegetation type. *Journal of Vegetation Science* 15 (6), pp.843–846. Available at: http://dx.doi.org/10.1111/j.1654-1103.2004.tb02327.x.

Smith, M.D. 2011. An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology* 99 (3), pp.656–663. Available at: http://dx.doi.org/10.1111/j.1365-2745.2011.01798.x.

Sperandii, M.G., Bazzichetto, M., Acosta, A.T.R., Barták, V. & Malavasi, M. 2019. Multiple drivers of plant diversity in coastal dunes: A Mediterranean experience. *Science of the Total Environment* 652 , pp.1435–1444. Available at: http://dx.doi.org/10.1016/j.scitotenv.2018.10.299.

Stace, C. 2019. *New Flora of the British Isles*. 4th ed. Cambridge: Cambridge University Press.

Stratford, C., Ratcliffe, J., Hughes, A.G., Roberts, J. & Robins, N.S. 2007. Complex interaction between shallow groundwater and changing woodland , surface water , grazing and other influences in partly wooded duneland in Anglesey , Wales. In: *Proceedings of the CDXXXV congress International association of hydrogeologists: groundwater and ecosystems.* International association of Hydrogeologists.

Stratford, C.J. 2014. *Survey and analysis of vegetation and hydrological change in English dune slack habitats.* Natural England.

Stratford, C.J., Robins, N.S., Clarke, D., Jones, L. & Weaver, G. 2013. An ecohydrological review of dune slacks on the west coast of England and Wales. *Ecohydrology* 6 (1), pp.162–171. Available at: http://dx.doi.org/10.1002/eco.1355.

Stuyfzand, P.J. 1993. *Hydrochemistry and Hydrology of the Coastal Dune area of the Western Netherlands*. Vrije Universiteit Amsterdam.

Stuyfzand, P.J.P.J. 1999. Patterns in groundwater chemistry resulting from groundwater flow. *Hydrogeology Journal* 7 (1), pp.15–27. Available at: http://dx.doi.org/10.1007/s100400050177.

Sundseth, K. 2015. *The EU birds and habitats directives – For nature and people in Europe*. Publications Office. doi: 10.2779/49288.

Sýkora, K.V., van den Bogert, J.C.J.M. & Berendse, F. 2004. Changes in Soil and Vegetation during Dune Slack Succession. *Journal of Vegetation Science* 15 (2), pp.209–218.

Tsoar, H. 2013. Critical Environments: Sand Dunes and Climate Change. *Treatise on Geomorphology: Volume 1-14* 1–14 (May), pp.414–427. Available at: http://dx.doi.org/10.1016/B978-0-12-374739-6.00314-6.

UKCEH & Dunescapes, U.S.D. and S.N. and D. 2021. *The Sand Dune Managers Handbook.* Produced for the Dynamic Dunescapes (DuneLIFE) project: LIFE 17 NAT/UK/00570; HG-16-08643.

Del Vecchio, S., Rova, S., Fantinato, E., Pranovi, F. & Buffa, G. 2022. Disturbance affects the contribution of coastal dune vegetation to carbon storage and carbon sequestration rate. *Plant Sociology* 59 (1), pp.37–48. Available at: http://dx.doi.org/10.3897/pls2022591/04.

Voortman, B.R., Bartholomeus, R.P., van Bodegom, P.M., Gooren, H., van der Zee, S.E.A.T.M. & Witte, J.P.M. 2014. Unsaturated hydraulic properties of xerophilous mosses: Towards implementation of moss covered soils in hydrological models. *Hydrological Processes* 28 (26), pp.6251–6264. Available at: http://dx.doi.org/10.1002/hyp.10111.

Voortman, B.R., Bartholomeus, R.P., van der Zee, S.E.A.T.M., Bierkens, M.F.P. & Witte, J.P.M. 2015. Quantifying energy and water fluxes in dry dune ecosystems of the Netherlands. *Hydrology and Earth System Sciences* 19 , pp.3787–3805. Available at: http://dx.doi.org/10.5194/hess-19-3787-2015.

Voortman, B.R., Bosveld, F.C., Bartholomeus, R.P. & Witte, J.P.M. 2016. Spatial extrapolation of lysimeter results using thermal infrared imaging. Available at: http://dx.doi.org/10.1016/j.jhydrol.2016.09.064.

Wamelink, G.W.W., Goedhart, P.W. & Frissel, J.Y. 2014. Why some plant species are rare. *PLoS ONE* 9 (7). Available at: http://dx.doi.org/10.1371/journal.pone.0102674.

Wamelink, G.W.W., Joosten, V., van Dobben, H.F. & Berendse, F. 2002. Validity of Ellenberg indicator values judged from physico-chemical field measurements. *Journal of Vegetation Science* 13 (2), pp.269–278. Available at: http://dx.doi.org/10.1111/j.1654-1103.2002.tb02047.x.

Wang, D. et al. 2023. Variation in mycorrhizal communities and the level of mycoheterotrophy in grassland and Forest populations of Neottia ovata (Orchidaceae). *Functional Ecology* 37 , pp.1948–1961. Available at: http://dx.doi.org/10.1111/1365-2435.14354.

Wang, R. et al. 2022. Recent increase in the observation-derived land evapotranspiration due to global warming. *Environmental Research Letters* 17 (2). Available at: http://dx.doi.org/10.1088/1748-9326/ac4291.

Waud, M., Brys, R., van Landuyt, W., Lievens, B. & Jacquemyn, H. 2017. Mycorrhizal specificity does not limit the distribution of an endangered orchid species. *Molecular Ecology* 26 (6), pp.1687–1701. Available at: http://dx.doi.org/10.1111/mec.14014.

Witte, A.J.M. et al. 2007. Bayesian Classification of Vegetation Types with Gaussian Mixture Density Fitting to Indicator Values Stable URL : http://www.jstor.org/stable/4499266 REFERENCES Linked references are available on JSTOR for this article : Bayesian classification of vegeta. 18 (4), pp.605–612.

Witte, J.P.M. et al. 2012. An ecohydrological sketch of climate change impacts on water and natural ecosystems for the Netherlands: Bridging the gap between science and society. *Hydrology and Earth System Sciences* 16 (11), pp.3945–3957. Available at: http://dx.doi.org/10.5194/hess-16-3945-2012.

Witte, J.P.M., Bartholomeus, R.P., Cirkel, D.G. & Kamps, P.W.T.J. 2008. *Ecohydrologische gevolgen van klimaatverandering voor de kustduinen van Nederland*. Niewegein.

Wösten, H. & Groenendijk, P. 2019. *Soil organic matter and its importance for water management*.

Wright, A.J., Mommer, L., Barry, K. & van Ruijven, J. 2021. Stress gradients and biodiversity: monoculture vulnerability drives stronger biodiversity effects during drought years. *Ecology* 102 (1), pp.1–10. Available at: http://dx.doi.org/10.1002/ecy.3193.

Yang, H. 2013. The case for being automatic: introducing the automatic linear modeling (LINEAR) procedure in SPSS statistics. *Multiple Linear Regression Viewpoints* 39 (2), pp.27–37.

Zhang, H. & Hiscock, K.M. 2010. Modelling the impact of forest cover on groundwater resources : A case study of the Sherwood Sandstone aquifer in the East Midlands , UK. *Journal* *of Hydrology* 392 (3–4), pp.136–149. Available at: http://dx.doi.org/10.1016/j.jhydrol.2010.08.002.