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Five-year carry-over effects in dune slack vegetation response to hydrology

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ABSTRACT

Dune slacks are biodiverse seasonal wetlands within sand dune systems, strongly influenced by the dynamics of the local groundwater regime. Future climate predictions indicate strong adverse impact on the hydrology and therefore ecology of these wetland ecosystems. In this study we aimed to find the most appropriate hydrological and ecological indicators to summarise dune slack plant community responses to hydrology over multiple years. We evaluated 80 hydrological metrics (weighted and un-weighted median, mean, minimum, maximum, mean spring level, averaged over 1–8 year duration, and 5 additional 1-year metrics) against plant community responses (variants of Ellenberg EbF moisture indicator). The data were drawn from 453 relevées in 17 dune slacks, using permanent quadrats and co-located piezometers, set up in 2010 with vegetation monitoring repeated six times until 2019. Within our study we found a strong relationship between multiple hydrology metrics and the plant community response, but this displayed inter-annual variation with different patterns and correlations between years. The best performing hydrology metric was the unweighted 5-year average mean spring water level (MSL), linked to unweighted mean EbF using vascular plant species only. Maximum water level (MAX) also performed well, but MSL was preferred as MAX can be enhanced or truncated by topography leading to anomalies for individual slacks. MSL is also flexible to implement within manual monitoring programmes, which could be targeted to 3-months per year over the spring as a minimum requirement. These findings provide simpler metrics for site managers to monitor potential hydrology and vegetation responses to climate change.

1. Introduction

Dune slacks are seasonal wetlands within coastal sand dune systems. They support high levels of plant and animal diversity, but are strongly influenced by the dynamics of the local groundwater regime (Grootjans et al., 2004). Dune slacks experience high inter- and intra-annual variation in the water table (Jones et al., 2006; Ranwell, 1959; Stratford et al., 2013). Seasonal flooding occurs in most years, depending on the type of dune slack, but the key defining characteristic is that the rooting zone is in contact with the water table for part of the year (Rhymes et al., 2014), with the water table typically within 1.5 m of the ground surface in summer (dry season) even for the drier variants of dune slacks (Curreli et al., 2013; Jones et al., 2021). These low-lying habitats can vary considerably along environmental gradients of hydrology, pH and age, resulting in a variety of dune slack communities (Berendse et al., 1998; Grootjans et al., 1998; Sýkora et al., 2004). Anthropogenic influences like eutrophication, drainage, water extraction and afforestation have contributed towards stabilization and drying of this dynamic habitat, reducing its area and degrading the condition of dune slack habitat (Bakker, 1981; Provoost et al., 2011; Rhind et al., 2007; Rhymes et al., 2014; van Dijk and Grootjans, 1993). In addition, future climate projections suggest a very high impact on dune slack habitats (Clarke and Ayutthaya, 2010; Curreli et al., 2013). Sea level and effective annual precipitation are important controls of the hydrology regime within a sand dune system. Sea level and coastal erosion influence the elevation and gradient of the water table, and climatic parameters like temperature and precipitation influence the annual recharge of the hydrological system (Kamps et al., 2008; Witte et al., 2012). Understanding the

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potential influence of climate change on dune slack wetlands is critical, but is currently hampered by incomplete understanding of how the hydrology regime affects vegetation, and which metrics best summarise those relationships. Therefore, there is a need to determine key indicators that are generally applicable for future research and management.

Relationships between dune slack habitat and hydrology have been studied for many years. Studies in the Netherlands have used hydrological metrics to describe hydrology management of dune slack plant communities, with a particular focus on the role of soil- and water-chemistry in plant responses (Aggenbach et al., 2002; Lammerts et al., 2001; Lammerts and Grootjans, 1998). In a UK context, most of the large dune sites have a hydrological system constrained by a relatively shallow continuous glacial till layer or other (semi-) impenetrable geological features, and approaches used so far have a number of limitations. Early hydrological studies (Jones, 1993; Ranwell, 1959) developed guidelines linking plant communities to water levels. However, these were based on very short durations of hydrological data, from 18 months to 2.5 years. While these are robust for determining relative differences in hydrological regime between plant communities, the short duration prevents use of absolute water levels to differentiate hydrological tolerances, since average annual groundwater levels can vary by 1 m between sequences of years (Stratford et al., 2013). More recent studies have attempted to update those guidelines with data from multiple sites (Davy et al., 2010). This suffered from a lack of spatial referencing, with vegetation communities often estimated from maps, sometimes created decades earlier. The first detailed UK study linking up-to-date vegetation mapping, hydrology and detailed geo-referenced and digital surveyed elevation by Differential GPS (to $<$ 1 cm vertical accuracy) was Curreli et al. (2013). This used four-year averages of hydrology metrics, and showed that the suite of wet to dry dune slack plant communities can be separated by 40 cm in the 4-year average winter water table (Curreli et al., 2013). The link between hydrology and dune slack vegetation has recently been revisited in a number of studies (Callaghan et al., 2021; Dwyer et al., 2021b, 2021a). However, none of these studies have investigated how duration of hydrological data influences the observed relationship with vegetation. To better understand the potential impact of climate change, particularly the role of inter-annual variability, there is a need to understand the short-to-medium term dynamics around hydrology and dune slack vegetation, which in turn can help explain the long-term dynamics. In order to reduce the dimensionality of the complex datasets involved, this requires an understanding of which are the most appropriate hydrological metrics and the most appropriate vegetation summary metrics.

Hydrology metrics are often used to summarize height of the phreatic groundwater zone, in order to understand general patterns of succession (Davy et al., 2006), niche boundaries of plant species (Aggenbach et al., 2002; Kooijman et al., 2016) or community composition (Curreli et al., 2013; Lammerts et al., 2001). The particular hydrological metrics used to describe or test relationships with vegetation vary in the literature. Mean spring water level (MSL) has been used to characterize vegetation communities or determine ecological niches (Käfer and Witte, 2004; Wamelink et al., 2002). 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. Fewer still have tested how the hydrology-vegetation relationship changes over different time frames of hydrological summary (Bartholomeus et al., 2008). Incorporating a longer range of temporal data is vital to understand the dynamics and response of dune slack communities around hydrological regimes in the context of managing these biodiverse systems. Analysing different types of hydrology metric is necessary, as each metric often encapsulates a certain part of the hydrology regime, with potentially different impacts on vegetation species (e.g. summer drought compared with spring waterlogging of the rooting zone). Better knowledge on these relationships and mechanisms will help monitor impacts of climate change.

Summary metrics which encapsulate response of the whole vegetation community are also useful to understand vegetation change, particularly in diverse plant communities where occurrence of low-frequency species can yield equally valuable information to that of the dominant species. Ellenberg indicators (Ellenberg et al., 1992; Hill et al., 2004) are frequently used as an integrator of community response to environmental conditions, including hydrology status (Diekmann, 2003; Schaffers and Sýkora, 2000). The Ellenberg indicator for soil moisture (EbF) values indicate conditions from dry (1) to wet (9) to very wet/ submerged (10–12). Previous studies have shown that EbF display high correlation coefficients with hydrology metrics and can be used as a quantitative measure for modelling or as part of monitoring to inform site management (Brunbjerg et al., 2012; Dwyer et al., 2021a; Ertsen et al., 1998; Käfer and Witte, 2004; Schaffers and Sýkora, 2000). The ecological indicator EbF can reveal small scale changes in vegetation community composition governed by the sensitivity of the component plant species to hydrological conditions (Curreli et al., 2013; Dwyer et al., 2021b). If these small-scale vegetation changes are sensitive to hydrology metrics, this can be especially useful for monitoring and management, particularly in the context of detecting ecological responses to climate change. Biodiversity measures can also be used to monitor vegetation responses, however these have been shown to differ with spatial resolution (Dwyer et al., 2022), and species richness may not always vary with hydrology due to inter-species dynamics within plant communities.

The condition of dune slack habitats across the UK has been classed as 'unfavourable' and has continued to decline during the last decade (Stratford, 2014). In order to guide evidence-based management to restore dune slack habitat to good ecological condition, there is an urgent need to better understand the relationship between dune vegetation and hydrological regime, with a particular focus on characterising plant community relationships against absolute water levels, and understanding the importance of within- and between-year variability in the context of climate change (Martins et al., 2018). Therefore, in this study we explored a variety of approaches to understand and reliably characterise the relationship between hydrology and dune slack vegetation. We aimed to provide a clear recommendation on which metric to use to guide future research and dune slack management. We tested a wide selection of hydrology metrics to understand the role of inter- and intra- annual variation in hydrology in terms of the response in vegetation composition over multiple years. Specifically, using co-located hydrology and vegetation metrics from dune slacks collected over a nine (vegetation) to thirteen (hydrology) year period, we addressed the following questions: I. Which hydrology metrics show the strongest relationship with dune slack vegetation mean EbF values? II. How does inter-annual variability affect the relationship? III. Which duration of hydrological data best represents the relationship between vegetation indicators and hydrology? This will increase our knowledge of climate-related responses and allow us to determine the most robust hydrology metrics to interpret change and to guide current and future management under climate change.

2. Materials and methods

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 divided by a rock ridge, consisting of Holocene aeolian calcareous sands that overlie glacial till deposits, resting on Palaeozoic and Precambrian basement (Bristow and Bailey, 1998). Between 1947 and

1965, the western side of the warren, including the rock ridge, was afforested with predominantly Corsican pine (*Pinus nigra* ssp. *Laricio*) (Hill and Wallace, 1989). The remaining east side of the site has developed as open dune grassland with four lines of parabolic dunes, with the interdune areas containing a high number of dune slacks. The site is managed by livestock grazing with sheep, cattle and merlod mynydd Cymreig since 1987 (Plassmann et al., 2010). Local climate is mildly oceanic with a 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.

2.2. Vegetation survey

The study uses multi-year data from permanently marked vegetation relevées in dune slacks. To gain a better understanding of relationships between vegetation and hydrology regime, an initial sample of 453 relevées were surveyed across 17 dune slacks at Newborough Warren in 2010 (Fig. 1) (Curreli et al., 2013). Sample size of the initial study aimed to represent and assess the full range of UK dune slack vegetation communities (SD13 – SD17 (Rodwell, 2000)), including a number of drier (non-wetland) dune vegetation types (SD7 – SD10) to define boundary conditions. Preliminary analysis of these relevées showed the sample was adequate to represent the hydrology gradient, in line with previous research on calibration of vegetation metrics (Ertsen et al., 1998) and dune slack research (Curreli et al., 2013; Dwyer et al., 2021a). Of these initial locations, 81 permanent quadrats (PQ) have been followed over time with an additional six repeat surveys between 2012–2019, giving seven time points in total for vegetation data (Table 1). Not all PQ were resurveyed in each year. Each dune slack contained 3 to 8 PQ of 1 m × 1 m, arranged in four directions (N, W, S, E) around a co-located piezometer. The spatial topography of the PQ was optimized to minimize spatial autocorrelation (minimum of 4 m distance from the piezometer), while also minimising additional corrections needed to extrapolate hydrological metrics from the adjacent piezometer (ideally within 7 m down- or up-gradient of the piezometer). Some cardinal point locations were re-located within the dune slack where topographic variability would result in a location outside the margin of dune slack vegetation, or on steep slopes. Slacks with more than four PQ were set up to include mini-transects to better understand groundwater variation within a slack. PQ were 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 plant species (Stace, 2019) and Atherton for bryophyte species (Atherton et al., 2010). To minimize surveyor bias all monitoring years were supervised by botany expert Hillary Wallace, with training for the surveyors before any relevées were recorded. Bryophyte species and other plant species have been sampled to confirm ID for expert evaluation to ensure correct identification.

2.3. Preliminary ecological indicator assessment

In order to select the most suitable vegetation indicators, we conducted a preliminary data assessment, focusing on Ellenberg indicators (nitrogen, moisture, light, reaction and salinity). as measures of realised community-mean environmental traits. As expected the Ellenberg indicator of soil moisture (mean EbF) showed a strong correlation with water table depth, but none of the other variables were strong enough to include alongside EbF. EbF displayed high inter- and intra-annual variance, i.e. it changed in tandem with hydrological variation, and was therefore the most suitable vegetation indicator for this study. Biodiversity metrics were not selected for this study, as previous research has indicated that relationships between hydrology and biodiversity vary at different levels of spatial scale (Dwyer et al. 2022), and the focus was on community-level metrics of change, not on the hydrological impacts on biodiversity *per se*.

2.4. Ellenberg indicator for soil moisture (EbF)

The mean EbF values for soil moisture were calculated for each relevée 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 programme R (v4.0.3, R Core Team, 2021). Preliminary analysis showed that the optimal correlation coefficients were obtained

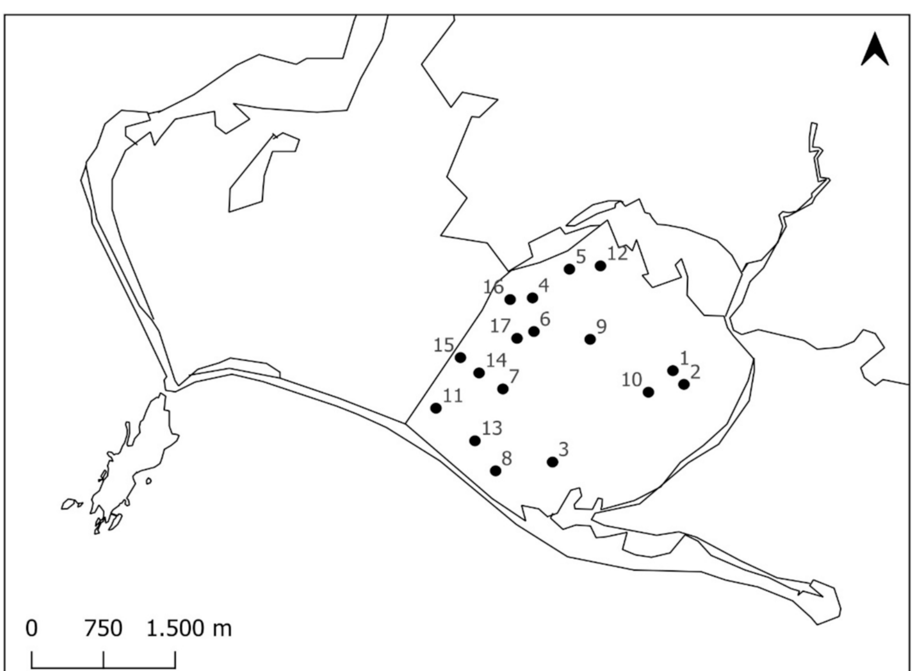

Fig. 1. Map of monitoring locations indicated with number (Table 1) of Newborough, Wales.

Table 1
Number of relevées recorded per co-located piezometer 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	T41	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

using the presence-only data (Appendix, Table A.2), similar to previous work on optimization of EbF for calibration (Käfer and Witte, 2004). There is a risk of over-weighting rare and low-cover species when using only presence-absence data (Schaffers and Sýkora, 2000). However, rare or uncommon 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), while dominant species often have a broader ecological niche. 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 hydrological variation than the cover-weighted EbF indicator. The risk of surveyor bias is also reduced when using presence-absence data compared to cover-weighted data, as differences in estimates of percentage cover can have a high influence on cover-weighted values. Preliminary analysis also showed higher correlation coefficients using mean EbF dependent on vascular plants only, compared with corelation coefficients of mean EbF dependent on both bryophytes and vascular plants (Appendix, Table A.2). Therefore, we used mean EbF for presence-absence of vascular plant species only for the analysis in this study.

2.5. Hydrology data

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

2.6. Topographical induced variation

To ensure high accuracy of the hydrology metrics for analysis, the elevations of all piezometers and PQ 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 PQ and piezometer to ensure accurate relationships between the hydrology and the vegetation data.

2.7. Hydrology metrics for co-located quadrats

To test the relationship between hydrology and plant community response, 80 hydrology metrics were calculated using the hydrological data from 2010 to 2019 (Appendix, Table A.1). Each "hydrology metric" summarizes a component of the local groundwater regime (Table 2), for example the minimum (MIN), mean, median or maximum (MAX) during a hydrology year. Following the convention in Curreli et al. (2013), 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 (Fig. 2).

Table 2
Hydrology metrics component list.

Hydrology metric Components	Description (+ period before vegetation monitoring)
MSL	Mean spring water level (1st March to 31st May)
MIN	Minimum 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 (1st June to 31st August)
Mean Winter	Mean winter water level (1st December to 28th February)

To calculate the multi-year hydrology metrics for this study, we averaged the hydrology metric components over a period of 1 up to 8 years. For the analysis of 2018 vegetation data, it was possible to use an 8-year average, but for comparison across years 2017 to 2019 it was only possible to calculate a 7-year average, since hydrological monitoring for some piezometers only started in 2010. For example, the 2-year average MAX, represents the average of the 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 A.1.

Equation (1). The weighted hydrology metric calculation

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

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

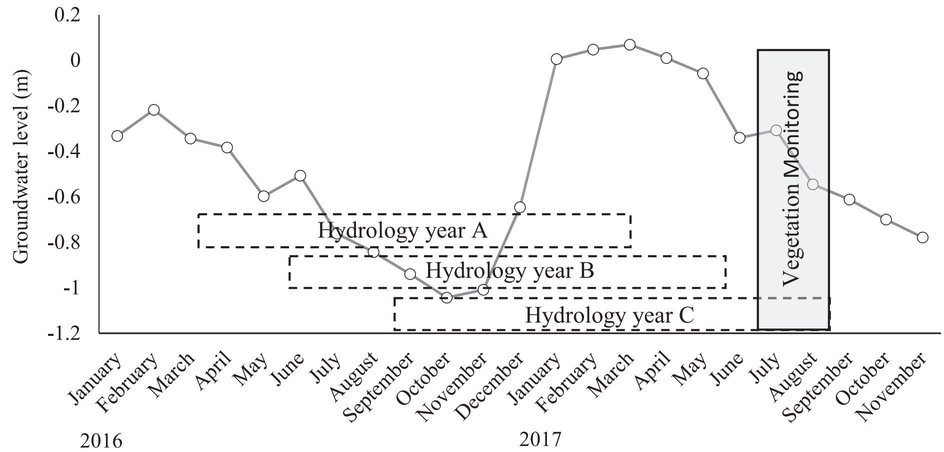

Fig. 2. Hydrograph of the groundwater level (m) per month of a typical dune slack, running from January 2016 to end of the year of 2017. Illustrating the choice of "hydrology year" with three different time periods: Hydrology years A, B and C are marked by dashed blocks. The light grey block marks the vegetation monitoring period corresponding to the hydrology year. Ground surface is 0 m, negative values represent water levels below ground surface.

long as $n = i$, the number of years included.

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

$$i = 3year, M = Mean_{,j=2018} = \frac{\sum(3^*M_{2018} + 2^*M_{2017} + 1^*M_{2016})}{\sum(3+2+1)} \quad (2)$$

2.8. Data analysis

In preliminary assessment of the dataset we assed patterns, trends and normality using plotting and statistical tests. The data indicated linear trends of mean EbF with multiple hydrology metrics, and no non-linear trends or interactions. Therefore, the Pearson's correlation test was used to assess relationships for the purposes of this study, since the goal was to evaluate which were the best metrics, rather than to build predictive models. Statistical analysis was undertaken in SPSS v.27. We discuss our approach below for the following steps:

2.8.1. 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 A.1) and the mean EbF values of the 2018 data (81 relevées, Table 1), all calculated for a single year. The year of 2018 was selected based on the longest available time period for the hydrology metrics in combination with the highest number of relevées. There is a potential risk of pseudo replication because of spatial autocorrelation without correcting for nesting within dune slacks or to co-located piezometers. However, this was deemed low risk, as the depth to water table for each quadrat is unique and is one of the dominant drivers of variation in dune slack vegetation.

2.8.2. 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 relevées was tested using the Pearson's correlation test between mean EbF values and selected hydrology metrics. Based on results from the first research question, the two highest performing hydrological metrics were selected (MAX and MSL) and assessed for multiple hydrology seasons (1–7 years). To gain more perspective to understand the inter-annual variation within the dune slack habitat, another subset of 47 relevées 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 1). Within this subset, 2 dune slacks have been selected to show inter-annual pattern of the mean EbF variation on dune slack level. We further plotted MSL as one of the best performing metrics from research question I against the mean EbF response for 2017, 2018 and 2019 with separate lines to visualize the inter-annual effect.

2.8.3. Hydrology year

To assess our chosen hydrological year period influenced relationships between hydrology and vegetation, three different variants of hydrological period were selected for sensitivity analysis (Fig. 2). These periods were: hydrological year A (1st of March to 28th of February), hydrological year B (1st of June to 31st of May, which can be regarded as the default standard "hydrological year") and hydrological year C (1st of September to 31st of August). To compare the different hydrological years, the subset of 69 relevées mean EbF data were re-analysed against the newly created hydrology metrics with Pearson's correlation test for the years 2017, 2018 and 2019.

3. Results

3.1. Which hydrology metrics show the strongest relationship with dune slack vegetation mean EbF values?

The Pearson's correlations coefficients (r) resulting from exploring the relationships between hydrology metrics and mean EbF ranged from r = 0.71 (moderate affinity) to r = 0.86 (high affinity) (Appendix, Table A.2, column – EbF 1a). The hydrology metrics component type with the highest affinity were the maximum water level (MAX) and spring mean water level (MSL) with positive correlations coefficients ranging from r = 0.83 to r = 0.86 (Fig. 3). Hydrology metrics component type 90th and 95th and the mean winter level resulted also in high correlation coefficients with mean EbF. Median water levels generally performed less well than the average (Mean) water levels, and the minimum water table (MIN) typically showed the weakest correlation coefficients with mean EbF values. In general, when multiple hydrology years were included in the calculation of the hydrology metrics, the relationship with mean EbF was stronger. The weighted metrics did not increase the strength of the correlations beyond that of unweighted metrics. Based on these findings, the non-weighted hydrology metrics based on component MAX and MSL were used for further analysis.

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

When testing the relationship using vegetation monitoring and hydrological metrics for different vegetation survey years (2017–2019), the Pearson's correlation coefficients of the sub-selection of 69 relevées, ranged from r = 0.73–0.85, depending on vegetation monitoring year, duration of the averaging period for hydrology (years included 1–7) and

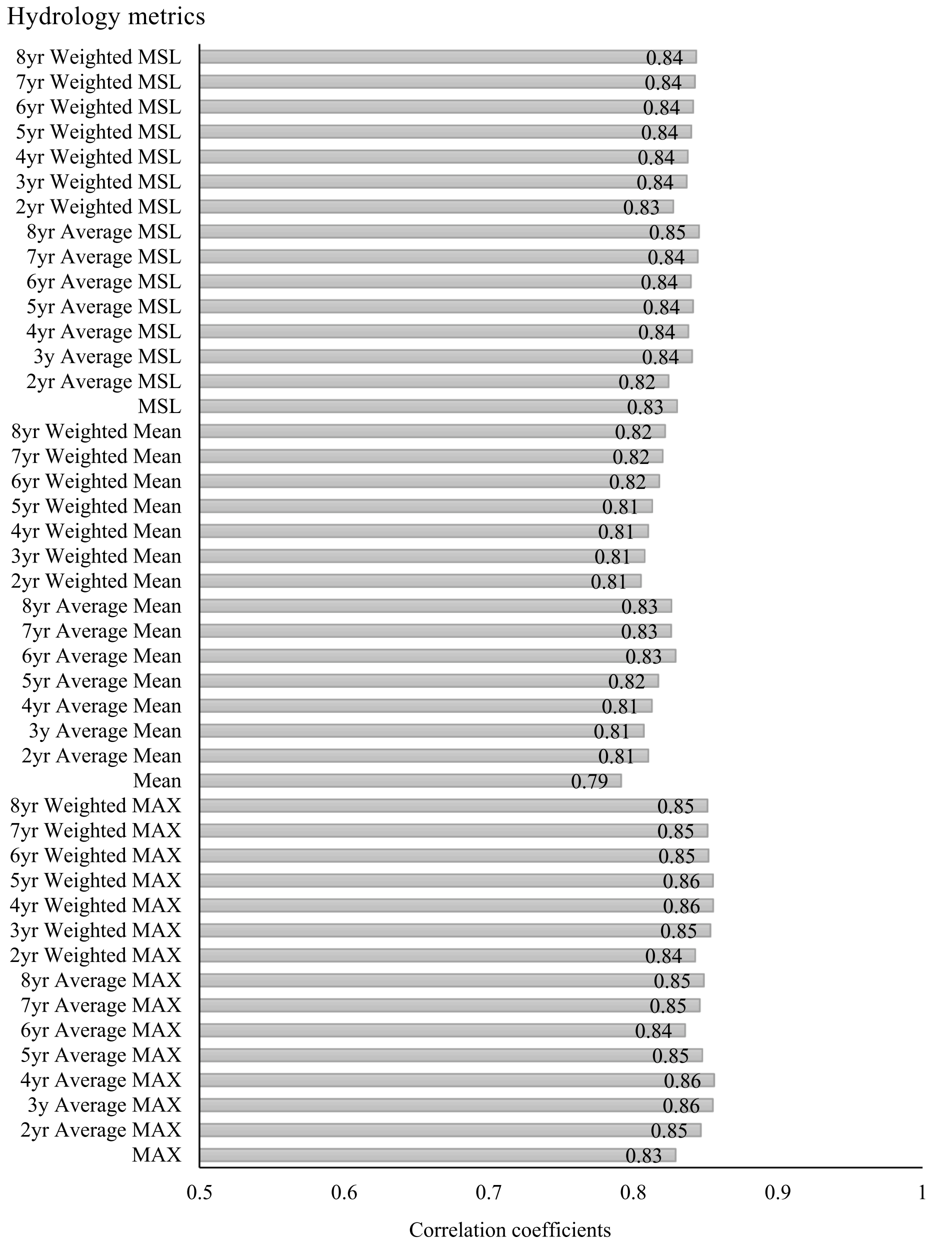

Fig. 3. Pearson's correlation coefficients between mean Ellenberg values (EbF) and families of hydrology metrics from 81 vegetation relevées (monitoring year = 2018). The displayed hydrology metrics contained the 1–8 hydrology year(s) average or weighted average of a hydrology metric component (mean water level, spring water level (MSL) or maximum water level (MAX)). All correlations were significant at $p < 0.05$. Full results for all metrics are in Appendix, Table A2.

hydrology metric (MAX or MSL) (Fig. 4, Panel B, D and F). The hydrology metrics linked to the correlation coefficients also differed considerably between years (Fig. 4, Panel A, C and E), particularly for the 1-year metrics, with 1-year MSL varying between −0.53 m and −0.27 m and 1-year MAX between −0.43 m and −0.20 m. The correlation coefficients of 2018 were reasonably constant for both MAX and MSL, varying between r = 0.78 and r = 0.82, and the averaging period had little effect on the relationship (Fig. 4, Panel D). However, different patterns were observed for 2017 and 2019, which were both drier years than 2018, where the correlation coefficients increased when averaging more seasons in the hydrology metric, particularly for the much drier year of 2019 (Fig. 4, Panel B and F). The best hydrology metric component (MAX or MSL) also differed between years. In single years, and over short-averaging periods, the most significant metric shifted: in 2017 MSL had higher positive correlation coefficients and MAX in 2019. The single highest positive correlation coefficient was found between the 3-year average MAX and mean EbF r = 0.848 in 2017. However, overall, across the three years (2017, 2018 and 2019) correlation coefficients of the relationship stabilises around the 5–7 hydrology years average (+/- weighted) and neither hydrology metric component (MAX or MSL) consistently performed better.

To gain a better understanding of the inter-annual variation found in the relationship between the hydrology metrics and mean EbF response, we plotted data from 47 relevées from multiple dune slacks (Panel A), and then two selected piezometers with a longer hydrological record, one wetter (NW4, Panel B)) and one drier (NW3, Panel C) in Fig. 5. Panel A summarises the annual variation for the hydrology metrics 1-year MIN, MAX and MSL of 47 relevées for the period 2010–2019. Metrics MAX and MSL display a similar pattern over time, but differs from metric MIN, where the inter-annual variation range of MIN is smaller and has a substantial different pattern from MAX and MSL in some years. The response of mean EbF to the hydrology metrics is broadly similar to that

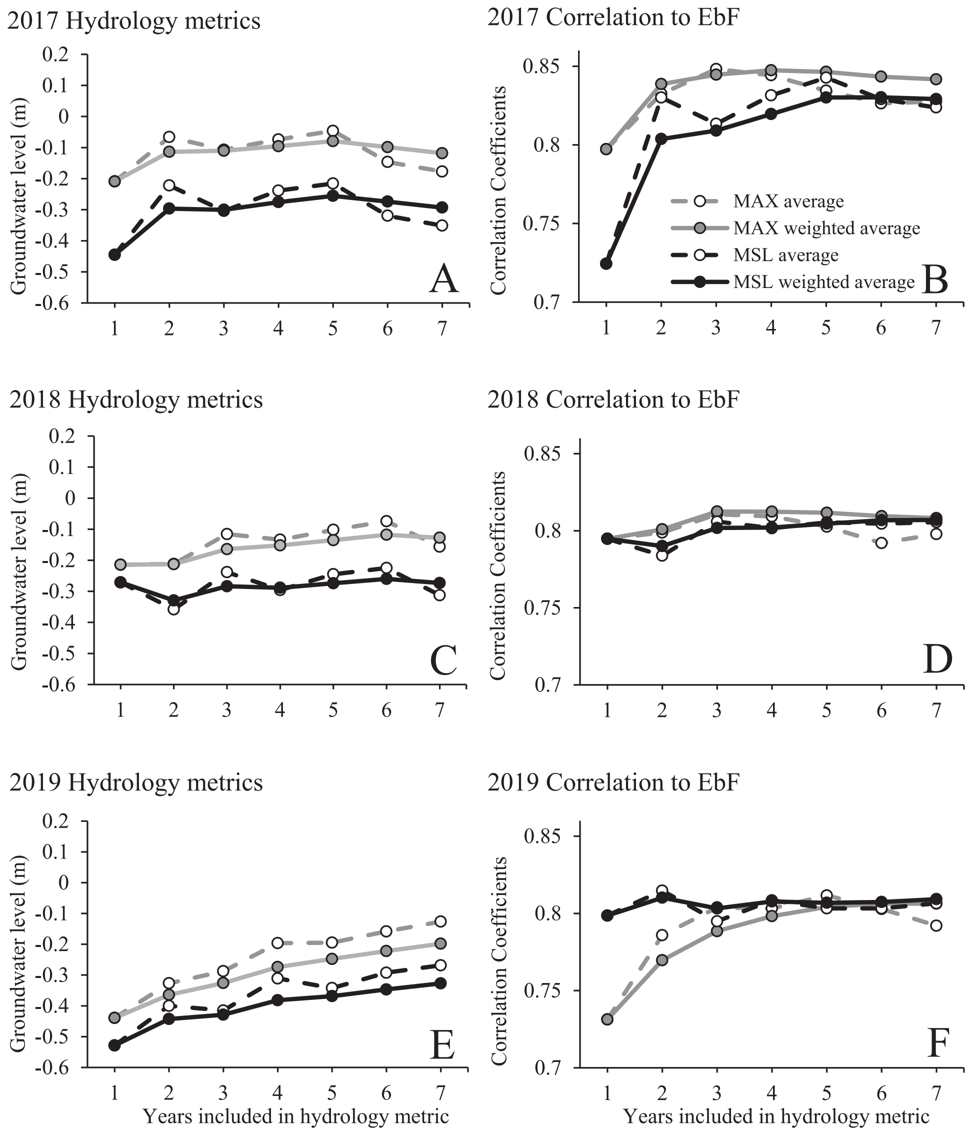

Fig. 4. An overview of the hydrology metric values (Panel A, C and E) and Pearson's correlations coefficients with mean EbF (Panel B, D and F) of 69 vegetation relevées for monitoring year 2017, 2018 and 2019. Each panel has data of 69 relevées, the monitoring year is displayed above the left upper corner 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 $p < 0.05$.

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). 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). While during the period 2010–2012 the decrease in mean EbF over this period is of similar magnitude (−0.17 mean EbF), but the decrease in MSL and MAX is much 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 1-year hydrology metrics suggests the presence of additional mechanisms governing the response of vegetation to changes in hydrology, such as time lags or carry-over effects in vegetation response to hydrology, or interactions with other parameters.

The time course of hydrology and mean EbF at two individual dune slacks is shown in Fig. 5 panel B (NW4, a wetter dune slack) and panel C (NW3, a drier dune slack), for the period 2007 – 2019 including the preceding three years hydrological regime. Absolute levels of the hydrology metrics MSL, MAX and MIN of dune slack NW3 were generally lower (representing drier conditions) compared with dune slack NW4. MAX levels in NW4 also show a characteristic that can occur in some slacks, where the MAX is truncated at higher water levels due to overland surface flow within the topography of the slack. The range of mean EbF values were lower in the drier dune slack (NW4 6.25–6.7 compared to NW3 5.85–6.2), reflecting the hydrological conditions, but also showed different inter-annual patterns. During the period of 2012–2013 there was a substantial increase observed in hydrology metrics MAX and MSL in both dune slacks, but unexpectedly NW3 showed a slight decrease in EbF (−0.05 mean EbF), while NW4 did have an increase in mean EbF (+0.15 mean EbF). Falls in water level summarised in the hydrology metrics generally resulted in a similar response in mean EbF across both dune slacks, however the decrease in mean EbF within dune slack NW3 tended to be greater than NW4. For example, the period 2018–2019, NW4 had a decrease of −0.06 mean EbF versus the much greater decrease in NW3 −0.23 mean EbF, while the decrease in MSL in

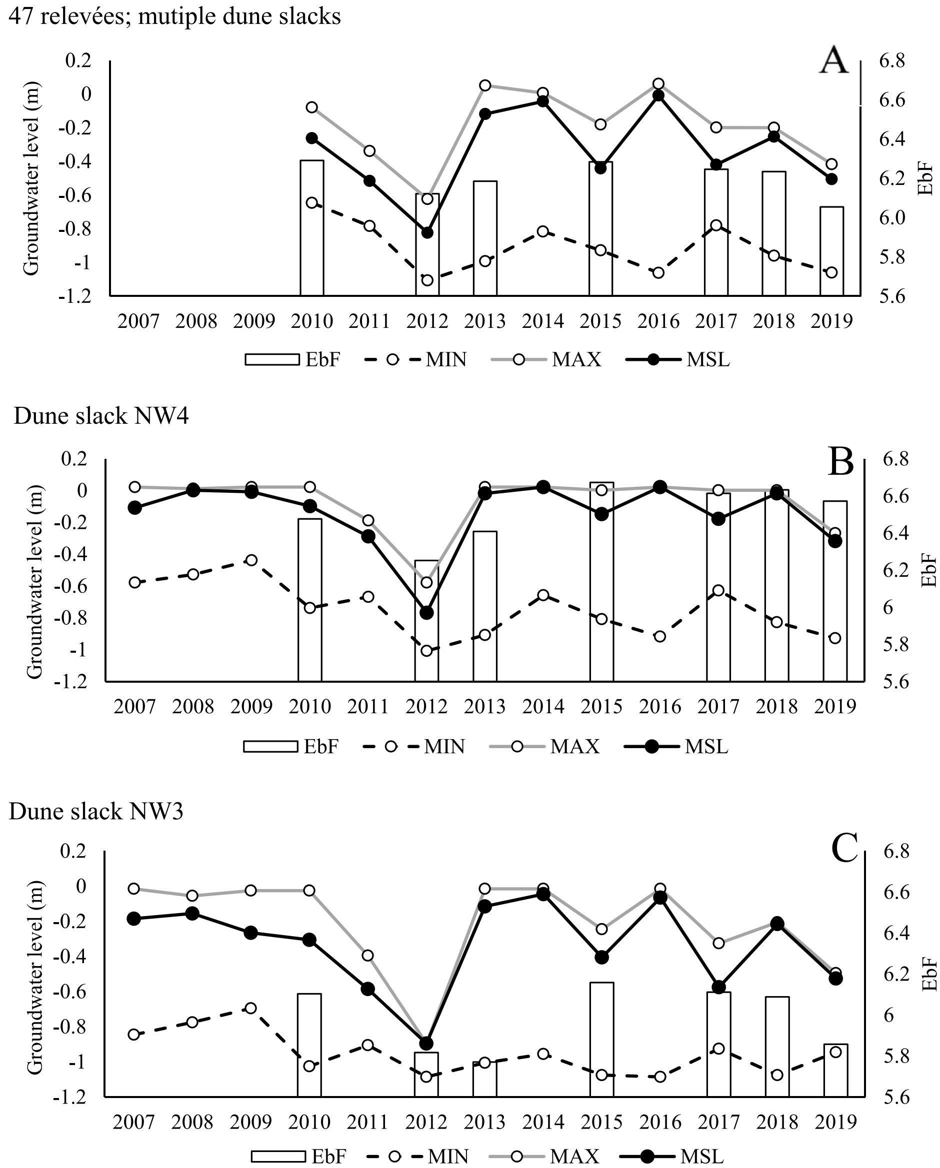

Fig. 5. The 1-year hydrology metrics (MAX, MSL and MIN) and mean EbF values for: 47 relevées (Panel A), dune slack NW4 (Panel B) and dune slack NW3 (Panel C), plotted over time (2007–2019). Hydrology metrics MIN, MAX and MSL are displayed with solid or dashed lines on the left y-axis (groundwater level, 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 metrics were 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 m, negative values represent water levels below ground surface.

both dune slacks was similar (−0.3 m). This suggests that there may be some differences in the vegetation response to hydrological change between types of dry and wet dune slacks.

To further analyse the effect of the inter-annual variation of the relationship between mean EbF and hydrology metrics MAX and MSL, we plotted linear trendlines and the values of mean EbF and the 5-year average of MAX and MSL (Fig. 6), as most of the correlation coefficients stabilized after including 5 hydrology years (Fig. 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, for both MSL and MAX. Overall, the results and data show the presence of inter-annual variation in the relationship between hydrology regime and the mean EbF response, which is still apparent to a lesser extent, even when using five-year averages of hydrological metrics.

3.3. *Which duration of hydrological data best represents the relationship between vegetation indicators and hydrology?*

The Pearson's correlation coefficients between mean EbF and the hydrology metrics resulting from hydrology year A, B and C were summarised in Table 3. Across all the hydrology metrics, the single highest correlation coefficient was found in hydrological year A, year 2017 with r = 0.89 for the 3-year average MSL, with hydrological year A performing better at short durations (1–2 yr average). However, when moving to longer averaging periods, hydrological years B and C performed slightly better than A, particularly for MAX. Overall, there were few substantial differences between the hydrological years' correlations, suggesting that the currently used method represented in hydrological year B is fit for purpose.

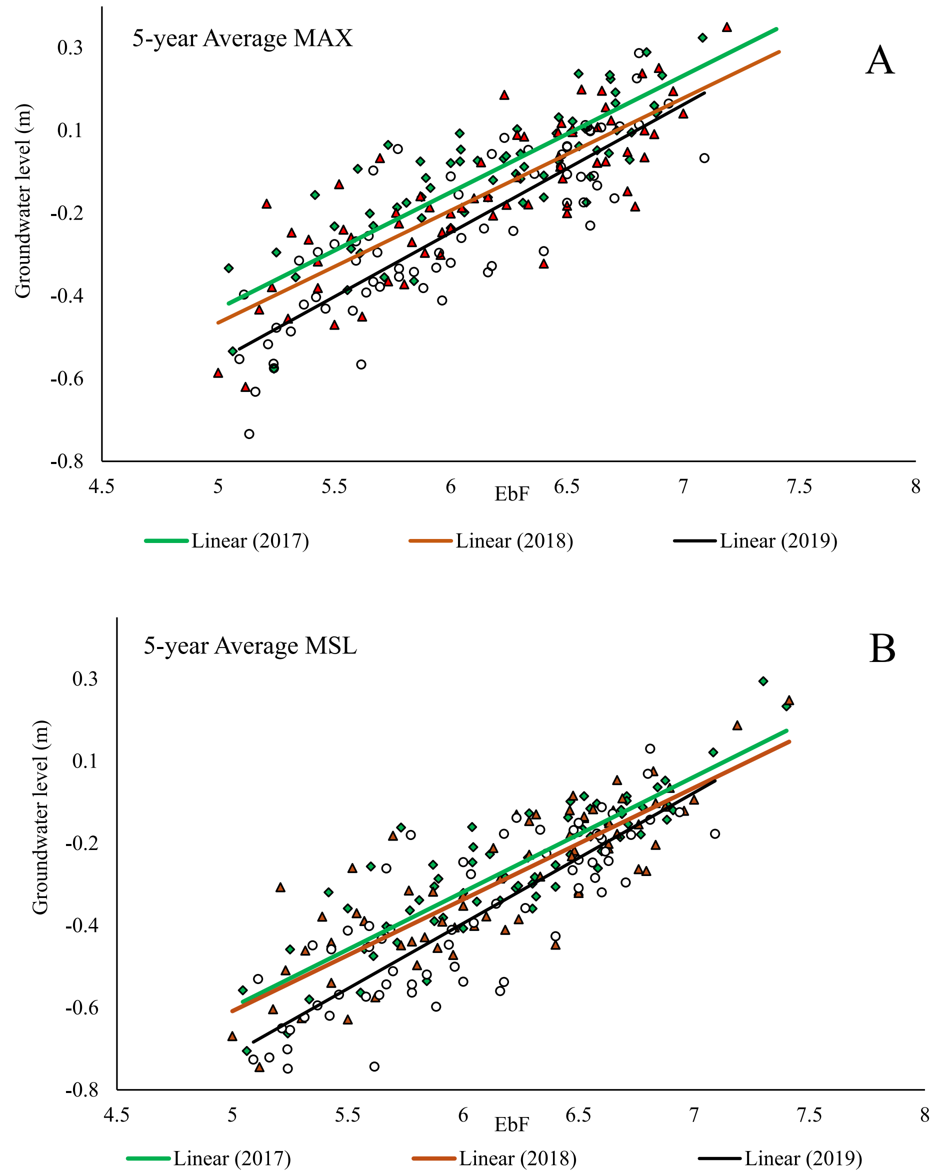

Fig. 6. Linear trendlines and corresponding values of 69 vegetation relevées between mean EbF against the 5-year average of MAX (panel A) and MSL (panel B) for the year 2017 (green line, plots = squares), 2018 (orange line, plots = triangles) and 2019 (black, plots = circles). Hydrology metrics MAX and MSL measure unit is groundwater level (m) on the y-axis, ground surface is 0 m, negative values represent water levels below ground surface. Correlation coefficients of the relationships are indicated in Table 3 with an *.

4. Discussion

This research demonstrates that there was a strong relationship between hydrology metrics and mean EbF in dune slacks, where hydrology metrics using the component MAX or MSL had the best ability to predict mean EbF response. Responses showed lag effects, with higher correlation coefficients gained by using longer averaging periods in the metrics. For the first time, we have tested different cumulative durations of water table metrics, and of those metrics with the highest correlation coefficients, the metric with most utility was the unweighted 5-year average MSL. The relationship between hydrology metrics and mean EbF displayed inter-annual variation with different patterns and correlations between years. There are strong indications that “dry” and “wet” years have different impacts on dune slacks and might be influenced by different duration carry effects or other environmental factors, depending on the type of dune slack. We discuss these findings in detail below per research question.

4.1. Which hydrology metrics show the strongest relationship with 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, 2021b). Our finding that hydrology metrics focusing on the wetter component of the hydrological regime (MAX and MSL) best explained the vegetation response suggests that wet conditions during a short period of the year are the dominant driver of plant responses. Plant species tend to have a strong response to short-term more extreme events compared to long-term more average conditions (Smith, 2011). Although summer drought was expected to also be an important hydrological influence, in line with other studies (Curreli et al., 2013) this was found to explain much less variation than MAX or MSL. Mechanisms for high water levels influencing vegetation composition might include waterlogging of the rooting zone, which is a substantial stressor for species with limited adaptations to flooding or the conditions that arise with waterlogging, particularly in spring when

Table 3
Summary table of the Pearson's correlation coefficients between mean EbF and hydrology metrics MAX and MSL, of 69 relevées per monitoring year (2017–2019). Hydrology year A, B, and C, each containing a different time period (Fig. 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 Fig. 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
1 yr MSL	0.81	0.78	0.85	1 yr MSL	0.74	0.82	0.81	1 yr MSL	0.74	0.82	0.81
2 yr Average MSL	0.89	0.86	0.82	2 yr Average MSL	0.88	0.81	0.83	2 yr Average MSL	0.88	0.81	0.83
3 yr Average MSL	0.89	0.85	0.84	3 yr Average MSL	0.86	0.86	0.82	3 yr Average MSL	0.86	0.86	0.82
4 yr Average MSL	0.89	0.87	0.84	4 yr Average MSL	0.88	0.85	0.84	4 yr Average MSL	0.88	0.85	0.84
5 yr Average MSL	0.89	0.86	0.83	***5 yr Average MSL**	**0.89**	**0.87**	**0.83**	5 yr Average MSL	0.89	0.87	0.83
6 yr Average MSL	0.88	0.87	0.83	6 yr Average MSL	0.88	0.87	0.84	6 yr Average MSL	0.88	0.87	0.84
7 yr Average MSL	0.87	0.86	0.82	7 yr Average MSL	0.87	0.87	0.84	7 yr Average MSL	0.87	0.87	0.84
1 yr MAX	0.75	0.81	0.85	1 yr MAX	0.76	0.82	0.72	1 yr MAX	0.76	0.82	0.72
2 yr Average MAX	0.74	0.86	0.84	2 yr Average MAX	0.87	0.81	0.79	2 yr Average MAX	0.87	0.81	0.79
3 yr Average MAX	0.77	0.84	0.84	3 yr Average MAX	0.86	0.86	0.80	3 yr Average MAX	0.86	0.86	0.80
4 yr Average MAX	0.79	0.83	0.80	4 yr Average MAX	0.88	0.85	0.80	4 yr Average MAX	0.88	0.85	0.80
5 yr Average MAX	0.79	0.82	0.77	***5 yr Average MAX**	**0.88**	**0.87**	**0.81**	5 yr Average MAX	0.88	0.87	0.81
6 yr Average MAX	0.84	0.81	0.77	6 yr Average MAX	0.86	0.87	0.81	6 yr Average MAX	0.86	0.87	0.81
7 yr Average MAX	0.85	0.83	0.75	7 yr Average MAX	0.85	0.86	0.81	7 yr Average MAX	0.85	0.86	0.81

plants are starting to grow (Jones, 1972; Parent et al., 2008; Schat, 1984), which might explain the importance of MSL as a response metric. Although other wetland studies have used multi-year averages of hydrology to explain vegetation responses (Käfer and Witte, 2004; Schaffers and Sýkora, 2000), there have been almost no consistent tests of the most appropriate averaging period. One study has looked at relationships over a longer time period, concluding that a 30-year average was most appropriate to obtain a generalisable response over different vegetation and soil types (Bartholomeus et al., 2008). However, the same study also found that rainfall levels preceding the vegetation survey year influenced the relationship. Those potentially contradictory findings suggest a tension between explaining short-term response of vegetation to hydrology and long-term climate conditions. Assuming that climate is stable, there is scope for ebb and flow in the dominance of individual species in response to drier or wetter years, with the long-term community composition remaining stable due to recovery of species from the seedbank or recolonization from nearby when the hydrological regime returns to a state that fits their niche. However, where a changing climate, or other factors such as drainage or altered recharge, disrupt the hydrological cycle such a quasi-stable state may not be maintained, and it becomes important to better understand the short- to medium-term responses of vegetation to groundwater variation. It is plausible that more recent hydrological conditions would have a greater influence on vegetation than conditions further back in time, yet our results did not show that "weighted" average hydrology metrics better explained variation compared with a simple arithmetic mean. While MAX and MSL explained roughly similar levels of variance, our data illustrated some potential challenges in using MAX, principally the truncation of high water levels in slacks where overland flow occurs. Use of MSL therefore brings a more consistently applicable metric across a wide range of contexts. It also brings advantages to site managers with limited resources to only conduct monitoring in a shorter duration within the year (March, April, May).

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

Similar differences in the community response that we found between dry and wet years have also been shown in other systems. For example, a carryover effect of drier conditions between years has also been found in *Cladonia* population dynamics, where an influence of decreased rainfall during one season was also found across the following years (Martins et al., 2018). In our study, the slower recovery of drier dune slacks compared to the more wetter dune slacks might be related to niche limitations for individual species within the dune slack vegetation community (Dwyer et al., 2022). This may in part be due to attributes of species linked to e.g. rooting depth and their potential for contact with the water table, and associated capillary rise (Ranwell, 1959; Rhymes et al., 2014). Another contributing factor may be the physiological mechanisms of different species to withstand waterlogging of the rooting zone (Pan et al., 2021). At a community level the average groundwater level niche is often considerably lower for dry slacks 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 accumulates faster and to greater depth in wetter communities (Grootjans et al., 2017; Jones et al., 2010; Sýkora et al., 2004). Soil organic matter influences plant community responses to hydrological conditions as it allows better retention of soil moisture, leading to different capacity to endure drought (Schaffers and 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 with wetter dune slacks, which recovered more quickly. Mechanisms of impact and recovery in response to drought operate on longer time scales than mechanisms of impact and recovery in response to flooding or high water table conditions. 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.

4.3. Which duration of hydrological data best represents the relationship between vegetation indicators and hydrology?

There has been limited research into the best way to calculate hydrology metrics to explain vegetation response, partly because many sites have lacked co-located vegetation and hydrology data for dune slacks. Within the field of hydrology, the term "hydrological year or season" is often used to describe a period of 12 months which encapsulates the key seasonal dynamics (e.g. min, max) of the hydrology regime within the ecosystem. Timing also depends on global location (northern or southern hemisphere), and climatic dynamics (seasonality, or seasons). The differences in outcome between calculations using our three definitions of hydrological year are small but may partly be explained by the relatively short duration of years assessed in this study. Longer durations of monitoring data (e.g. > 8 years) may include periods of unusual rainfall pattern and hydrological behaviour, such as the low double winter peak rather than a single higher peak observed in datasets from Jones et al. (2006). However, the current selection of hydrological year starting 1st June should in principle be maximally organised to capture a winter recharge peak which tends to be more variable in timing than the summer minimum and can occur any time during the autumn to spring period from around September through to

March. Other periods could be considered if needed when looking at different (hydrology) metrics.

5. Conclusion and recommendations

Dune slack habitat is highly dependent on the hydrological regime, which makes it vulnerable to future climate change. This study re-establishes the strong direct relationship between hydrology and vegetation, using hydrology metrics as indicators to predict plant community responses. 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 unweighted MSL as a monitoring metric allows site managers to obtain data more easily 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. Or, once a few years of full data collection have taken place to establish the overall hydrological regime, this gives flexibility to then reduce monitoring frequency to the spring period, if staff time or funding resources become constrained. Nonetheless, the ideal situation is to collect both hydrological and ecological response data over much longer time periods. The hydrology metric can also function as an early detection indicator, in which the value of the 5-year MSL can serve as a proxy to indicate thresholds or potential "status" of dune slack plant communities on site. By setting a standard for dune slack monitoring, we provide a link between management and research, but which may also be useful for other vegetation types strongly linked to hydrology. Our study highlights the essential role of long-term monitoring for both hydrology and vegetation studies to better understand these complex ecological systems. Such data are the only way to gain an improved understanding of dune slack resilience to hydrological change.

Hydrology metrics can be used to develop climate scenario predictions about plant community shifts or to determine resilience or thresholds. The ability to predict thresholds of vegetation responses to changes in water table is of high importance for management and conservation of dune slack habitat. Both the inter-annual variation in responses, and the differences observed across wet and dry dune slack types, suggest that there is a need for further research of plant community response dynamics in relation to climate change. A focus on individual species with response curves that could serve as indicators for management (Dwyer et al., 2021b; Wierda et al., 1997) and principle response curves can help to understand temporal dynamics in community shifts (Auber et al., 2017; van den Brink et al., 2009). Multivariate methods, like canonical-, GAMMS or mixed model- approaches, would help to further analyse the relationship between hydrology and vegetation response on higher spatial levels to answer more in-depth questions on the influence of other environmental variables, as has been done with biodiversity metrics (Dwyer et al., 2022, 2021b). Studying more dune slacks with different hydrological regimes (e.g. atypical regimes where hydrology is partly mediated by artificial drainage, such as on golf courses) or other topographical regions could provide more insights and context in the full scale of the dune slack ecotype. Understanding the impact of regional characteristics (geology, topography, climate) on the hydrology regime would also help to understand the dynamics behind the inter-annual variability among the hydrology metrics. By incorporating the influence of precipitation and temperature on recharge, it would also be possible to model the impact of climate scenarios, thereby predicting future impacts of climate change on dune slack plant communities. This will be an important step to guiding management and conservation strategies. Overall, the research in this study has contributed to enable the next step for dune slack research and those managing dune slacks for their high biodiversity and conservation value to respond to climate change.

CRediT authorship contribution statement

Lisanne van Willegen: Writing – original draft, Writing – review & editing, Formal analysis, Investigation, Methodology. **Hilary Wallace:** Supervision, Software, Methodology, Investigation. **Angela Curreli:** Supervision, Methodology, Investigation. **Ciara Dwyer:** Writing – review & editing, Software, Methodology. **John Ratcliffe:** Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Davey L. Jones:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Graham Williams:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Martin Hollingham:** Validation, Methodology, Investigation. **Laurence Jones:** Writing – review & editing, Visualization, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.113016.

Data availability

Data will be made available on request.

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