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Original Articles

Environmental modifiers of the relationship between water table depth and Ellenberg's indicator of soil moisture

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ABSTRACT

Ellenberg indicator values for plant species are widely used metrics in ecology, providing a proxy measure of environmental conditions, without direct measurements. They integrate environmental conditions over time since species will only persist where conditions are favourable. Ellenberg moisture (F) values summarise the hydrological environment experienced by plants. However, the relationship between indicator values and hydrological metrics appears to be influenced by a range of other abiotic and biotic factors, limiting our ability to fully interpret Ellenberg F. Focussing on Ellenberg F, we evaluated how the unweighted mean plant community F value to hydrology, specifically water table depth, is influenced by other environmental factors, ground cover type and alpha diversity in UK seasonal coastal wetlands (dune slacks). As expected, water table depth had the strongest influence on unweighted mean Ellenberg F. We show that unweighted mean Ellenberg F was more sensitive to changes in water table levels for plant communities that were more nutrient limited, when the organic matter layer was thicker and there was less bare ground cover. Unweighted mean Ellenberg F was consistently lower for a given water table depth, when there was lower atmospheric nitrogen deposition, lower loss of ignition (a measure of organic matter content) and more diverse plant communities. These findings help us to better interpret what Ellenberg F indicator values tell us about hydrological conditions, by understanding the factors which alter that relationship.

1. Introduction

Ellenberg indicator values allocate a score to a plant species based on its environmental preferences (Ellenberg, 1991). They have been defined for the majority of temperate European plant species and are used to provide a measure of environmental conditions, without direct measurements, and to detect changes in the environment (Britton et al., 2017; Diekmann, 2003; Ellenberg, 1991). Ellenberg moisture (F) values range from species growing on dry soils (score 1), to wet soils (score 9), to emergent or submerged aquatic species (scores 10–12). They are valuable because they can be combined as a biological indicator that represents the integrated response of the plant community to the hydrological regime that has been experienced (Curreli et al., 2013; Diekmann, 2003; Ertsen et al., 1998; Schaffers and Sýkora, 2000; Wamelink et al., 2002). As such, they are likely more meaningful than metrics derived from direct, short-term, measurements of the physical environment. However, because ecological indicators such as Ellenberg's moisture values integrate a complex range of ecological processes, this can also make interpretation difficult in an ecological and habitat management context. In addition to the hydrological regime, community mean Ellenberg F values in seasonal wetland habitats may be influenced by a wide range of abiotic and biotic factors, either through their direct impact on soil moisture availability, or impacts on plant responses to soil moisture.

There are clear mechanisms by which community Ellenberg F values might be affected by other potential drivers. Nitrogen deposition can affect the drought tolerance of plants, making some species more vulnerable to drought events (Pivovaroff et al., 2016; Zhong et al., 2019). Climatic conditions can alter community responses. For instance, Curreli et al. (2013) demonstrated in UK dune slacks that climate driven hydrological changes may shift wet dune slacks to dry dune slacks, which is likely to have a significant impact plant community

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composition. In coastal sand dune systems, tidal flooding or saline intrusion from sea water and salt spray can lead to increased salinity in dune slacks (Everard et al., 2010), with potential impacts on plant-soil interactions and plant community patterns (Delaune et al., 1987). Soil organic matter can also alter plant responses as thicker organic matter depth may buffer plants from a low water table due to its greater water-holding capacity (Bordoloi et al., 2019; Boyle et al., 1989; Minasny et al., 2015), but in grasslands it has been shown to decrease soil moisture by increasing aggregation and so infiltration (Fischer et al., 2019). An increase in soil organic matter may also increase nitrogen mineralisation (Grootjans et al., 2008; Shahrudin, 2014). This increase in nutrient availability may cause a shift in species competition from nutrients towards light as the limiting resource (Berendse et al., 1998; Lammerts et al., 1999). Disturbances such as grazing in sand dunes, indicated by high bare ground cover and low forb cover (Millett and Edmondson, 2013), may alter Ellenberg F values as early successional species may not reflect the F values seen in more stable communities. Alpha diversity metrics could help to understand the relationship between hydrology and Ellenberg F by explaining species tolerances. For instances, in lower diversity communities, dominant species may have a wider niche (Lou et al., 2018), and therefore be relatively tolerant of water table changes. These biotic and abiotic controls may distort the ability to directly interpret hydrological conditions through the measure of Ellenberg F. The extent and nature of these interactions is poorly understood, therefore limiting our ability to fully interpret Ellenberg F (Silvertown et al., 2006). As such, there is a need to explore which factors can alter the relationship between the Ellenberg F values of a wetland plant community and the hydrological regime it experiences.

In this study, we investigated a range of potential abiotic and biotic controls over the relationship between hydrology and Ellenberg F in coastal wetlands (dune slacks). Dune slacks are low-lying seasonal wetlands found between dune ridges in coastal sand dunes, which are often nutrient-poor. They are formed when bare sand is disconnected from the beach or when wind erodes the sand to the water table or capillary layer (Ranwell, 1960). They are valuable systems for understanding hydrology – plant community interactions because dune slack formation, and therefore their plant and soil development is influenced by the hydrological regime (Curreli et al., 2013; Dwyer et al., 2021). Successional processes are also important in structuring dune slack plant communities, with shifts from bare sand and pioneer species, to the accumulation of organic matter and increase in shrubs and grasses (Grootjans et al., 1991). They are also habitats of high conservation importance (JNCC, 2021). In this study, we explored the following four questions: (1) Is there a relationship between Ellenberg F values (unweighted mean) and hydrology (average water table depth). Is the relationship between Ellenberg F (unweighted mean) and average water table depth altered by (2a) environmental factors (atmospheric deposition, climate, soil characteristics, salinity – mean community unweighted Ellenberg salinity and proxied by distance to the coastline, and fertility – proxied by plant tissue nutrient content), (2b) ground cover type and (2c) alpha diversity of the plant community.

Methods

1.1. Coastal sand dune site selection

Coastal sand dune sites were selected to represent a range of geographic and climatic variability across the United Kingdom (Fig. 1, Appendix A). We included sites with existing hydrological data and, where this was not available, we installed dipwells to monitor water levels. Surveys were undertaken in between 06/2017 – 08/2018.

1.2. Plant community composition, Ellenberg indicator values, ground cover type and alpha diversity

Across the 12 sand dune sites, 41 dune slacks were surveyed, and 164 quadrats were sampled. In each dune slack four quadrats (1 m by 1 m) were located 4 m north, east, south, and west around a central point (the dipwell). Percentage cover data of vascular plants, non-vascular, bare ground and dead matter were recorded. Vascular plants were identified to species level; nomenclature follows Stace (2019).

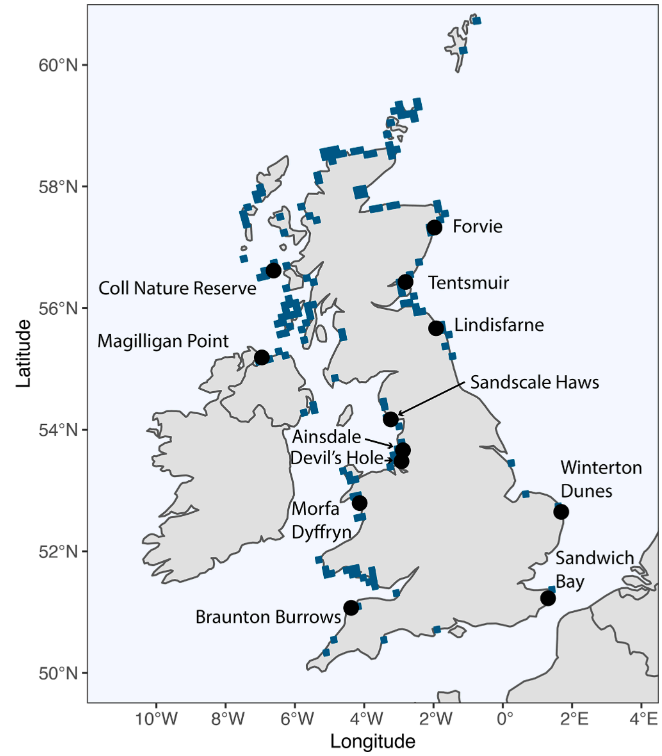

Fig. 1. Locations of the 12 coastal sand dune sites in this study. The blue grids represent the 10 km presence of humid dune slacks (EU Habitats Directive Annex I habitat - H2190). The map image source was downloaded from R package *rworldmap* (South, 2011). The gridded data was downloaded from Eionet Central Data Repository (2020).

Mean unweighted Ellenberg F values (EllF), and mean unweighted Ellenberg salinity (S) values (EllS) were calculated using UK Ellenberg indicator values for vascular plants, taken from the PlantATT database (Hill et al., 2004). Mean unweighted Ellenberg values were chosen as it provides information on the mean F or mean S of the species in the community rather than that of the dominant species in a weighted mean, in addition it avoids the problem of unequal maxima (peaks) of species (Schaffers and Sýkora, 2000). Here we use the term Ellenberg F and Ellenberg S to refer to the general ecological indicator. We use the acronym EllF to refer to the unweighted community mean Ellenberg F, and the acronym EllS to refer to the unweighted community mean Ellenberg S.

To explore whether ground cover type explains differences in EllF, we classified species into woody (W), graminoids (GR), forb (FO) and non-vascular (NV). Species were grouped based on growth form, to reduce complexity in the community and because these different groups of species have shared characteristics. Woody species typically indicate large roots and might be more adapted to drought conditions, forbs typically have a taproot system, whereas graminoids predominantly have a more lateral rooting system, therefore occupying different niches for nutrient competition (Bossuyt et al., 2005; Moor et al., 2017; Rossatto et al., 2014). We also included the category bare ground (BG) which can be used to give a measure of the available space, disturbance or an indication of the age of the dune slack (Sýkora et al., 2004). Dead matter (DM) cover may give a measure of leaf litter which may help to reduce water loss from the soil surface (Li et al., 2014).

To explore whether alpha diversity explains differences in the relationship between EllF and hydrology, species richness was calculated for each quadrat and Shannon diversity, Simpson diversity and Pielou evenness were calculated based on the percentage cover in each quadrat. These were calculated using the package *BiodiversityR* in R (R Core Team, 2020) (Table 1).

1.3. Atmospheric deposition, climate data and salinity

Atmospheric deposition data was downloaded from the Concentration Based Estimated Deposition (CBED) dataset (CBED, 2021). This consists of 5 km average gridded data of oxidised nitrogen (NO_2/NO_3) and reduced nitrogen (NH_3/NH_4), which combined is total nitrogen (TN). This was averaged over a 30-year period (1987–2017) because this is the period shown to be the most important influence on community composition (Payne et al., 2019). Climate data were downloaded from the HadUK-Grid. This consisted of 5 km gridded data of mean, maximum and minimum annual temperature, and mean annual precipitation (Met Office et al., 2020). This was averaged over a 10-year period which has been shown to be correlated with plant community change (Britton et al., 2017). Distance to coastline was used as a proxy for salinity (from salt deposition) (Lammerts et al., 1999), as salt deposition decreases with distance from the coastline. Data was downloaded from an ESRI shape file from OS OpenData Downloads (Ordnance Survey, 2021) This ESRI shapefile included a boundary high water polyline shapefile, which

Table 1
Variables used for linear mixed effects models (LMM). Ranges represent the differences between the quadrats. Asterix denotes variables removed due to colinearity with other variables. Maximum mean annual temperature (MaxAT) and mean annual temperature (MAT), minimum mean annual temperature (MinAT) and MAT, loss on ignition (LOI) and loss of carbonates (LOC), nitrogen content (N) and phosphorous content (P) were the correlated pairs. MaxAT, MinAt, LOC and N removed from analysis as they had the largest mean absolute correlation. Presented are the unscaled variables.

	Code	Range
1. Water table metric		
Average water table depth (4 years) (cm)†	AWTD	−276 – 25
2a. Environmental variables		
Atmospheric deposition		
Total nitrogen ($NO_2/NO_3/NH_3/NH_4$) deposition (keq ha^{-1} yr^{-1}) [or as kg ha^{-1} yr^{-1}]	TN	0.6 – 1.2 [8.4 – 16.8]
Climate		
Mean annual temperature (°C)	MAT	8.5 – 11.3
Maximum mean annual temperature (°C) *	MaxAT	11.9 – 14.8
Minimum mean annual temperature (°C) *	MinAT	5.2 – 8.1
Mean annual precipitation (mm)	Prec	626 – 1631
Soil characteristics		
Soil organic matter depth (cm)	OM depth	0 – 15
Loss on ignition (%) of soil organic matter	LOI	0 – 45
Loss of carbonates (%) of soil organic matter *	LOC	0 – 53
Salinity		
Unweighted mean Ellenberg salinity (S)	EllS	0 – 1.3
Distance to coastline (m)	DisC	30–1100
Vascular leaf sample analysis		
Nitrogen content (%) *	N	1.4 – 2.6
Phosphorus content (%)	P	0.1 – 0.4
Potassium content (%)	K	0.8 – 2.4
2b. Ground cover type		
Woody (%)	W	0 – 125
Graminoid (%)	GR	2 – 99
Forb (%)	FO	0 – 98
Non-vascular (%)	NV	0 – 98
Bare ground (%)	BG	0 – 98
Dead matter (%)	DM	0 – 40
2c. Alpha diversity		
Species richness	RI	3 – 23
Shannon diversity	SHA	0.5 – 2.8
Simpson diversity	SIM	0.2 – 0.9
Pielou evenness	PE	0.3 – 0.9

†AWTD – negative values are below ground surface, positive values above ground surface.

was imported into QGIS (version 3.10.11-A Coruña) (QGIS Development Team, 2021). To calculate distance of the quadrats to the sea, locations of the quadrats were imported using *add text Delimited Text* layer. In the field, the location and elevation of each quadrat was recorded to < 10 mm vertical accuracy using a differential GPS (DGPS) (Trimble R6, Trimble, 2013). In the vector analysis tool, *distance to nearest hub* was used to calculate the distance (in m) of the quadrat to the nearest high-water polyline shapefile.

1.4. Hydrological modelling

Dune slack water table levels were measured from a single dipwell in each slack and recorded using data loggers or a buzzer stick. The frequency (e.g., daily, weekly, or monthly), length of data collection (3–45 years) and gaps in data collection varied for each slack. To overcome these differences in the dune slack hydrological data, daily water table values were modelled using the software Menyanthes for each of the 41 dune slacks (Bartholomeus et al., 2008; KWR, 2020). Menyanthes uses climate data and measured water table depths to model daily groundwater levels. Daily climate data required included mean temperature (°C), precipitation (mm), and potential evapotranspiration (PET) (mm). PET was calculated using the Penman-Monteith formula (Allen et al., 1994), function *ET. PenmanMonteith* in the R package *Evapotranspiration* (Guo et al., 2016). Data required for PET included maximum, minimum and average temperature (°C), relative humidity (%) precipitation (mm), daily sunshine hours (hour) and wind speed (m s^{-1}).

1.5. Quadrat-level hydrological metrics

For statistical analysis, an average 4-year water table depth (AWTD) was calculated to reflect the impacts hydrology has on unweighted mean Ellenberg F (EllF). This was based on modelled daily values over a 4-year hydrological period (01/06/2014 – 30/05/2018). Studies have demonstrated Ellenberg F responses to average water table depth (Curreli et al., 2013; Schaffers and Sýkora, 2000), and a 4-year average is consistent with other dune slack studies (Curreli et al., 2013).

To calculate quadrat-level hydrological metrics, a DGPS was used to record the location and elevation of each dipwell and quadrat (Trimble R6, Trimble, 2013). Based on the differences in elevation between the dipwell and quadrat, a 4-year mean metric was calculated for each quadrat. This metric was based on the modelled data for that dipwell.

1.6. Soil characteristics

For every quadrat, soil samples (5 cm in diameter by 15 cm in depth) were collected. These samples were taken just outside of the quadrat, on the south-west corner. The thickness of the soil organic matter (OM depth) was measured in each sample. Soil organic matter and mineral horizons were separated. These samples were dried at 40 °C, passed through a 2 mm sieve (to remove roots) and weighed. Samples were dried at 105 °C for 16 h to remove moisture. Loss on Ignition (LOI) at 550 °C for two hours in a furnace was used to provide an estimate of organic matter, and the difference between LOI at 550 °C and 950 °C (for four hours) provided an estimate of loss of carbonate content (LOC). Presented here are the results for LOI and LOC for the organic matter horizon.

1.7. Vascular leaf sample analysis

To provide a measure of plant available nutrients at each dune slack, leaf samples were collected to determine the level of plant tissue nitrogen (N), phosphorous (P) and potassium (K) in each dune slack. Leaf samples (with no apparent damage) were collected from common dune slack species. Species sampled included the grass species: *Agrostis stolonifera, Holcus lanatus;* sedges: *Carex arenaria*, *Carex flacca*, *Carex nigra*, *Carex oederi* and *Carex rostrata*; forbs: *Galium palustre*, *Galium verum* and

Hydrocotyle vulgaris; and woody species: *Salix repens.* Leaves were dried in an oven for three days at 60 °C and ground up to a fine powder using a ball mill prior to analysis by an elemental analyser to determine nutrients (N, P, K) (Forest Research, 2021).

1.8. Data analysis

Data analysis was performed using R (v.4.0.3) (R Core Team, 2020). For vascular plants, a total 162 species were analysed. Four quadrats were removed from analysis due to missing soil characteristic data. In total 12 sand dune sites, 41 dune slacks and 160 quadrats were analysed.

We used linear mixed effects models (LMM) to explore (1) the relationship between EllF and AWTD and whether (2a) environmental factors, (2b) ground cover type and (2c) alpha diversity metrics can help to explain the variability in F values in addition to that of the water table (Table 1). LMM were chosen as they account for the nested design (quadrat nested within dune slack, and dune slack nested within sand dune site). All variables were rescaled to standard deviations from the mean using the *scale* function in the *base* package in R (R Core Team, 2020). This enabled us to directly compare effect sizes between predictor variables. For each set of variables, we compared four models: (1) a single level null model, (2) multilevel null model, (3) random intercept model and (4) random slope and intercept model. We used a LMM using the function *lmer* in package *lme4*, with a Gaussian distribution (Bates et al., 2015). A log likelihood ratio test was used to compare the (2) multilevel null model with the (1) single level null model, using the function *logLik* in the package *stats*. This would test the significance of the dune slack nested within sand dune site. A likelihood ratio test was used to compare the (3) random intercept model (intercept of AWTD to vary randomly with dune slack nested with sand dune site) and the (2) multilevel null model to see if the addition of AWTD reduced the amount of variation at sand dune site and dune slack, using the function *anova* in the package *stats* (R Core Team, 2020). A likelihood ratio test (using the function *anova*) was used to compare (3) random intercept model with (2) multilevel null model to see if AWTD differed across sand dune site and dune slack. A likelihood ratio test (using the function *anova*) was used to compare (4) random slope and random intercept model (intercept and slope of AWTD to vary randomly with dune slack nested with sand dune site) with the (3) random intercept model to see if AWTD varied with dune slack nested with sand dune site.

As AWTD varied with dune slack nested within sand dune site, a (4) random slope and random intercept model was selected for all models (1, 2a, 2b and 2c). This is because we are interested in establishing what other factors alter the relationship between AWTD and EllF. To identify the most parsimonious model, backward elimination was carried out on non-significant fixed effects terms using the function *step* (with reduce. random = FALSE), with maximum likelihood estimation (REML = FALSE) in the package *lmerTest* (Kuznetsova et al., 2017). Co-linearity between predictor variables was assessed with a correlation matrix using the function *corr* in the package *boot* (Canty and Ripley, 2020). We visualised the data using the function *corrplot.mixed* from the package *corrplot* (Wei et al., 2017). For pairs of variables with correlation coefficients greater than 0.7, one of the pair of correlated variables was removed which had the largest mean absolute correlation, reducing the environmental variables from 12 to 8 (Table 1: 1−2a). As we were interested in whether (2b) ground cover type could help to predict unweighted mean Ellenberg values and explain the variation in unweighted mean F values, the total percentage cover of each functional group for each quadrat was tested in separate models (Table 1: 2b). As (2c) alpha diversity metrics were correlated, separate models were run for each alpha diversity metric (Table 1: 2c). Model residuals were checked for overdispersion and heteroscedasticity using visual plots. Presented in Tables 2 to 5 is the full model using residual maximum likelihood (REML = TRUE) estimation, which was selected using maximum likelihood (REML = FALSE). Maximum likelihood can provide smaller p-values than residual maximum likelihood. However, residual maximum likelihood are presented as they compute the Satterthwaite degrees-of-freedom correction and give unbiased estimators (Alday, 2021).

To display the interactions effects from the LMMs the R package *interactions* was used (Long, 2019). For interactions between variables in

Table 2
Results of linear mixed effects models (LMM) of average water table depth (AWTD) against unweighted mean Ellenberg F (EllF) (all variables scaled).

	Estimate	Std.Error	df	t value	Pr(>|t|)
Intercept	−0.102	0.176	11.103	−0.581	0.573
AWTD	0.603	0.143	6.244	4.224	0.005

Table 3
Results of linear mixed effects models (LMM) of physical environment variables and the average water table depth (AWTD) against unweighted mean Ellenberg F (EllF) (all variables scaled). Abbreviations. OM depth (organic matter depth), P (phosphorous content), LOI (loss on ignition) and TN (total nitrogen).

	Estimate	Std. Error	df	t value	Pr(>|t|)
Intercept	−0.102	0.155	8.432	−0.658	0.528
AWTD	0.580	0.115	7.111	5.052	0.001
OM depth	0.117	0.052	131.94	2.247	0.026
P	0.131	0.079	22.747	1.666	0.109
LOI	0.117	0.059	85.516	1.988	0.050
TN	0.329	0.154	9.067	2.132	0.062
AWTD × OM depth	0.134	0.051	54.052	2.594	0.012
AWTD × P	−0.486	0.123	39.235	−3.954	<0.001

Table 4
Results of linear mixed effects models (LMM) of functional group bare ground (BG) and the average water table depth (AWTD) against unweighted mean Ellenberg F (EllF) (all variables scaled).

	Estimate	Std.Error	df	t value	Pr(>|t|)
Intercept	−0.065	0.175	11.093	−0.369	0.719
BG	−0.088	0.049	130.842	−1.965	0.052
AWTD	0.630	0.126	6.125	5.012	0.002
BG × AWTD	−0.071	0.035	71.146	−2.061	0.043

Table 5
Results of linear mixed effects models (LMM) of alpha diversity metrics and the average water table depth (AWTD) against unweighted mean Ellenberg F (EllF) (all variables scaled).

	Estimate	Std.Error	df	t value	Pr(>|t|)
(a) Richness (SR) and the average water table depth (AWTD) against unweighted mean Ellenberg F (EllF)					
Intercept	−0.088	0.167	11.003	−0.528	0.608
AWTD	0.545	0.122	6.653	4.456	0.003
SR	−0.159	0.046	138.991	−3.466	<0.001
(b) Shannon diversity (SHAN) and the average water table depth (AWTD) unweighted mean Ellenberg F (EllF)					
Intercept	−0.089	0.165	10.952	−0.540	0.600
AWTD	0.565	0.125	6.255	4.538	0.004
SHAN	−0.167	0.045	144.228	−3.756	<0.001
(c) Simpson diversity (SIM) and the average water table depth (AWTD) unweighted mean Ellenberg F (EllF)					
Intercept	−0.097	0.170	11.109	−0.570	0.580
AWTD	0.583	0.132	5.921	4.415	0.005
SIM	−0.117	0.041	140.941	−2.825	0.005
(d) Pielou evenness (PE) and the average water table depth (AWTD) unweighted mean Ellenberg F (EllF)					
Intercept	−0.098	0.171	11.086	−0.575	0.577
AWTD	0.592	0.133	5.786	4.450	0.005
PE	−0.094	0.042	141.039	−2.252	0.026

the final models which were statistically significant, interaction plots (of the unscaled variables) were plotted for separate LMMs (random slope and random intercept models) using the function *interact_plot*. The +/− 1 standard deviation from the means were plotted using the same function. Fig. 3 summarises interaction effects in the LMMs in Tables 2–5.

2. Results

2.1. Water table depth and unweighted mean Ellenberg F

As AWTD becomes more positive (i.e. wetter, along a gradient of drier slacks to wetter slacks), EllF of plant species in the community increases (from plants generally found in drier conditions to those generally found in wetter conditions) (Fig. 2, Table 2). For all the models where other environmental variables, cover type, and diversity metrics were included, AWTD retained the strongest relationship with EllF.

2.2. Environmental variables

OM depth altered the relationship between AWTD and EllF values. EllF of species in plant communities where the substrate contained a deeper organic matter layer were more sensitive to differences in AWTD (i.e. the relationship had a steeper slope) than those with a shallower organic matter layer (i.e. the relationship had a shallower slope) (Table 3, Fig. 3a). Plant tissue P and N concentrations were positively correlated (Table 1), therefore only the response with P was analysed. EllF of species in plant communities with higher available nutrients (P and N), were far less sensitive to changes in AWTD than those which were more nutrient limited (Table 3, Fig. 3b). Other environmental variables did not alter the AWTD-EllF relationship but did have important overall impacts on EllF. For communities growing in soil which had relatively high LOI the EllF of plants in the community was consistently higher than those with lower LOI (Table 3, Fig. 3c). For communities growing at coastal sand dune sites which received relatively high levels of total atmospheric nitrogen deposition (TN) EllF was consistently higher than those receiving lower levels of historic total atmospheric nitrogen deposition (Table 3, Fig. 3d). LOI and TN were marginal in their significance. MaxAT, MinAt, LOC and N removed from the model prior to analysis due to co-linearity (Table 1). The main effects of K and Prec and their impact on the AWTD-Ell F relationship were not statistically significant, therefore was not included in the final model. DisC and EllS had no impact on EllF, therefore was not included in the final model.

2.3. Ground cover type

The only ground cover type with any impact on EllF was the percentage cover of bare ground. For communities with a larger amount of bare ground EllF was less responsive to changes in AWTD than for communities where there was less bare ground. The result of this is that where the water table was furthest below the ground surface, communities with more BG had a higher EllF than those with less, but when water table levels increased, this difference disappeared (Table 4, Fig. 3e).

2.4. Alpha diversity

Species richness, Shannon diversity, Simpson diversity and Pielou evenness did not alter the AWTD-EllF relationship but did have important overall impacts on EllF. For communities that had a higher species richness, EllF was consistently lower (plants indicating drier conditions) than those communities that had lower species richness (plants indicating wetter conditions) for a given water table depth (Table 5a, Fig. 3f). For communities that had a higher Shannon diversity, EllF was consistently lower (drier conditions) than those communities that had lower Shannon diversity (wetter conditions) (Table 5b, Fig. 3f). For communities that had a higher Simpson diversity, EllF was consistently lower (drier conditions) than those communities that had lower Simpson diversity (wetter conditions) (Table 5c, Fig. 3f). For communities that had a higher Pielou evenness (more even communities), EllF was consistently lower (drier conditions) than those communities that had lower Pielou evenness (less even communities and wetter conditions) (Table 5d, Fig. 3f).

3. Discussion

Our research demonstrates that while there is a strong relationship between the widely used ecological indicator Ellenberg F (unweighted

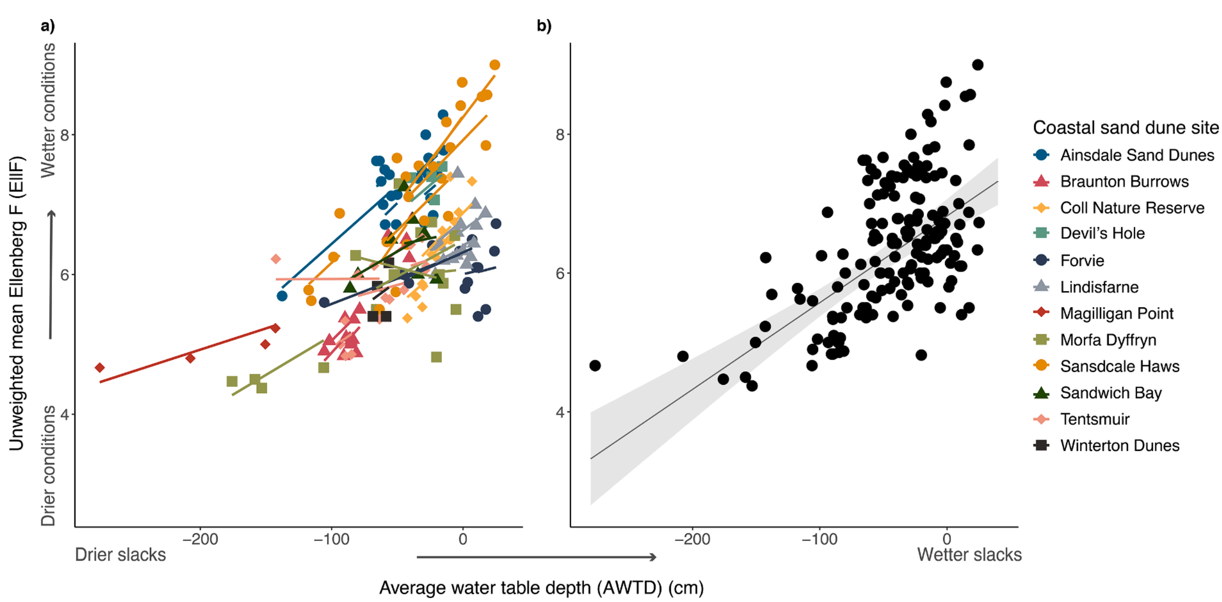

Fig. 2. The relationship between average water table depth (AWTD) (cm) and the unweighted mean Ellenberg F (EllF) of plant species in the community. Presented are EllF and AWTD for 1 × 1 m quadrats within dune slacks. Points which are the same colour are dune slacks located within the same coastal sand dune site. a) Each line represents the modelled relationship between AWTD and EllF for quadrats within an individual dune slack. b) the single grey line and grey confidence intervals represents the linear relationship (and 95% CI) between AWTD and EllF across all the dune slacks.

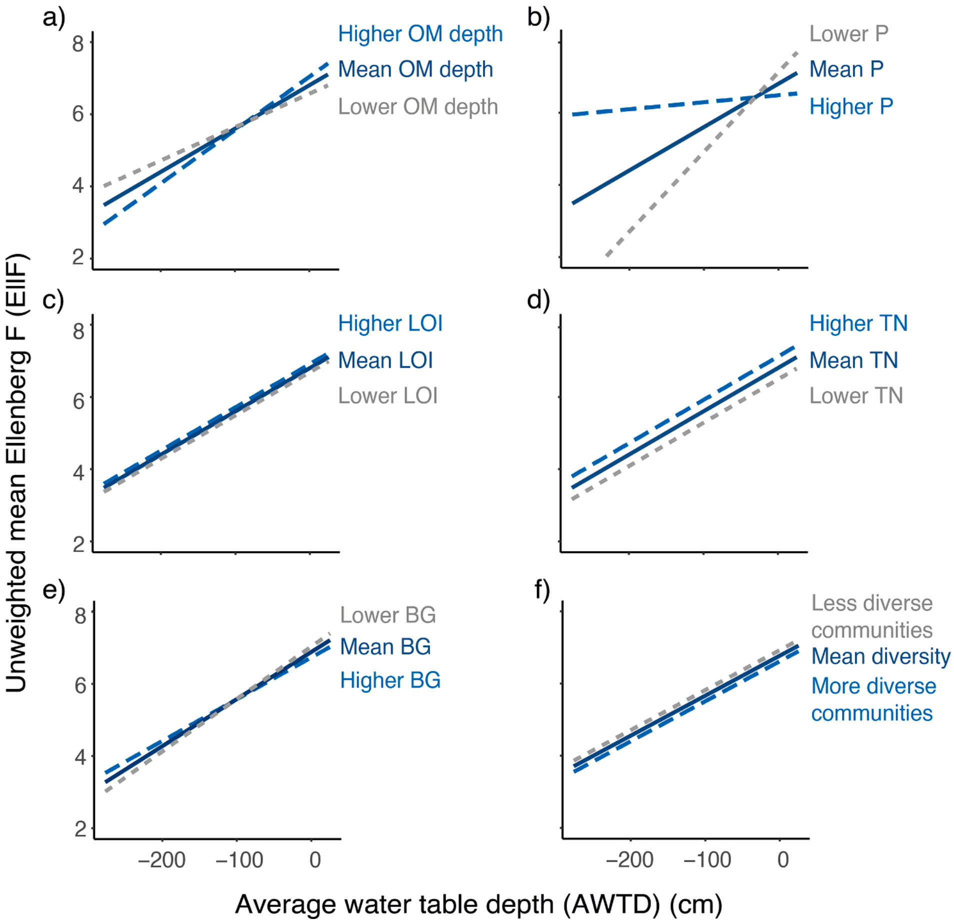

Fig. 3. Predictions of (4) random slope and random intercept linear mixed effects models (LMM). Presented are unscaled outputs for visualisation of the how the relationship between unweighted mean Ellenberg F (EllF) and average water table depth (AWTD) is altered with (a) organic matter depth (OM depth) and (b) phosphorus content (P) and (e) bare ground cover (BG). The AWTD-EllF relationship was not altered by (c) loss on ignition (LOI), (d) total atmospheric nitrogen deposition (TN), and (f) alpha diversity of plant communities, but did impact overall EllF. Calculation of the upper (light blue – – –) and lower lines (grey - - -) are based on ± 1 standard deviation of the input variable from the mean (dark blue ——).

mean) (EllF) and average water table depth (AWTD), this relationship is modified by other biotic and abiotic factors. This illustrates that interpreting unweighted mean Ellenberg F as an indicator of the hydrological conditions experienced by plants needs to account for other factors which might have important ecological impacts. EllF was more sensitive to changes in AWTD for communities that were more nutrient limited and where the soil had a deeper OM depth layer and less bare ground. EllF was consistently lower, for a given AWTD, for communities that are more diverse, in sand dune sites with lower TN and where the soil had a lower LOI. These responses might be due to these factors altering species tolerance of waterlogging or drought, alternatively they themselves might modify soil water status. These findings have important implications for the conservation of the dune slacks as local factors need to be considered if management strategies are based on unweighted mean Ellenberg F values.

Measured parameters such as average annual groundwater level (Curreli et al., 2013; Schaffers and Sýkora, 2000), mean spring groundwater (Ertsen et al., 1998; Runhaar et al., 1997; Wamelink et al., 2002), average highest and lowest groundwater (Schaffers and Sýkora, 2000) have been shown to be correlated with Ellenberg F. Diekmann (2003) showed the importance of using Ellenberg F to determine the wetness of a habitat and assess local conditions. In dune slacks, dipwells are often used to monitor the depth to the water table, providing information on seasonal and inter-annual changes (Jones et al., 2017). However, the installation and monitoring of dipwells is costly. Our results show that there is a strong relationship with EllF and AWTD, therefore EllF may be a suitable indicator for hydrology in dune slacks, but with caveats.

Soil organic matter depth, bare ground cover and plant nutrient status - phosphorus (and nitrogen content as they were positively correlated – see Table 1) altered the relationship between EllF and AWTD. Soil organic matter improves water-holding capacity of the soil (Bordoloi et al., 2019; Minasny et al., 2015). Ertsen et al. (1998) demonstrated that unweighted mean Ellenberg F was related to water table depth, but that this relationship differed with soil type (sandy, clayey, and peaty soil). Supporting the findings of Ertsen et al., (1998), we found that wet slacks with thicker OM had higher F values. However, by contrast we found that EllF values were lower (plants adapted to drier conditions) in quadrats with thicker OM depth in drier slacks, which was not expected. One reason for this might be the impact of OM on soil aggregation. An experimental study by Fischer et al. (2019) in grasslands found that more soil OM resulted in greater soil aggregation, causing faster drainage and therefore drier soils. Alternatively, the interaction may indicate the relationship is related to successional development stage (OM accumulates over time). For older slacks there is more likelihood of patterns from initial colonisation having weakened and distributions more closely reflect species' preferences along hydrological gradients (Bartelheimer and Poschlod, 2016). This possible explanation is supported by the patterns observed with bare ground cover. We found that plant communities with higher BG (younger dune slacks) have lower EllF than those with less BG when the water table is close to the surface, with the opposite true when the water table is far below the surface (Berendse et al., 1998; Lammerts et al., 1999). This suggests that at mature sand dune sites (low BG, high OM) there is greater potential for niche differentiation to have occurred whilst patterns on more disturbed sand dune sites (high BG, low OM) may reflect arrival times more (Bossuyt et al., 2005; Bossuyt et al., 2003). Bare ground can also indicate if the slack has recently been disturbed such as grazing, which may affect the EllF value (Millett and Edmondson, 2015; Millett and Edmondson, 2013; Plassmann et al., 2010).

Our results demonstrate that plant communities in nutrient-poor conditions (low P and N) have a lower EllF value than plant communities in nutrient-rich conditions, for a given water table depth. This is difficult to interpret, but one possible reason for this may be that the nutrient-poor communities are more sensitive to changes in AWTD, as they contain more specialised species (Grootjans et al., 2008). For instance, many dune slack species are smaller, have a lower nutrient demand and may develop tussocks, which are efficient in recycling nutrients (Ernst and Van Der Ham, 1988; Grootjans et al., 2008). Additionally, nutrient-poor conditions have plant communities that are typically stress tolerant (Grime, 1977). Adaptation to nutrient-poor conditions include higher rooting depth and higher percentage of roots, adaptations that are also beneficial in drought tolerant conditions (Moor et al., 2017). As average water table depth represents water table depth over time, it may be the case that nutrient-poor plant assemblages have been able to tolerate drier conditions that may occur during the hydrological regime for any given water table depth. Another explanation for our finding could be due to the selection of plant samples for nutrient analysis. Different species can have different nutrient concentrations in their leaves (Bombonato et al., 2010; Shtangeeva et al., 2017). Therefore, the results may reflect differences in species selection across slacks.

We also showed that LOI and TN was marginally significant, and alpha diversity was significant in altering the intercept of the relationship between AWTD and EllF. LOI affected EllF consistently regardless of AWTD. LOI is used to estimate organic matter, therefore the increase in LOI may indicate higher water holding capacity, hence changes in the intercept but not the slope of the relationship (Bordoloi et al., 2019). Nitrogen deposition may have a direct physiological effect on plants. It can cause a shift towards nutrient demanding species, by outcompeting the species that are adapted to stress-tolerance and low nutrients (Ceulemans et al., 2017; Hautier et al., 2009; Stevens et al., 2018). It can alter the drought tolerance of species (Pivovaroff et al., 2016; Zhong et al., 2019), as well as seed bank dynamics (Plassmann et al., 2008). Alternatively, it may be that there is a correlation between EllF and total atmospheric nitrogen deposition where a change in one driver may result in changes in indicator values for another (Pakeman et al., 2008). Our results do not suggest there is an interaction, only a change in intercept suggests EllF is affected by total atmospheric nitrogen deposition levels. Alpha diversity affected EllF consistently regardless of AWTD. Overall, for a given AWTD, the more diverse and more evenly distributed communities had a lower EllF value (drier conditions) than less diverse/less evenly distributed (wetter conditions). One explanation for this, is that the species which dominate less diverse and more even communities may have a wider niche (Lou et al., 2018). Therefore, these species may be more tolerant of changes in water table depth. Whereas more diverse communities, which may contain more species that are highly specialised (Markham, 2014; Martorell et al., 2015; Thuiller, 2004) and this specialisation may be linked to drought tolerance.

We detected no significant effect of climate on the relationship between EllF and AWTD. It may be that climate only drives changes in the water table, but does not differentiate plant responses to the hydrology, or that other factors are masking the effects. Pakeman et al.'s (2015) long term Scottish re-survey concluded that coastal plant communities appear resistant to climate change, perhaps because geographic isolation limits species dispersal. Another reason may be that along the climatic gradient there is species turnover, with the species replaced are of the same Ellenberg F values hence why no trend was detected. We detected no effect of salinity (EllS and DisC) as a potential modifier of EllF responses, which suggests there is no saline groundwater influence and no substantial effect of salt-spray induced salinity in the communities we studied. This supports general findings of UK dune slacks that salinity does not appear to exert a major influence on the vegetation communities of secondary dune slacks (Ranwell, 1959; Willis et al., 1959). Ranwell, (1959) demonstrated in a sand dune system in Wales that there was no tidal influence of groundwater. In addition, our EllS for quadrats ranged from 0 to 1.3 indicating that the plant communities experience only slight influences of salt, most likely from salt spray. We also found that cover type (apart from bare ground) had no effect on the relationship between EllF and AWTD. Using cover type helps to summarise complex information. However there is a trade-off between using simple cover types and fine-scale information such as plant traits (Douma et al., 2012; Duckworth et al., 2000; Moor et al., 2017).

We used unweighted mean Ellenberg F values. An alternative is to use weighted mean values. Weighted mean Ellenberg F values (based on percentage cover) take into account dominance (Smart and Scott, 2004). As a result, if conditions change rapidly, they may show a clearer response to fluctuations in water table depths. However, weighted mean value assume that species will have a unimodal response to changes and that species occurrences are closer to their optimum response (Schaffers and Sýkora, 2000). Biased results may arise if there are differences in the occurrence of an indicator value in the regional species pool. Nevertheless, we found that AWTD predicts unweighted mean Ellenberg F (EllF) well.

4. Conclusion

This study demonstrates that the response of the commonly used ecological indicator of soil hydrological status – unweighted mean Ellenberg F – to average water table depth shows some dependency on other biotic and abiotic factors. We showed that water table depth had the strongest influence on unweighted mean Ellenberg F. However, unweighted mean Ellenberg F was more sensitive to changes in water table levels when plant communities were nutrient limited, had a thicker organic matter layer and less bare ground cover. We also demonstrated that for a given water table depth, unweighted mean Ellenberg F was consistently lower, when total atmospheric nitrogen deposition is lower, loss of ignition (estimate of organic matter) is lower and plant communities were more diverse. This research has important implications for the conservation of these dune systems as these findings demonstrate that Ellenberg F is strong ecological indicator of soil hydrology, but that it should be used critically in practice as a range of factors modify the relationship between Ellenberg F and hydrological regime.

CRediT authorship contribution statement

Ciara Dwyer: Conceptualization, Formal analysis, Visualization, Writing – original draft. **Jonathan Millett:** Conceptualization, Formal analysis, Visualization, Supervision, Writing – review & editing. **Robin J. Pakeman:** Conceptualization, Formal analysis, Visualization, Supervision, Writing – review & editing. **Laurence Jones:** Conceptualization, Formal analysis, Visualization, Supervision, Writing – review & editing.

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

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