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Relations between vegetation and water level in groundwater dependent terrestrial ecosystems (GWDTEs)

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ABSTRACT

Alkaline wetlands and fens are groundwater dependent, terrestrial ecosystems (GWDTEs) existing throughout the temperate zone. They contain a large number of protected and endangered plant species and their ecological status is threatened by insufficient groundwater quality and quantity. However, management and conservation of fens are constrained by limited knowledge on the relations between vegetation and measurable hydrological conditions. This study investigates the relations between vegetation and water level dynamics in groundwater dependent wetlands in Denmark.

A total of 35 wetland sites across Denmark were included in the study. The sites represent a continuum of wetlands with respect to vegetation and hydrological conditions. Water level was measured continuously using pressure transducers at each site. Metrics expressing different hydrological characteristics, such as mean water level and low and high water level periods, were calculated based on the water level time series. A complete plant species list was recorded in plots covering 78.5 m^2 at each site. Community metrics such as total number of species and the number of bryophytes were generated from the species lists and Ellenberg Indicator scores of moisture, pH and nutrients were calculated for each site.

The water level correlates with the number of typical fen species of vascular plants, whereas bryophytes are closer connected to the stable water level conditions provided by groundwater seepage. The water level variability is proved to be a significant limiting factor for species diversity in wetlands, which should be considered along with the fertility in order to access the habitat quality. The study provides new insight in the water level preferences for GWDTEs which is highly needed in the management and assessment of anthropogenic damage to these ecosystems.

KEYWORDS

Alkaline wetlands, hydrology, vegetation, Ellenberg indicator values

1 Introduction

Groundwater dependent, terrestrial ecosystems (GWDTEs) include a range of wetland types including fens, alkaline springs, dune slacks, wet meadows and in some situations also bogs and transition mires, which are of conservation concern in the temperate zone worldwide due to a high species diversity and presence of many endangered species (Van Diggelen et al. 2006, Wassen et al 2005). In heavily populated regions human uses of the groundwater resource is considered as a major threat to these sensitive plant communities (Van Diggelen et al. 2006). In Europe, the Water Framework Directive (WFD) prescribes that GWDTEs are identified, mapped and taken into consideration in the assessment of the availability and quality of groundwater. In practice, however, addressing the policies regarding conservation and GWDTEs remains problematic due to the lack of operational criteria for assessment of wetland status and thresholds above which damage is expected (Whiteman et al. 2010). Therefore, quantitative relations are needed between the hydrology and the ecological status of GWDTEs.

Plant communities of GWDTEs are especially vulnerable to hydrological changes; however, their dependency on groundwater seepage is only partially understood. A constant alkaline groundwater supply keeps sediments and pore water highly buffered and prevents acidification (Boomer and Bedford 2008b) and reduces the availability of phosphorus (Wassen et al. 2015). Furthermore, the groundwater inflow sustains a water level close to the land surface most of the year and waterlogged conditions prevent aeration of organic matter and, hence, limit acidification and nutrient mineralization (Almendinger and Leete 1998, Verhoeven et al. 1996). The limited nutrient and oxygen availability in the root zone prevents more competitive species from invading the habitat thereby reducing compositional change and maintaining a high species diversity (Kotowski et al. 2006). When the topsoil is unsaturated, periodic filling of soil pores with rainwater may occur (Schot et al. 2004) and this further increases the risk of acidification and increased nutrient mineralisation (Grootjans et al. 1988). Infiltration of nutrient rich surface water e.g. following a flooding event may also result in increased nutrient availability (Beumer et al 2007, Banach et al. 2009, Cusell et al. 2015).

The water table dynamics greatly influence redox conditions which again control internal binding and release of phosphorus, which is considered the limiting nutrient in wetland ecosystems (Lucassen et al. 2005). The position of the water table is only indirectly connected to these controlling chemical processes, and it does not take into account the variability in capillary rise which is often pronounced in GWDTE soils. Schaffers and Sýkora (2000) showed that there is a stronger correlation between soil water content and vegetation than between water table depth and vegetation for a wide range of plant communities from dry to wet soils. However, under very wet conditions, as in GWDTEs, it is here argued that the water level is a better and more robust measure because it is easy to measure, highly comparable and representative for the area surrounding the measurement point.

Previous studies have revealed significant correlation between mean water table and the relative number of hydrophytes in dune areas, heathlands, bogs and fens in the Netherlands (Runhaar et al. 1997). Wheeler (1999) emphasizes the difficulties of finding clear patterns between species composition and water table gradients across sites due to the large spatial and temporal variability of the water table dynamics. There are studies showing significant correlations between vegetation and mean water table metrics, while other studies indicate that extreme events or the frequency and duration of water level fluctuations significantly influence the vegetation composition (Wheeler

1999). However, species typical of GWDTEs are known to be highly sensitive to increased nutrient availability (e.g. Bedford et al. 1999, Bergamini and Pauli 2001) and thus, considering the trophic status along with water table measures is necessary for a reliable assessment of status of these habitats (Andersen et al. 2013). In this study, continuous water level registrations between 2004 and 2010 are analysed to identify measures that correlate with the vegetation in 35 Danish GDWTEs. A high temporal resolution of water level data in the study makes it possible to derive statistical measures and test the correlation with vegetation composition. The objectives of the study can be summarised as follows:

- To investigate relations between water level metrics and characteristic vegetation in alkaline GWDTEs
- To establish quantitative models linking water level metrics to vegetation metrics which can be operationally useful in the management of alkaline GWDTE sites.

2 Materials and methods

Data from 35 GWDTEs located across the northern and eastern part of Denmark was analysed (Fig. 1). Of the 35 sites, 29 are classified as *alkaline fens* within the NATURA 2000 network. A categorisation of the remaining six sites was conducted by vegetation based classification according to the Habitats Directive (Ejrnæs et al. 2004; Nygaard et al. 2099). Three sites were thereby categorised as *alkaline fens,* one as *calcareous fens with Cladium mariscus and species of the caricion davallianae* and two as *molinia meadows on calcareous, peaty or clayey- silt-laden soils*. The occurrence of alkaline GWDTEs in the western part of Denmark is very limited due to flat terrain, sandy soils, and absence of alkaline groundwater aquifers. Therefore, the spatial occurrence of alkaline GWDTEs in Denmark is represented by the selected sites.

2.1 Water level

Water level data was collected using pressure transducers for continuous registration. Some systems automatically compensate for barometric pressure, while others use a reference atmosphere recording. The original water level series were sampled with varying density between 30 min and 24 h, and there were a few minor gaps in the data. All data was therefore averaged to continuous time series of daily mean values. The time series were trimmed so that only whole years were used and annual measures could be calculated correctly. Most data was collected as a part of the Danish monitoring programme supplemented with four additional stations from other projects (Ejrnæs et al. 2010, Johansen et al. 2011).

Water level time series were analysed from each of the 35 sites in order to link water level metrics and vegetation composition. The general approach used in ecology is to relate the water table to the ground surface level. In some wetland habitats, the ground surface is, however, not easily defined due to the micro-topographic variability. In order to obtain a base level for the water level we used the stable winter water level as the base level. A stable water level near the terrain surface was typically observed from November to April (Fig. 2). We calculated this base level as the 90 % quantile of the water level time series and denoted H_{90}. For sites where the soil surface was homogeneous and precise ground levels were obtained, the differences between H_{90} and the actual ground level were found to be within a few centimetres. This approach is only applicable at sites where the water table is close to or equal to the terrain surface during winter periods and without long term inundation from a nearby stream or lake.

The overall minimum water level, H_{min}, was calculated as the minimum of all observed values, which reflects the water level during the driest period recorded at the site. Different ways of representing the water level variability is tested by the metrics H_{mean}, H_{20}, H_{IQR} (definitions are given in Table 1). The Dry_{dur} is the share of time where the water table is more than 50 cm below the base level (H_{90}). Previous vegetation studies primarily deal with spring or summer water levels. Therefore, we calculated the mean water level in the periods April-June ($H_{\text{mean Apr.-Jun.}}$) and July-August ($H_{\text{mean Jul.-Aug.}}$). To evaluate the effect of a rapidly changing water table, the mean water level variance over periods of three days throughout July and August (Var_3) was calculated. Table 1 summarises all water level metrics.

2.2 Vegetation

The vegetation data constitutes complete species lists recorded in one 78.5 m^2 plot (circle with radius = 5 m) on each of the 35 sites. On 19 sites, the vegetation plots were centred on the corresponding water level well, while on the remaining sites we used similar vegetation registrations from the Danish monitoring programme from the plot closest to the well; the distance ranging from 2-60 metres.

The typical species used for evaluation of conservation status were masked from a list published by Ejrnæs et al. (2009). The list contains potential typical species of alkaline wetlands, fens and springs, which are referred to in the Habitats Directive (European Commission 1992) and the corresponding CORINE biotopes (European Commission 1991). The list was further supplemented with species from Nordic habitats (Påhlsson 1994) referred to in the Interpretation manual (European Commission 2007). Species, which do not predominantly occur in alkaline fens or springs were excluded from the list (See appendix A, Table A.1 for the total species list). We added the list of species used in this study because it makes it possible to compare with future studies.

For each site, the vegetation data were used to calculate average Ellenberg Indicator values. The Ellenberg indicator system is an expert system that is partly based on measured data, but mainly on expert knowledge and experience of the optimal environmental conditions for single plant species (Ellenberg et al. 1991, Wamelink et al. 2002). Ellenberg values were averaged over all species present in a plot and were used as surrogate for measured environmental conditions (Diekmann 2003). The Ellenberg indicator system has a score for nitrogen (*EN*) in the range of 1-9, which describes the nutrient availability and potential productivity. An *EN* value of 1 indicates extremely infertile sites and a score of 9 indicates extremely nutrient-rich conditions. The Ellenberg R value (*ER*) indicates soil reaction and ranges from 1 to 9 where 1 is extreme acidity and 9 indicates basic reaction only found on high pH soils. Ellenberg F (*EF*) is the moisture indicator between 1 and 12 where 1 is an indicator of extremely dry sites and 12 represent permanently submerged plants. Throughout the study, we used Ellenberg indicator values calibrated to the British flora (Hill et al. 1999). Danish studies have shown that the ratio between the parameters EN and ER, also referred to as the “nutrient ratio”, correlates particularly well with the number of typical species in Danish, alkaline fens and springs (Andersen et al. 2013).

Table 2 shows the vegetation parameters used in the study. The number of typical species (*T*) is used as a measure of habitat conservation status (Andersen et al. 2013). However, a large scatter in the link between typical species and the water level was expected. Therefore, it was examined whether or not correlations would improve by excluding typical species with $EF<8$ in the metric T_{wet}. Bryophytes are more directly dependent on a shallow water table than vascular plants, due to the lack of vascular tissue for the transport of water from greater depths. The total number of bryophytes (*B*), the typical bryophytes (*TB*) and the relative number of bryophytes (B_{rel}) were also used as metrics to characterise the bryophyte community. The highest observed number of typical bryophytes in the study was only 7, which is problematic when trying to obtain highly significant correlations. The total number of species (S_{tot}) and the relative number of hydrophytes (H_{rel}), based on *EF* scores, provide alternative metrics based on all observed species. Finally, the mean Ellenberg indicator values *EN, ER, EF* and the ratios $EN\ ER^{-1}$ and $EN\ EF^{-1}$ were included as metrics in the analyses.

2.3 Relations between water level and vegetation

Spearman rank correlation coefficients (*Rho*) were calculated between all combinations of hydrological metrics (Table 1) and the vegetation metrics (Table 2) along with the probability of the two parameters being uncorrelated (P_{val}).

Plotting vegetation metrics against the four water level metrics (H_{min}, H_{IQR}, H_{mean} and Dry_{dur}), quantile regression analysis was used to test the consistency of tendencies by subdividing the x-axis into seven categories and finding the highest scoring sites within each of these subdivisions. Fitting a line through the seven highest scoring points, the intersection with the x-axis represents the point where vegetation scores are zero due to limitation by hydrological conditions, whereas the intersection with the y-axis represents the point where water level is not a limiting factor.

Further, multivariate Poisson regression techniques were applied to model the species diversity as a function of water level metrics and additional explanatory variables. The purpose was to explain some of the expected residual variation in the regressions. The Poisson distribution was assumed to be valid, since the response variable (number of species) is a small but non-negative integer value. The statistics toolbox in MATLAB was used to conduct the analysis. The Poisson regression model expresses the log outcome as a linear function of a set of predictors:

$$\log(\mu) = \eta = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k \qquad (1)$$

where μ is the mean of the response variable and η is the linear combination of the coefficients β_i and the independent variables x_i so that

$$\mu = \exp(\eta) \qquad (2)$$

In order to analyse the residuals of the initial regression models two additional Poisson regression models linking Ellenberg indicators and hydrological metrics were established. Model 1 predicts the number of typical species, and model 2 predicts the number of bryophytes. Both models are based on the mean water level in July-August ($H_{mean\ Jul.\text{-}Aug.}$) and nutrient ratio ($EN\ ER^{-1}$) as explanatory variables. In combination with the nutrient ratio, $H_{mean\ Jul.\text{-}Aug.}$ is the hydrological metric provided the best prediction.

This yields following expressions for the applied models based on equations (1) and (2):

$$Model\ 1: T_{pred} = \exp\left(b_0 + b_1\left(\frac{EN}{ER}\right) + b_2\left(H_{mean\ Jul.-Aug.}\right)\right) \qquad (3)$$

$$Model\ 2: B_{pred} = \exp\left(c_0 + c_1\left(\frac{EN}{ER}\right) + c_2\left(H_{mean\ Jul.-Aug.}\right)\right) \tag{4}$$

T_{pred} and B_{pred} are the predicted number of typical species and bryophytes respectively. The coefficients $\bar{b}$ and $\bar{c}$ are determined by linear regression.

3 Results

3.1 Water level and vegetation dataset

Within the 35 sites, registration of water level started in 2004 while the main part of the dataset only covers the period 2007 to 2009. The average length of the water level time series is 3.5 years, but only five months are overlapping (30 June 2008 to 4 Dec 2008) between all stations. The eastern and western parts of the country are equally well-represented by the data for all years.

3.2 Relations between water level and vegetation metrics

The correlation between the total number of typical species, *T*, and the hydrological measures was significant on a 5 % level for 6 of 8 water level metrics. The highest direct correlation with typical species was obtained for H_{IQR} (*Rho* = -0.38*) while correlations with the short term variability (Var_3) and spring mean ($H_{mean\ Apr.-Jun.}$) were insignificant. As expected, the number of bryophytes were closer related to the hydrology than vascular plants with highly significant ($p<0.01$) correlations with all water level metrics. Also for bryophytes, H_{IQR} showed the highest correlation (*Rho* = -0.54**). The number of typical species and bryophytes decrease with increasing annual amplitude in water level.

The Ellenberg moisture indicator (*EF*) correlates significantly with all water level metrics, however, *EF* is by far closest related to the short term variability expressed by Var_3 (*Rho* = -0.68***). The highest correlation between a water level metric and a vegetation metric was obtained between the inner quartile range of the water level H_{IQR} and the relative number of bryophytes B_{rel} (*Rho* = -0.69***). The relative number of bryophytes was, furthermore, very closely related to the ratio between the Ellenberg nutrient and moisture indicators $EN\ EF^{-1}$ (*Rho* = -0.79***). All spearman rank correlation coefficients and P-values between quantitative metrics (Table 1 and Table 2) are listed in appendix B, Table B.1.

At high and stable water levels the observed habitat quality expressed as the number of typical species ranges from poor to high (left on all graphs, Fig. 3), while at the dry sites (right on all graphs, Fig. 3), the number of typical species is always low indicating that water level is a limiting factor. For all four vegetation metrics such limitation occurs when the minimum water level (H_{min}) is around 1.5 m. A good agreement on this point was found between different vegetation metrics. Across different water level metrics the location of the intersection with the y-axis did not change much either. So despite a large scatter in the relations between vegetation and water level there seems to be a clear upper limit to all vegetation metrics which is constrained by water level conditions.

A considerable scatter in the water level vegetation relations was found (Fig. 4). The *nutrient ratio* ($EN\ ER^{-1}$) has been shown to correlate well with the number of typical species and, hence, this nutrient indicator may explain some of the residual variation in the regressions of typical species and bryophytes against hydrological metrics. Based on the models in Fig. 5, we found bryophytes to be more dependent on a high and stable water table than the typical species collectively. The explanatory value of the mean water level was highly significant in model 1 ($p<0.01$) and very highly significant in model 2 ($p<0.001$). In both cases, the nutrient ratio explained a larger share of the variance than the water level (Table 3 and Table 4). The results of applying multivariate regression to predict the number of typical species (model 1) and bryophytes (model 2) are shown in Fig 5.

4 Summary and discussion

The study comprised 35 alkaline GWDTEs located throughout Denmark, thus comprising a representative sample of Danish GWDTEs with respect to hydrology and vegetation composition. We found significant relationships between the number of typical fen species and 6 out of 8 hydrology metrics and highly significant relationships between water level metrics and the number of bryophyte species, while bryophyte species richness decreases with increasing annual water level amplitude. The established models confirmed that bryophytes are more dependent on a high and stable water level than vascular plants.

The proposed models (3) and (4) indicate a change in the number of typical species by a factor 2 and a change in the number of bryophytes by a factor 3 corresponding to the observed range of water level. This applies to sites where the presence of species and hence diversity is primarily limited by water level conditions. Comparable results have been reported elsewhere (Duval et al. 2012) and Ilomets et al. (2010) conclude that the number and cover of fen species decreases sharply when the seasonal water level fluctuations exceed 25 cm within the Paraspõllu calcareous-rich fen in northern Estonia. Our proposed models can be used as tools for evaluating the conservation status and determining the limiting factor for species diversity in Danish GWDTEs. The models can also predict the expected changes in species diversity due to changes in water level conditions. Care must be taken when interpreting the results. The underlying assumption is that water level and nutrient availability are independent parameters. For small seasonal changes in water level, the assumption can be valid, but for large water level fluctuations the nutrient availability is likely to change significantly as a consequence of internal eutrophication (Almendinger and Leete 1998, Verhoeven et al. 1996) and changing redox conditions (Boomer and Bedford 2008a, Boomer and Bedford 2008b) at least until a new equilibrium state has been established.

The strongest correlation (*Rho* = 0.68) for the Ellenberg moisture indicator *EF,* was found with the short term water level variability in the summer period (Var_3). The short term variability is highly dependent on soil texture, where permeable clayey soils show a higher amplitude of water level fluctuations during summer periods compared to that of highly permeable sandy soils. Ertsen et al. (1998) have shown that non-linear relationships between *EF* and water level apply best to clayey soils while linear relationships provide the best fit for peaty and sandy soils. However, the individual soil classes did not improve the amount of variance explained in their models. Our results indicate that the *EF* score is related closer to the short term water level dynamics and soil texture than to the mean annual or mean seasonal water level metrics. The number of typical species and the number of bryophytes are, on the other hand, not closely related to this short term variability, but rather to the annual or seasonal dynamics. An additional explanation to the poor correlation between typical species and *EF* is that species preferring wet conditions occur along the entire gradient of nutrient status. Species typical of alkaline fens and springs may share a general preference of wet conditions. However, the range in nutrient availability is limited to the low end of the nutrient gradient. These results are in agreement with the results of Andersen et al. (2013), where a similar weak correlation between typical fen species and EF was found.

Wet conditions clearly result in a larger share of bryophyte species compared to vascular plant species as indicated by the highly significant relationships between the water level measures and the relative number of bryophytes B_{rel}. The relative number of bryophytes is closely related to Ellenberg N, and in particular the ratio between Ellenberg N and Ellenberg F. In other words, the number of bryophytes becomes prominent when the conditions are wet and nutrient poor. This is in agreement with the results of Mälson and Rydin (2007), who found that bryophytes disappeared from alkaline fen areas shortly after drainage, and several studies have shown inhibition or competitive disadvantage with increased nutrient availability (Bergamini and Pauli 2001, Kooijman 2012, Andersen et al. 2016) or even toxic effects of especially ammonium on fen bryophytes (Paulissen et al. 2004, Verhoeven et al. 2011).

A strong, positive correlation between *EN* (nutrient score) and *ER* (pH score) was demonstrated for the sites in this study. This acidity-alkalinity gradient from bogs to rich fens is often interpreted as a nutrient availability gradient with associated changes in species richness and productivity caused by changes in nutrient availability (Bedford et al. 1999). The fen species typically depend on low values of *EN* and high values of *ER*. Both *EN* and *ER* correlate positively with the magnitude of seasonal water table fluctuations. The positive correlation between *EN* and low water table can be caused by oxygen penetrating the soil, followed by an internal release of nutrients due to soil mineralisation or by an input of groundwater low on cations thereby reducing immobilisation of phosphorus (Boomer and Bedford 2008a, Niedermeier and Robinson 2009). On the other hand phosphorus is more effectively bound to iron when periodic aeration of the peat occurs (Lucassen et al. 2005, Smolders et al. 2006). There is no commonly accepted explanation to the positive correlation between *ER* and water table fluctuations. It is, however, well known that a number of processes such as sulphur oxidation and nitrification decrease alkalinity when oxygen is available while sulphate reduction and denitrification increase alkalinity when no oxygen is available (McLaughlin and Webster 2010). However, as the water table fluctuations increase so does the oxygen availability which should then lead to acidification (Van Haesebroeck et al. 1997). A possible explanation to this could be that evaporative effects increase the concentration of minerals. Large seasonal fluctuations in the water table are due to the evapotranspiration being larger than the groundwater inflow during dry spring and summer periods. Excessive rainfall during fall and winter brings the water level close to the terrain surface again. This in terms leads to increased concentrations of dissolved minerals including Ca-ions and thereby increases in alkalinity. So, groundwater inflow provides the minerals that prevent acidification of fens, however, the largest alkalinity could be present for low-intermediate groundwater fluxes where evapotranspiration becomes important. Another possible explanation of the positive correlation between ER and water table fluctuations may be the strong positive correlation between *ER* and *EN* (*Rho* = 0.76). In that respect, the correlation possibly reflects a shift in vegetation towards more competitive species, than a shift towards a more alkaline environment.

5 Conclusions

The water level correlates with the number of typical fen species, whereas bryophytes are closer connected to the stable water level conditions provided by groundwater seepage. We found significant relationships between the number of typical fen species and 6 out of 8 hydrology metrics and highly significant relationships between water level metrics and the number of bryophyte species. Bryophyte species richness decreases with increasing annual amplitude in water level fluctuations. The established models confirmed that bryophytes are more dependent on a high and stable water level than vascular plants.

The strongest correlation for the Ellenberg moisture indicator EF, was found with the short term water level variability in the summer period (Var3). The relative number of bryophytes is closely related to Ellenberg N, and in particular the ratio between Ellenberg N and Ellenberg F.

Our proposed models can be used as tools for evaluating the conservation status and determining the limiting factor (nutrients or hydrology) for species diversity in Danish GDWTEs. The relative number of bryophytes to total species is very closely related to water level conditions, which can be useful in situations where no or limited water level data is available. The models can also predict the expected changes in species diversity due to changes in water level conditions. The water level variability is proved to be a significant limiting factor for species diversity in GDWTEs, emphasizing the importance of considering optimal hydrology along with the fertility in order to access the habitat quality.

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FIGURES

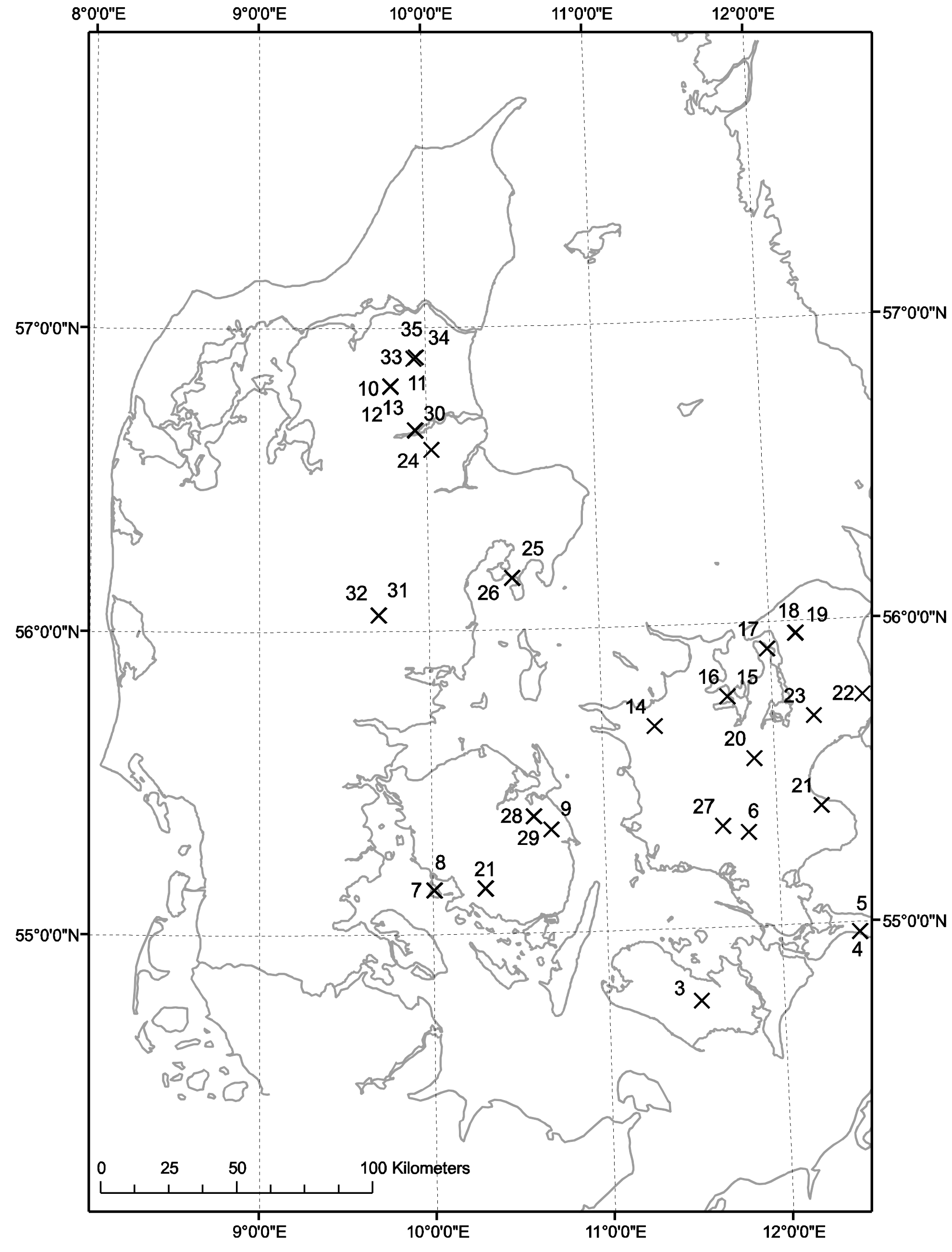

Fig. 1 Location of the 35 sites concentrated in northern and eastern Denmark.

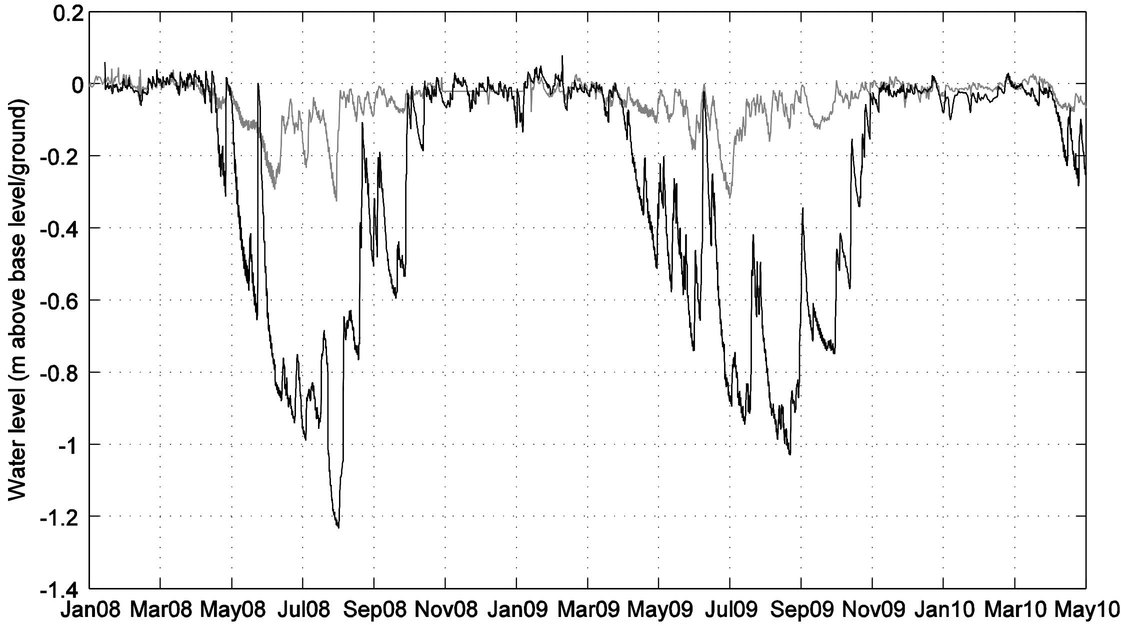

Fig. 2 Example of water level time series analysed. The grey line represent a site with a minor lowering of the water table in the summer period, and the black line represent a site with a more dynamic summer water table.

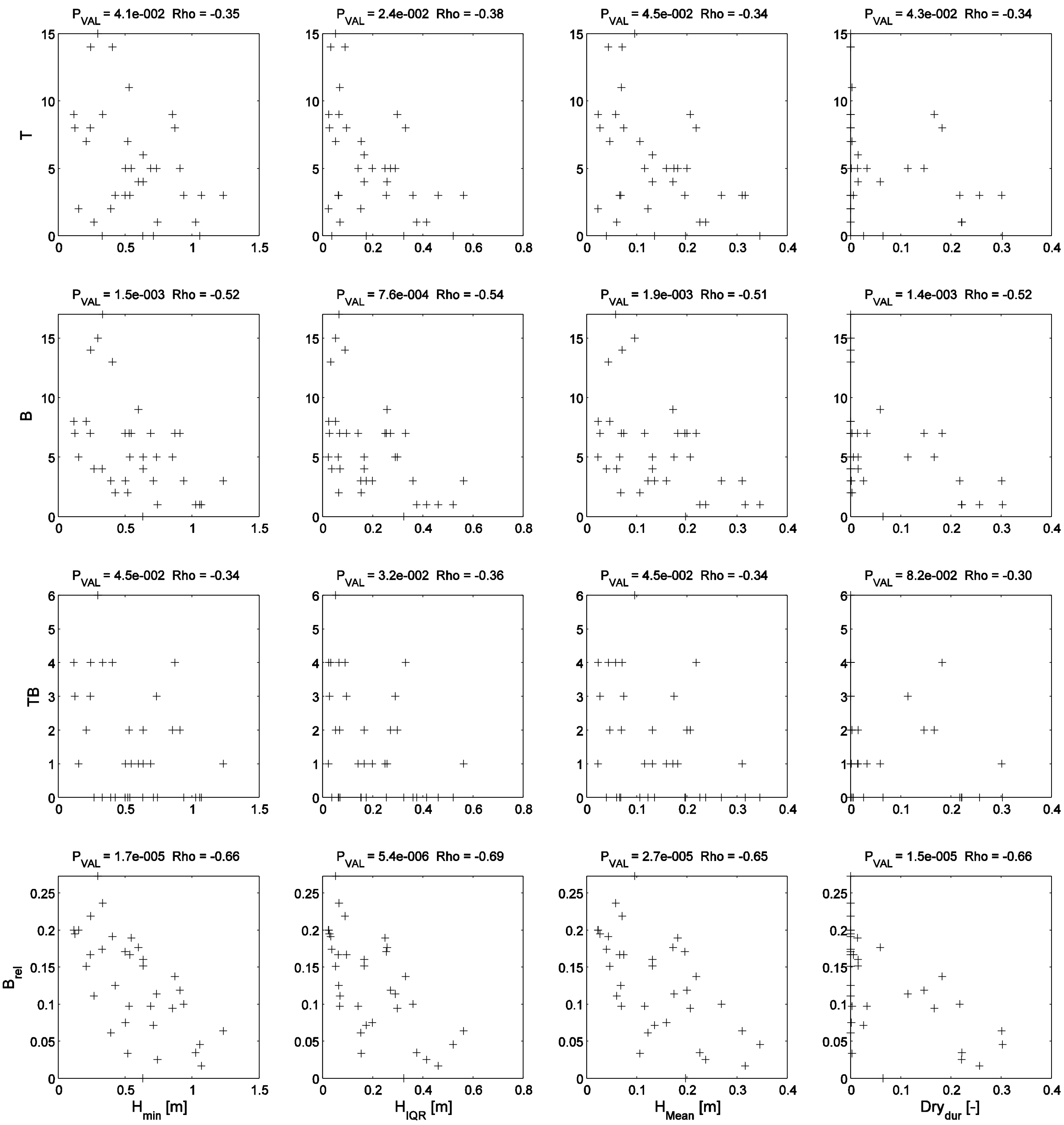

Fig. 3. Four vegetation measures *T, B, TB,* B_{rel} plotted against four water level measures H_{min}, H_{IQR}, H_{mean}, Dry_{dur}. *Rho* and P_{val} based on Spearman's rank correlation is shown

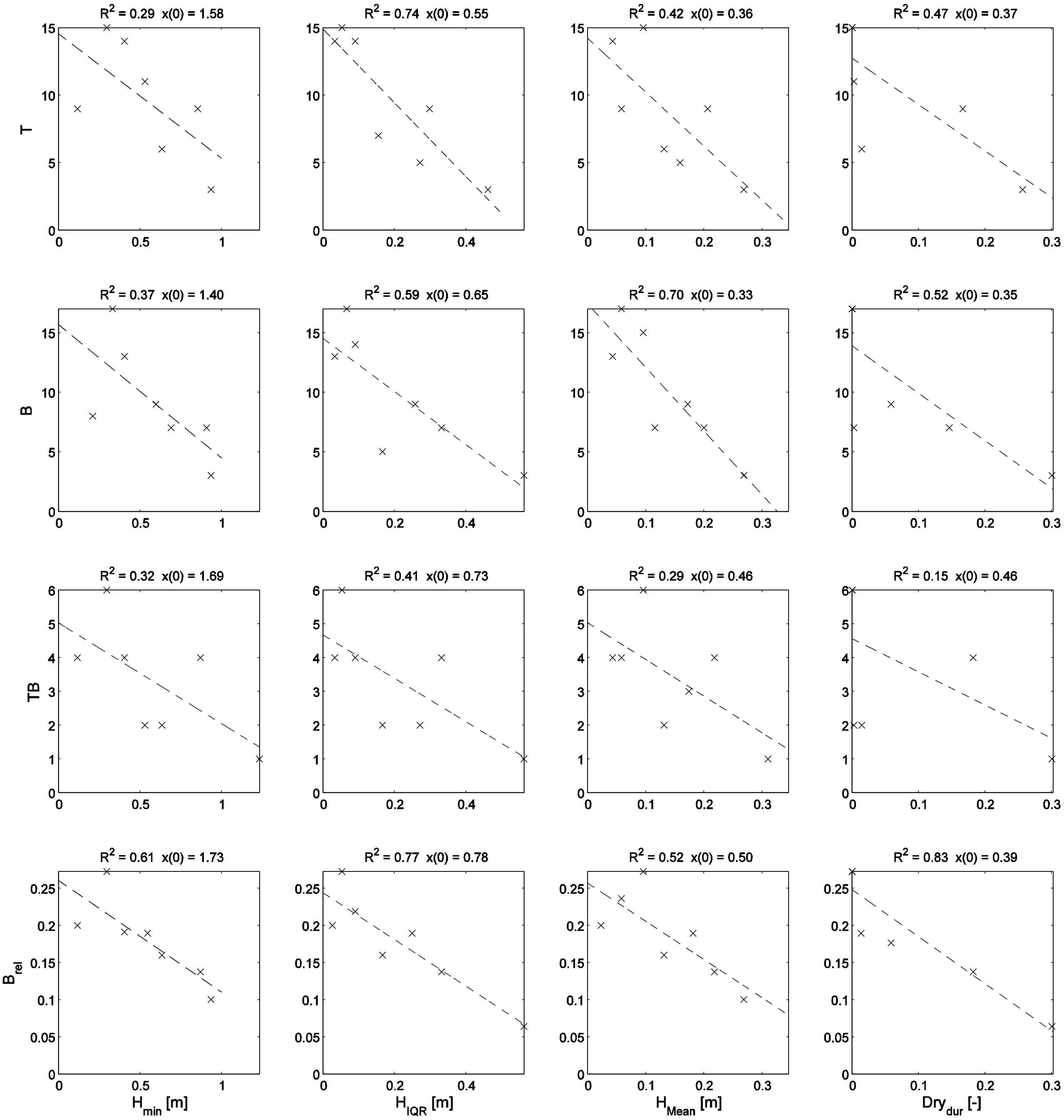

Fig. 4. The highest scoring point along seven subdivision of the x-axis each containing 5 observation points. The dashed line represents a linear model of these maximum values with the shown R^2 value and intersect with the water level axis equal to x(0)

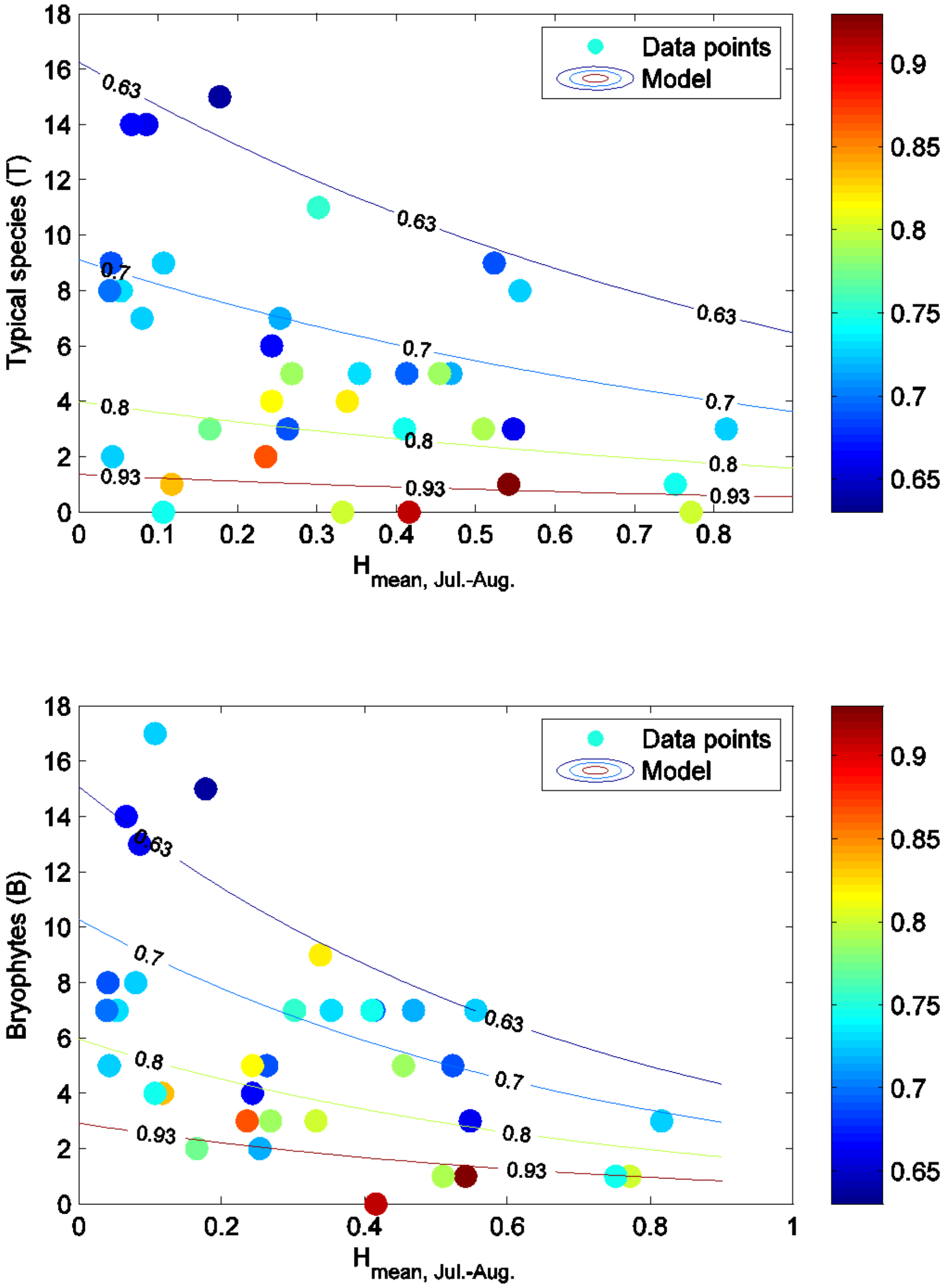

Fig. 5. Visualisation of Poisson regression model 1 (upper) and model 2(lower) using a Poisson distribution for the predicted variables *T* and *B.* The contour lines are values of the nutrient ratio *EN* ER^{-1}. The original data points are shown with respect to the x-axis and y-axis.

TABLES

Table 1. Statistical measures calculated from water level time series and observed ranges at study sites

Symbol	**Unit**	**Observed range**	**Definition**
H_{min}	m	0.12 – 1.23	H_{90}- lowest observed water level
H_{mean}	m	0.02 - 0.35	H_{90}- Mean observed water level
H_{20}	m	0.04 - 0.73	H_{90}- Water level drawdown exceeded 20 per cent of the time
H_{IQR}	m	0.02 - 0.56	H_{75}-$H_{25,}$ Inner quartile range of water level
Dry_{dur}	%	0-30 %	H < (H_{90} – 50 cm), *r*elative duration of period with more than 50 cm to the water table
$H_{mean\ Apr.-Jun.}$	m	0.02 - 0.40	H_{90}- mean observed water level in April to June
$H_{mean\ Jul.-Aug.}$	m	0.04 - 0.82	H_{90}- mean observed water level in July to August
Var_3	m	7e-5 - 8e-3	Mean variance evaluated over periods of 3 days during July and August

Table 2. Vegetation parameters: examined and observed ranges at study sites.

Symbol	**Unit**	**Observed range**	**Definition**
T	Number	0-15	Number of typical species
T_{wet}	Number	0-6	Number of typical species where Ellenberg F (moist) score ≥8
B	Number	0-17	Number of bryophytes
TB	Number	0-6	Number of typical bryophytes
B_{rel}	%	0-27	Relative number of bryophytes
S_{tot}	Number	16-72	Total number of species
H_{rel}	%	18-74	Relative number of all species with Ellenberg F score ≥8
EN	Score	3.5-6.0	Mean Ellenberg N (nutrient) score
ER	Score	4.9-6.4	Mean Ellenberg R (pH) score
EF	Score	5.9-8.2	Mean Ellenberg F (moist) score
$EN\ ER^{-1}$	Ratio	0.63-0.93	Ratio between *EN* and *ER* - the “nutrient ratio”

Table 3. Statistics of model 1 using a Poisson distribution for the predicted variable

Typical species	**Coefficient estimates b**	**Std. error of b**	**p-value of b**
b_0 **(intercept)**	8.00***	0.99	4.8e-16
b_1 ***Ellenberg N/R***	-8.27***	1.40	3.1e-9
b_2 $H_{mean, Jul.-Aug.}$	-1.02**	0.38	7.5-e-3

Table 4. Statistics of model 2 using a Poisson distribution for the predicted variable

Bryophytes	**Coefficient estimates c**	**Std. error of c**	**p-value of c**
c_0 **(intercept)**	6.16***	0.89	4.4e-12
c_1 ***Ellenberg N/R***	-5.47***	1.25	1.2e-5
c_2 $H_{mean, Jul.-Aug.}$	-1.39***	0.38	2.4e-4

Appendix A

Table A.1 Typical species of alkaline springs (S) and rich fens (F) (Ejrnæs et al. 2009), number of presences as typical species in other EU- member states and frequency of occurrence in current study. Species marked by grey colour are excluded due to more frequent occurrence in other habitats in Denmark. Bryophytes are marked by bold.

Species	**Habitat**	**Corine /other**	**EU-presences**	**Occurences in current dataset (35 plots)**
Aneura pinguis	**S**	**Corine 54.251, 54.54.52, 54.541, Nordisk min.3.4.2.1**	**4**	**2**
Briza media	F		0	10
Bryum pseudotriquetrum	**S, F**	**Corine 54.2, Nordisk min.3.4.2.1**	**9**	**11**
Calliergonella cuspidata	**S**	**Corine 54.4, Nordisk min.3.4.2.1**	**1**	**32**
Campylium protensum	**F**	**(Corine 54.2 "and others")**	**0**	**3**
Campylium stellatum	**S, F**	**Corine 54.2, 54.23**	**8**	**9**
Cardamine amara	S	Corine 54.113	1	0
Carex dioica	F	Corine 54.25	10	1
Carex hostiana	F	Corine 54.2	6	1
Carex lepidocarpa	F	Corine 54.121, 54.2	8	5
Carex nigra	F	Corine 54.23	0	21
Carex pulicaris	F	Corine 54.21	4	2
Carex viridula	F	Corine 54.2 (c. flava)	7	3
Cratoneuron filicinum	**S**	**Corine 54.12, Nordisk min.3.4.2.1**	**13**	**7**

Ctenidium molluscum	**F**	**Corine 54.2**	**2**	**1**
Dactylorhiza incarnata	F	Corine 54.2	6	3
Dicranum bonjeanii	**F**	**Nordisk min. 3.5.2.3**	**0**	**2**
Eleocharis quinqueflora	F	Corine 54.2, 54.23	14	1
Epipactis palustris	S, F	Corine 54.2, 54.23	14	9
Equisetum telmateia	S	Corine 54.12	1	0
Eriophorum angustifolium	F	Corine 54.4	1	10
Fissidens adianthoides	**F**	**Corine 54.2, Nordisk min.3.4.2.1**	**6**	**3**
Hypericum tetrapterum	S		0	5
Juncus articulatus	S	Corine 54.23	0	21
Juncus inflexus	S	Nordisk min.3.4.2.1, (corine 37.241, 37.242)	1	0
Juncus subnodulosus	F	Corine 54.2, Nordisk min.3.4.2.1	12	11
Limprichtia cossonii	**S, F**	**Corine 54.2, 54.23, Nordisk min.3.4.2.1**	**2**	**3**
Liparis loeselii	F	Corine 54.2	7	1
Lychnis flos-cuculi	S, F		0	15
Menyanthes trifoliata	S, F	Corine 54.422	0	8
Montia fontana ssp. fontana	S	Corine 54.111	0	0
Nasturtium microphyllum	S	Corine 53.4	0	0
Nasturtium officinale	S	Corine 53.4	0	0
Palustriella commutata	**S**	**Corine 54.12, Nordisk min.3.4.2.1**	**16**	**0**
Palustriella falcata	**S**	**Corine 54.12, Nordisk**	**3**	**0**

		min.3.4.2.1		
Parnassia palustris	F	Corine 54.21, 54.23	10	1
Pedicularis palustris ssp. palustris	F	Corine 54.422	0	4
Philonotis calcarea	**S**	**Interpret. manual 7220,(corine 54.2 ”and others..”)**	**13**	**0**
Philonotis fontana	**S**	**Corine 54.111**	**2**	**0**
Pinguicula vulgaris	S, F	Corine 54.12, 54.2, 54.23	10	0
Potentilla erecta	F	Corine 54.23	0	11
Ranunculus flammula	S	Corine 54.422	0	12
Rumex acetosa ssp. acetosa var. Hydrophilus	S		0	0
Sphagnum teres	**F**	**Nordisk min. 3.4.3.2, (Nordisk min. 3.4.1.3)**	**2**	**2**
Sphagnum warnstorfii	**F**	**Nordisk min. 3.4.2.1, , 3.4.3.2**	**0**	**0**
Stellaria alsine	F	(corine-spring 54.113),	0	0
Succisa pratensis	F	Corine 37.31	0	11
Tomentypnum nitens	**S, F**	**Nordisk min. 3.4.2.1, 3.4.3.2**	**4**	**4**
Triglochin palustris	S, F		4	11

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Appendix B

Table B.1 Spearman rank correlation coefficients (upper right) and p-values (lower left) for all combinations of water level and vegetation measures. n.s. is not significant (p>0.05)

	Rho	Vegetation measures												Water level measures							
Pval		***T***	T_{wet}	***B***	***IB***	B_{rel}	H_{rel}	S_{tot}	***EN/ER***	***EN/EF***	***EF***	***EN***	***ER***	H_{min}	H_{IQR}	H_{20}	H_{mean}	Dry_{dur}	H_{mean} Apr.-Jun.	H_{mean} Jul.-Aug.	Var_3
Vegetation measures	***T***		0.84	0.76	0.87	0.53	0.33	0.61	-0.65	-0.39	0.32	-0.33	0.10	-0.35	-0.38	-0.35	-0.34	-0.34	-0.31	-0.37	-0.23
	T_{wet}	2E-10		0.65	0.63	0.43	0.49	0.54	-0.44	-0.40	0.44	-0.29	-0.02	-0.36	-0.34	-0.33	-0.31	-0.40	-0.29	-0.35	-0.33
	B	2E-7	3E-5		0.80	0.83	0.33	0.50	-0.53	-0.55	0.36	-0.46	-0.26	-0.52	-0.54	-0.53	-0.51	-0.52	-0.45	-0.49	-0.45
	IB	1E-11	5E-5	8E-9		0.63	0.23	0.47	-0.55	-0.31	0.24	-0.22	0.16	-0.34	-0.36	-0.35	-0.34	-0.30	-0.31	-0.37	-0.25
	B_{rel}	1E-3	1E-2	7E-10	4E-5		0.43	0.02	-0.57	-0.79	0.47	-0.64	-0.45	-0.66	-0.69	-0.66	-0.65	-0.66	-0.61	-0.66	-0.58
	H_{rel}	n.s.	3E-3	6E-2	n.s.	1E-2		-0.12	-0.14	-0.52	0.95	-0.14	-0.10	-0.47	-0.36	-0.34	-0.35	-0.42	-0.40	-0.48	-0.65
	S_{tot}	1E-4	7E-4	2E-3	4E-3	n.s.	n.s.		-0.18	0.14	-0.15	0.04	0.18	0.00	-0.02	-0.02	-0.01	-0.04	0.04	0.00	0.10
	EN/ER	2E-5	8E-3	1E-3	6E-4	4E-4	n.s.	n.s.		0.71	-0.10	0.80	0.28	0.22	0.36	0.31	0.28	0.23	0.22	0.26	0.05
	EN/EF	2E-2	2E-2	7E-4	n.s.	2E-8	1E-3	n.s.	2E-6		-0.52	0.88	0.67	0.56	0.65	0.61	0.59	0.59	0.56	0.57	0.49
	EF	n.s.	8E-3	3E-2	n.s.	4E-3	9E-19	n.s.	n.s.	1E-3		-0.11	-0.07	-0.51	-0.41	-0.39	-0.40	-0.45	-0.45	-0.50	-0.68
	EN	n.s.	n.s.	5E-3	n.s.	3E-5	n.s.	n.s.	7E-9	2E-12	n.s.		0.76	0.35	0.50	0.45	0.43	0.43	0.36	0.35	0.16
	ER	n.s.	n.s.	n.s.	n.s.	7E-3	n.s.	n.s.	n.s.	1E-5	n.s.	1E-7		0.35	0.47	0.46	0.45	0.46	0.38	0.33	0.20
level	H_{min}	4E-2	3E-2	1.5E-3	5E-2	2E-5	4E-3	n.s.	n.s.	4E-4	2E-3	4E-2	4E-2		0.89	0.89	0.89	0.96	0.86	0.94	0.84

	H_{IQR}	2E-2	5E-2	7.6E-4	3E-2	5E-6	4E-2	n.s.	3E-2	3E-5	2E-2	2E-3	5E-3	1E-12		0.99	0.98	0.89	0.93	0.92	0.65
	H_{20}	4E-2	n.s.	1.1E-3	4E-2	1E-5	4E-2	n.s.	n.s.	1E-4	2E-2	6E-3	5E-3	6E-13	1E-27		1.00	0.88	0.95	0.93	0.64
	H_{mean}	5E-2	n.s.	1.9E-3	5E-2	3E-5	4E-2	n.s.	n.s.	2E-4	2E-2	1E-2	7E-3	7E-13	2E-25	8E-36		0.88	0.95	0.93	0.64
	Dry_{dur}	4E-2	2E-2	1.4E-3	n.s.	2E-5	1E-2	n.s.	n.s.	2E-4	6E-3	1E-2	5E-3	5E-19	2E-12	3E-12	6E-12		0.82	0.91	0.79
	$H_{mean\ Apr.\text{-}Jun.}$	n.s.	n.s.	6.4E-3	n.s.	9E-5	2E-2	n.s.	n.s.	4E-4	7E-3	3E-2	2E-2	3E-11	3E-16	1E-17	3E-18	1E-9		0.92	0.70
	$H_{mean\ Jul.\text{-}Aug.}$	3E-2	4E-2	2.6E-3	3E-2	1E-5	4E-3	n.s.	n.s.	4E-4	2E-3	4E-2	n.s.	6E-17	2E-15	5E-16	3E-16	2E-14	3E-15		0.76
	Var_3	n.s.	n.s.	7.3E-3	n.s.	2E-4	3E-5	n.s.	n.s.	3E-3	6E-6	n.s.	n.s.	2E-10	3E-5	3E-5	4E-5	1E-8	2E-6	1E-7	