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Topographically controlled soil moisture drives plant diversity patterns within grasslands

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Abstract Grasslands are recognized as biodiversity hotspots in Europe. However, protection and management of these habitats are currently constrained by a limited understanding of what determines local grassland plant diversity patterns. Here, we combined vegetation records (8,639 inventory plots) from 258 semi-natural grasslands with fine-resolution topographic data based on light detection and ranging technology to investigate the importance of topography—particularly topographically controlled soil moisture—for local and regional grassland plant diversity patterns across a 43,000 km^2 lowland region (Denmark). Specifically, we examined the relationships between five vegetation measures representing species composition and richness as well as functional composition (Ellenberg indicator values) and four functional topographic factors representing topographic wetness, potential solar radiation, heat balance and wind exposure. Topography emerged as an important determinant of diversity patterns in both wet and dry grasslands throughout the study region, with topographic wetness being the strongest correlate of the main local (within-site) and regional (among-sites) gradients in species composition and species' average preferences for soil moisture. Accordingly, topography plays an important role in

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shaping grassland plant diversity patterns both locally and regionally throughout this lowland European region, with this role mainly driven by topographically controlled soil moisture. These findings suggest hydrology to be important to consider in the planning and management of European grasslands.

Introduction

Among European vegetation types, grasslands are known for their high levels of biodiversity, they provide important ecosystem services, and are important habitats for many red-listed light-loving and nitrophobic plant species (Bruun and Ejrnæs 1998; Gibson 2009; Zavaleta et al. 2010). However, the actual drivers of local grassland plant diversity patterns are incompletely understood and hence conserving and managing these semi-natural habitats is challenging.

Many studies of the determinants of local (~100–1,000 m extent) vegetation patterns in grasslands have focused on anthropogenic effects and soil pH (Saunders et al. 1991; Collins et al. 1998; Hansson and Fogelfors 2000; Stevens et al. 2004; Maskell et al. 2010; Reitalu et al. 2010), although also with some attention to other abiotic factors and topography (e.g., Bennie et al. 2006; Perring 1959). Though, the general importance of topography for shaping local grassland vegetation patterns remain poorly understood as do the mechanisms involved. Notably, most studies of local vegetation patterns in grasslands include only one or a few sites and consequently the generalizability of their results is uncertain. Topography is considered an indirect variable (Guisan and Zimmermann 2000), and by tradition mostly thought of as a substitute of temperature in mountainous regions where it is recognized as an important determinant of regional vegetation patterns (e.g., Vázquez and Givnish 1998; Grytnes 2003). Locally and especially in lowlands, topography is commonly believed to be less important for plant diversity patterns (Willis and Whittaker 2002; Pearson and Dawson 2003, but see Svenning 1999; Ejrnæs and Bruun 2000; Moeslund et al. 2011).

Topography controls local vegetation patterns in many wetlands as only minute changes in elevation may confer large differences in soil moisture and thus strong gradients in plant species composition and richness (Vivian-Smith 1997; Silvertown et al. 1999; Økland et al. 2008). While variation in elevation in dry habitats is unlikely to induce water logging, it may still affect water availability, for example by controlling the proximity to the ground water table or local drainage patterns. Moreover, soil moisture is known to affect nutrient availability even in dry habitats (Rodriguez-Iturbe et al. 1999; Loiseau et al. 2005). Consequently, topographically controlled soil moisture is an obvious candidate for being a main controller of local plant diversity patterns in grasslands.

Besides having strong effects on local hydrology, topography additionally affects patterns in local temperature and irradiation as well as local exposure to wind. Temperature is one of the most widely recognized determinants of continental-to-global scale vegetation patterns (Willis and Whittaker 2002; Pearson and Dawson 2003), yet its effects on local plant diversity are much less acknowledged (Olivero and Hix 1998; Bennie et al. 2008). Wind has contingent effects on soil grain size characteristics (Parker 1952; Barbour et al. 1974) as well as on local temperature and water loss from plants and soil (Gates 1980;

Knapp 1985), but how it affects plant diversity patterns within grasslands is largely unstudied (Ennos 1997).

Local topography-vegetation patterns in grasslands have previously been studied (Perring 1959; Knapp 1985; Amezaga et al. 2004; Bennie et al. 2006; Li et al. 2009), but the dearth of topography and plant data at fine resolution across large regions have limited scientists' ability to assess the general importance of topography for plant diversity patterns within grasslands. In the present study we combined novel digital terrain data based on Light Detection and Ranging (LiDAR) technology (Vierling et al. 2008) with accurately georeferenced vegetation data to remedy this situation. Using vegetation data from 258 humid and dry grasslands in Denmark, we address the following specific study questions: (1) how strongly does topography control local plant diversity patterns within grasslands? (2) To what extent are vegetation-topography relationships driven by topographically controlled soil moisture? (3) Is this control more important in relatively wet grasslands?

Materials and methods

Study sites

This study included plant species abundance data from 258 protected Danish grasslands of special conservation interest to the European Union; i.e., all Danish grasslands categorized as a 6000-series habitat (semi-natural grasslands) in Annex 1 of the Habitats Directive (Fig. 1; Table 1) (Council of the European Communities 1992; Commission of the European communities 2002). Most of these grasslands feature a high plant diversity compared to other European habitat types and constitute important environments for rare and red-listed plant species such as orchids (Orchidaceae). The majority of the sites are grazed and harbour a number of characteristic grassland specialists that are non-competitive in shade and under nutrient-rich conditions (Bruun and Ejrnæs 1998). The dataset included a total of 1,079 plant species, subspecies, and varieties.

Vegetation data

As part of the Danish National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environment (NOVANA, Svendsen et al. 2005), 40 (occasionally 20 or 60) circular vegetation plots (5 m radius) has been laid out randomly within each grassland site. Presence/absence of plant taxa in these plots is inventoried at least every sixth year. In addition, abundances of all plant species within a 0.25 m^2 quadrat at the plot centre are recorded by the pinpoint method, i.e., as the number of presences in a 4 by 4 rectangular grid (16 cells) laid out in the quadrat. A plant is considered present if it touches a stick inserted vertically in each grid cell. Here, we extracted inventory data from the NOVANA database for 2004–2009. Data from all years were lumped together and duplicates and erroneous values (e.g., saltmarsh species recorded in an inland dry grassland site) removed, resulting in a final data set covering 8,639 plots from the 258 grassland sites.

To analyse the effect of topography on different components of the local (within-site) vegetation patterns the following five vegetation measures (detailed below) were computed for each plot: (1–3) mean (abundance weighted) Ellenberg indicator values (EIVs, Ellenberg et al. 2001) for soil moisture (EIV_{moist}), pH (EIV_{reac}), and nitrogen content (EIV_{nitro}), (4) species richness, and (5) the 1st axis value from a within-site Detrended correspondence analysis (DCA) of plot species abundances. The EIVs represent measures

Fig. 1 The study area
(Denmark). The digital terrain
model used in this study is
superimposed upon the area,
and the 258 grassland sites under
study is shown as *circles* (dry
grasslands) and *triangles* (wet
grasslands)
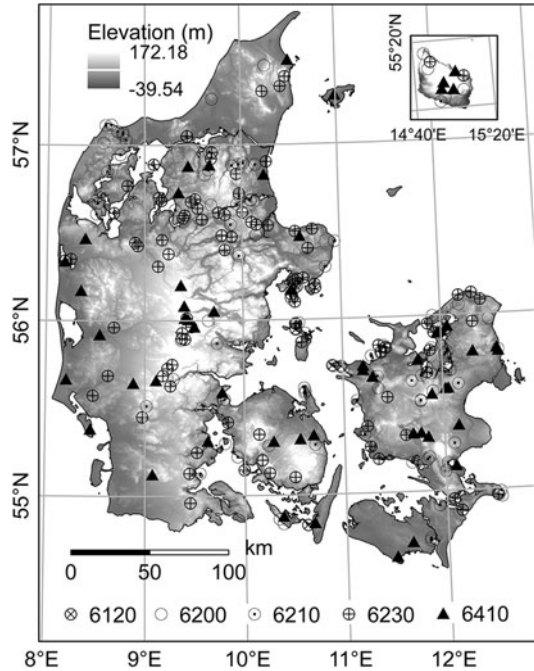
of the niche gradients related to hydrology and other soil conditions and act as measures of
functional plant composition. Where possible the updated EIVs presented by Hill et al.
(1999) for the British Isles were used since these correspond best to the conditions pre-
ferred by plant species in Denmark. Values for taxa missing in Hill et al. (1999) were taken
from Ellenberg et al. (2001) (first priority) or from Landolt et al. (2010) (second priority).
The scale of the latter values was stretched to match the scale of the original EIVs: Landolt
indicator value (LIV) 1 (minimum) corresponds to EIV 1, LIV 5 (maximum) to EIV 9
(reaction and nitrogen) or EIV 12 (for soil moisture). For the species not found in any of
these sources, we estimated the values mainly based on information from Danish floras
(Online Resource 1). Subspecies and varieties were mostly kept separate as they often have
divergent environmental preferences; hereby, we derived the most precise mean indicator
values possible for the taxa present in a plot. However, if a subspecies or a variety in a plot
was not consistently identified at each plot inventory, the nearest higher taxon was con-
sidered instead. Species richness was the number of vascular plant taxa in each plot. The
DCA 1st axis represents the main floristic gradient within each grassland site. To addi-
tionally analyse regional (among-sites) vegetation patterns, site means were calculated for
EIV_{moist}, EIV_{reac}, EIV_{nitro}, and species richness. Additionally, since among-sites compar-
ison of values from local (within-site) DCAs is meaningless, a regional DCA was per-
formed including all 8,639 plots and site means of the resulting 1st axis were computed.

Topographic data

Elevation data originated from a 1.6-m resolution LiDAR based (Vierling et al. 2008)
digital terrain model (DTM) covering all Denmark (Fig. 1, vertical precision:
0.10–0.15 m) (National Survey and Cadastre 2008). A recent study has shown that a

Table 1 An overview of the habitat types included

NATURA 2000 habitat code	Habitat description	Characteristic plant species	n
6120	Extremely dry calcareous grasslands on sand	*Aira caryophyllea, Allium schoenoprasum* var. *schoenoprasum, Cardaminopsis arenosa, Carex ligerica, Cerastium semidecandrum, Dianthus deltoides, Erophila verna, Festuca polesica, Helichrysum arenarium, Herniaria glabra, Koeleria glauca, Myosotis stricta, Petrorhagia prolifera, Phleum arenarium, Silene conica, S. otites, Trifolium striatum, Vicia lathyroides*	6
6200	Dry impoverished grasslands	These grasslands lack a sufficient number of characteristic species to be categorized into either 6210 or 6230, typically due to agricultural improvement as a consequence of cultivation and/or fertilization	25
6210	Dry calcareous grasslands	*Anacamptis morio, Anthyllis vulneraria* s.l., *Arabis hirsuta* var. *hirsuta, Brachypodium pinnatum, Bromopsis erecta, Campanula glomerata* ssp. *glomerata, Carex caryophyllea, Carlina vulgaris* ssp. *vulgaris, Centaurea scabiosa, Koeleria pyramidata, Leontodon hispidus, Medicago sativa* ssp. *falcata, Neotinea ustulata, Orchis mascula, O. purpurea, Primula veris, Sanguisorba minor* ssp. *minor, Scabiosa columbaria*	79
6230	Dry acidic grasslands	*Antennaria dioica, Arnica montana, Carex ericetorum, C. pallescens, C. panicea, Festuca ovina, Galium saxatile, Gentiana pneumonanthe, Hypericum perforatum, Hypochoeris maculata, Lathyrus linifolius, Nardus stricta, Pedicularis sylvatica* ssp. *sylvatica, Platanthera bifolia* ssp. *bifolia, Polygala vulgaris, Potentilla erecta, Pseudorchis albida, Veronica officinalis, Viola canina*	94
6410	Wet grasslands on calcareous, peaty or clayey-silt-laden soils	In calcareous parts: *Carex flacca, C. nigra, C. pallescens, Inula salicina, Dianthus superbus, Juncus subnodulosus, Molinea caerulea, Primula farinosa, Selinum carvifolia, Serratula tinctoria, Tetragonolobus maritimus* In non-calcareous parts: *Crepis paludosa, Dianthus deltoides, Galium uliginosum, Juncus conglomerates, J. acutiflorus, Lotus pedunculatus* var. *pedunculatus, Luzula multiflora* ssp. *multiflora, Ophioglossum vulgatum, Potentilla erecta, P. anglica, Viola palustris, V. persicifolia*	54

The number of sites (*n*) of the different grassland types is also given. Nomenclature follows Mossberg and Stenberg (2005)

horizontal resolution of approximately 10 m is optimal for working with the datasets incorporated here (Moeslund et al. 2011). Hence, the DTM was aggregated (mean) to 9.6 m resolution (for simplicity referred to as 10 m resolution) and the topographic variables below are consequently all in this resolution. To gain insight into the roles played by soil moisture and other functional environmental factors in vegetation-topography relationships, we computed four functional topographic variables described in detail below (heat index, potential solar radiation, a topographic wetness index, and wind exposure).

We adapted the heat index proposed by McCune and Keon (2002) as a rather simple measure of the potential heat load in a given spot based on topographic aspect alone.

Aspect was computed using the "Aspect" tool (default settings) in the Spatial Analyst module of ArcGIS 10 (ESRI, Redlands, CA, USA). Subsequently, the heat index was calculated according to: $(1 - \cos(\theta - 45))/2$, where θ is the aspect in degrees.

To more fully represent heat load and light intensity, we also employed a more complex measure, namely potential solar radiation. This measure was produced using the "Area Solar Radiation" tool (default settings except that the time configuration was: "whole year (2009) with monthly interval") in the aforementioned module of ArcGIS 10.

Topographic wetness was represented by a topographic wetness index (TWI), which is proportional to the potential wetness of a given spot (Beven and Kirkby 1979; Wilson and Galant 2000). The TWI of a DTM cell (i) is given by $\ln(A_s/\tan(\theta_i))$, where A_s is the specific catchment area associated with i (detailed below) and θ_i is the slope angle of i (Wilson and Galant 2000). A_s is defined as A_u/L_i, where A_u is the area of the upslope cells draining into i and L_i is the dimension of i measured as the width of the cell in the direction orthogonal to the water flow direction. The calculations of A_u and L_i are based on outputs from flow accumulation and flow direction computer algorithms (Wilson and Galant 2000). Recently, Kopecký and Čížková (2010) recommended the use of multiflow direction algorithms for vegetation ecology studies. We followed this recommendation and used SCALGO Hydrology ver. 1.0.5 (SCALGO, Aarhus, Denmark) which implements the multiflow direction algorithm developed by Quinn et al. (1991) as well as a flow accumulation algorithm. From these data, we computed the TWI in ArcGIS 10 using the above formula. See flowchart in Online Resource 2 for details of the calculation.

We represented topographically controlled wind exposure by adapting the method described by Mikita and Klimánek (2010). The Hillshade tool in the "Spatial Analyst" module of ArcGIS 10 creates a shaded relief from a DTM by considering the azimuth (compass direction) and altitudinal angles of an artificial illumination source. Used with an altitude angle of 5°, the resulting hillshade can be interpreted as the potential wind exposure from a given direction (Boose et al. 1994; Mikita and Klimánek 2010). Initially, one hillshade raster was created for each of the following compass directions: 0°, 30°, 60°, 90°, 120°, 150°, 180°, 210°, 240°, 270°, 300° and 330°. In Denmark, wind is not equally distributed among the compass directions (Cappelen and Jørgensen 1999). To account for this we incorporated data on general wind speed and direction: for each compass direction a map of average wind speed and a map of frequency for that particular wind direction were created by interpolating (Inverse Distance Weighting, IDW) data from 62 weather stations distributed throughout Denmark (Cappelen and Jørgensen 1999). The IDW calculations were conducted using the "IDW" function in the "Geostatistical Analyst" module in ArcGIS 10 with default settings (default power = 2). We used an output cell size of 250 m as the general wind speed and direction is unlikely to change markedly over shorter distances. These two maps were used for weighting (equal weights) the potential impact of wind as represented by the corresponding hillshade layers, allowing us to compute a map of weighted-average potential wind exposure for all of Denmark.

Data analysis

For each grassland site the five vegetation measures were individually regressed against all four topographic variables using ordinary least squares (OLS) multiple regression models to establish the general relationships between local (within-site) vegetation and topography (1,290 models in total). Being particularly interested in the importance of topographic wetness for each of the five vegetation measures, we additionally conducted local (within-site) Spearman correlations of each of the five vegetation measures against plot TWI values

(1,290 correlations in total). To analyse the importance of topographic wetness for grassland vegetation patterns among-sites, regional (including all 258 sites) OLS models regressing each vegetation measure (site means) against the site mean TWI were also built (5 models in total). Suspecting a certain amount of spatial autocorrelation in the model results, Moran's I (Legendre and Legendre 1998) was calculated for the residuals of these regional models. As spatial autocorrelation was detected for some models (not shown), we also reran the above regional OLS models as spatial error simultaneous auto-regressive (SAR$_{err}$) models (Kissling and Carl 2008). To investigate differences between wet and dry grasslands in the importance of TWI for local as well as regional vegetation patterns the Spearman correlation results (local) and the results from the regional OLS and SAR analyses were reported for three site categories: all, wet grasslands only, and dry grasslands only (see Results and Table 1). Since soil moisture may affect both nitrogen content and the pH value in a site, one may speculate that TWI correlates with EIV$_{nitro}$ and EIV$_{reac}$ only because it correlates with EIV$_{moist}$. To test for such effects, we conducted OLS multiple regressions of each of the vegetation measures against TWI and EIV$_{moist}$ following Freckleton (2002) to reveal if there is still an effect of TWI after potential effects of EIV$_{moist}$ has been accounted for. Finally, to analyse if the strength of the local TWI-vegetation relationships depend on continuous site-level soil wetness conditions, the absolute coefficients (representing the strength of the local within-site relationships) from the TWI-vegetation Spearman correlations were regressed (OLS) against the mean and the standard deviation of the TWI per grassland site.

All statistics were conducted using the R statistics programming environment ver. 2.15.0 and 2.14.2 (R Development Core Team 2012). The 'vegan' package ver. 2.0-1 (Oksanen et al. 2011) was used for DCA calculations, and the 'spdep' package ver. 0.5–46 (Bivand et al. 2012) was used for SAR modelling.

Results

The functional topographic variables were all important for shaping the local (within-site) grassland vegetation patterns (Table 2). On average the topographic variables explained 13 % ($R^2_{adjusted}$) of the variation in local vegetation patterns and models for all vegetation measures were statistically significant in >30 % of the grasslands (i.e., more than expected by chance). For the vegetation measure with the strongest link to topography in each grassland site (in some sites this measure was EIV$_{moist}$, in some species richness, etc.), on average 32 % (R^2_{adj}) of its variance was explained by the topographic variables.

Overall, the most important topographic factors for local grassland vegetation patterns were TWI and to a lesser extent potential solar radiation (Table 2). Conversely, the vegetation measures most strongly controlled by topography were EIV$_{moist}$ and, secondarily, the main local floristic gradient (DCA 1st axis) (Table 2). The strongest specific vegetation-topography link was between EIV$_{moist}$ and TWI (Table 2).

Local relationships between EIV$_{moist}$, EIV$_{reac}$, and EIV$_{nitro}$ and TWI were all predominantly positive, while local species richness generally declined with increasing TWI (Fig. 2). Regionally (among-sites), TWI also had strong links to EIV$_{moist}$ and the main regional floristic gradient (DCA 1st axis). Links to other vegetation components were weaker, but significant, even after accounting for spatial autocorrelation (Table 3) and effects of EIV$_{moist}$ on EIV$_{nitro}$ and EIV$_{reac}$ (Online Resource 3).

We found no differences in the importance of TWI for local vegetation patterns in dry compared to wet grasslands except for its relationship to EIV$_{nitro}$ (Fig. 2). Furthermore,

Table 2 Results for the local ordinary least squares (OLS) multiple regression models of the five grassland vegetation measures against the four functional topographic explanatory variables

	Full model $R^2_{adjusted}$	Explanatory variables (partial R^2)			
		Heat	Solar	TWI	Wind
EIV_{moist}	0.16^a	$0.12^{bc,a}$	$0.18^{b,a}$	$0.32^{a,a}$	$0.09^{c,a}$
EIV_{nitro}	0.13^b	$0.13^{a,a}$	$0.18^{a,a}$	$0.22^{a,b}$	$0.21^{a,a}$
EIV_{reac}	0.09^c	$0.08^{b,a}$	$0.23^{a,a}$	$0.23^{a,b}$	$0.19^{a,a}$
DCA_{1-axis}	0.14^{ab}	$0.10^{b,a}$	$0.19^{ab,a}$	$0.26^{a,b}$	$0.17^{ab,a}$
SpRich	0.12^{bc}	$0.11^{b,a}$	$0.24^{a,a}$	$0.19^{ab,b}$	$0.12^{b,a}$

The average $R^2_{adjusted}$ for the multiple linear regressions (full model) is given for each vegetation measure along with the average partial R^2 (Legendre and Legendre 1998) for each of the explanatory variables (given as its fraction of the full model R^2_{adj}). These were compared row-wise (only partial R^2, superscript before comma) and column-wise (for partial R^2 indicated by the superscript after comma). Different letters indicate significantly different values (Student's t test, $P < 0.05$, corrected for multiple comparisons following Narum's (2006) modified false discovery rate method). For all vegetation measures the full model was statistically significant in more than 30 % of the grassland sites

SpRich: species richness, DCA_{1-axis}: 1st axis scores of local (within-site) Detrended Correspondence Analyses of species abundances. EIV_{moist}, EIV_{nitro}, and EIV_{reac}: the Ellenberg indicator values for soil moisture, nitrogen content, and pH respectively

Heat: heat index, solar: potential solar radiation, TWI: topographic wetness index, wind: wind index

hydrological conditions (mean and standard deviation of TWI) within each grassland site did at most weakly influence the strength of the local vegetation-wetness relationships (Table 4).

Discussion

Here we present the first geographically comprehensive (>250 sites with >8,600 plots in total) study of the importance of topography and the underlying driving mechanisms for local plant diversity patterns in lowland humid and semi-dry grassland types. Generally, topography was important for local (within-site) and regional (among-sites) vegetation patterns in these grasslands, and particularly topographic wetness (TWI) played a main role. Locally, solar radiation was the second most important.

The importance of elevation for shaping local vegetation patterns is well recognized for wetlands (Vivian-Smith 1997; Silvertown et al. 1999; Økland et al. 2008; Moeslund et al. 2011) and topography is also sometimes considered important locally in other habitats (Svenning 1999; Eiserhardt et al. 2011). Still, the general importance of topography at local scales and notably the mechanisms behind such control remain to be elucidated, as topography may mediate the effects of a wide range of factors (e.g., Guisan and Zimmermann 2000; Svenning 2001). In this study, topographic wetness (TWI) was the functional topographic driver most important for local vegetation patterns even though grasslands are much drier than wetlands (mean TWI for grasslands in Denmark within the NATURA 2000 network is 6.5; for the wetlands excluding lakes it is 8.9), and hence elevation effects on soil moisture should be weaker in these relatively dry habitats (see Introduction). A possible explanation for this finding is that soil moisture affects a number of factors important for plant growth beyond the availability of water. For example, soil moisture has previously been demonstrated to affect the amount of nitrogen available to
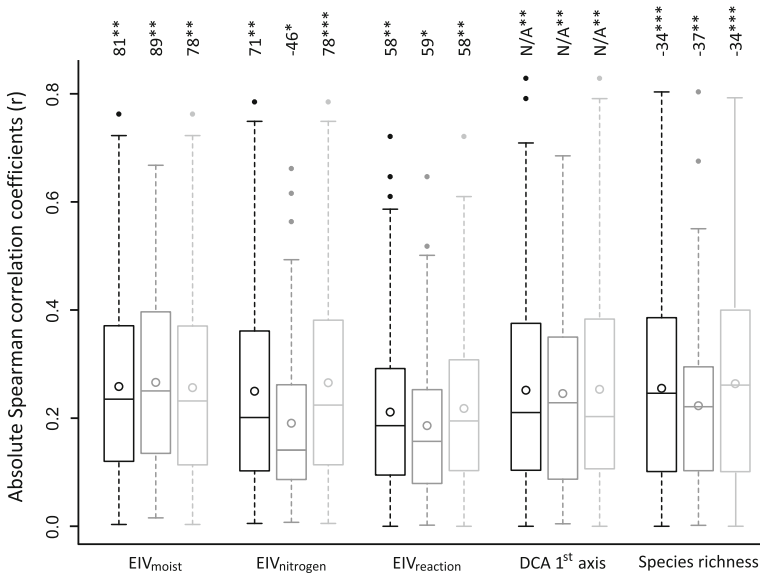
Fig. 2 Absolute Spearman correlation coefficients (*r*, denoting relationship strengths) for correlations within 258 Danish grassland sites between five vegetation measures (*x*-axis) and the topographical wetness index (TWI). *Black boxes* represent results for the full analysis including all sites. *Dark grey boxes* represent results for wet grasslands only and *light grey boxes* for dry grasslands. *Numbers above boxes* show the percentage of positive correlations. A *minus* emphasizes that the majority of correlations were negative. For DCA 1st axis, the correlation directions (positive/negative) are arbitrary and hence meaningless therefore percentages are not given. The mean coefficient for EIV_{reac} in all grasslands was significantly (Student's *t* Test, $P < 0.05$) lower than the corresponding means for the rest of the vegetation measures. The mean coefficient in wet grasslands for EIV_{nitro} was significantly (Student's *t* Test, $P < 0.05$) lower than the corresponding coefficient for dry grasslands. *Dots* are outliers, *circles* are means. Upper extreme, upper quartile, median, lower quartile and lower extreme are represented for each *box*. For abbreviations, see Table 2. Significance levels: * >5 % significant correlations ($P < 0.05$), ** >15 %, *** >30 %

plants through its impact on mineralization rates (Giesler et al. 1998; Rodriguez-Iturbe et al. 1999; Loiseau et al. 2005). Furthermore, subsurface water is likely to transport dissolvable cations and nitrogen compounds towards the lower-lying relatively wet sites potentially affecting both pH (Zinko et al. 2006) and soil nitrogen content. This agrees with our finding that TWI had clear positive links to the species' preferences for both nitrogen (EIV_{nitro}) and pH (EIV_{reac}). We note that low-lying parts of grasslands are also more likely to include former fields (here the habitat code 6200) (Fritzbøger and Odgaard 2010), and since these may be more nutrient-rich than grasslands on soils never used for agriculture, this legacy might contribute to these TWI relationships. Potential solar radiation was additionally among the most important topographic variables for local vegetation patterns in the present study. Notably, it was the second most important controller of EIV_{moist}. Hence, topography probably controls soil moisture through at least two mechanisms, namely by controlling groundwater flow and precipitation water accumulation (Wilson and Galant 2000) and by controlling the amount of incoming solar radiation, thereby affecting the evaporation and evapotranspiration rates (Cantlon 1953). However, the direct effect of solar radiation on local temperatures (Bennie et al. 2008; Suggitt et al. 2011) may also contribute to its effects on local vegetation patterns.

Table 3 Results for regional (among sites) ordinary least squares (OLS) and simultaneous auto-regressive (SAR) models of five vegetation measures (site means) against the site mean (μ) topographic wetness index (TWI), and for species richness also against the standard deviation (σ) of TWI per site

| | OLS models | | | | | | SAR models | | | | | | | | |
| | All grasslands | | Wet | | Dry | | All grasslands | | | Wet | | | Dry | | |
	b	R^2	b	R^2	b	R^2	B	R^2_{full}	R^2_{env}	b	R^2_{full}	R^2_{env}	b	R^2_{full}	R^2_{env}
SpRich ~ TWI(μ)	−0.26***	0.07	0.00	0.00	−0.24***	0.06	−0.24***	0.14	0.07	0.00	0.00	0.00	−0.21**	0.11	0.06
SpRich ~ TWI(σ)	0.01	0.00	0.03	0.00	0.04	0.00	0.03	0.10	0.00	0.06	0.01	0.00	0.06	0.09	0.00
DCA$_{1\text{-axis}}$ ~ TWI(μ)	0.72***	0.52	0.08	0.01	0.49***	0.24	0.71***	0.52	0.52	0.14	0.07	0.01	0.45***	0.30	0.24
EIV$_{moist}$ ~ TWI(μ)	0.75***	0.57	0.15	0.02	0.39***	0.15	0.74***	0.57	0.57	0.15	0.02	0.02	0.36***	0.20	0.15
EIV$_{nitro}$ ~ TWI(μ)	−0.21***	0.04	0.10	0.01	−0.20**	0.04	−0.20***	0.23	0.04	0.00	0.51	0.01	−0.18**	0.16	0.04
EIV$_{reac}$ ~ TWI(μ)	−0.25***	0.06	0.13	0.02	−0.37***	0.13	−0.21***	0.41	0.06	0.07	0.45	0.02	−0.3***	0.38	0.13

For all grasslands, wet grasslands, and dry grasslands the standardised regression coefficient (b) is shown along with its significance level. For the OLS models the model R^2 value is also given. For the SAR models both the full model (both space and environment) pseudo R^2 (R^2_{full}) as well as the environment-only pseudo R^2 (R^2_{env}, comparable and often more or less equal to the OLS R^2 value) are presented (Kissling and Carl 2008)

For abbreviations, see Table 2 (note that the DCA 1st axis values used here was taken from the regional DCA based on all plots in the study region)

Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4 Results from ordinary least squares (OLS) regressions of absolute correlation coefficients (denoting the strengths of correlations between five different vegetation measures and the topographic wetness index (TWI) among plots within grassland sites) against the site level means or standard deviations of TWI

| Correlation pair	Site mean TWI					
	All grasslands		Wet		Dry	
	b	R^2	B	R^2	b	R^2
SpRich–TWI	−0.14*	0.02	0.06	0.00	−0.15*	0.02
DCA_{1-axis}–TWI	−0.08	0.00	−0.06	0.00	−0.09	0.01
EIV_{moist}–TWI	−0.07	0.00	−0.03	0.00	−0.16*	0.03
EIV_{reac}–TWI	−0.06	0.00	0.03	0.00	−0.01	0.00
EIV_{nitro}–TWI	−0.22***	0.05	0.21	0.05	−0.17*	0.03
Site level standard deviation of TWI						
SpRich–TWI	0.06	0.00	0.07	0.00	0.07	0.00
DCA_{1-axis}–TWI	0.07	0.00	0.13	0.02	0.06	0.00
EIV_{moist}–TWI	0.16**	0.03	0.21	0.05	0.15*	0.02
EIV_{reac}–TWI	0.08	0.01	0.01	0.00	0.10	0.01
EIV_{nitro}–TWI	0.13*	0.02	0.18	0.03	0.16*	0.03

For all grasslands, wet grasslands and dry grasslands the standardised regression coefficient (b) and its significance level are shown along with the R^2 value for the model

For abbreviations, see Table 2

Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Besides being important for the functional composition in terms of species' preferences for soil moisture and nitrogen, topographic wetness was also important for local patterns in the floristic composition (DCA 1st axis) and the species richness. The first is not surprising as it is well known that species composition may change with soil moisture (Burke et al. 1998; Ejrnæs and Bruun 2000), although the current study is the first to show that the main local floristic gradient within grasslands is generally linked to topography and in particular to topographic wetness. The relationship between species richness and TWI was negative. The relationship between productivity and species richness in grasslands is generally believed to be unimodal, i.e., with species richness peaking at an intermediate level of productivity (Janssens et al. 1998; Gibson 2009). Given the generally high soil nitrogen content throughout the study region today (Ellermann et al. 2007), it is likely that the Danish grasslands span intermediate to high productivity levels and hence the species richness decrease with soil nitrogen content could still be consistent with an overall uni-modal relationship to the full productivity gradient. Notably, the richness decrease could be a consequence of increasing competition from tall-growing nitrophilic herbs. This explanation is corroborated by the fact that the plant's preferences for nitrogen (EIV_{nitro}) were highest in the wetter grassland zones, indicating these areas to be more nutrient rich.

Topographic wetness (TWI) was also important for regional (among-sites) variation in all vegetation measures and particularly had strong links to both the main floristic gradient in grasslands throughout the study region (DCA 1st axis) and species' preferences for soil moisture. These effects were linked to overall differences between wet and dry grasslands (Fig. 3) and showed that soil moisture is also important for regional grassland plant diversity patterns. In a previous study of regional diversity patterns in Danish grasslands, Ejrnæs and Bruun (2000) found the main floristic gradient (1st DCA axis) to primarily
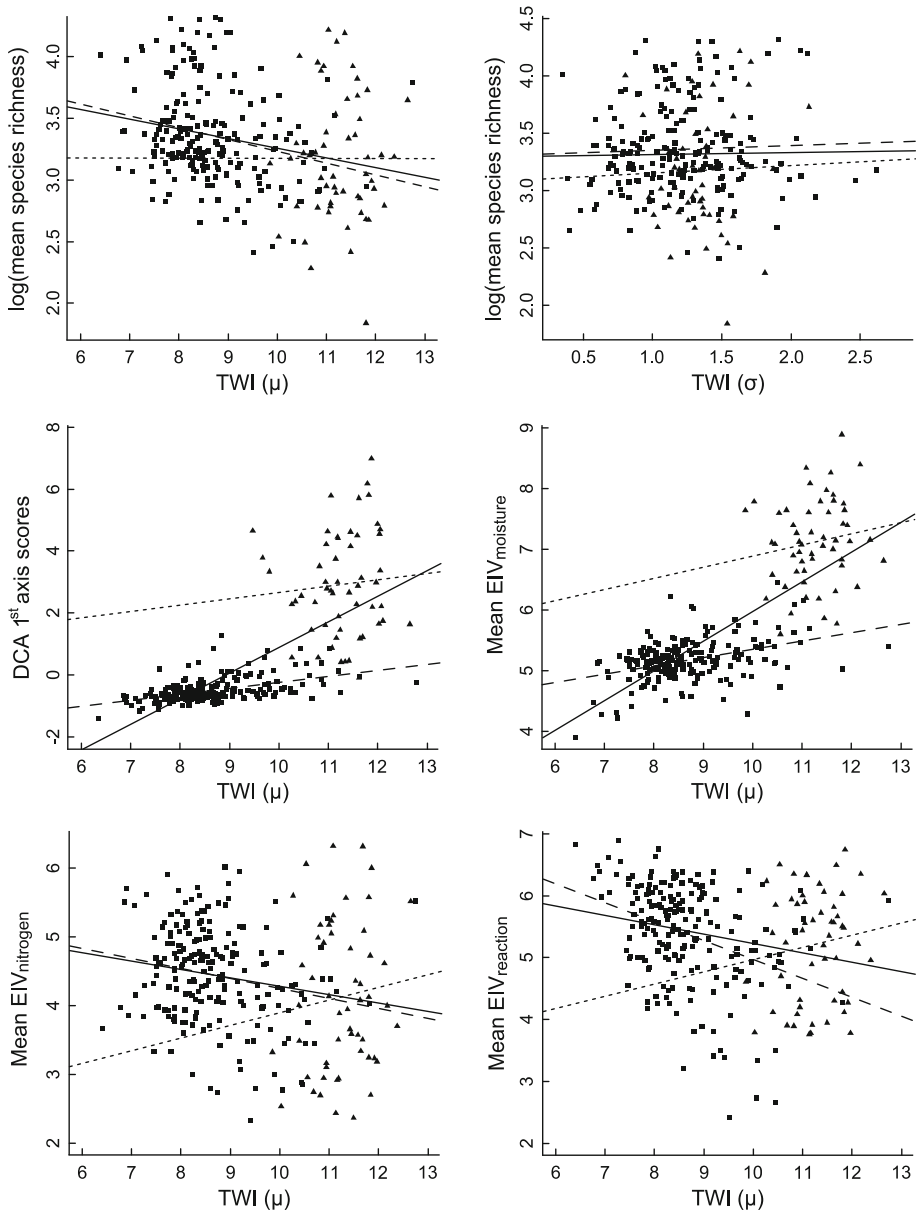
Fig. 3 Graphs showing values for the five vegetation measures (site means, *y*-axes) plotted against the site means (μ) of the topographical wetness index (TWI) and for species richness also against the standard deviations (σ) of TWI for each site. For illustrative purposes linear regression lines are drawn for all grasslands (*full lines*), for the wet grasslands (*dotted lines, triangular dots*), and for the dry grasslands (*dashed lines, square dots*). For modelling results related to these *plots*, see Table 3. For abbreviations, see Table 2 (but note that the DCA 1st axis values used here was taken from the regional Detrended Correspondence Analysis (DCA) including all plots in the study)

have links to soil pH, continentality and potential spring solar radiation, interpreted as a gradient going from warm and dry calcareous sites to cold and humid acidic sites, and they identified the 2nd DCA axis to be mainly linked to soil water conditions. Based on these results, Ejrnæs and Bruun (2000) point to yet another effect of topography, namely its potential long-term effect on soil formation, leaching and acidification. Warm, steep and eroded slopes are well protected against leaching and acidification by high evapotranspiration and constant exposure of fresh mineral soil. These suggestions are partially consistent with our findings, with differences potentially reflecting that Ejrnæs and Bruun (2000) excluded formerly cultivated grasslands and the wetter part of the moisture gradient as well as other methodological differences.

The strength of the local vegetation-TWI relationships did not differ between wet and dry grasslands overall and was at most weakly affected by the mean hydrological conditions and variations herein. This indicates that vegetation-topography relationships are equally strong across the soil moisture gradient, which is somewhat surprising as topographically controlled soil moisture gradients could be expected to be strongest in wet habitats, as flooding and associated effects such as anoxia will only occur here (Silvertown et al. 1999). However, under dry conditions water is potentially more limiting for plant growth than in wetlands (Burke et al. 1998; Flanagan and Johnson 2005) and this might explain why soil moisture is similarly important for plant diversity patterns here.

Conclusion

Using data from 8,639 plots distributed within 258 wet and dry grassland sites, we made the first geographically comprehensive evaluation of the importance of topography for local grassland plant diversity patterns and the underlying mechanisms, with specific emphasis on topographically controlled soil moisture. Topography emerged as an important determinant of vegetation patterns in both wet and dry semi-natural grassland habitats throughout the study region, with TWI being the strongest correlate of the main local (within-site) and regional (among-sites) gradients in species composition and with a particularly strong link to species' preferences for soil moisture (EIV_{moist}) at both scales. The results demonstrate that topography plays an important role in shaping local and regional vegetation patterns in grasslands in this North-western European region and that this role is mainly driven by topography's effect on soil moisture. Thus, it is imperative to consider hydrology in the planning and management of European grasslands, notably given the often strong anthropogenic effects on the ground-water table and flooding regimes (Eckhardt and Ulbrich 2003).

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