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The contribution of the spatial hydrological niche to species diversity in rare plant communities of English floodplain meadows

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Abstract   The hydrological niche is one of the few below ground spatial environmental niches, which has been shown to structure English floodplain meadows and other European and African herbaceous ecosystems. However, both the relative contribution of hydrological heterogeneity to the structure of English floodplain meadows across spatial scales and the forms of the individual species' responses to hydrological heterogeneity remain largely unknown. Here, we use a survey database of 2440 evaluation units sampled in 15 English floodplain meadows to dissect the spatial architecture of this metacommunity and describe the relationship between the abundance of individual species and hydrological heterogeneity. Of the tested species, 65% responded to spatial hydrological heterogeneity, with both monotonic and hump-shaped responses. We found that between-site beta-diversity is much stronger than within-site beta-diversity, with between-site scale hydrological variation explaining twice as much variation in community structure as within-site scale. This leads to the conclusion that a conservation strategy of rare plant communities should include not only the preservation of the diversity of local hydrological regimes, but also, specially, the inclusion in the conservation system of as many and environmentally varied local plant communities as possible.

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Introduction

The maintenance of species diversity in ecological guilds is explained by the theory of species coexistence via equalizing and stabilizing mechanisms (Chesson 2000a). The latter increase intra-specific competition relative to inter-specific competition (Chesson and Warner 1981; Chesson 2000b; Yuan

and Chesson 2015) and may depend on the differential response of species to physical heterogeneity in either space or time (Chesson 1985). Physical heterogeneity typifies environmental plant niches, which are additionally qualified as spatial (rather than as temporal) if they refer to spatially structured features of the physical environment. This is so because plants, being permanently exposed to above- and below-ground abiotic stress created by environmental heterogeneity (Mcgill et al. 2006) such as drought, chemical toxicity (Nagajyoti et al. 2010) or shade (Valladares and Niinemets 2008), have reacted by evolving complex mechanisms to tolerate simultaneous adverse conditions (van Loon 2015; Thoen et al. 2017). The environmental niche, which basically corresponds to Hutchinson's concept (Hutchinson 1957; Leibold 1995) and is related to Grubb's regeneration niche (Grubb 1977), links the theory of species coexistence with the evolution of ecological specialization (Kassen 2002), niche dynamics (Pearman et al. 2008) and global change (Valladares et al. 2015).

The hydrological niche is a spatial environmental niche that has been postulated to stabilize species coexistence in English floodplain meadows (Silvertown et al. 1999), South African fynbos (Araya et al. 2011) and Iberian grasslands (García-Baquero et al. 2016). In studies of these habitats, within-site hydrological heterogeneity along topographic gradient was understood as a physical feature that creates, at a fine scale, patchy conditions of varying water deficit stress (due to soil drying) and oxygen deficit stress (due to waterlogging). Niche conservatism was not detected in floodplain meadows (Silvertown et al. 2006) and fynbos (Araya et al. 2012), suggesting that the hydrological niche might be evolutionarily labile. Other studies highlight an importance of the temporal aspect of hydrology, e.g. frequency and duration of floods to be responsible for hydrological niche liability (e.g. Shepeleva 2018).

Floodplain meadows are discrete habitats ('field sites') that are organized in space; hence, the set of still existing field sites can be understood as a metacommunity (Leibold et al. 2004; Cottenie 2005). However, the relative contribution of hydrological heterogeneity to the structure of these plant communities across spatial scales (within- and between-site) remains largely unknown. We sampled 15 English floodplain meadows (field sites) representing species-rich mesotrophic plant communities of MG4 and MG8 types of British National Vegetation Classification (Rodwell 1992), which have high conservation status in the UK and are included in European Emerald network of protected habitats. Botanical, hydrological and spatial data from 2440 quadrats were analysed to (i) assess which hydrological descriptor performs best for explanatory purposes; (ii) dissect the spatial architecture of the above metacommunity and (iii) describe the shape of the individual species' responses versus hydrological heterogeneity. For this purpose, we use the concept of beta-diversity as non-directional variation (rather as species turnover) in community structure (Anderson et al. 2011) combined with multivariate multiscale spatial analysis (Dray et al. 2012; Declerck et al. 2011), and generalised additive mixed models (Zuur et al. 2010). This paper describes our findings, discusses the applicability of our results to the conservation of floodplain meadows and provides the data and R code (R Core Team 2017) needed to replicate them.

Material and methods

We sampled floodplain meadows on alluvial soils (*Deschampsion cespitosae* Horvatić 1930=*Alopecurion pratensis* Passarge 1964) (Mucina et al. 2016) using a two-stage sampling design (Thompson 2012). Fifteen field sites in England were selected (Table S1 in Online Resource 1 presents detail of their location, climate and soils). The cover of vascular plant species was recorded (Table S2) in c.160 (on average) systematically placed 1 m^2 quadrats (=evaluation units) within each site. The number of samples taken from each site was chosen to adequately represent the microtopographic and botanical variation within the site. Water-table depth was modelled for each botanical quadrat for a growing season (March–September) and averaged for 5-year period (Noest 1994; Gowing et al. 2002), and ten different hydrological descriptors tested (Table S3). Plant nomenclature followed Tutin et al. (1964–1980).

For statistical analyses, a dataset of four matrices was constructed. The first was a species matrix of $n=2440$ quadrats $\times p=189$ plant species (Table S2), where each element represented the normalized cover of species. Normalization is a standardization method that makes *row* margin sum of squares equal to one, thereby removing

variability due to differences in productivity. The second matrix was a survey design matrix of $n = 2440$ quadrats $\times f = 3$ factors [quadrat identity, field site, and region (England)]. The third matrix was an environment matrix of $n = 2440 \times q = 10$ soil properties (Table S3). The fourth matrix was a geographic matrix of $n = 2440 \times c = 2$ Cartesian spatial coordinates (X and Y). R software was used for data analysis (R Core Team 2017). Supporting information provides complete R coding (Online Resource 2). Data sufficient to reproduce our data analysis are available from the corresponding author on request.

Data exploration (focussing on symmetry, extreme values and co-linearity) demonstrated the similarity of the information conveyed by the ten hydrological descriptors (Online recourse 1, Figs. S1 and S5), particularly once between-site variability has been taken into account (Online recourse 1, Figs. S2–S4). Easily comparable with other parameters, median Water Table Depth (mWTD) has been chosen as the best parameter for explanatory purposes, due to its symmetry and simplicity, as well as relative lack of extreme values. Non–metric multidimensional scaling (NMDS) (Kruskal 1964; Legendre and Legendre 2012) was selected to explore the relationship between community structure (species composition and abundance) and sites and hydrological heterogeneity. The main underlying species gradients were obtained via this technique for unconstrained ordination, which preserves the ordering among objects and may be used on the basis of any distance measure (Legendre and Legendre 2012). This was achieved via function metaMDS() of the package vegan (Oksanen et al. 2016), on the basis of the Hellinger distance (Legendre and Gallagher 2001). To reduce initial data dimensionality and facilitate a simplified ordination in two dimensions, only the 50 species with frequency > 10% were considered. The smooth surface corresponding to mWTD was overlaid onto the previously defined species ordination through function ordisurf() (Fig. 1).

For **dissecting the spatial architecture of the metacommunity,** we partitioned species diversity across spatial scales (Crist et al. 2003) and tested the partitioning against random expectation (Summerville et al. 2003). The partitioning was performed according to (Eq. 1):

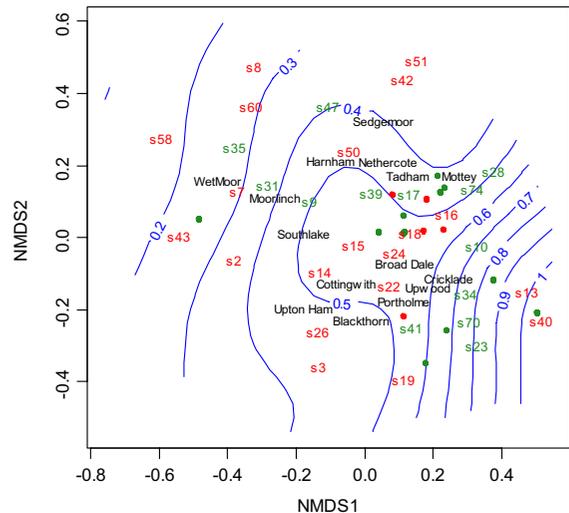**NMDS ordination with fitted smooth surface (mWTD)**

Fig. 1 Main species gradients (unconstrained ordination) described by non-metric multidimensional scaling (NMDS; Hellinger distance). Only species with frequency > 10% have been considered ($n = 2440$). Non-metric goodness-of-fit of the ordination: $R^2 = 95.1\%$; stress $= 0.22$. Graminoids are indicated in red; forbs, in green. The trend surface for mWTD (median Water Table Depth), in m and depicted by blue lines, was overlaid onto the species ordination *after* concluding the NMDS procedure. Significance of trend surface: $F = 148.2$; adj.-$R^2 = 35.3\%$ ($p < 0.001$); field sites goodness-of-fit: adj.-$R^2 = 60.6\%$ ($p < 0.001$). **Key to species** (to avoid crowding, some species are represented by just a point with no legend): s1, *Agrostis capillaris* (0.23, 0.02); s2, *Agrostis stolonifera*; s3, *Alopecurus pratensis*; s4, *Anthoxanthum odoratum* (0.08, 0.12); s5, *Bromus commutatus* (0.17, 0.02); s6, *Bromus racemosus* (0.11, − 0.22); s7, *Carex disticha*; s8, *Carex nigra*; s9, *Cardamine pratensis*; s10, *Centaurea nigra*; s11, *Cerastium fontanum* (0.22, 0.13); s12, *Cynosurus cristatus* (0.18, 0.11); s13, *Dactylis glomerata*; s14, *Deschampsia cespitosa*; s15, *Festuca pratensis*; s16, *Festuca rubra*; s17, *Filipendula ulmaria*; s18, *Holcus lanatus*; s19, *Hordeum secalinum*; s20, *Lathyrus pratensis* (0.24, − 0.25); s21, *Leontodon autumnalis* (0.04, 0.02); s22, *Lolium perenne*; s23, *Lotus corniculatus*; s24, *Phleum pratense*; s25, *Plantago lanceolata* (0.21, 0.17); s26, *Poa trivialis*; s27, *Polygonum amphibium* (− 0.49, 0.05); s28, *Prunella vulgaris*; s29, *Ranunculus acris* (0.11, 0.02); s30, *Ranunculus bulbosus* (0.50, − 0.21); s31, *Ranunculus repens*; s32, *Rhinathus minor* (0.37, − 0.12); s33, *Rumex acetosa* (0.11, 0.01); s34, *Sanguisorba officinalis*; s35, *Senecio aquaticus*; s36, *Silaum silaus* (0.18, − 0.35); s37, *Taraxacum officinale* (0.11, 0.06); s38, *Trifolium pratense* (0.23, 0.14); s39, *Trifolium repens*; s40, *Trisetum flavescens*; s41, *Vicia cracca*; s42, *Agrostis canina*; s43, *Alopecurus geniculatus*; s47, *Caltha palustris*; s50, *Carex hirta*; s51, *C. panicea*; s58, *Glyceria fluitans*; s60, *Juncus articulatus*; s70, *Potentilla reptans*; and s74, *Trifolium dubium*

Table 1 Partition of variation results for the floodplain meadow metacommunity at two spatial scales using partial redundancy analysis (RDA) on Hellinger-transformed species composition and abundance data ('community structure')

Source of variation	Response is community structure				p-value
	R^2_{adj} (%)	DF_{model}	DF_{res}	F	
(A) Hydrological heterogeneity (mWTD polynomials)	5.56	3	2436	48.85	< 0.0001
(B) Between-site scale					
Meadow sites (14 'indicator' variables)	34.92	14	2425	94.47	< 0.0001
Hydrological heterogeneity|Meadow sites	2.33	3	2422	31.07	< 0.0001
Meadow sites|Hydrological heterogeneity	31.50	14	2422	88.08	< 0.0001
(C) Within-site scale					
MEM_{ws} (38 staggered spatial variables)	8.58	38	2401	7.03	< 0.0001
Hydrological heterogeneity|(MEM_{ws} + Meadow sites)	1.06	3	2384	16.34	< 0.0001
MEM_{ws}|Hydrological heterogeneity + Meadow sites)	8.11	38	2384	10.42	< 0.0001

Tests are based in 10,000 permutations. The [meadow sites] component represents spatial variation in 15 field sites. MEM_{ws} represents model components that describe within-site spatial variation (38 staggered MEM spatial variables)

R^2_{adj}, multivariate species composition variation explained by model; DF_{model}, degrees of freedom of model; DF_{res}, residual degrees of freedom

$$\gamma = \alpha_1 + \beta_1 + \beta_2, \tag{1}$$

where α_1 is the mean species number in the quadrats, β_1 is the variation (beta-diversity) among quadrats (within a site), β_2 is the variation among field sites and γ is the total species number. The mean species number in the field sites, α_2, is (Eq. 2)

$$\alpha_2 = \alpha_1 + \beta_1. \tag{2}$$

The procedure was carried out using the function adipart() of the vegan (Oksanen et al. 2016).

We dissected multivariate variation in community structure at the within-site and between-site scales and quantified the extent of hydrological control (mWTD) and spatial models (Declerck et al. 2011) (Table 1; Figs. 2 and 3). To dissect community structure into hydrological and spatial components, we followed Declerck et al. (2011). First, we used constrained ordination (Redundancy Analysis or RDA), i.e. multivariate (multiresponse) linear regression followed by a principal component analysis on the fitted values (Legendre, and Legendre 2012; Wollenberg 1977), to construct environmental and spatial models at each spatial scale. We then tested the unique contributions of the hydrological (Hydrological heterogeneity\|Spatial model) and spatial (Spatial model\|Hydrological heterogeneity) components at
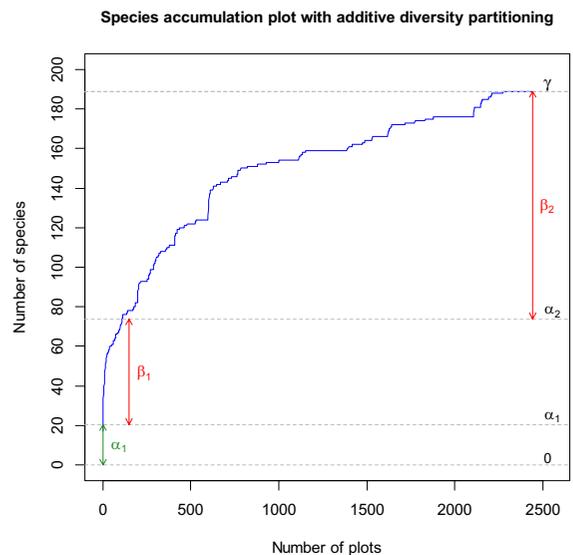

Species accumulation plot with additive diversity partitioning

Fig. 2 Species accumulation plot ('collector curve') with observed components of alpha- and beta-diversity overlaid. Beta-diversity among field sites is the greatest source of variation, i.e. $\beta_2 > \beta_1$. Despite using 15 sites in which nearly 200 species were recorded, the curve has not yet reached saturation. 24 species (12.7%) had frequency less than 10% but greater than 5%; and 115 (61%) had frequency < 5%. Note that $\gamma = \alpha_1 + \beta_1 + \beta_2 = \alpha_2 + \beta_2$. α_1 = mean species number in quadrats; β_1 = beta-diversity among quadrats (= within-field-site beta-diversity); β_2 = beta-diversity among field sites (floodplain meadows); γ = total species number
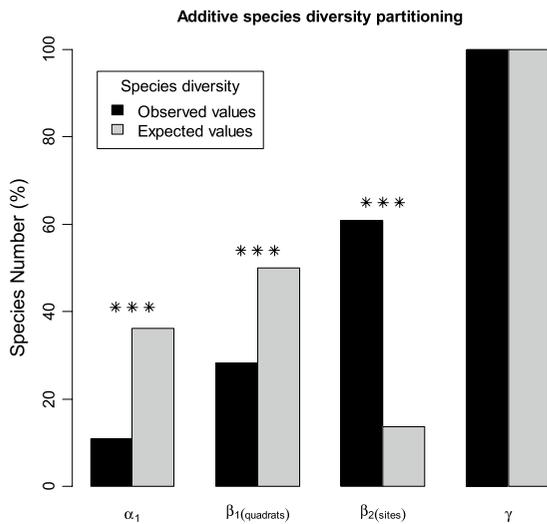
Additive species diversity partitioning

Fig. 3 Additive partitioning of species richness. The estimates of observed and expected values were computed using normalized abundances and are graphically given as percentages. All the observed alpha- and beta-diversity components differ from those expected by chance: α_1 and β_1 are significantly less than expected, whereas β_2 is significantly greater than expected. The effect size for β_2 is conspicuously large. ***p-value < 0.001. α_1 = mean species number in quadrats; β_1 = beta-diversity among quadrats (= within-field-site beta-diversity); β_2 = beta-diversity among field sites (floodplain meadows); γ = total species number

each spatial scale by means of permutation-based variation partitioning (Borcard et al. 1992). Prior to analysis, abundance data were Hellinger-transformed (Legendre and Gallagher 2001), which, in the context of RDA-based direct ordination (Legendre and Legendre 2012), gives the Hellinger distance. This transformation makes species data amenable to testing via RDA analysis.

The above spatial model was built at the between-site scale using 14 indicator variables (Dalgaard 2008) (Meadow Sites component). This set of 14 variables represents factor site, which has 15 levels (one level per field site). We also built a spatial model at the within-site scale; with two separate parts. The first was the same set of indicator variables used at the between-site scale. The second was created using staggered MEM (Moran's eigenvector maps) spatial variables (spatial templates) (Dray et al. 2006), here called 'MEM$_{ws}$' component. This second component represents spatial relationships among quadrats (i.e. within site) and uses 38 MEM variables, arranged in blocks (one block per field site).

This approach is appropriate for nested structures (Declerck et al. 2011) such as those considered here. The class of MEM variables used in this study were previously called Principal Coordinates of Neighbour Matrices or PCNM (Legendre and Legendre 2012). The MEM$_{ws}$ components were created using P. Legendre's "create.MEM.model()" function [published in Declerck et al. 2011]. All RDA tests were carried out using the rda() function of the vegan package in R software.

Generalised Additive Mixed Modelling (GAMM) (Zuur et al. 2010) was employed to study the form of the relationships between the normalized abundance of species and median water table depth (Table 2; Figs. 4, 5, 6, and 7). Only 74 species with relative frequency > 0.05 were tested. GAMM regression was carried out with function gamm() of package mgcv (Wood 2011) and using the so-called P- splines (Eilers and Marx 1996), which combine a B-spline basis with a discrete penalty on the basis coefficients. Between-site variability was modelled by means of a random factor. Spatial autocorrelation in residuals was investigated via experimental semivariograms (Cressie 1993) estimated with function Variogram() of package nlme (Pinheiro et al. 2016) and, when needed (i.e. in the presence of spatial autocorrelation in GAMM residuals), models were re-fitted introducing autoregressive processes (Pinheiro and Bates 2000) via the argument 'correlation' of gamm().

Results

One hundred and eighty-nine (189) species (Table S2 in Online Resource 1) were recorded, although only 50 of them (26.4%) had a relative frequency > 10%. Among these, 49% were 'graminoids' (Poaceae, Cyperaceae and Juncaceae) and 51% were 'forbs' (all other species). The forbs *Ranunculus acris*, *Cardamine pratensis* and *Rumex acetosa*, and the grasses *Anthoxanthum odoratum*, *Cynosurus cristatus*, *Holcus lanatus* and *Poa trivialis* were the most frequent species. The average value ($n = 2440$ quadrats) for median Water Table Depth (mWTD) was 0.490 with 95% CI (0.480, 0.499); its standard deviation was 0.232 with 95% CI (0.226, 0.239).

The main species gradients in the metacommunity (Fig. 1), obtained without external reference to environmental variability, were strongly associated

Table 2 Generalised Additive Mixed Modelling results for 74 species with frequency across quadrats ($n = 2440$) greater than 5%

Species	Freq. (%)	F (edf)	p-value	R^2 (%)	SR	σ^2_S	σ^2	σ_S/σ	Φ (AR)
Agrostis stolonifera	53.3	71.98 (3.02)	<0.0001	2.48	C (−)	0.0279	0.0445	0.79	0.3671
Alopecurus geniculatus	11.2	7.75 (1.60)	0.0016	0.89	C (−)	0.0003	0.0031	0.29	0.1973
Anthoxanthum odoratum	68.3	20.30 (3.21)	<0.0001	1.69	HS	0.0107	0.0169	0.79	0.3100
Arrhenatherum elatius	8.9	52.83 (4.71)	<0.0001	19.60	SS (+)	0.0003	0.0021	0.35	0.2595
Bellis perennis	9.0	5.36 (2.10)	0.0043	0.17	X (+)	0.0000	0.0003	0.29	0.1725
Briza media	5.1	32.58 (4.60)	<0.0001	9.42	HS	0.0001	0.0007	0.42	0.2044
Bromus commutatus	16.8	39.52 (3.57)	<0.0001	8.20	SS (+)	0.0005	0.0014	0.57	0.2578
Bromus racemosus	21.2	11.34 (3.97)	<0.0001	4.89	HS	0.0015	0.0043	0.59	0.4293
Caltha palustris	10.6	11.49 (2.23)	<0.0001	1.94	C (−)	0.0014	0.0070	0.44	0.1419
Cardamine pratensis	20.5	9.48 (2.43)	<0.0001	2.92	C (−)	0.0062	0.0282	0.47	0.4330
Carex disticha	60.9	11.81 (1.00)	0.0006	2.59	L (−)	0.0004	0.0018	0.49	0.2037
Carex nigra	18.0	7.94 (2.03)	0.0003	3.77	C (−)	0.0005	0.0123	0.21	0.2998
Centaurea nigra	40.7	21.34 (3.82)	<0.0001	0.97	HS	0.0091	0.0205	0.67	0.2795
Cynosurus cristatus	61.2	32.74 (2.00)	<0.0001	1.69	X (+)	0.0146	0.0169	0.93	0.3725
Dactylis glomerata	15.6	241.4 (2.00)	<0.0001	30.50	C (+)	0.0011	0.0028	0.63	0.2824
Deschampsia cespitosa	20.5	18.18 (1.00)	<0.0001	0.01	L (−)	0.0011	0.0095	0.34	0.2095
Eleocharis palustris	9.0	7.64 (2.84)	0.0001	2.89	C (−)	0.0036	0.0128	0.53	0.2707
Elymus repens	7.1	13.53 (3.39)	<0.0001	1.58	C (−)	0.0003	0.0022	0.36	0.1532
Festuca arundinacea	5.7	7.00 (2.18)	0.0007	0.48	C (−)	0.0006	0.0031	0.45	0.1389
Festuca rubra	58.4	21.58 (2.68)	<0.0001	1.33	X (+)	0.0258	0.0219	1.08	0.2278
Filipendula ulmaria	44.8	3.04 (2.02)	0.0474	0.35	X (−)	0.0060	0.0230	0.51	0.2173
Galium palustre	6.6	5.80 (2.44)	0.0018	0.90	C (−)	0.0000	0.0002	0.37	0.1768
Galium verum	7.8	19.09 (3.01)	<0.0001	2.05	HS	0.0005	0.0030	0.42	0.1522
Glyceria fluitans	13.9	12.23 (4.41)	<0.0001	1.15	SS (−)	0.0027	0.0115	0.48	0.2478
Lathyrus pratensis	31.0	23.51 (4.29)	<0.0001	7.51	HS	0.0004	0.0021	0.41	0.1127
Leontodon hispidus	6.8	6.24 (3.86)	<0.0001	0.33	HS	0.0002	0.0006	0.56	0.1635
Leucanthemum vulgare	7.7	54.74 (6.33)	<0.0001	30.70	HS	0.0006	0.0018	0.56	0.3401
Lolium perenne	58.2	44.37 (2.77)	<0.0001	16.10	C (+)	0.0039	0.0153	0.51	0.3736
Lotus corniculatus	16.0	18.36 (2.00)	<0.0001	3.20	X (+)	0.0005	0.0031	0.42	0.2302
Lychnis flos-cuculi	8.8	9.93 (5.16)	<0.0001	4.53	HS	0.0000	0.0002	0.44	0.2025
Lysimachia nummularia	8.0	20.79 (3.02)	<0.0001	0.82	C (−)	0.0000	0.0008	0.25	0.0370
Oenanthe fistulosa	6.4	4.32 (1.32)	0.0280	0.94	C (−)	0.0001	0.0011	0.37	0.1997
Oenanthe silaifolia	8.7	14.47 (3.47)	<0.0001	0.60	C (−)	0.0001	0.0009	0.32	0.0402
Plantago lanceolata	42.0	10.84 (3.88)	<0.0001	3.68	HS	0.0014	0.0097	0.38	0.2552
Polygonum amphibium	23.9	13.04 (2.28)	<0.0001	2.09	C (−)	0.0006	0.0038	0.40	0.2870
Potentilla reptans	11.1	15.16 (3.83)	<0.0001	3.52	HS	0.0001	0.0009	0.35	0.3575
Prunella vulgaris	15.9	14.16 (4.80)	<0.0001	4.63	HS	0.0003	0.0014	0.49	0.1760
Ranunculus acris	77.0	16.11 (2.00)	<0.0001	0.34	HS	0.0012	0.0083	0.38	0.2348
Ranunculus bulbosus	11.4	31.84 (3.84)	<0.0001	9.47	HS	0.0003	0.0015	0.49	0.0690
Ranunculus repens	56.8	4.80 (2.00)	0.0083	2.19	X (−)	0.0235	0.0381	0.79	0.3087
Rumex acetosa	64.7	13.00 (2.43)	<0.0001	1.10	X (+)	0.0010	0.0023	0.65	0.1134
Sanguisorba officinalis	34.2	16.71 (2.72)	<0.0001	2.37	HS	0.0166	0.0391	0.65	0.2334
Senecio aquaticus	21.6	7.98 (2.38)	0.0002	1.14	C (−)	0.0016	0.0036	0.67	0.3181
Taraxacum officinale	46.1	15.31 (2.34)	<0.0001	3.25	X (+)	0.0007	0.0020	0.59	0.1631
Trifolium pratense	43.7	4.99 (2.00)	0.0069	0.49	HS	0.0020	0.0068	0.54	0.2343
Trifolium repens	57.3	26.29 (2.00)	<0.0001	1.04	HS	0.0038	0.0089	0.65	0.1519

Table 2 (continued)

Species	Freq. (%)	F (edf)	p-value	R^2 (%)	SR	σ^2_S	σ^2	σ_S/σ	Φ (AR)
Trisetum flavescens	13.6	95.3 (5.83)	< 0.0001	34.4	HS	0.0010	0.0035	0.28	0.3254
Vicia cracca	16.4	12.16 (2.60)	< 0.0001	1.45	C (+)	0.0004	0.0027	0.37	0.1342

The reported R^2-, F-, and p-value correspond to the smoothers used to model the relationship between species' normalized abundance and median water table depth. Models for the species *Agrostis capillaris*, *Alopecurus pratensis*, *Carex hirta*, *Cerastium fontanum*, *Cirsium arvense*, *Festuca pratensis*, *Holcus lanatus*, *Hordeum secalinum*, *Luzula campestris*, *Phleum pratense*, *Poa trivialis*, *Rhinathus minor*, and *Silaum silaus* did not converge appropriately. Models for *Agrostis canina*, *Carex acuta*, *C. acutiformis*, *C. panicea*, *Juncus acutiflorus*, *J. articulatus*, *J. effusus*, *Leontodon autumnalis*, *Poa pratensis*, *Ranunculus flammula*, *Trifolium dubium*, *Stellaria graminea*, and *Succisa pratensis* were not significant (p-value > 0.05)

Freq., relative frequency across quadrats ($n = 2440$); *edf*, estimated degrees of freedom; *SR*, shape of relationship; σ^2_S, between-site variance; σ^2, residual variance; Φ (*AR*), parameter of the autoregressive model used to control for spatial autocorrelation in residuals; *L*, linear; *X*, curvilinear convex; *C*, curvilinear concave; *HS*, hump-shaped; *SS*, sigmoid-shaped; (+), increasing; (−), decreasing. See Fig. 4 and Online Resource 1, S6–S8
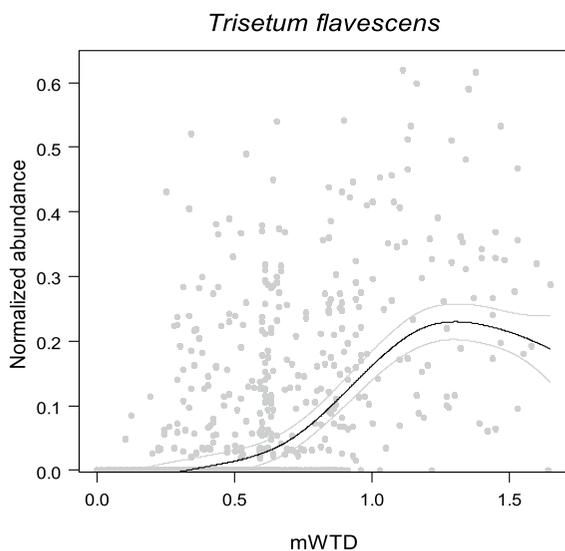

Fig. 4 Observed (dots) and fitted (smoother with 95% confidence bands) relationship between *Trisetum flavescens* normalized abundance and median water table depth. The species had frequency across quadrats ($n = 2440$) = 13.6%. This hump-shaped relationship explains $R^2 = 34.4\%$ of the observed variation ($F = 95.3$ on 5.83 estimated degrees of freedom; p-value < 0.0001). Between-site observed variance is $\sigma^2_S = 0.0010$ ($\sigma_S = 0.0312$) and residual variance is $\sigma^2 = 0.0035$ ($\sigma = 0.0590$). The autoregressive model included to control for spatial autocorrelation in model residual has parameter $\Phi = 0.3254$. See Table 2

with hydrological heterogeneity (in a diagonal direction). The driest end corresponded to species such as *Ranunculus bulbosus*, and *Trisetum flavescens*; the wettest end, to species such as *Persicaria amphibia*, *Juncus articulatus*, *Senecio aquaticus* and *Glyceria fluitans*. Grasses and forbs were found throughout the overlaid hydrological gradient, but grasses tended to avoid the driest niches (Fig. 1). Page: 9

Variation in species abundance was much better explained by mWTD for species that one would consider good 'indicators' of dry soil conditions ($R^2 = 7.5$–34%) compared to those indicative of the wet soils ($R^2 = 0.01$–3.8%) (Table 2).

Beta-diversity component, the between-site—β_2, is the largest observed component (Fig. 2); moreover, it is significantly greater than expected by chance (Fig. 3). Within-site diversity—β_1 appeared to be smaller than β_2. That shows the greatest source of plant diversity variation occurs between, not within field sites. Besides, β_1, the beta-diversity component at the within-site scale (within field sites) is significantly smaller than expected by chance.

The contribution of hydrological heterogeneity to the explanation of beta-diversity, in general terms, is c. 6% of multivariate variation in community structure (Table 1). At the between-site scale (Table 1), both the [Hydrological heterogeneity|Meadow sites] and the [Meadow sites|Hydrological heterogeneity] components are significant, suggesting that meadow community structure is explained by both hydrological heterogeneity and meadow identity. However, meadow identity explained about thirteen times more variation in meadow community structure than hydrological heterogeneity. This indicates the presence of other, potentially strong, drivers that were not measured in this study.

At the within-site scale (Table 1), both the [Hydrological heterogeneity|(MEM$_{ws}$+Meadow sites)] and the
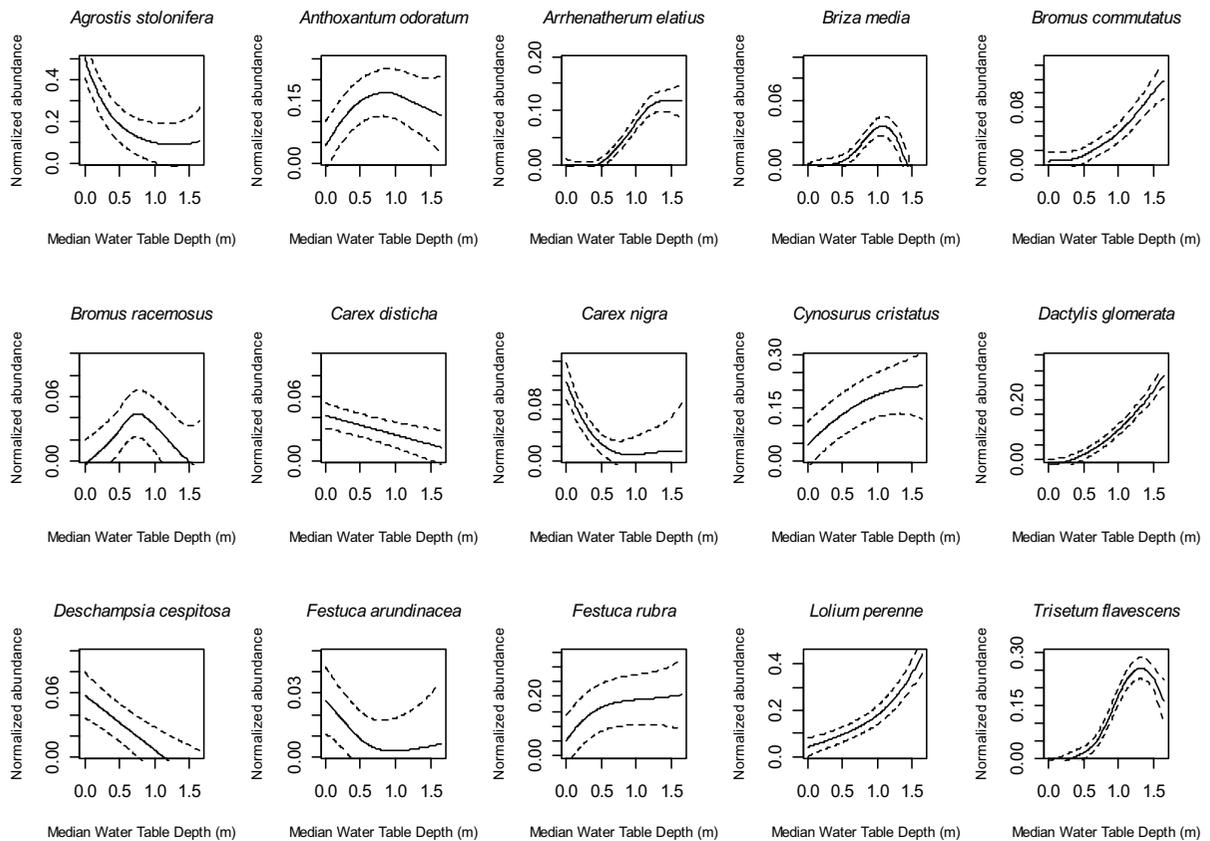
Fig. 5 Smoothers with 95% C.I. (dashed lines) corresponding to the GAMMs fitted for 15 frequent graminoids found in English floodplain meadows. The smoothers depict the relationship between normalized abundance and median water table depth. For statistical details, see Table 2

the [MEM_ws|Hydrological heterogeneity + Meadow sites] components are significant. This indicates that meadow community structure is explained by both hydrological heterogeneity and the fine-grained spatial models (MEM templates), which may be due to either spatially structured non-hydrological variation of the physical environment, unspecified biological processes (also spatially structured), or both. In terms of explained variation in meadow structure, the component [MEM_ws|Hydrological heterogeneity + Meadow sites] is nearly eight times greater than [Hydrological heterogeneity|MEM_ws + Meadow sites] component, which indicates the relative strength of unspecified ecological factors other than hydrological heterogeneity at this within-field-site scale.

The shapes of individual species' responses are displayed in Figs. 5 and 6. Significant GAMMs were fitted for 65% (48 out of the 74) of tested species

(i.e. of the species with relative frequency > 0.05), with average model fit adj.-R^2 = 4.3% (Table 2 and Figs. 4, 5, 6, and 7). Monotonic and hump-shaped relationships between the normalised abundance of species and mWTD constituted 63% and 37% of the responses, respectively. Figures S6–S8 (Online Resource 1) confirm the impression that all hydrological descriptors convey essentially the same information.

Median Water Table Depth was considered the best descriptor for explanatory purposes. The ten hydrological descriptors initially considered in this work are correlated among themselves (Online Resource 1, Table S3; Fig. S1) and thereby convey essentially the same information, which becomes clearer when data are considered site by site (Online Resource 1, Figs. S2–S4). For this reason, the choice of median Water Table Depth (mWTD) as the best
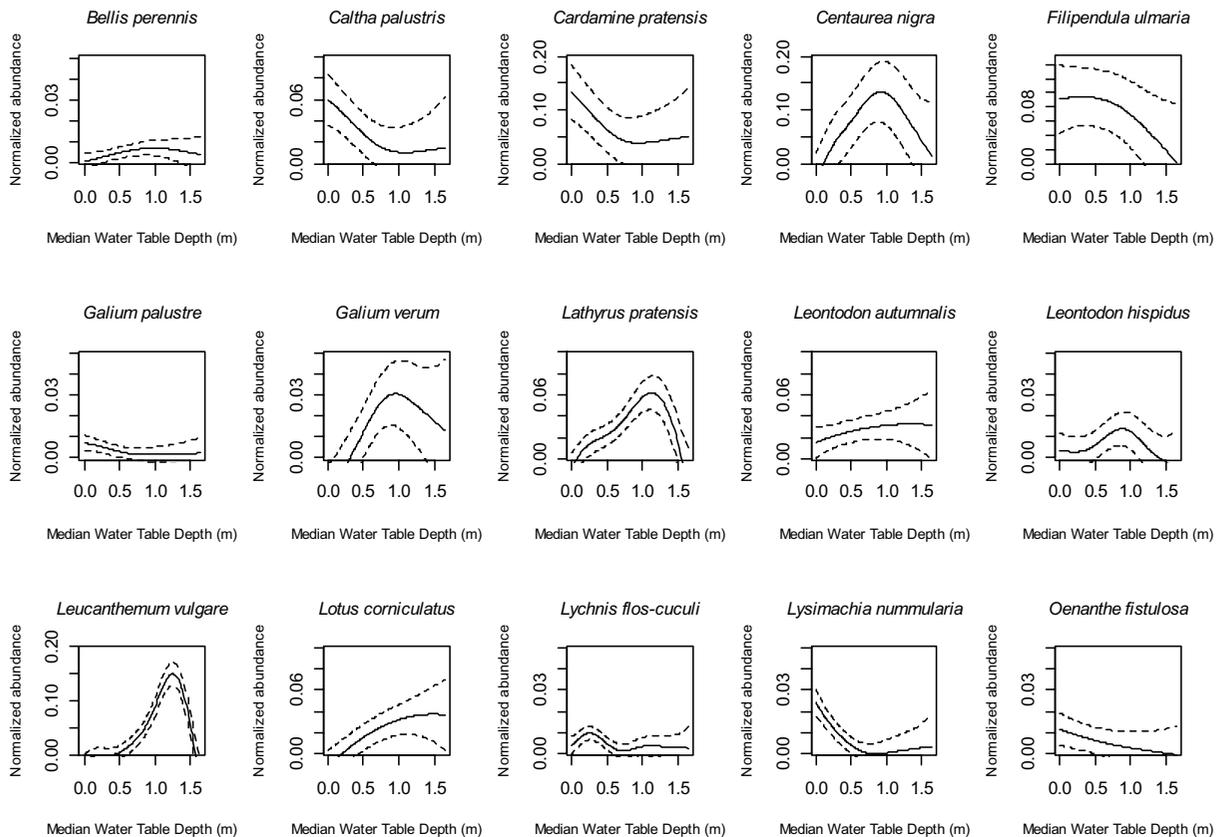
Fig. 6 Smoothers with 95% C.I. (dashed lines) corresponding to the GAMMs fitted for 15 frequent forbs found in English floodplain meadows. The smoothers depict the relationship between normalized abundance and median water table depth. For statistical details, see Table 2

hydrological descriptor for additive (GAMM) and linear (RDA) explanatory modelling purposes has been based on judgement that considered statistical and pragmatic criteria. Thus, and given co-linearity, preference has been given (i) to direct measurements on a continuous scale (e.g. AWTD or mWTD) over derived measurements (e.g. EA or EB) or measurements on a discrete scale (e.g. DF or DB), (ii) to comparatively symmetric descriptors (mWTD) over comparatively skewed descriptors (e.g. DF or DA) and (iii) to descriptors lacking, also comparatively, extreme values (Online Resource 1, Fig. S5).

Discussion

Between-site beta-diversity component (β_2) is spatially structured. It is the largest diversity component

and, besides, it is (much) greater than expected by chance alone (Figs. 2 and 3). This means that the greatest observed source of variation in meadow structure (61% of species) occurs at this scale, i.e. among field sites (Crist et al. 2003; Summerville et al. 2003). On the other hand, the largest contribution of hydrological heterogeneity to the explanation of beta-diversity also occurs at this scale, with hydrological heterogeneity at the between-site scale contributing to the explanation of community structure twice that at the within-site scale (Table 1). This confirms the insights from Fig. 1. However, the amount of variability in meadow structure explained by spatial hydrological heterogeneity at this scale is relatively small.

Most variability in between-site meadow structure was unexplained by spatial hydrological heterogeneity, which indicates that temporal factors or the presence of unmeasured processes (Declerck et al. 2011;
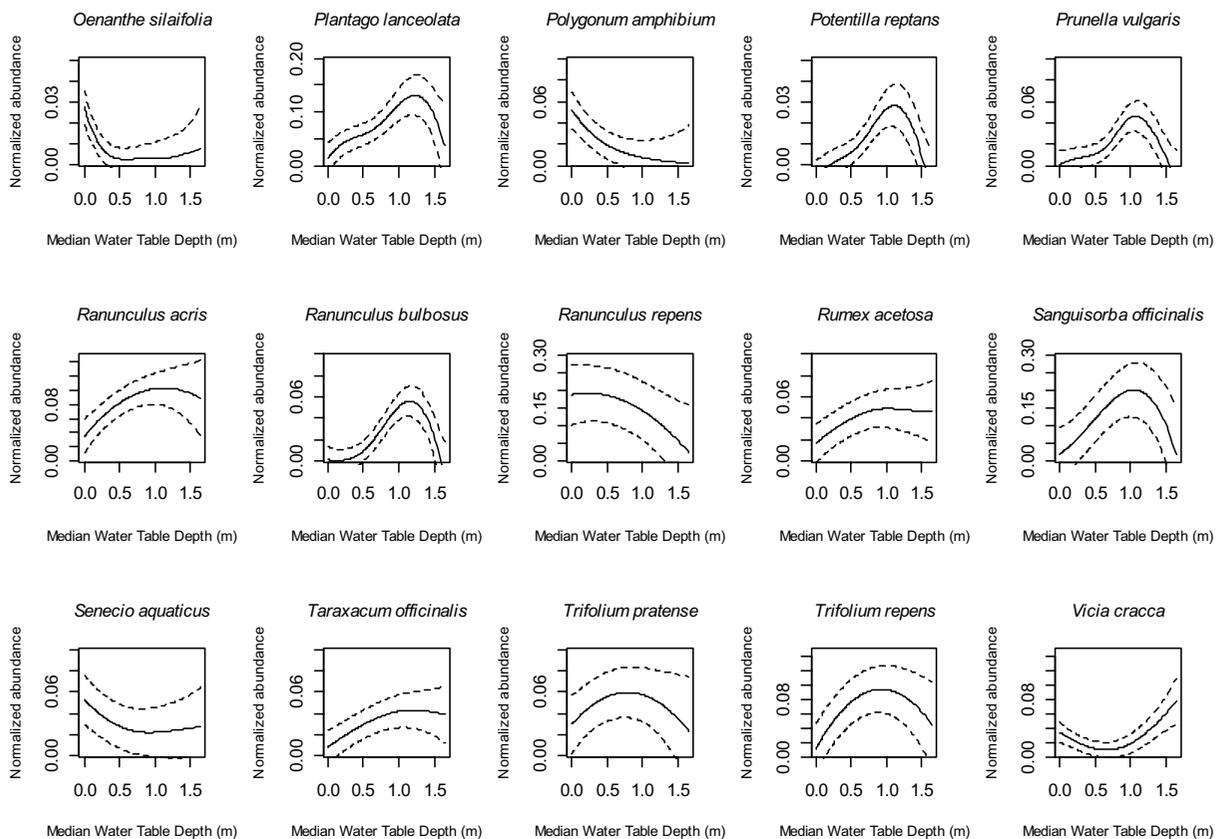
Fig. 7 Smoothers with 95% C.I. (dashed lines) corresponding to the GAMMs fitted for 15 frequent forbs found in English floodplain meadows. The smoothers depict the relationship between normalized abundance and median water table depth. For statistical details, see Table 2

Dray et al. 2012) can have strong effect. Long-term studies on floodplain meadows (e.g. Ermakova and Sugorkina 2016; Shepeleva 2018) suggest that the frequency and duration of floods drive vegetation composition. At the between-site spatial scale, non-specified variation of the physical environment (e.g. climate gradients or geological variation) plays a substantial role (Leibold et al. 2004; Cottenie 2005; Kucherov et al. 2020). Given the usual structure of the landscape in industrialized countries, it seems likely that the role of dispersal limitation (Wagner et al. 2013) may be relevant also in the case of floodplain meadows. Remaining English floodplain meadows are isolated from each other (Rothero et al. 2016). The inclusion in the relevant conservation network of as many and as environmentally diverse field sites as possible will be beneficial, because (as strongly suggested by Fig. 2) it will likely imply the inclusion in the system of new meadow species.

Within-site beta-diversity component, β_1 (Figs. 2 and 3), is smaller than the between-site beta-diversity component and, besides, it is significantly less (28% of species) than expected just by chance (50% of species). The contribution of spatial hydrological heterogeneity to the explanation of beta-diversity at the within-site scale is about half that at the between-site scale, but still significant (Table 1).

At this local spatial scale, besides the contribution of hydrological heterogeneity to the explanation of beta-diversity, there exists a strong [MEM$_{ws}$|Hydrological heterogeneity + Meadow sites] component. Since the only descriptor of the physical environment that has been introduced in the environmental model is spatial hydrological heterogeneity, this strong component indicates (Declerck et al. 2011;

Dray et al. 2012) that meadow community structure is locally (co-)explained also by fine-grained non-hydrological variation of the physical environment, by unspecified processes with biotic origin (e.g. clonal dispersion), or by both (Leibold et al. 2004; Cottenie 2005).

Species' individual responses are well explained by spatial hydrology. The GAMM results (Table 2) show that the 65% of meadow species that were sufficiently frequent to be tested respond to hydrological heterogeneity in a way that is consistent both with Fig. 1 and the environmental/spatial models summarised in Table 2. The amount of variance in community structure explained by the hydrological niche is similar in both cases. Since appropriate sampling methods and data from 15 field sites have been used, it seems reasonable to consider these results as widely representative of English species-rich floodplain meadows. Consistent with the previously reported segregation patterns (Silvertown et al. 1999), monotonic responses (63% of the fitted models) were either increasing or decreasing with increasing mWTD (i.e. with increased soil drying), thereby contributing to species segregation over hydrological heterogeneity. The hump-shaped responses (37% of the fitted models) often, but not always, contribute to segregation. For example, the graphical comparison (Fig. 5) of *Bromus racemosus*, *Anthoxanthum odoratum*, *Briza media* and *Trisetum flavescens* shows that these species substitute each other as conditions are getting drier. By contrast, *Ranunculus bulbosus*, *Potentilla reptans*, *Prunella vulgaris* and *Sanguisorba officinalis* (Fig. 7), albeit with differing normalised abundances, appear to occupy essentially the same hydrological niche.

These results are similar to those obtained for an Iberian *dehesa* meadows and an alpine grassland (García-Baquero et al. 2016), although with the difference that in the Iberian ecosystems, in which only presence–absence data were used, the average model fit was estimated to be adj.-$R^2 = c.20\%$, i.e. about four times greater than the current estimation for floodplain meadows (adj.-$R^2 = c.5\%$). This difference might be accounted for via different hypothesised explanations, but the following explanations may be of importance. First, only presence–absence data were used in the Iberian case, while normalised abundance was used in the floodplain meadows case. Second, both within- and between-site

variation in community structure and hydrological heterogeneity were used in the floodplain meadows case, whereas only within-site variation was used in the Iberian case. The inclusion of between-site variability increases the representativeness of the underlying data and enlarges the range of the hydrological gradient studied here, but it may also increase the noise in the data due to unexplained random variation.

Further work is clearly needed on how relevant functional traits rule fundamental niches over hydrological gradients and how this translates into the realized niche within real communities (Mcgill et al. 2006). For this purpose, the existing database (containing community, environment and spatial data) should be complemented with information on functional traits, such as resistance to water loss on drying (Baastrup-Spohr et al. 2015); physiological traits, such as stomatal conductance or water use efficiency, might also be potentially useful (Belluau and Shipley 2017). Plant phylogenies would also be useful and can be obtained from public databases (Qian and Jin 2016). Finally, novel statistical approaches that allow for linking observational community data with phylogeny, traits, environmental variables and space are already available and can be implemented with R software (Pavoine et al. 2011).

The modelling process here implemented via GAMMs (a flexible approach for univariate regression) and RDA (a technique based on multivariate linear regression) has tested, broadly speaking, the null hypothesis that the distribution of vascular plant species in floodplain meadows is not related with hydrological heterogeneity that occurs in space. For so doing, both species composition and hydrological heterogeneity have been expressed at the level of evaluation units (quadrats), using, for the latter variable, a location measure (the median) of a hydrological descriptor (Water Table Depth) which was in fact measured also in time. This means that in order to gain the ability of testing for the spatial hydrological niche, temporal hydrological variation has been excluded. Temporal aspects of the hydrological niche, such as regeneration (Grubb 1977) and duration of floods (Shepeleva 2018), are important for vegetation dynamics. Because, for a given quadrat, change in water table depth can be expressed (or represented) as a function of time,

the relatively new field of Functional Data Analysis (Ramsay and Silverman 2005) and, in particular, the several available techniques for functional regression might prove to provide the appropriate statistical tools.

Conclusions

We conclude that median Water Table Depth (mWTD) is the best of the ten available hydrological descriptors, at least for its use as an explanatory variable of meadow community structure in additive and linear spatial models. While this choice allows for modelling the spatial hydrological niche of meadow plants, it does not facilitate observation of temporal variation.

Most tested species (65%), forbs as well as graminoids, responded significantly to hydrological heterogeneity, with the normalised abundance (cover) of species being related to hydrological heterogeneity either with monotonic (increasing or decreasing) or with hump-shaped responses. Species hydrological optima (maximum normalised abundance) are observed throughout the whole measured hydrological gradient.

Hydrological heterogeneity drives, c.6% of meadow community structure (i.e. species abundance and composition), and does so at two increasing spatial scales (within- and between-site). Partitioning of plant beta-diversity and the subsequent explanation of this partitioning in terms of hydrological versus unmeasured variables have led us to suggest that a conservation strategy for English meadows based on the present results should promote not only the conservation of local hydrological regimes, but also the inclusion of as many distinct hydrological systems within the network of sites with conservation designations. Further research into the effect of restoring connectivity between field sites on plant community structure is likely to be relevant for conservation purposes, because the high inter-site beta-diversity identified here could reflect dispersal limitation or impeded gene flow between sites.

Declarations

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