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 fifteen 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, specially, the inclusion in the conservation system of as many and environmentally varied local plant communities as possible.

Keywords: beta-diversity; meta-community; median water table depth; multivariate multiscale spatial analysis; species co-existence.

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). When this occurs, 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 (Mahajan and Tuteja 2006), 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; Atkinson and Urwin 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 2016). In these studies, 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 meta-community (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 fifteen 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 have been analysed to i) assess which hydrological descriptor performs best for explanatory purposes; ii) dissect the spatial architecture of the above meta-community; 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 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). The cover of vascular plant species was recorded (Table S2) in c.160 (on average) systematically placed 1m² quadrats (= evaluation units) within each 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 (focusing on symmetry, extreme values and co-linearity) demonstrated the similarity of the information conveyed by the ten hydrological descriptors (Online recourse 1, Fig. S1 and S5), particularly once between-site variability has been taken into account (Online recourse 1, Fig. 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 meta-community**, 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 (equation 1): $\gamma = \alpha_1 + \beta_1 + \beta_2$, 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 (equation 2): $\alpha_2 = \alpha_1 + \beta_1$. 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 and Fig. 2-3). 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 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 Neighbor 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; Fig. 4-7). 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

189 species (Table S2 in Online Resource 1) were recorded, although only 50 of them (26.4%) had 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 meta-community (Fig. 1), obtained without external reference to environmental variability, are strongly associated with hydrological heterogeneity (in a diagonal direction). The driest end corresponds to species such as *Ranunculus bulbosus*, and *Trisetum flavescens*; the wettest end, to species such as *Polygonum amphibium*, *Juncus articulatus*, *Senecio aquaticus* and *Glyceria fluitans*. Grasses and forbs are found throughout the overlaid hydrological gradient, but grasses tend to avoid the driest niches (Fig. 1). Page: 8

The variation in abundance of the species that one would consider good ‘indicators’ of the dry soil conditions is much better explained by mWTD ($R^2 = 7.5\text{-}34\%$) comparing to the wet soil specialists (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, which indicates 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 strong latent processes.

At the within-site scale (Table 1), both the [Hydrological heterogeneity | (MEM_{ws} + Meadow sites)] and 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 the Figures 5-6. 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 $\text{adj.-}R^2 = 4.3\%$ (Table 2 and Fig. 4-7). Monotonic and hump-shaped relationships between the normalised abundance of species and mWTD constituted 63% and 37% of the responses, respectively. The Figures S6-S8 (Online Resource 1) confirm the impression that all hydrological descriptors convey essentially the same information.

Discussion

Median Water Table Depth is best descriptor for explanatory purposes. The ten hydrological descriptors initially considered in this work are correlated among themselves (Online Recourse1, Table S3 and Fig. S1) and thereby convey essentially the same information, which becomes clearer when data are considered site by site (Online recourse 1, Fig. S2-S4). For this reason, the choice of median Water Table Depth (mWTD) as the best hydrological descriptor for additive (GAMM) and linear (RDA) explanatory modeling purposes has been based on judgment 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 recourse 1, Fig. S5). These criteria led us to judge that the use of mWTD was the best descriptor among the available ones for explanatory purposes.

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 (Fig. 2-3). 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 Figure 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 strong latent processes (Dray et al. 2012; Declerck et al. 2011) can have larger effect. Long-term studies on floodplain meadows (e.g. Ermakova and Sugorkina 2016; Shepeleva 2018) suggest frequency and duration of floods driving vegetation composition. At the between-site spatial scale, non-specified variation of the physical environment (e.g. climate gradients or geological variation) play 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 net of as many and 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 (Fig. 2-3), 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 (Dray et al. 2012; Declerck et al. 2011) 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 65% of meadow species that were sufficiently frequent to be tested, respond to hydrological heterogeneity in a way that is consistent both with Figure 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 $\text{adj.-}R^2 = \text{c.}20\%$, i.e. about four times greater than the current estimation for floodplain meadows ($\text{adj.-}R^2 = \text{c.}5\%$). This difference might be accounted for via different hypothesised explanations, but the next facts are likely to provide credible explanations. 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 no doubt increases the representativeness of the underlying data and contributes to enlarge the range of the hydrological gradient here studied, but it also likely increases noise (unexplained random variation).

Further work 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) seems likewise to be promising. For this purpose, the existing database (which by now contains 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 needed, but they can be easily 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.

4.6. 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 modeling 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, after our estimation, 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 latent and hydrological processes, have led us to suggest that a conservation strategy of English meadows based on the present results should promote not only the preservation of local hydrological regimes, but, specially, the inclusion in the conservation system of as many and environmentally varying field sites as feasible. Further research about the effect of restoring connectivity between field sites on meadow community structure is likely to be relevant for conservation purposes.

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Declarations

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Availability of data and material. The datasets generated during and analysed during the current study are available from the corresponding author on reasonable request.

Code availability R code is supplied in ESM

Authors' contributions. DG originally formulated the idea, DG, HW, GG-B developed methodology, HW conducted fieldwork, HW, DG generated data for analysis, DG, GG-B developed the mathematical models, GG-B performed statistical analyses and wrote the manuscript.

References

- Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson NG (2011) Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14:19-28.
- Araya YN, Silvertown J, Gowing DJ, McConway KJ, Linder HP, Midgley G. (2011) A fundamental, eco-hydrological basis for niche segregation in plant communities. *New Phytol.* 189:253-258.
- Araya YN, Silvertown J, Gowing DJ, McConway KJ, Linder HP, Midgley G (2012) Do niche-structured plant communities exhibit phylogenetic conservatism? A test case in an endemic clade. *J. of Ecol.* 100:1434-1439.
- Atkinson NJ, Urwin PE (2012) The interaction of plant biotic and abiotic stresses: from genes to the field. *J. of Exp. Bot.* 63:3523-3543.
- Baastrup-Spohr L, Sand-Jensen K, Nicolajsen SV, Bruun HH, Halvorsen R (2015) From soaking wet to bone dry: predicting plant community composition along a steep hydrological gradient. *J. of Veg. Sci.* 26:619-630. DOI: [10.1111/jvs.12280](https://doi.org/10.1111/jvs.12280)
- Belluau M, Shipley B (2017) Predicting habitat affinities of herbaceous dicots to soil wetness based on physiological traits of drought tolerance. *Ann. of Bot.* 119:1073-1084.
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the Spatial Component of Ecological Variation. *Ecol.* 73:1045-1055. doi.org/10.2307/1940179
- Chesson P (2000a) Mechanisms of Maintenance of Species Diversity. *Annual Rev. of Ecol. and Syst.* 31:343-366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>
- Chesson P (2000b) General theory of competitive coexistence in spatially-varying environments. *Theor. Popul. Biol.* 58:211-237.

370 Chesson PL, Warner RR (1981) Environmental Variability Promotes Coexistence in
 371 Lottery Competitive Systems. *Am. Naturalist*. 117:923-943.

372 Chesson PL (1985) Coexistence of competitors in spatially and temporally varying
 373 environments: A look at the combined effects of different sorts of variability. *Theor. Popul.*
 374 *Biol.* 28:263-287.

375 Cottenie K (2005) Integrating environmental and spatial processes in ecological
 376 community dynamics. *Ecol. Lett.* 8:1175-1182.

377 Cressie NAC (1993) *Statistics for Spatial Data*. Wiley, New York.

378 Crist TO, Veech JA, Gering JC, Summerville KS (2003) Partitioning species diversity
 379 across landscapes and regions: A hierarchical analysis of alpha, beta, and gamma diversity.
 380 *Am. Naturalist*. 162:734-743. DOI: 10.1086/378901

381 Dalgaard P (2008) *Introductory Statistics with R*, 2 nd edn. Springer, New York.

382 Declerck SAJ, Coronel JS, Legendre P, Brendonck L (2011) Scale dependency of
 383 processes structuring metacommunities of cladocerans in temporary pools of High-Andes
 384 wetlands. *Ecography*. 34:296-305. <https://doi.org/10.1111/j.1600-0587.2010.06462.x>

385 Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive
 386 framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Modelling*.
 387 196:483-493.

388 Dray S, Péliissier R, Couteron P, Fortin M, Legendre P, Peres-Neto P, Bellier E, Bivand
 389 R, Blanchet FG, Ceres M, Dufour A-B, Heegaard E, Jombart T, Munoz F, Oksanen J,
 390 Thioulouse J, Wagner H (2012) Community ecology in the age of multivariate multiscale
 391 spatial analysis. *Ecol. Monographs*. 82:257-275. 10.1890/11-1183.1.

392 Eilers PHC, Marx BD (1996) Flexible Smoothing with B-splines and Penalties.
 393 *Statistical Sci.* 11:89-102.

394 Ermakova IM, Sugorkina NS (2016) Study of Plant Communities on Zalidovskie Luga
395 Meadow. Youcaxton Publications, Oxford.

396 García-Baquero G, Silvertown JS, Gowing DJ, Valle CJ (2016) Dissecting the
397 hydrological niche: soil moisture, space and lifespan. *J. of Veg. Sci.* 27:219-226.

398 Gowing D, Lawson C, Youngs E, Barber K, Rodwell J, Prosser M, Wallace H,
399 Mountford J, Spoor G (2002) The water regime requirements and the response to
400 hydrological change of grassland plant communities: DEFRA-commissioned project
401 BD1310, Final report to the Department for Environment, Food and Rural Affairs. Cranfield
402 University, Silsoe, UK.

403 Grubb PJ (1977) The maintenance of species richness in plant communities: The
404 importance of the regeneration niche. *Biol. Reviews of the Cambridge Philosophical Soc.*
405 52:107-145.

406 Hutchinson GE (1957) Population studies. *Animal ecology and demography. Concluding*
407 *remarks. Cold Spring Harbor Symposia on Quantitative Biology.* 22:415-427.

408 Kassen R (2002) The experimental evolution of specialists, generalists, and the
409 maintenance of diversity. *J. of Evol. Biol.* 15:173-190.

410 Kruskal JB (1964) Nonmetric multidimensional scaling: A numerical method.
411 *Psychometrika.* 29:115-129.

412 Kucherov IB, Shchukina KV, Tatarenko IV, Parinova TA, Volkov AG, Neskryabina ES,
413 Cherednichenko OV, Savinykh NP, Perestoronina ON, Shabalkina SV, Pyzhikova EM,
414 Tsyrenova MG (2020) Great burnet floodplain meadows along Euro-Siberian longitudinal
415 gradient. *Botanical Journal.* 105:1169–1190.

416 Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for
417 ordination of species data. *Oecologia.* 129:271-280.

418 Legendre P, Legendre L (2012) Numerical Ecology, 3 rd edn. Elsevier Science,
 419 Amsterdam.

420 Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt
 421 RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity
 422 concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7: 601-613.

423 Leibold MA (1995) The Niche Concept Revisited: Mechanistic Models and Community
 424 Context. *Ecol.* 76:1371-1382.

425 Mahajan S, Tuteja N (2005) Cold, salinity and drought stresses: An overview. *Arch. of*
 426 *Biochem. and Biophys.* 444:139-158.

427 McGill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding Community Ecology
 428 from Functional Traits. *Trends in Ecol. and Evol.* 21. 178-85. 10.1016/j.tree.2006.02.002.

429 Mucina L, Bueltmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A, Šumberová K,
 430 Willner W, Dengler J, Gavilán R, Chytrý M, Hájek M, Di Pietro R, Iakushenko D, Pallas J,
 431 Daniëls F, Bergmeier E, Guerra A, Ermakov N, Tichý L (2016) Vegetation of Europe:
 432 Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal
 433 communities. *Applied Veg. Sci.* 19. 3-264. 10.1111/avsc.12257.

434 Nagajyoti PC, Lee KD, Sreekanth TVM (2010) Heavy metals, occurrence and toxicity
 435 for plants: a review. *Environmental Chemistry Lett.* 8:199-216.

436 Noest V (1994) A hydrology - vegetation interaction model for predicting the occurrence
 437 of plant species in dune slacks. *J. of Environmental Management* 40: 119-28.

438 Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin P, O'Hara RB, Simpson G,
 439 Solymos P, Stevens MHH, Wagner H (2016) vegan: Community Ecology Package. R
 440 package version 2.4-1 [cited 2017 January 25].

441 Pavoine S, Vela E, Gachet S, de Bélair G, Bonsall MB (2011) Linking patterns in
 442 phylogeny, traits, abiotic variables and space: a novel approach to linking environmental

443 filtering and plant community assembly. *J. of Ecol.* 99:165-175. Doi: 10.1111/j.1365-
 444 2745.2010.01743.x

445 Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space
 446 and time. *Trends Ecol. Evol.* 23:149-58. doi: 10.1016/j.tree.2007.11.005.

447 Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team (2016) nlme: Linear and
 448 Nonlinear Mixed Effects Models. R package version 3.1-128.

449 Pinheiro JJ, Bates DM (2000) *Mixed-Effects Models in S and S-PLUS*. Springer, NY.

450 Qian H, Jin Y (2016) An updated megaphylogeny of plants, a tool for generating plant
 451 phylogenies and an analysis of phylogenetic community structure. *J. of Plant Ecol.* 9:233-
 452 239.

453 R Core Team (2017) R: A language and environment for statistical computing. 2017:
 454 version 3.4.0. R Foundation for Statistical Computing, Vienna, Austria.

455 Ramsay JO, Silverman BW (2005) *Functional Data Analysis*, 2nd edn. Springer-Verlag,
 456 NY.

457 Rodwell JS (ed) (1992) *British Plant Communities*. 3 Grasslands and Montane
 458 communities. Cambridge, CUP.

459 Rothero E, Lake S, Gowing D (eds) (2016) *Floodplain meadows: Beauty and Utility*. A
 460 technical handbook. Floodplain Meadows Partnership, Milton Keynes.

461 Shepeleva LS (2018) *Structure and dynamics of meadow communities in the Middle*
 462 *River Ob floodplain*. Tomsk University Publishing, Tomsk.

463 Silvertown J, McConway K, Gowing G, Dodd M, Fay MF, Joseph JA, Dolphin K (2006)
 464 Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proc. of*
 465 *the Royal Soc. B-Biol. Sci.* 273(1582):39-44.

466 Silvertown J, Dodd M, Gowing DJ, Mountford JO (1999) Hydrologically defined niches
 467 reveal a basis for species richness in plant communities. *Nature*. 400(6739):61-63.

468 Summerville KS, Boulware MJ, Veech JA, Crist TO (2003) Spatial Variation in Species
 469 Diversity and Composition of Forest Lepidoptera in Eastern Deciduous Forests of North
 470 America. *Conserv. Biol.* 17:1045. <https://www.jstor.org/stable/3588861>
 471 Thoen MP, Davila Olivas NH, Kloth KJ, Coolen S, Huang PP, Aarts MG, Bac-Molenaar
 472 JA, Bakker J, Bouwmeester HJ, Broekgaarden C, Bucher J, Busscher-Lange J, Cheng X,
 473 Fradin EF, Jongsma MA, Julkowska MM, Keurentjes JJ, Ligterink W, Pieterse CM, Ruyter-
 474 Spira C, Smant G, Testerink C, Usadel B, van Loon JJ, van Pelt JA, van Schaik CC, van
 475 Wees SC, Visser RG, Voorrips R, Vosman B, Vreugdenhil D, Warmerdam S, Wiegiers GL,
 476 van Heerwaarden J, Kruijer W, van Eeuwijk FA, Dicke M (2017) Genetic architecture of
 477 plant stress resistance: multi-trait genome-wide association mapping. *New Phytol.* 213:1346-
 478 1362. doi: 10.1111/nph.14220.
 479 Thompson SK (2012) *Sampling*, 3rd edn. Wiley, New York.
 480 Tutin TG, Heywood VH, Burges NA, Moore DM, Valentines DH, Walters M, Webb DA
 481 (eds) (1964-1980) *Flora Europaea*. Vol. 1-5. Cambridge University Press, Cambridge.
 482 Valladares F, Niinemets Ü (2008) Shade Tolerance, a Key Plant Feature of Complex
 483 Nature and Consequences. *Annual Review of Ecol., Evol. and Syst.* 39:237-257.
 484 Valladares F, Bastias CC, Godoy O, Granda E, Escudero A (2015) Species coexistence
 485 in a changing world. *Frontiers in Plant Sci.* 6:866. DOI=10.3389/fpls.2015.00866
 486 van Loon LC (2015) The Intelligent Behavior of Plants. *Trends in Plant Sci.* 21:286-294.
 487 Wagner HH, Rico Y, Lehnert H, Boehmer HJ (2013) Process-based long-term evaluation
 488 of an ecological network of calcareous grasslands connected by sheep herding. *Ecography.*
 489 36:374-382. <https://doi.org/10.1111/j.1600-0587.2012.07463.x>
 490 Wollenberg A (1977) Redundancy analysis an alternative for canonical correlation
 491 analysis. *Psychometrika.* 42:207-219.

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. of the Royal Statistical Soc. (B)*. 73:3-36.

Yuan C, Chesson P (2015) The relative importance of relative nonlinearity and the storage effect in the lottery model. *Theor. Popul. Biol.* 105:39-52.

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2010) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

Electronic Supplemental Material (ESM):

Online Resource 1. Supplementary Tables and Figures.

Online Resource 2. R code.

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'). Tests are based in 10 000 permutations. The [meadow sites] component represents spatial variation in fifteen 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.

Source of variation	Response is community structure				
	R^2_{adj} (%)	DF _{model}	DF _{res}	F	p -value
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

Table 2. Generalised Additive Mixed Modelling results for 74 species with frequency across quadrats ($n = 2440$) greater than 5%. The reported R^2 -, F -value, 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, S3-S5.

Species	Freq. (%)	F (edf)	p -value	R^2 (%)	SR	σ^2_s	σ^2	σ_s/σ	Φ (AR)
<i>Agrostis stolonifera</i>	53.3	71.98 (3.02)	$<$ 0.0001	2.48	C (-)	0.0279	0.0445	0.79	0.3671
<i>Alopecurus geniculatus</i>	11.2	7.75 (1.60)	0.0016	0.89	C (-)	0.0003	0.0031	0.29	0.1973
<i>Anthoxanthum odoratum</i>	68.3	20.30 (3.21)	$<$ 0.0001	1.69	HS	0.0107	0.0169	0.79	0.3100
<i>Arrhenatherum elatius</i>	8.9	52.83 (4.71)	$<$ 0.0001	19.60	SS (+)	0.0003	0.0021	0.35	0.2595
<i>Bellis perennis</i>	9.0	5.36 (2.10)	0.0043	0.17	X (+)	0.0000	0.0003	0.29	0.1725
<i>Briza media</i>	5.1	32.58	$<$	9.42	HS	0.0001	0.0007	0.42	0.2044

		(4.60)	0.0001						
<i>Bromus</i>	16.8	39.52	<	8.20	SS	0.0005	0.0014	0.57	0.2578
<i>commutatus</i>		(3.57)	0.0001		(+)				
<i>Bromus racemosus</i>	21.2	11.34	<	4.89	HS	0.0015	0.0043	0.59	0.4293
		(3.97)	0.0001						
<i>Caltha palustris</i>	10.6	11.49	<	1.94	C (-)	0.0014	0.0070	0.44	0.1419
		(2.23)	0.0001						
<i>Cardamine</i>	20.5	9.48	<	2.92	C (-)	0.0062	0.0282	0.47	0.4330
<i>pratensis</i>		(2.43)	0.0001						
<i>Carex disticha</i>	60.9	11.81	0.0006	2.59	L (-)	0.0004	0.0018	0.49	0.2037
		(1.00)							
<i>Carex nigra</i>	18.0	7.94	0.0003	3.77	C (-)	0.0005	0.0123	0.21	0.2998
		(2.03)							
<i>Centaurea nigra</i>	40.7	21.34	<	0.97	HS	0.0091	0.0205	0.67	0.2795
		(3.82)	0.0001						
<i>Cynosurus</i>	61.2	32.74	<	1.69	X	0.0146	0.0169	0.93	0.3725
<i>cristatus</i>		(2.00)	0.0001		(+)				
<i>Dactylis glomerata</i>	15.6	241.4	<	30.50	C	0.0011	0.0028	0.63	0.2824
		(2.00)	0.0001		(+)				
<i>Deschampsia</i>	20.5	18.18	<	0.01	L (-)	0.0011	0.0095	0.34	0.2095
<i>cespitosa</i>		(1.00)	0.0001						
<i>Eleocharis</i>	9.0	7.64	0.0001	2.89	C (-)	0.0036	0.0128	0.53	0.2707
<i>palustris</i>		(2.84)							
<i>Elymus repens</i>	7.1	13.53	<	1.58	C (-)	0.0003	0.0022	0.36	0.1532
		(3.39)	0.0001						
<i>Festuca</i>	5.7	7.00	0.0007	0.48	C (-)	0.0006	0.0031	0.45	0.1389
<i>arundinacea</i>		(2.18)							
<i>Festuca rubra</i>	58.4	21.58	<	1.33	X	0.0258	0.0219	1.08	0.2278
		(2.68)	0.0001		(+)				
<i>Filipendula</i>	44.8	3.04	0.0474	0.35	X (-	0.0060	0.0230	0.51	0.2173
<i>ulmaria</i>		(2.02)			)				
<i>Galium palustre</i>	6.6	5.80	0.0018	0.90	C (-)	0.0000	0.0002	0.37	0.1768
		(2.44)							

<i>Galium verum</i>	7.8	19.09 (3.01)	< 0.0001	2.05	HS	0.0005	0.0030	0.42	0.1522
<i>Glyceria fluitans</i>	13.9	12.23 (4.41)	< 0.0001	1.15	SS (-)	0.0027	0.0115	0.48	0.2478
<i>Lathyrus pratensis</i>	31.0	23.51 (4.29)	< 0.0001	7.51	HS	0.0004	0.0021	0.41	0.1127
<i>Leontodon hispidus</i>	6.8	6.24 (3.86)	< 0.0001	0.33	HS	0.0002	0.0006	0.56	0.1635
<i>Leucanthemum vulgare</i>	7.7	54.74 (6.33)	< 0.0001	30.70	HS	0.0006	0.0018	0.56	0.3401
<i>Lolium perenne</i>	58.2	44.37 (2.77)	< 0.0001	16.10	C (+)	0.0039	0.0153	0.51	0.3736
<i>Lotus corniculatus</i>	16.0	18.36 (2.00)	< 0.0001	3.20	X (+)	0.0005	0.0031	0.42	0.2302
<i>Lychnis flos-cuculi</i>	8.8	9.93 (5.16)	< 0.0001	4.53	HS	0.0000	0.0002	0.44	0.2025
<i>Lysimachia nummularia</i>	8.0	20.79 (3.02)	< 0.0001	0.82	C (-)	0.0000	0.0008	0.25	0.0370
<i>Oenanthe fistulosa</i>	6.4	4.32 (1.32)	0.0280	0.94	C (-)	0.0001	0.0011	0.37	0.1997
<i>Oenanthe silaifolia</i>	8.7	14.47 (3.47)	< 0.0001	0.60	C (-)	0.0001	0.0009	0.32	0.0402
<i>Plantago lanceolata</i>	42.0	10.84 (3.88)	< 0.0001	3.68	HS	0.0014	0.0097	0.38	0.2552
<i>Polygonum amphibium</i>	23.9	13.04 (2.28)	< 0.0001	2.09	C (-)	0.0006	0.0038	0.40	0.2870
<i>Potentilla reptans</i>	11.1	15.16 (3.83)	< 0.0001	3.52	HS	0.0001	0.0009	0.35	0.3575
<i>Prunella vulgaris</i>	15.9	14.16 (4.80)	< 0.0001	4.63	HS	0.0003	0.0014	0.49	0.1760
<i>Ranunculus acris</i>	77.0	16.11 (2.00)	< 0.0001	0.34	HS	0.0012	0.0083	0.38	0.2348
<i>Ranunculus</i>	11.4	31.84	<	9.47	HS	0.0003	0.0015	0.49	0.0690

<i>bulbosus</i>		(3.84)	0.0001						
<i>Ranunculus repens</i>	56.8	4.80 (2.00)	0.0083	2.19	X (-)	0.0235	0.0381	0.79	0.3087
<i>Rumex acetosa</i>	64.7	13.00 (2.43)	< 0.0001	1.10	X (+)	0.0010	0.0023	0.65	0.1134
<i>Sanguisorba officinalis</i>	34.2	16.71 (2.72)	< 0.0001	2.37	HS	0.0166	0.0391	0.65	0.2334
<i>Senecio aquaticus</i>	21.6	7.98 (2.38)	0.0002	1.14	C (-)	0.0016	0.0036	0.67	0.3181
<i>Taraxacum officinale</i>	46.1	15.31 (2.34)	< 0.0001	3.25	X (+)	0.0007	0.0020	0.59	0.1631
<i>Trifolium pratense</i>	43.7	4.99 (2.00)	0.0069	0.49	HS	0.0020	0.0068	0.54	0.2343
<i>Trifolium repens</i>	57.3	26.29 (2.00)	< 0.0001	1.04	HS	0.0038	0.0089	0.65	0.1519
<i>Trisetum flavescens</i>	13.6	95.3 (5.83)	< 0.0001	34.4	HS	0.0010	0.0035	0.28	0.3254
<i>Vicia cracca</i>	16.4	12.16 (2.60)	< 0.0001	1.45	C (+)	0.0004	0.0027	0.37	0.1342

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 x 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 caespitosa*; 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, *Rhinanthus 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*

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 fifteen sites in which nearly two hundred 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

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

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

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

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

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

NMDS ordination with fitted smooth surface (mWTD)

Figure 1.

Species accumulation plot with additive diversity partitioning

Figure 2.

Figure 3.

Trisetum flavescens

Figure 4.

Figure 5.

Figure 6.

Figure 7.