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RESEARCH ARTICLE

Simulated effects of floodplain restoration on plant community types

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Abstract

Aims: Channelization and artificial embankments have altered the natural flood regime of many rivers, impacting the hydrological characteristics of floodplain ecosystems and their biological communities. This study was undertaken on a floodplain meadow to assess spatial patterns of plant communities in relation to soil physical and chemical conditions, and the impacts of floodplain restoration that involved embankment-removal.

Location: River Glaven, Hunworth, Norfolk, UK.

Methods: Fine-scale plant and soil chemistry sampling was conducted prior to embankment removal, and hydrological and climatological conditions were monitored prior to and after embankment removal. Hydrological/hydraulic modelling simulated groundwater levels for a 10-year period to assess changes in soil aeration stresses and plant community composition following embankment-removal.

Results: Hydrology was identified as the primary driver of plant community composition. Soil fertility was also important. Unique continuous measurements of vadose dissolved oxygen concentrations using oxygen optodes indicated strong coupling between water table depth and root zone dissolved oxygen concentrations. Reinstatement of overbank flows did not substantially affect aeration stress across most of the meadow because of pre-existing wet conditions. However, along the river-floodplain ecotone, aeration stress increased substantially from conditions normally associated with dry grassland to those characteristic of fen communities ($p < 0.05$).

Conclusions: This restored water table regime may be suitable for more diverse plant assemblages. Benefits of flooding for increased species richness and transport of propagules may, however, be over-ridden without accompanying water level management during the growing season, or hay removal to balance additional supply of nutrients from river floodwater and sediment. Our results show that hydrological/hydraulic modelling combined with quantitative measures of plant water-requirements can provide practical and adaptive management tools to estimate the response of floodplain communities to changing water regimes.

KEYWORDS
cumulative aeration stress index, ecohydrology, floodplain restoration, MIKE SHE, wet grassland

1 | INTRODUCTION

Lowland wet grassland, defined in Britain as grassland growing less than 200 m above sea-level subject to periodic freshwater flooding (Jefferson & Grice, 1998), is often characterised by high biodiversity and recognised for its multiple ecosystem services and high nature conservation value (Habel et al., 2013). However, river channelisation and artificial embankments, drainage, and inorganic fertilisers have altered the hydro-ecology of these habitats (Entwistle et al., 2019), contributing to widespread declines in wet grassland biodiversity (McGinlay et al., 2017). In an effort to re-establish river–floodplain connections and more dynamic flood-pulsed hydrological regimes that are characteristic of species-rich floodplains, river restoration in the form of embankment removal and the reconfiguration of river channels is an increasingly popular management strategy in Europe and globally (Bernhardt et al., 2005; Palmer et al., 2005; Klimkowska et al., 2007; Gumiero et al., 2013; Smith et al., 2014).

Predictions of floristic responses to modified hydrological conditions that allow an optimisation of wet grassland management for biodiversity require an understanding of the relationship between the soil moisture and oxygen status of the root environment. A wet grassland's hydrological regime is a critical factor determining its plant community (Kennedy et al., 2003; Araya et al., 2011). Floodplain grassland vegetation is influenced by variations in water table depth and the magnitude–frequency characteristics of flood events (Poff et al., 1997), which in turn control root zone oxygen status (Barber et al., 2004). Soil variables including nutrient availability and site management history may also have important effects (Kalusová et al., 2009; Michalcová et al., 2011; Kaiser & Ahlborn, 2021).

Plant species have individual tolerance ranges to aeration stress with species separation along fine-scale hydrological gradients. These have been investigated using both qualitative (Ellenberg, 1974) and quantitative (Gowing et al., 1998; Silvertown et al., 1999) methods. Gowing et al. (1997) used a cumulative stress index based on water table position to predict root zone aeration stress and to account for spatial patterns in UK wet-meadow plant communities. Water table depth, which is relatively easy to monitor, represents a useful descriptor of soil water content and air-filled porosity (Hillel, 1998). However, air-filled porosity and soil oxygen status are not always strongly correlated. Soil oxygen concentration is a function of diffusion from the soil surface, and consumption from respiration in the profile. Thus, where respiration exceeds diffusion, soil pores may be filled primarily with respiratory and fermentation products (e.g. CO_2, CH_4, H_2S) rather than oxygen. Direct measures of oxygen status in response to changing hydrological conditions are therefore required to establish the degree to which water table position can be used as a proxy for plant aeration stress.

Niche and habitat suitability models of plant sensitivity to moisture regime, such as the cumulative aeration stress index, can guide management of wetland vegetation and environmental restoration, especially when linked to predictive tools such as physically-based hydrological models (e.g. Booth & Loheide, 2012; Thompson et al., 2017). The length of time required to restore plant communities following management interventions can be substantial (e.g. >10 years; Woodcock et al., 2006; Lindsay, 2010). Thus, hydrological/hydraulic modelling, combined with appropriate habitat suitability models, can simulate the expected long-term hydrological and ecological effects of restoration on a range of wetland plant communities.

In this study, fine-scale floristic, chemical, soil moisture, and topographic data for a lowland wet meadow were used to assess links between spatial patterns of plant communities and soil physical and chemical conditions. Water table simulations from coupled MIKE SHE-MIKE 11 hydrological/hydraulic models (Clilverd et al., 2016) were used to evaluate root zone aeration stresses before and after restoration that removed river embankments. The following research questions are addressed: (i) what are the importance of soil moisture and nutrient status in controlling plant community composition on a disconnected floodplain meadow; (ii) what is the relationship between water table depth and oxygen content in the root zone; and (iii) what are the likely long-term vegetation impacts of floodplain restoration?

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted at Hunworth Meadow on the River Glaven, a small (17 km long) lowland chalk river in North Norfolk, UK (Figure 1). The meadow extends along a 400-m reach of the Glaven and is 40–80 m wide. An agricultural drainage ditch runs parallel to the river and at the time of the study was partially blocked. The Meadow's alluvial soils are approximately 2 m thick and classified as sandy loam (Clilverd et al., 2013).

The Riven Glaven's discharge follows the typical annual hydrograph of a chalk stream, with the largest discharges in winter (mean flow: 0.26 $m^3\ s^{-1}$) (Clilverd et al., 2016). Glaven river water at the study site has a mean pH of 7.3 and is eutrophic (mean nitrate and phosphate concentrations: 6.2 mg NO_3^--N L^{-1} and 0.1 mg P L^{-1} respectively; Clilverd et al., 2013). Restoration, involving removal of embankments along the 400 m reach, was undertaken in March 2009 (Appendix S1). This lowered the surface by on average 0.6 m to align the riverside elevation with that of the floodplain (Appendix S1)

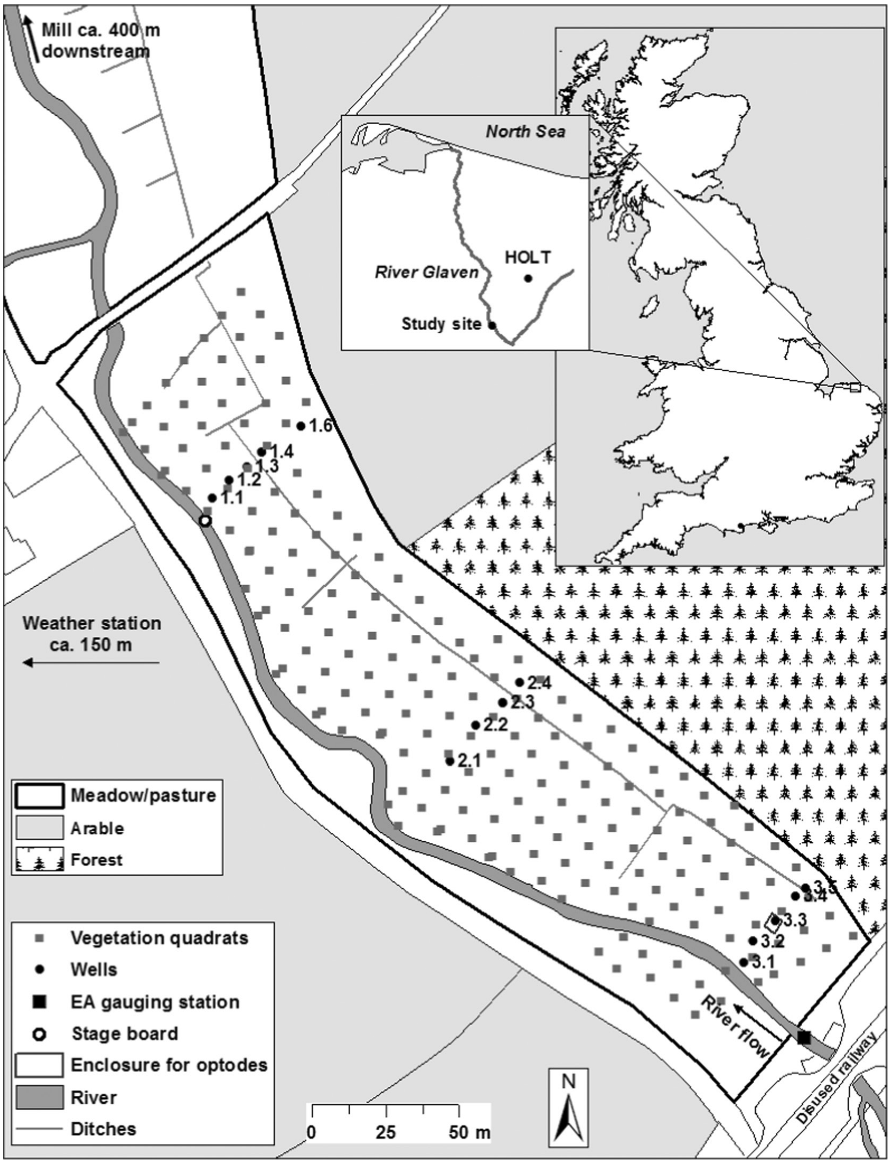

FIGURE 1 Hunworth meadow restoration site on the river Glaven, North Norfolk. The woodland and arable border along the northeast of the meadow delineates the base of a hillslope. The river Glaven and location of the study site at Hunworth are shown in the inset.

(cross sections of the floodplain are presented in Clilverd et al., 2013, 2016). Restoration was aimed at enhancing river–floodplain hydrological connectivity, improving floodwater storage, and establishing a more variable floodplain hydrological regime to enable diversification of wet-meadow vegetation.

2.2 | Sampling protocol

Vegetation surveys across the entire meadow prior to restoration were conducted before restoration (late June 2008) using a regular 10 m × 10 m sampling grid and 1-m^2 quadrats (n = 206) (Figure 1). It was not possible to conduct a vegetation survey after the restoration due to additional in-stream restoration works at the site and land management changes (see section 4 *Discussion*). Percentage composition of all plant species was estimated visually and typically exceeded 100% due to vegetation layering. Concurrently, soil moisture content was measured at a subset of points (n = 138) that were evenly spaced and aligned to the botanical grid using a ML-2X soil moisture ThetaProbe (Delta-T Devices, Cambridge, UK). Soil samples were collected before restoration on 29 Aril 2008 across the meadow at depths of 10–20 cm (n = 113). Bulk density and porosity were calculated from the difference in the volume of saturated and dry soil (Elliot et al., 1999) collected using bulk density rings (I.D. = 53 mm, height = 51 mm, volume = 100 cm^3) from the top 0–0.2 m of soil. Samples were stored in a cooler with ice until return to the laboratory, where they were frozen pending analysis.

Elevation of the meadow, river embankments and channel was surveyed before and after restoration using a differential Global Positioning System (dGPS) (Leica Geosystems SR530 base station receiver and Series 1200 rover receiver, Milton Keynes, UK). Water table elevation was monitored hourly before and after restoration from February 2007 till August 2010 at 10 shallow wells (1–2 m depth), using Solinst (Georgetown, Canada) pressure transducers (Levelogger Gold 3.0) (Figure 1) (see Clilverd et al., 2013).

2.3 | Soil chemistry analyses

Plant-available nutrients were determined using standard extraction methods. Nitrate and ammonium were extracted with potassium chloride (Robertson et al., 1999). Potassium, calcium, magnesium, and sodium were extracted using ammonium acetate (Hendershot et al., 2008). Phosphate was analysed using the 'Olsen-P' sodium bicarbonate method (Schoenau & O'Halloran, 2008). Inorganic nitrogen species and phosphorus were analysed colorimetrically using an automated continuous flow analyser (SAN++, SKALAR, Delft, The Netherlands). Base cation analysis was conducted using a Vista-PRO inductively coupled plasma optical emission spectrometer (ICP-OES) with an SPS3 autosampler (Varian, Palo Alto, USA).

2.4 | Oxygen concentration in soil pores

An Aanderra 4175 oxygen optode (Nesttun, Norway) connected to a Campbell Scientific CR1000 datalogger (Loughborough, UK) monitored dissolved oxygen (DO) concentration at 30-min intervals in saturated and unsaturated soil pore spaces in the rooting zone (0–0.10 m below the surface) at an upstream well transect (Well 3.3) (Figure 1) between January and December 2010. Two oxygen optodes used to measure DO in well water on the floodplain from 2009–2010 (Clilverd et al., 2013) responded similarly to the soil optode measurements reported herein. Calibration of the optode was checked periodically using a zero-oxygen solution (sodium sulphite saturated in deionised water) and 100% saturated solution (deionised water bubbled with air). The optodes measure partial pressure of DO and respond equally when measuring in air and air-saturated freshwater (Bittig & Körtzinger, 2015). Hence, in addition to measurements of oxygen concentration in shallow groundwater, the optode provided unique data on oxygen concentrations in soil air. The amount of DO in water at equilibrium with air is given by Henry's Law (see Weiss & Price, 1980). Oxygen saturation values in air are calculated assuming 100% relative humidity, a pressure of one atmosphere and zero salinity (Aanderaa, 2006). Dry air can result in slightly higher (up to 3%) oxygen measurements than air that is 100% saturated with water vapour since dry air can hold more oxygen. This effect is expected to be minimal in soil, particularly at Hunworth Meadow where the water table was close to the optodes throughout the monitoring period. Wetting and drying of the sensors can lead to a maximum error of 2% (Aanderaa, 2006).

2.5 | Biodiversity and multivariate analysis

Diversity patterns of the floodplain vegetation were analysed using the Shannon Index, which is the most used measure of α-diversity (Jost, 2006; Reddy et al., 2009; Stein et al., 2010).

The Shannon Index (H') expresses heterogeneity of an assemblage, and was calculated as:

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportional abundance (% cover) of the ith species (Magurran, 2004).

Spatial variation in plant community composition and soil environmental conditions were investigated using correspondence analysis (CA) and canonical correspondence analysis (CCA) (Lepš & Šmilauer, 2003) in CANOCO 4.5 for Windows (Microcomputer Power, Ithaca, NY, USA). Since elevation and soil moisture content were significantly correlated ($y = -23.301x + 523.45$, $r^2 = 0.52$, $p < 0.05$), and soil moisture ($n = 138$) was not available for all vegetation plots ($n = 206$), elevation was used as a proxy for soil moisture. Prior to analysis, data were tested for normality using normal probability plots and the Kolmogorov–Smirnov test. Where necessary, data were log-transformed to achieve normality. Multicollinearity among the environmental variables was tested using Pearson and Spearman correlation coefficients.

2.6 | Hydrological/hydraulic modelling

Pre- and post-restoration coupled hydrological/hydraulic models of the meadow were developed using MIKE SHE-MIKE 11 (DHI, Southampton, UK) (Clilverd et al., 2016). Dynamic coupling of 1D MIKE 11 river models and the MIKE SHE models enabled simulation of river–aquifer exchange, inundation from the river onto the floodplain and overland flow to the river (Thompson, 2004). Fine model discretization (5 m × 5 m) was used to characterise small-scale variations in topography that control soil water content, water table depth and influence habitat suitability for plant species (Wheeler et al., 2004). MIKE SHE models were driven by daily precipitation and Penman–Monteith potential evapotranspiration (Monteith, 1965) derived from an on-site weather station (MiniMet SDL 5400, Skye) supplemented by the UK Met Office meteorological station at Mannington Hall. Daily discharge from the Environmental Agency gauging station (#034052) immediately upstream of Hunworth Meadow provided the upstream MIKE 11 boundary (Figure 1).

The pre-restoration model was calibrated and validated against observed groundwater elevation for two consecutive 12-month periods (22 February 2007–14 March 2008 and 15 March 2008–15 March 2009), the end of the latter coinciding with embankment removal. Calibrated parameter values were applied to the post-restoration model enabling validation for the subsequent 16-month period (29 March 2009–25 July 2010). Model performance in terms of water table level was assessed using the Pearson correlation coefficient (R), the Nash–Sutcliffe coefficient (NSE) and root mean squared error (RMSE). A good fit was achieved for most wells (Appendix S2).

To assess the impacts of embankment removal, the pre-restoration (embanked) and post-restoration (no embankment) models were run under identical climatic and river flow conditions for a 10-year period (2001–2010), for which continuous meteorological and river discharge data were available (post-2010 discharge data were affected by in-stream reprofiling and could not be included). Detailed descriptions of the models, their parameterisation, calibration/validation, and results are provided by Clilverd et al. (2016).

2.7 | Aeration stress index

An aeration stress index for each well location was estimated by determining sum exceedance values for aeration stress (SEV_{as}), calculated as the integral of the difference between the water table depths and a reference water table depth:

$$SEV_{as} = \int_{1}^{N} (D_{ref} - D_{W}) dt$$

where SEV_{as} is sum exceedance value, the number of weeks for which the aeration threshold was exceeded multiplied by the height which the water table exceeded it, given in units of metre weeks (m weeks), which increases in value with aeration stress; N is the number of weeks in the active growing season for grasses (March–September; Gowing, Lawson, Youngs, et al., 2002; Gowing, Lawson, Youngs, Barber, et al., 2002); D_W is the average depth to the water table (m) and D_{ref} is the reference water table (0.34 m) where air-filled porosity at the surface equals 0.1 (threshold porosity expected for aeration stress in plants; Wesseling & van Wijk, 1975; Gowing et al., 1998). D_{ref} was established by measuring the water release characteristic (pF curves) of topsoils (0–10 cm) (n = 15) using a manual 08.01 sandbox (Eijkelkamp, Giesbeek, The Netherlands). Air-filled porosity was calculated as the difference between water content of the soil and saturated water content (Gowing et al., 1998). Assuming soil rigidity, the 10% threshold porosity occurred at the surface when the water table was on average less than 0.34 m below the ground surface (Wesseling & van Wijk, 1975). This reference water table depth is comparable to the 0.35 m threshold used by Gowing et al. (1998) for a UK peat-based wet grassland.

Using MIKE SHE-MIKE 11-simulated pre- and post-restoration water table elevations, average water table depths during the growing season and SEV_{as} were calculated for each of the vegetation plots (n = 206). These values were compared with known tolerances of meadow plant communities established by Gowing et al. (1998) and Wheeler et al. (2004) to assess potential compositional change in plant communities in response to embankment removal.

3 | RESULTS

3.1 | Groundwater hydrology and soil moisture gradients

Mean water table depth during the wettest summer of the study period (2007) was predominantly between 0 and 0.6 m (Figure 2). Even during the driest summer (2009), the water table was frequently in the root zone (ca. top 30 cm). However, elevated regions such as the embankments remained dry for most of the summer (>95% of the time) (Figure 2a). Soil moisture increased in a downstream (northwesterly) direction in conjunction with declining elevation (Appendix S3a,b). It ranged from 11% to 30% along the river embankments, where pre-restoration surface elevation was 0.4–1.1 m above the meadow, to 100% (waterlogged conditions) at the downstream end of the meadow (Appendix S3b).

3.2 | Soil nutrient status

Analysis of plant-available nutrients revealed moderately fertile conditions, with mean Olsen-P and plant-available potassium concentrations of 9.2 mg P kg^{-1} (range: 0.1–34 mg P kg^{-1}) and 1.6 mg K^+ g^{-1} (range: 0.4–4.8 mg K^+ g^{-1}) respectively. Plant-available ammonium and nitrate concentrations were, on average, 32.5 mg NH_4^+-N kg^{-1} (range: 5.7–249.9 mg NH_4^+-N kg^{-1}) and 2.9 mg NO_3^--N kg^{-1} (range: below detection to 25.2 mg NO_3^--N kg^{-1}) respectively. Soils were high in calcium (mean: 2.6 mg Ca^{2+} g^{-1}). Plant-available N:P ratios were low, averaging less thasn 5:1 (Table 1).

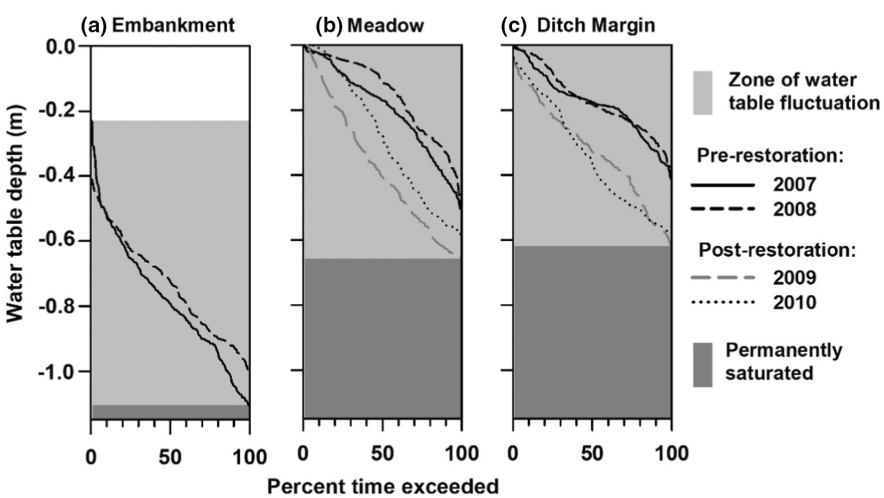

FIGURE 2 Water table duration curves derived from mean daily water table depth below the soil surface (0.0 m) during the active growing season for grasses (March–September inclusive; Gowing, Lawson, Youngs, Barber, et al., 2002) for three representative wells across the floodplain, (a) on the embankment (well 3.1), (b) middle meadow (well 3.3), and (c) ditch margin (well 1.3).

3.3 | Vegetation community composition

A total of 88 plant species were encountered within 206 quadrats. Average species richness was low at eight species m^{-2} but varied substantially (range: 1–16 species m^{-2}) (Table 2), with highest species richness more often encountered on the embankments. Shannon Index of diversity averaged 1.4 ± 0.4 (Table 2), suggesting low heterogeneity of the plant assemblages on Hunworth Meadow.

Three distinct vegetation groups were identified: an MG1 *Arrhenatherum elatius* grassland on the embankments, an OV28 *Agrostis stolonifera–Ranunculus repens* grassland community in the main meadow, and an MG10 *Holcus lanatus–Juncus effusus* floodsward along the ditch, with some overlap between meadow and ditch margin communities (Table 2).

Correspondence analysis axis 1, which explained 16% of total species variability (Table 3), appears aligned to a gradient in plant moisture tolerance. Plants tolerant of waterlogging (e.g. *Equisetum fluviatile*, *Juncus effusus* and *Juncus inflexus*) are negatively associated with axis 1 and less waterlogging-tolerant species (e.g. *Arrhenatherum elatius*, *Urtica dioica*, *Lolium perenne* and *Dactylis glomerata*) from the embankment are at the other end of the gradient (Appendix S4a,b). Putting aside the strong differences between the embankment and the rest of the meadow, many meadow samples were clustered together at the centre of the axis. Species closely associated with these samples were *Holcus lanatus*, *Ranunculus repens* and *Festuca pratensis*, and the dense clustering indicates little variation in community composition amongst these samples. This analysis was restricted to the first axis due to the arch effect shown in Appendix S4, indicative of a quadratic dependence of the second ordination axis on the first ordination axis (Lepš & Šmilauer, 2003).

Variations in micro-topography, that serve as a proxy for variations in soil moisture (Appendix S3a,b), were closely linked to plant positioning in the CCA plot along axis 1 ($r = 0.79$; $p < 0.05$; Figure 3; Table 4; Appendix S5). Soil fertility was a secondary predictor of plant species composition; plant-available ammonium and phosphorus were closely correlated with CCA axis 2 ($p < 0.05$) (Figure 3). The plant assemblage on the embankments was clearly separated from the remaining vegetation, being characterised by low soil moisture and higher phosphorus availability (Figure 3).

TABLE 1 Soil ($n = 113$) chemistry of Hunworth meadow along the vegetation transects [mean ± 95% confidence interval (CI)]

Soil:	Mean ± 95% CI
pH (*in situ*)	6.09 ± 0.23
Organic matter content (%)	13.64 ± 1.50
Bulk density ($g\,m^{-3}$)	0.69 ± 0.07
Ca^{2+} ($mg\,g^{-1}$ dry soil)	2.64 ± 0.36
Na^{+} ($mg\,g^{-1}$ dry soil)	0.08 ± 0.01
Mg^{+} ($mg\,g^{-1}$ dry soil)	0.11 ± 0.01
K^{+} ($mg\,g^{-1}$ dry soil)	1.64 ± 0.16
NH_4^{+} ($mg\,N\,kg^{-1}$ dry soil)	32.46 ± 5.02
NO_2^{-} ($mg\,N\,kg^{-1}$ dry soil)	0.28 ± 0.09
NO_3^{-} ($mg\,N\,kg^{-1}$ dry soil)	2.86 ± 0.75
Olsen-P ($mg\,P\,kg^{-1}$ dry soil)	9.20 ± 1.23
N:P ratio ($NH_4^{+}+NO_3^{-}$/Olsen-P)	4.89 ± 0.61

3.4 | Soil oxygen status

Oxygen status of surface soil pores was closely linked with water table depth (Figure 4). During waterlogging, DO concentrations responded rapidly (within one day), and soil pores in the root zone were filled with anoxic groundwater (mean DO = 0.74 ± 0.15 μM; 0.22 ± 0.04% DO saturation). As the water table fell, DO concentration increased close to atmospheric levels typically within 3–6 days. This response was quicker, typically 1–2 days, if the duration of

TABLE 2 Species richness and British national vegetation classification (NVC) communities found across the meadow assigned using the average goodness of fit value produced in TABLEFIT (Hill, 1996)

Community	Species richness (no m^{-2})	Species diversity (Shannon index)	Main vegetation type	NVC mesotrophic grassland communities assigned by TABLEFIT (goodness of fit)
Embankment	10 (3–16)	1.6 (0.8–2.3)	*Arrhenatherum elatius*	MG1 (88), MG1 (82), W24 (80)
Middle meadow	7 (1–13)	1.3 (0–2.1)	*Agrostis stolonifera–Ranunculus repens*	OV28 (68), MG10 (60)
Ditch	8 (4–16)	1.3 (0.6–2.3)	*Holcus lanatus–Juncus effusus*	MG10 (82), M23 (75), OV28 (71)

TABLE 3 Eigenvalues and cumulative percentage variance for each correspondence analysis (CA) axis of the vegetation data

Axes		1	2	3	4
Embankment, meadow, and ditch:	Eigenvalues:	0.674	0.554	0.447	0.373
	Cumulative percentage variance of species data:	15.7	28.7	39.1	47.8
Sum of all eigenvalues:					4.283

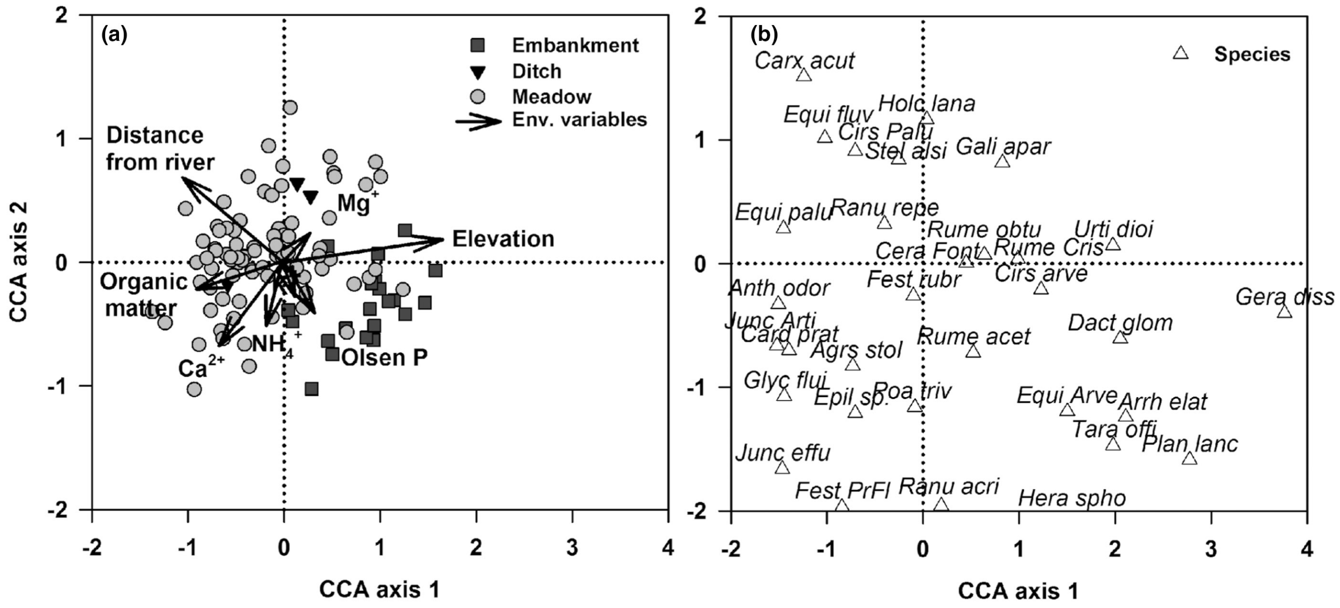

FIGURE 3 Constrained canonical correspondence analysis (CCA) of species composition on environmental variables showing (a) embankment, middle meadow and ditch sample points, and (b) the associated species. Correlations of the soil variables (elevation, distance from the river, organic matter content, calcium, ammonium, Olsen-P, magnesium, and potassium concentrations) with the two main axes are shown by the arrows. In total, 67 species were analysed from 108 samples that spanned 31 transects across the Hunworth meadow. See Appendix S7 for full species names.

TABLE 4 Eigenvalues and cumulative percentage variance for each constrained canonical correspondence analysis (CCA) axis of the vegetation and environmental data, and summary of the Monte Carlo test

Axes	1	2	3	4	
Eigenvalues:	0.419	0.169	0.077	0.058	
Species–environment correlations:	0.794	0.631	0.558	0.448	
Sum of all eigenvalues					4.241
Test of significance:	First axis				All axes
F-ratio	10.634				2.635
P-value	0.002				0.002

Note: Forward selection of the environmental variables is shown in Appendix S5.

waterlogging was less than one week. During the growing season, vadose DO averaged 295 ± 5 μM (88 ± 2% DO saturation), being close to atmospheric levels (Figure 4).

3.5 | Hydrological and habitat suitability models

Flooding of the meadow was simulated by the pre- and post-restoration models. However, for the former, flooding only occurred due to elevated groundwater levels following large precipitation events. Such flooding was mainly restricted to lower-lying areas, while embankments remained dry (Figure 5a). After restoration, flooding also occurred due to overbank inundation (Figure 5b) and both the extent and depth of surface water increased, especially close to the river, along the ditch, and in the lower part of the meadow (see Clilverd et al., 2016, for detailed results).

SEV_{as} derived for the floodplain grid cells of the pre- and post-restoration models averaged 4.3 ± 3.8 and 4.8 ± 3.9 m weeks (p = 0.1665) respectively, suggesting a high degree of aeration stress (MG4 communities typically tolerate SEV_{as} values between 0–1 m weeks; see community SEV_{as} thresholds in Figure 6 and Appendix S6). The highest parts of the meadow, that is, on the embankment (pre-restoration) or adjacent to the hillslope, had the lowest values of SEV_{as} (<0.2 m weeks), and plants in these areas are expected to experience little to no aeration stress. Restoration produced large increases in aeration stress immediately next to the river. Mean SEV_{as} increased from 0.4 (range: 0–2.8) m weeks before embankment removal to 2.5 (range: 0–15) m weeks ($p < 0.05$) after restoration (Figure 6a). Conversely, aeration stress decreased along the ditches after embankment removal.

The simulated restored water table regimes in some parts of the meadow satisfy target hydrological conditions for an MG8 species-rich floodplain meadow community (Figures 6, 7), or an MG13 inundation grassland community (Figures 6, 7). During wetter years (e.g. 2007), overbank inundation and surface flooding result in groundwater levels which exceed tolerable limits for both communities. However, since they can endure occasional overbank flows (Figure 7b,d), and wet conditions do not occur year on year or across

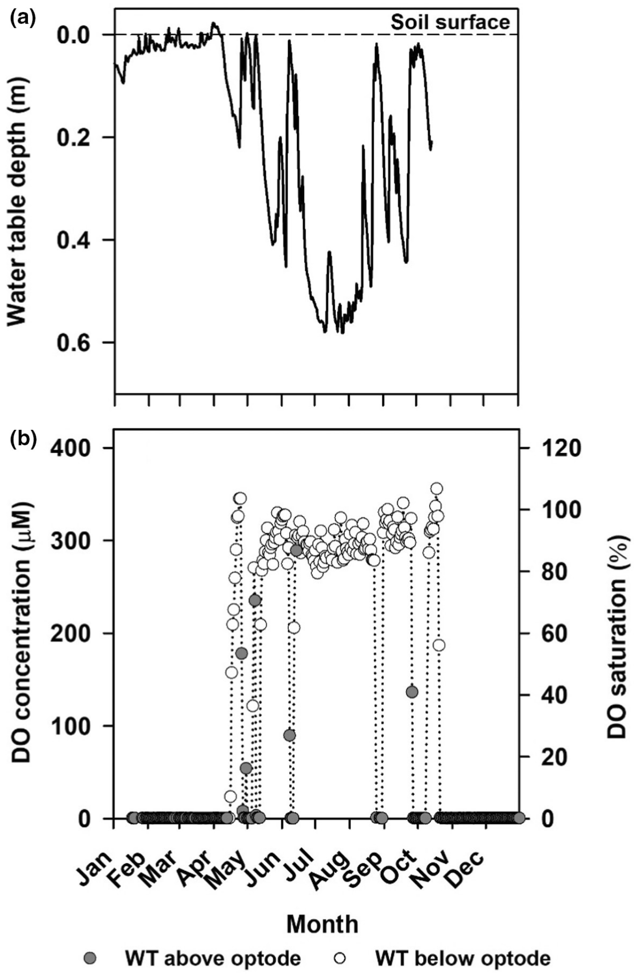

FIGURE 4 (a) Relationship between mean daily dissolved oxygen (DO) concentration in soil and mean daily water table (WT) depth, and (b) time series of DO concentration for 2010. The DO optode was buried in soil 0.10 m below the ground surface.

the entire meadow, there is potential for sustained establishment of these diverse plant communities. Restored conditions are nonetheless too wet for an MG4 species-rich hay meadow since the respective plant species cannot tolerate soil waterlogging at any time of year (Figure 7f).

4 | DISCUSSION

4.1 | Hydrological controls on floodplain processes and plant communities

Overbank flows affect soil moisture and nutrient status, which are important for floodplain ecological functioning (Junk et al., 1989; Tockner & Stanford, 2002). Embankments on Hunworth Meadow resulted in infrequent (>10-year recurrence interval) overbank flow events, which severely impeded exchanges of water and nutrients between the river and its floodplain. Whilst hyporheic exchange may, in some hydrogeological settings, be important for linking biological and chemical processes (i.e. nutrient uptake and cycling) that occur in rivers and their floodplains (Krause et al., 2017), subsurface flows on Hunworth Meadow are in the order of only cm day^{-1} (Clilverd et al., 2013). Without regular overbank events the floodplain was essentially disconnected from the river. Despite this, groundwater levels were generally close to the surface, and during periods of high rainfall, the root zone was often waterlogged due to groundwater flooding. The embankments would then restrict surface water drainage towards the river (Clilverd et al., 2016).

Seasonal timing of flooding, high water tables, and accompanying aeration stresses, play important roles in structuring wetland plant communities (Robertson et al., 2001; Gaberščik et al., 2018; Keddy & Campbell, 2020). Summer flood duration is particularly important, and a less dynamic soil water regime promotes plant

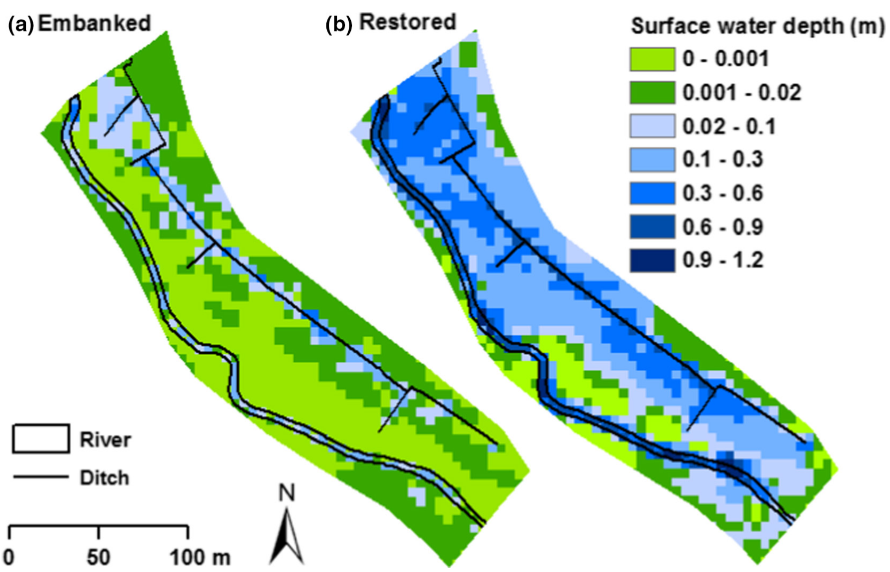

FIGURE 5 Comparison of simulated surface water extent for the embanked (a) and restored (b) scenarios during a representative river flood event (28/05/07; discharge = 1.9 m^3 s^{-1}).

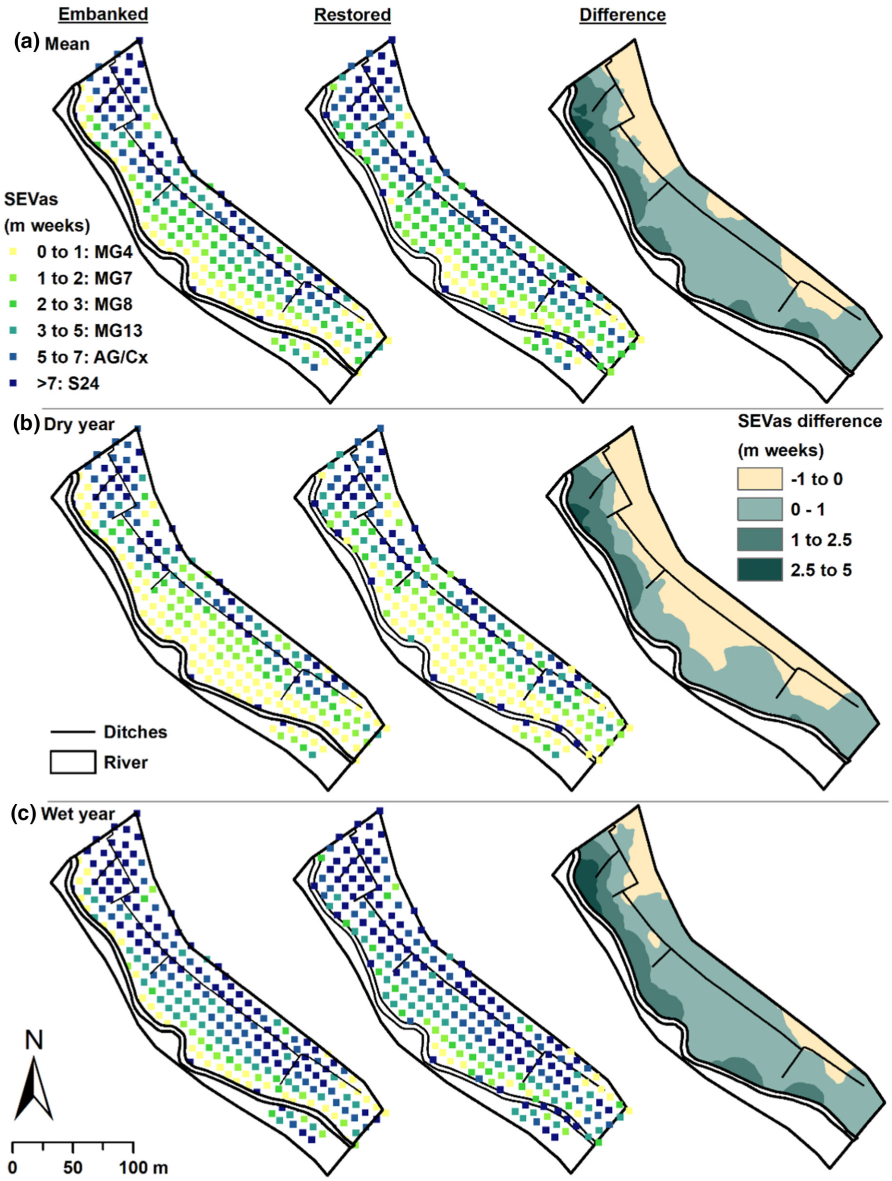

FIGURE 6 Simulated sum exceedance values for aeration stress (SEV_{as}) for the embanked and restored scenarios across the meadow during the active grass growing season (March–September inclusive; Gowing, Lawson, Youngs, Barber, et al., 2002) for (a) average conditions (2001–2010), (b) a dry year (2002), and (c) a wet year (2007). The difference across the meadow is shown using the kriging interpolation function in ArcGIS.

communities characterised by stress-tolerant, competitive perennials (Joyce, 1998). Indeed, the relatively wet and stable hydrological conditions of the embanked Hunworth Meadow supported a species-poor community dominated by a degraded *Holcus lanatus–Juncus effusus* (NVC MG10 type) flood-sward.

Ordination of the botanical data suggested that soil moisture, represented by elevation, was the dominant environmental influence on vegetation distribution. This agrees with earlier studies (e.g. Silvertown et al., 1999; Dwire et al., 2006). The degree of waterlogging, and resultant root zone aeration stresses, control plant functioning, productivity and survival (Visser et al., 2003). Wet, anoxic soil conditions persisted in winter and intermittently in the growing season in both the embanked and restored Hunworth Meadow. This is likely to be a major factor controlling plant assemblages. In addition to oxygen deprivation, wetland plants are affected by accompanying changes in soil chemistry. Anaerobic conditions lead to higher phosphorus availability due to the reduction of iron complexes and phosphorus desorption in low redox soils (Zeitz & Velty, 2002), and lower amounts of available nitrogen for plants due to the limitation of nitrification and loss of nitrate via denitrification (Pinay et al., 2007).

Soil fertility was a lesser, secondary driver of plant species composition. Topsoils were of intermediate phosphorus fertility, probably due to historic agricultural fertiliser additions. Hence, as in many nutrient-rich habitats, Hunworth Meadow exhibited a high dominance of a few plant species. Biodiversity of mesotrophic plant communities generally declines in response to increased nutrient supply (Willems et al., 1993; Aerts et al., 2003). More diverse grassland communities require plant-available phosphorus concentrations within the range of 5–10 mg P kg^{-1} (Gowing, Lawson, Youngs, et al., 2002; Gowing, Lawson, Youngs, Barber, et al., 2002; Michalcová et al., 2011). Average topsoil concentration at Hunworth was at the upper limit of this range, and in numerous samples exceeded 15 mg P kg^{-1}. In contrast, nitrate concentrations in soil pore water and soil were typically low, likely associated with prolonged winter waterlogging and anoxia, and high demand from soil

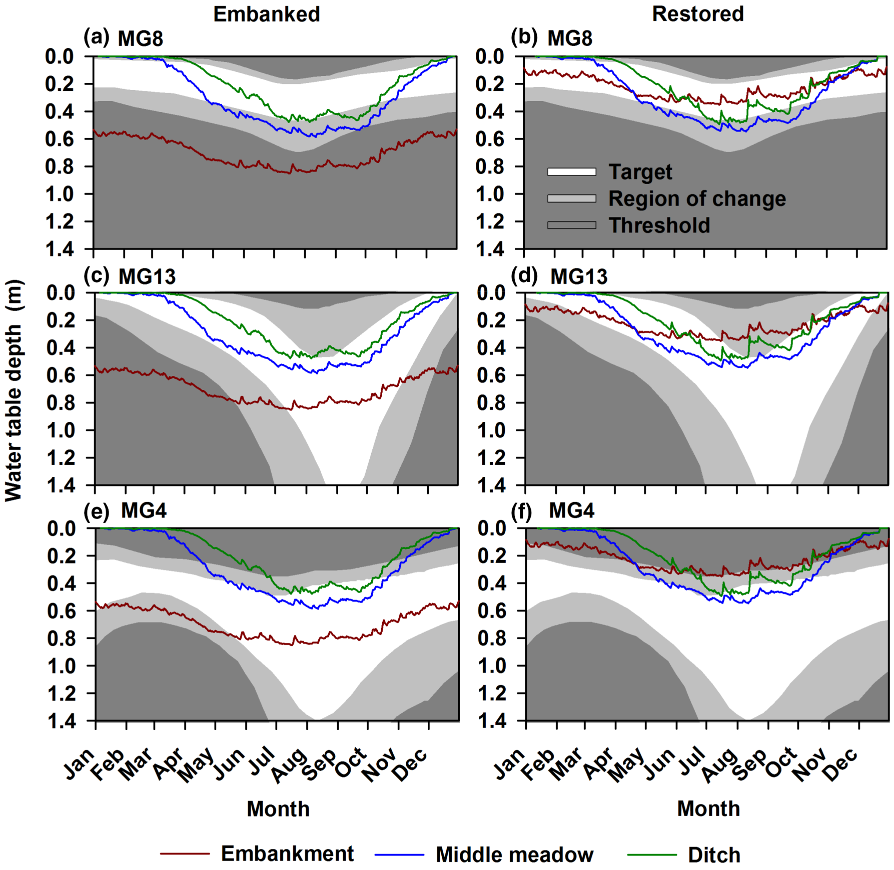

FIGURE 7 Simulated (a, c, e) pre- and (b, d, f) post-restoration mean (2001–2010) water table depth for three representative locations across the meadow: the river margin (well 3.1), middle meadow (well 2.1), and ditch margin (well 2.4) superimposed upon ecohydrological guidelines for (a, b) MG8, (c, d) MG13 and (e, f) MG4 British NVC grasslands from Wheeler et al. (2004). The target areas (white) represent conditions required for the community; conditions that fall outside of this target area regularly result in community change (light grey); the threshold areas (dark grey) indicate the more extreme wet or dry conditions that if experienced in one year only will result in community change.

microbes and plants. The resource balance hypothesis suggests that plant species diversity is highest when nutrient supply ratios (N:P) are balanced, which favours high species coexistence (Braakhekke & Hooftman, 1999). In contrast, low species richness on Hunworth Meadow likely results from combined effects of high aeration stress due to waterlogging, high available phosphorus, and nitrogen limitation. Therefore, regular management interventions, especially hay cutting, may be required to balance additional inputs of allochthonous phosphorus supplied by floods following river–floodplain reconnection (Linusson et al., 1998; Wheeler et al., 2004).

4.2 | Water regime of the restored floodplain meadow

Hydrological and hydraulic modelling indicates that under restored conditions, large floods on Hunworth Meadow are fairly infrequent (return period approximately three years) and typically short-lived (less than one day). Indeed, observations of overbank flows onto the meadow confirm that floodwaters recede quickly, normally within one day. This is likely to minimise negative impacts of widespread inundation on plant diversity (e.g. Baldwin et al., 2001), particularly if inundation occurs in winter. In contrast, smaller-scale flooding at the river–floodplain margin (i.e. within 5 m of the river) is simulated as occurring much more regularly (return period, 0.2 years) and persisting for longer (2–3 days). This results in a more hydrologically connected river–floodplain ecotone. Simulated water table elevation was higher after embankment removal due to lower surface elevation and increased floodwater storage on the meadow. However, there are also periods of drier conditions since surface water can now drain back to the river more freely (Clilverd et al., 2016) thereby reducing the effects of large floods. These findings may reduce concerns of land managers who do not wish to lose productive grazing land to floodwater but are interested in ecosystem benefits of river restoration.

Low soil aeration under waterlogged conditions was demonstrated using a novel oxygen optode approach that directly measured vadose DO concentrations to identify when plants begin to experience oxygen stress. High DO concentrations were consistent with low aeration stress values, confirming that air-filled porosity and soil oxygen status were directly linked. These findings validate the use of water table position as a proxy of aeration status in wetland soils, which underpins the SEV_{as} index. This method has tremendous potential for assessing the impacts of waterlogging and accompanying aeration stresses on wetland plants. However, it is possible that when DO is present in the top 34 cm of soil (the reference zone for aeration stress), deeper roots may experience some aeration stress. In addition, the delayed response of DO to falling water tables after saturation may lead to longer periods of aeration stress than predicted by water table depth alone if prolonged waterlogging (more than one week) were to occur during the growing season. Further work could examine changes in the soil oxygen–moisture relationship with depth, during overbank inundation, and in different soils.

4.3 | Predicting plant community composition change

Modelled water tables for a 10-year period allowed the quantification of the hydrological effects of embankment removal for a range of climate and river flow conditions, including extreme high- and low-flow years. Reinstatement of overbank flows did not substantially affect root saturation and aeration stress, largely because prior to embankment removal the meadow was already very wet and groundwater flooding typical during wet periods. However, an exception was the embankment area, where SEV_{as} increased dramatically from 0 m weeks (i.e. dry grassland) to approximately 7 m weeks (i.e. fen) ($p < 0.05$). This area is likely to undergo the greatest plant community change, from species intolerant of flooding (e.g. *Arrhenaterum elatius* and *Dactylis glomerata*) to plants that tolerate waterlogged soils throughout most of the growing season (e.g. *Phalaris arundinacea*, *Ranunculus acris* and *Cardamine pratensis*). These species are already present in wetter parts of the meadow and could colonise along the restored river banks.

Species-rich MG4 meadows require less waterlogging than observed and simulated at Hunworth Meadow. Interestingly, before restoration, the hydrological regime along the embankments was suited to dry grassland communities. It is likely that other factors (e.g. high fertility, seed dispersal limitation) limited colonisation of embankments by MG4 grassland. Michalcová et al. (2011) reported that increased plant diversity in UK wet mesotrophic grasslands is most likely when SEV_{as} values are between 0 and1 m weeks. Gowing, Lawson, Youngs, et al., 2002 and Gowing, Lawson, Youngs, Barber, et al., 2002 presented average SEV_{as} values of ca. 2.5 m weeks (upper limit: ca. 4.5 m weeks) as the favoured water regime of species-rich MG8 *Cynosurus cristatus*–*Caltha palustris* grazing marsh communities, and ca. 3.2 m weeks (upper limit: ca. 6 m weeks) for MG13 *Agrostis stolonifera*–*Alopecurus geniculatus* inundation grassland communities. The restored water table regime in parts of Hunworth Meadow may be suitable for MG8 or MG13 grassland communities. Indeed, some particularly characteristic species of MG8 (e.g. *Cynosurus cristatus*, *Cirsium palustre*, *Carex hirta*) and MG13 (e.g. *Agrostis stolonifera*, *Rumex crispus*, *Alopecurus geniculatus*) were present on the meadow before restoration. However, SEV_{as} values after restoration are near the upper limits for these more diverse plant assemblages, and although there is a gradient of hydrological change across the meadow that could support a range of communities, drier conditions would still be required during parts of the growing season to achieve the greatest increases in plant species diversity.

Changes in the quality of floodwater on the meadow may reduce aeration stress during waterlogging. Whereas prior to restoration, the meadow was dominated by oxygen-depleted groundwater (mean: 0.6 mg O_2 L^{-1}), the restored flooding regime includes overbank flows of oxygen-rich river water (mean: 10.8 mg O_2 L^{-1}). Passive diffusion of DO from the water column into submerged terrestrial plants, that is, *Rumex palustris*, is an important source of oxygen (Mommer et al., 2004). Thus, submergence with oxygen-rich river water may reduce oxygen shortages and stress on plant functioning, and thereby significantly affect which species can survive.

A botanical study of wet meadows along the River Glaven by Wotherspoon (2008) identified a number of sites of higher botanical value in terms of species richness (mean: 15–20 species m^{-2}) compared to Hunworth Meadow (mean: 8 species m^{-2}). Post-restoration these local species pools may provide sources of hydrochorically deposited propagules during overbank flows (e.g. Merritt et al., 2010), providing that embankments along the river upstream do not limit seed dispersal. Additional restoration works at Hunworth Meadow that involved the creation of a new, narrower, and more geomorphically diverse, meandering river channel, were carried out after the main period of fieldwork reported in this study and were followed by grazing management changes. Hence it is not possible to observe the effects of embankment removal only on the current vegetation assemblage.

4.4 | Management implications

Conservation efforts for UK wetlands are particularly focused on MG4 and MG8 species-rich wet meadows (Manchester et al., 1999). Based on the hydrological and soil physical and chemical conditions presented herein, three management options are proposed to maximise the botanical value where waterlogging persists following embankment removal: (1) restoration and maintenance of existing ditch networks to lower the water table during the growing season and promote more favourable conditions for species-rich MG8 communities; (2) reinstatement of traditional grazing and hay cutting to reduce nutrient loading from flood-deposited sediments, and address the dominance of competitive grasses and tall species such as rushes (*Juncus* spp.) (e.g. Proulx & Mazumder, 1998; Woodcock et al., 2006); and (3) reintroduction of species (e.g. hay spreading from local meadows) to supplement the local species pool, which may be particularly important at restoration sites that are seed-poor due to previous river regulation and habitat fragmentation (e.g. Bissels et al., 2004; Walker et al., 2004; Baasch et al., 2016).

Following embankment removal, and over the last few years, Hunworth Meadow has flooded approximately 1–3 times each year (Sayer, personal observation), verifying our modelled results. It is undoubtedly a key water store in the Glaven catchment throughout which much of the river is embanked and largely disconnected from its floodplain. Reinstatement of overbank flooding and improved interconnectivity along the river corridor could result in a natural dispersal-driven diversification of floodplain plant communities, which combined with more targeted introduction techniques could greatly enhance conservation value.

5 | CONCLUSIONS

The methods employed in this study to investigate the hydrological and ecological impacts of floodplain restoration provide powerful and practical scientific and management tools to assess changes in habitat suitability for target vegetation communities. The study employs a novel combination of field data that describe the distribution of vegetation species, hydrological conditions (in particular water table depth), soil nutrient status and continuous measurements of vadose dissolved oxygen using oxygen optodes (that in itself provides a unique data set) with high resolution hydrological/hydraulic modelling. Results demonstrate strong coupling between water table depth and root zone DO concentrations and show that the relationship between oxygen status and water table fluctuations in floodplain soils can assist the understanding of spatial and temporal distributions of lowland wet-meadow vegetation.

Embankment removal created a more natural flood-pulsed hydrological regime, characterised by more regular, short-duration inundation of the meadow that will likely improve river–floodplain ecosystem functioning (e.g. enhanced habitat connectivity and heterogeneity) that can inform agri-environment planning and practice. Changes in the quality of flooding, that is from long-term waterlogging with oxygen-poor groundwater to short-term pulses of oxygen-rich river water, should reduce aeration stress during submergence, and create flood conditions that are much more easily tolerated by a variety of wet-meadow plant species. This study has important implications for the rehabilitation, maintenance, and resilience of floodplain plant communities.

AUTHOR CONTRIBUTIONS

All authors contributed to methodology. Hannah Clilverd and Carl Sayer collected field data. Catherine Heppell, Jan Axmacher, Charlie Stratford, and Helene Burningham assisted in the laboratory and field. Hannah Clilverd constructed models, analysed data, and led the writing of the manuscript, Julian Thompson contributed to model development, and critiqued first drafts of the manuscript. Carl Sayer, Catherine M. Heppell and Jan Axmacher each contributed to drafts.

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DATA AVAILABILITY STATEMENT

Data are provided within the manuscript and Appendices S1–S7. Where further data are required, data are available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Photos of the River Glaven at Hunworth Meadow before and immediately after embankment removal.

Appendix S2. Observed and simulated groundwater depths for three representative wells on Hunworth Meadow for the calibration and validation periods.

Appendix S3. Topography and associated moisture gradient on the embanked floodplain meadow.

Appendix S4. Correspondence analysis (CA) of the vegetation data.

Appendix S5. Forward selection of environmental parameters for constrained canonical correspondence analysis (CCA).

Appendix S6. Vegetation type and associated sum exceedance values for aeration stress (SEV_{as}).

Appendix S7. Species names, frequency of presence and mean relative cover of each plant species used in the CANOCO ordination analyses.

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