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Landscape-scale ecohydrological mapping demonstrating how flood inundation water quality types relate to floodplain vegetation communities

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ABSTRACT

Landscape-scale ecohydrological mapping is commonly restrained to one-dimensional ecohydrological transect studies or two-dimensional vegetation distributions lacking adequate spatial coverage of explanatory hydrological data. The objective of this paper is to construct a two-dimensional (semi-3D) landscape-scale ecohydrological map based on vegetation distribution maps and detailed spatial, multi-year, floodplain inundation water quality data. The dataset comes from the near-natural Biebrza floodplain mire in Poland encompassing 658 inundation water quality analyses over the period 2002–2012, covering 17 different vegetation communities of freshwater marshes and rich fens. The data represent the main hydrological gradients from valley edge to river encompassing groundwater seepage, local stagnant precipitation influences and river flooding and drainage. We used chi-squared Haberman residuals analysis to correlate communities to inundation water quality types, resembling river water and three different types of groundwater. Out of 17 communities, six showed a preference for river water, three showed a preference for clean groundwater, four for diluted groundwater and one for polluted groundwater. For three communities, no significant preference was found. Spatial patterns in vegetation and attributed water quality preference can be linked to three dominant hydrological processes at the landscape scale, i.e. discharge of clean and polluted groundwater near the valley edges, dilution of exfiltrated groundwater with local snowmelt and precipitation water and flooding with river water along the river. The ecohydrological relations are depicted in two-dimensional maps and a semi-3D diagram with typical cross sections.

KEY WORDS wetland; floodplain mire; vegetation communities; water quality; landscape ecohydrological mapping

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INTRODUCTION

Wetlands provide 40% of the renewable ecosystem services (Costanza *et al*., 1997), despite their global cover of only 6% (OECD (Organisation for Economic Cooperation and Development), 1996). However, wetlands are being degraded (Brinson and Malvárez, 2002; Dudgeon *et al*., 2006), which endangers the performance of ecosystem services. Climate change processes might further exacerbate the degradation (STRP (Scientific and Technical Review Panel of the Ramsar Convention on Wetlands), 2002; Erwin, 2009).

Dominant factors for wetland vegetation are light (Kotowski *et al*., 2001; Kotowski *et al*., 1998), temperature, water quantity (Wheeler and Shaw, 1995) and water quality. These factors form the basis for classifications of wetlands using multiple gradients: (i) groundwater, surface water or rainwater fed, (ii) nutrient richness and base richness of the feeding water, and (iii) water level dynamics affecting production and decomposition (e.g. Zoltai and Vitt, 1995; Bridgham *et al*., 1996; Wheeler and Proctor, 2000).

In natural floodplains, typically, gradients in hydrological processes can be found with seepage of upland groundwater being dominant at the valley edges and flooding becoming more dominant in the direction of the river. In between these extremes, groundwater–surface water interactions play a role, as well as possible addition of local precipitation (Keizer *et al*., 2014; Schot and Winter, 2005). From an ecohydrological viewpoint, these gradients are often reflected in the distribution of floodplain vegetation communities with rich-fen vegetation fed by upland groundwater at the valley edges, freshwater marshes in river flood zone, and mixed and precipitation

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influenced wetland types like poor fens and bogs in the intermediate zone (e.g. Wheeler, 1980a, 1980c; Yabe and Onimaru, 1997; Wassen and Barendregt, 1992; Wassen *et al*., 2002; Schipper *et al*., 2007). Freshwater marshes are treeless wetlands on mineral soil and a characteristic element of river floodplains (Ward *et al*., 2002). They are well buffered because of the inflow of HCO_3^--rich surface water or groundwater. Rich fens are species-rich, low-productive treeless wetlands on organic substratum, fed by base-rich groundwater (Wheeler and Proctor, 2000).

The influence of water quality on wetland vegetation communities is mainly a function of the amount of available nutrients in flood inundation water and in shallow soil water as derived from groundwater seepage or precipitation (Wheeler and Proctor, 2000; Lamers *et al*., 2006; Wassen, 1995). Hydrobiogeochemical processes in the soil play an important role in regulating the amount of nutrients available for wetland plants, mainly as a function of climate, soil type and hydrological processes affecting water level dynamics and the quality of inflowing water. Base-richness and water level are important controls on nutrient availability (Koerselman *et al*., 1993; Lamers *et al*., 2006). Water quality in surface water-fed and groundwater-fed wetlands shows varying degrees of nutrient richness and base richness, affecting vegetation community differences between those wetland types.

Many ecohydrological studies show how water quality correlates to fen and marsh vegetation, notably in the northern United States, Canada and Europe. Vegetation communities and gradients in water quality were shown to be closely related for a Minnesota peatland (Glaser *et al*., 1990), fens in West Virginia's Appalachian Plateau (Walbridge, 1994) and Canadian fens in boreal Alberta (Vitt and Chee, 1990; Zoltai and Vitt, 1995). Relations between water quality and vegetation communities for European fens and freshwater marshes were shown in the UK (Wheeler, 1980a, 1980b, 1980c; Wheeler and Giller, 1982; Boyer and Wheeler, 1989), in the Netherlands (Grootjans *et al*., 1988; Wassen *et al*., 1989; Bootsma and Wassen, 1996), Poland (Wassen *et al*., 2002) and in the Western Carpathians (Chytrý *et al*., 2003; Hájková *et al*., 2004; Rozbrojová and Hájek, 2008; Koczur and Nicia, 2013) and Tatra Mountains (Sekulová and Hájek, 2009).

The relations between water quality and wetland vegetation can be studied in different ways. Vegetation communities or plant species can be correlated to environmental variables using multiple types of statistical techniques (Kleyer *et al*., 2012), e.g. canonical correspondence analysis (CA) (Ter Braak, 1987; Sarvade *et al*., 2016), multivariate regression trees (De'Ath, 2002) and generalized linear models (Guisan *et al*., 1999). These techniques adequately describe the environmental preferences of the vegetation community or plant species, but lack a spatial dimension. Spatial relations can be studied in transects that cover a typical gradient in the environment (e.g. wetness, elevation and observed pattern in vegetation communities; Wassen *et al*., 2002; Schipper *et al*., 2007). With this approach, the one-dimensional spatial context of the vegetation communities can be taken into account to determine possible causes of observed relations. However, upscaling to the landscape scale requires multiple, adequately placed transects and interpolation. Thirdly, two-dimensional remote sensing is often used to map vegetation communities (Chormański *et al*., 2011; Martínez-López *et al*., 2014), but lacks mapping of water quality parameters.

Studies on the relations between water quality and vegetation community often focus on one type of vegetation community (e.g. species-rich communities) or wetland type (e.g. calcareous springs, freshwater marshes and oxbows). They rarely cover the entire floodplain wetland gradient from valley edge to river, encompassing all vegetation communities typical for the hydrological steering processes of groundwater seepage, river flooding and local precipitation. Also, water quality sampling sizes often are relatively small, and rarely repeated sampling over several years is conducted, raising doubts as to representativeness of the acquired data.

In this paper, we combine floodplain-wide water quality mapping with remote sensing-derived vegetation communities, and use typical transects and landscape ecological knowledge to explain how inundation water quality influences vegetation communities. We aim to determine whether water quality properties can be inferred from the spatial distribution of rich-fen and freshwater marsh communities. For this, we use a comprehensive dataset that circumvents the inadequacies of most previous research. It consists of a large inundation water quality dataset ($n = 658$), covering 17 different vegetation communities of freshwater marshes and rich fens from the Biebrza Lower Basin in Poland. The data presents a unique opportunity to study water quality–vegetation community relations and processes fundamental to river floodplain ecosystem restoration (Palmer *et al*., 2008) because of (1) the absence of large-scale human alteration in hydrology in the catchment (Wassen *et al*., 1992), except for some small-scale pollution from agricultural settlements; (2) the sustained presence of near-natural rich-fen and marsh vegetation (Pałczynski, 1986); (3) the presence of a complete floodplain gradient from valley edge to river, in which the influence of the main interacting hydrological forces of groundwater seepage, river flooding and drainage, and local precipitation are all present and reflected in the vegetation communities; and (4) the extensive base of knowledge on hydrology, water quality and vegetation communities. We derive ecohydrological relations between flood inundation water quality (notably major ions, base-richness and nutrients) and vegetation communities to produce ecohydrological maps on the landscape scale.

METHODOLOGY

Study area characteristics

The field study was conducted in the Biebrza Lower Basin floodplain marshes and rich fens (NE Poland; 22°30′–23° 60′E, 53°30′–53°75′N; catchment area: 7000 km^2; see Figure 2 for location). In the lower basin (453 km^2), flooding occurs annually following snowmelt starting between February and April, but the extent of flooding and the zone inundated with river water varies from year to year (Okruszko, 1990; Grygoruk *et al*., 2011; Ignar *et al*., 2011). The floodplain (100–106 m amsl) remains flooded until May/June with inundation water depth varying spatially with distance from the river from more than 1·00 to 0·10 m (Chormański *et al*., 2011). The ice-marginal valley widens from 3 km in the north to more than 15 km in the south and is bordered by a sand and gravel moraine plateau (130–165 m amsl). Because of differences in elevation, the surrounding moraines and the local dunes act as groundwater recharge areas, while the river valley acts as groundwater discharge zone (Pajnowska and Wienclaw, 1984). Mean annual precipitation is 585 mm (1979–2008). January–April is generally dry (143 mm), while the summer months June, July and August are relatively wet (261 mm) (data obtained from Institute of Meteorology and Water Management – National Research Institute (Poland)).

Inundation water quality data

For the Biebrza Lower Basin, a large database of chemical water quality analyses of flood inundation water is present. A total of 1154 analyses from samples taken over the period 2001–2012 were classified by Keizer *et al*. (2014) into water types that could be related to principal water sources in the study area. The main variation in inundation water quality can be attributed to mineral richness and pollution, including nutrients (NO_3^- and K^+). *K*-means cluster analysis on principal component analysis scores showed four clusters, which were related to principal water sources in the study area. The clusters showed varying degrees of mineral richness and pollution and were termed river water, clean groundwater, polluted groundwater and diluted groundwater (Keizer *et al*., 2014). With respect to nutrients, river water is high in NO_3^- and polluted groundwater is high in PO_4^{3-}. River water and polluted and clean groundwater are relatively high in base ions compared with diluted groundwater. In the current paper, these water quality types are related to wetland vegetation communities.

Of the 1154 inundation water samples used in Keizer *et al*. (2014), only water samples taken within polygons of the modified vegetation map (next section) were retained in the current analysis. Samples from 2001 were omitted from the dataset as that year had a very low peak flow (below bankfull at the upstream inflow point during the sampling moment). The final dataset consisted of 658 inundation water samples. Water quality parameters for the four water quality types are presented in Table I.

Vegetation communities data

A detailed vegetation map based on aerial imagery was utilized (Matuszkiewicz, 2000), which covers the Biebrza National Park in the Lower Basin. Vegetation communities were attributed by ground truth visual inspection. In the current study, some communities were discarded because they are not a vegetation community in the strict sense, or they covered a too small area (<5 ha), or had too little inundation water samples (<5). The discarded vegetation communities were a mosaic of two communities (except Mosaic of Sedges and *Magnocaricion*), forest, dense bushes, crop communities and aquatic vegetation. Some vegetation communities were merged into one because

Table I. Mean and standard deviation of water quality parameters for the 658 water quality samples used in this study.

Water type	River water	GW clean	GW diluted	GW polluted
n	249	146	140	123
Electrical Conductivity ($\mu S\,cm^{-1}$)	400 (47)	402 (120)	238 (49)	410 (112)
pH (–)	7·9 (0·3)	7·3 (0·3)	7·1 (0·3)	7·2 (0·4)
Ca^{2+}	65 (16)	60 (23)	39 (13)	77 (25)
Mg^{2+}	12 (3)	13 (5)	7 (2)	14 (4)
Na^+	6·7 (2·1)	5·0 (1·6)	4·6 (1·4)	7·1 (2·4)
K^+	2·7 (1·1)	1·0 (0·8)	1·1 (1·5)	2·3 (1·9)
Cl^-	9·3 (2·5)	5·0 (1·7)	6·6 (2·3)	9·5 (4·0)
SO_4^{2-}	28·7 (7·9)	5·2 (7·6)	8·8 (10·3)	18·5 (18·3)
PO_4^{3-}	0·06 (0·05)	0·06 (0·28)	0·17 (0·60)	0·42 (0·85)
NO_3^-	3·31 (2·96)	0·07 (0·09)	0·21 (0·30)	0·22 (0·49)
NH_4^+	0·20 (0·42)	0·11 (0·14)	0·15 (0·19)	0·28 (0·70)

The samples are categorized as water types according to the clustering of inundation water samples of 2002–2012 from the Biebrza Lower Basin by Keizer *et al*. (2014).
All units in $mg\,l^{-1}$, unless indicated otherwise.
GW, groundwater.

they were subtypes of the same higher-order community. The modified vegetation map consisted of 17 vegetation communities, which were used for further analysis.

Correlation analysis of inundation water quality and vegetation communities

Correlation of vegetation community distribution to inundation water quality type distribution was carried out by a chi-squared test (Monte Carlo with 2000 replicates) and Haberman-adjusted residual analysis (Haberman, 1973). This method follows Grootjans *et al.* (1988); Wassen *et al.* (1989) and De Mars *et al.* (1997). A chi-squared test requires that the expected values are not 'too small'. Similar to Grootjans *et al.* (1988), we used 'no expected frequency < 1'. Two *Molinion* vegetation communities did not meet this criterion and were merged with two other *Molinion* communities into one class *Molinion*/*Molinietum*. The inundation water quality type that showed highest positive correlation to a vegetation community (Haberman-adjusted residual) was attributed to (all polygons of) that vegetation community. We call that water quality type the attributed water quality preference of that vegetation community. The spatial distribution of the attributed water quality preference is shown for the 12 most common vegetation communities as based on area coverage. The remaining communities only cover 5% of the area. To obtain more insight in the similarities of the vegetation types with respect to the attributed water quality types, a CA (Benzécri, 1973; Nanadic and Greenacre, 2007) was performed on the cross-table and presented in an asymmetric biplot. Water quality type points are plotted as principal coordinates; vegetation points are plotted as contribution coordinates (contribution coordinates are principal coordinates corrected for the weight of the vegetation community and the dimension eigenvalue). This combination most clearly revealed the association between water quality and vegetation.

Verification of the attributed water quality preference was carried out by comparison of total numbers of observed inundation water quality samples with the attributed preferred water quality type of vegetation communities.

Additional insight in differences between water quality properties of vegetation communities is provided by means and standard deviations of water quality parameters (Electrical Conductivity (EC), pH, major ions and nutrients) for all vegetation communities with significant numbers of inundation water samples (>30) and total polygons area with water samples on the vegetation map (>500 ha). This resulted in seven vegetation communities. Kruskal–Wallis multiple comparison tests were performed to determine significant differences in water quality parameters between those vegetation communities. All statistics were performed in R 3.1.1 (R Core Team, 2014).

Spatial verification of inundation water types – vegetation communities correlations

Spatial verification of the degree of (mis)match was analysed by construction of maps confronting observed water quality types at water sampling locations with the spatial coverage of attributed water quality preference of vegetation communities. Verification of the spatial distribution of vegetation attributed to river water was also carried out by comparison to the spatial extent of river water flood using independent hydrodynamic modelling data (50% flood probability extent; Grygoruk *et al.*, 2011) and extent of river inundation water quality (2002; average peak discharge; Chormański *et al.*, 2011).

RESULTS

Correlations between inundation water quality and vegetation communities

A chi-squared analysis on the cross-table of water quality types and vegetation communities showed significant differences (χ^2 339·3; $p < 0{\cdot}001$). Most of the vegetation communities (14 out of 17) were found to be significantly correlated ($p < 0{\cdot}05$) to at least one of the inundation water quality types (Table II). Three vegetation types (*Caricetum elatae*, *Caricetum rostratae* and *Molinion*/*Molinietum*) were not significantly correlated to any of the water types. The significantly correlated vegetation communities were attributed to river water ($n = 6$), clean groundwater ($n = 3$), diluted groundwater ($n = 4$) and polluted groundwater ($n = 1$). River water shows the strongest correlation to vegetation communities, followed by clean groundwater, diluted groundwater and polluted groundwater, respectively.

The CA biplot (Figure 1) shows the strong correlation between river water and its six attributed vegetation communities. Communities that plot further from the centre of the diagram indicate stronger associations to water quality. Close relations are also seen for polluted groundwater and clean groundwater with their attributed vegetation communities. For diluted groundwater the attributed communities diverge most from their related water quality point possibly indicating transitional/mixing stages with the other water quality types. Communities that have no attributed water quality preference plot closest to the centre of the CA biplot confirming absence of correlation to water quality, although they incline towards the group of river water-attributed communities, which is also evident from their spatial distribution (Figure 3).

Verification of the attributed inundation water quality preference based on vegetation matches well with the observed water types (Table III). Vegetation with river water preference shows a correct attribution in 74% of the cases (145 out of 197), which was also corroborated by

Table II. Correlations between vegetation communities and water quality types (after Keizer *et al*., 2014).

Attributed water quality preference	Vegetation community	χ^2	Water quality types			
			River	GW clean	GW diluted	GW polluted
River water	*(a) Sedges and Magnocaricion*	***	+	–	–	·
	(b) Rushes and Phragmition	***	+++	·	·	·
	(c) Phragmitetum communis	***	+++	·	·	–
	(d) Glycerietum maximae	***	+++	–	– –	·
	(e) Caricetum gracilis	***	+++		– –	·
	(f) Agropyro-Rumicion crispi	***	+++	–	– – –	·
GW clean	*(g) Carici-Agrostietum caninae*	***	– – –	+++	·	·
	(h) Carici-Agrostietum caninae (*Caricetum diandra*)		–	+++	·	·
	(i) Filipendulion		·	++		
GW diluted	*(j) Caricetum appropinquatae*	**	– – –	++	+++	–
	(k) Caricetum diandrae (*Caricetum appropinquata*)	***	– – –	·	+++	·
	(l) Caricetum diandrae	***	– –	–	+++	·
	(m) Carici-Agrostietum caninae (*Caricetum appropinquata*)		·		+	·
GW polluted	*(n) Caricetum lasiocarpae*	***		·	+	+++
No preference	*(o) Molinion/Molinietum*	**	·	·	–	·
	(p) Caricetum rostratae		·	·		·
	(q) Caricetum elatae	***	·	·	·	·

Levels of significance of χ^2 test and adjusted residuals analysis (Haberman, 1973).
χ^2: $^{**}p < 0{\cdot}01$; $^{***}p < 0{\cdot}001$. Adjusted residuals: $^{\cdot}p > 0{\cdot}05$, $^{-}p < 0{\cdot}05$, $^{+}p < 0{\cdot}05$, $^{--}p < 0{\cdot}01$, $^{++}p < 0{\cdot}01$, $^{---}p < 0{\cdot}001$, $^{+++}p < 0{\cdot}001$, –/+: avoidance/preference to water type. GW, groundwater.

the CA biplot (Figure 1), where river water and the associated communities are strongly differentiated from the other water types and their associated communities. Vegetation with an attributed preference for one of the groundwater types matches the observed water quality type in only 42–48% of the cases, indicating these vegetations also show correspondence to other groundwater types, notably diluted groundwater (Figure 1). When the three groundwater types are merged, the correct attribution increases to 87% (299 out of 344). Within the vegetation with no preference, groundwater and river water types are equally represented.

For the seven most abundant vegetation communities based on available numbers of inundation water samples and total area coverage, additional insight in water quality parameters is presented in Table IV.

The general pattern is one of high pH, base-richness, pollutants and nutrients (N and K) in vegetation with a preference for river water (*Glycerietum maximae* and *Caricetum gracilis*) and somewhat lower concentrations in vegetation with a preference for groundwater-derived inundation water. Phosphorus is low in river water and clean groundwater-attributed communities, and particularly high in the community with polluted groundwater preference (*Caricetum lasiocarpae*), the latter also having the lowest pH.

Spatial match of inundation water types and vegetation communities

When comparing observed inundation water quality from water samples with the spatial distribution of attributed water quality preference of the communities (Figure 2), insight is obtained in the spatial match between the two (cf., Table III). In general, there is a good spatial match between observed inundation water quality (river water flooding, groundwater discharge and diluted by precipitation and snowmelt; Keizer *et al*., 2014) and vegetation preference. Vegetation with river water preference is predominantly found in a zone along the river stretching from north to south. Vegetation with attributed clean groundwater preference is mainly found in the northern and central part, adjacent to the river dune complex, with some local occurrences further away from the edges. Vegetation with attributed diluted groundwater preference is observed mainly in the southern part where groundwater is diluted at a large scale by precipitation and snowmelt water because of the isolated location distant from both groundwater and river water influence. A similar type of intermediate position is seen for some local occurrences in the northern part in the middle of the gradient from the river to the valley edge. Vegetation with attributed polluted groundwater preference is predominantly located along the moraine edges in the east where groundwater seepage

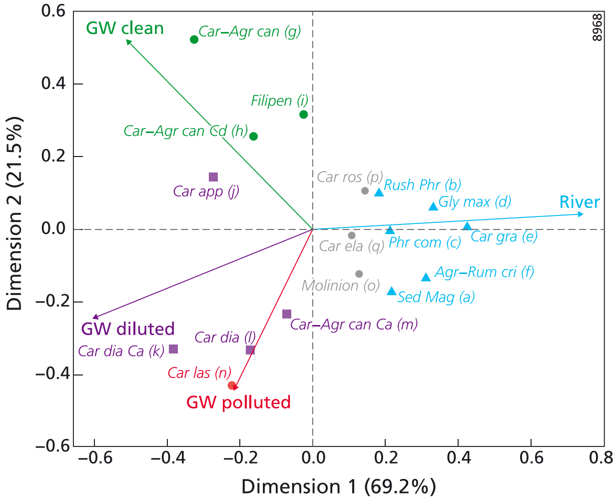

Figure 1. Correspondence analysis biplot (dimensions 1 and 2) of the vegetation of the Biebrza Lower Basin, showing associations between inundation water quality types and vegetation communities. Colours in the diagram show the different water quality types and attributed water quality preference of the vegetation communities (Table II; Figure 2). Vegetation community names are as follows: *Car-Agr can*, *Carici-Agrostietum caninae*; *Car-Agr can Cd*, *Carici-Agrostietum caninae* (*Carex diandra*); *Filipen*, *Filipendulion*; *Rus Phr*, *Rushes and Phragmition*; *Phr com*, *Phragmitetum communis*; *Gly max*, *Glycerietum maximae*; *Sed Mag*, *Sedges and Magnocaricion*; *Agr-Rum cri*, *Agropyro-Rumicion crispi*; *Car gra*, *Caricetum gracilis*; *Car app*, *Caricetum appropinquatae*; *Car-Agr can Ca*, *Carici-Agrostietum caninae* (*Carex appropinquata*); *Car dia*, *Caricetum diandrae*; *Car dia Ca*, *Caricetum diandrae* (*Carex appropinquata*); *Car las*, *Caricetum lasiocarpae*; *Molinion*, *Molinion/Molinietum*; *Car ros*, *Caricetum rostratae*; *Car ela*, *Caricetum elatae*. Letters after the name correspond to Table II. For information about the average chemical composition of the water quality types, see Table I. The arrows point in the direction of maximum change of water quality related to that arrow. The length of an arrow indicates the strength of the correlation with the ordination axes, so it is indicative of the strength of their relation with the pattern of community variation. The distribution of communities over the diagram indicates the relative position of the communities with respect to the water quality types.

However, there are some mismatches in attribution. Firstly, in the northern and central part, inundation samples belonging to river water are frequently (42% of the samples) observed within vegetation with a clean or diluted groundwater preference. Secondly, in the central and southern part, samples belonging to polluted and clean groundwater are in 26% of the cases observed within vegetation with a river water preference. Thirdly, within the vegetation with clean groundwater preference, as already presented in Table III, other groundwater types are frequently observed, notably in occurrences of these vegetation communities in the northern and south-western part. Lastly, polluted groundwater is often (90% of the samples) found outside vegetation with attributed polluted groundwater preference. It should be noted that although this type is termed 'polluted', this is predominantly linked to high phosphorous while the concentrations of other pollution indicators (Cl^-, SO_4^{2-}, K^+ and $Na^{+)}$ are low in comparison with, e.g. similar wetlands in the Netherlands (Wassen *et al*., 1996).

Figure 3 presents the spatial distribution of the 12 most common vegetation communities (based on total polygons area) and their attributed water quality preference. Their position in the landscape can be explained from the main operating hydrological processes determining inundation water quality zonation. For *Phragmitetum communis*, *G. maximae*, *Carici-Agrostietum caninae* (*Carex diandra*), *Caricetum appropinquata*, *C. lasiocarpae* and *C. elatae*, examples are shown in Figure 4.

Table III. Verification of attributed water quality preference for vegetation communities (Table II, columns 1 and 2) by comparison with observed inundation water quality types (after Keizer *et al*., 2014) of samples located within corresponding community polygon.

		Observed water quality type				
		River	GW clean	GW diluted	GW polluted	*Sum*
Attributed water quality preference	River water	145 (74%)	12	9	31	*197*
	GW clean	29	72 (46%)	33	22	*156*
	GW diluted	16	41	68 (42%)	38	*163*
	GW polluted	0	3	10	12 (48%)	*25*
	No preference	59	18	20	20	*117*
	Sum	*249*	*146*	*140*	*123*	658

GW, groundwater.

i Communities with attributed river water preference, *P. communis*, *C. gracilis* and *G. maximae*, are located in the riparian zone. The latter occupies the zone very close to the river channel, while *C. gracilis* is originates from recharge in the agricultural uplands. Vegetation with no water quality preference is found in adjacent to the river water zone (in line with the CA biplot) and bordered by groundwater preference vegetations on the other side. observed also more distant from the river channel where flooding occurrence is less frequent, shallower and for shorter periods.

ii Communities with attributed clean groundwater preference *Carici-Agrostietum caninae* (and variety with *C.*

Table IV. Water quality properties on the level of single parameters (mean and standard deviation) for vegetation communities.

	Vegetation community	*Glycerietum maximae (d)*	*Caricetum gracilis (e)*	*Carici-Agrostietum caninae (g)*	*Caricetum appropinquata (j)*	*Caricetum diandrae (Carex appropinquata) (k)*	*Caricetum lasiocarpae (n)*	*Caricetum elatae (q)*
	Water quality preference	River	River	GW clean	GW diluted	GW diluted	GW polluted	No preference
	n	35	64	86	65	89	25	94
	area (ha)	512	852	578	1510	1114	253	1033
	EC	401 (36)^{ab}	406 (78)^{a}	425 (137)^{a}	310 (85)^{c}	337 (150)^{c}	313 (65)^{c}	345 (83)^{bc}
	pH	8·0 (0·3)^{a}	8·0 (0·4)^{a}	7·5 (0·3)^{b}	7·2 (0·4)^{c}	7·1 (0·2)^{cd}	6·9 (0·2)^{d}	7·5 (0·4)^{b}
Major ions	Ca^{2+}	66 (14)^{ab}	72 (21)^{b}	72 (24)^{b}	47 (16)^{d}	54 (25)^{cd}	51 (11)^{cd}	57 (17)^{ac}
	Mg^{2+}	12 (4)	13 (3)	11 (5)	11 (4)	12 (5)	13 (4)	12 (4)
	Na^{+}	6·6 (2·8)^{abc}	6·6 (1·9)^{b}	6·1 (1·6)^{b}	5·3 (1·8)^{acd}	5·1 (1·7)^{cd}	4·3 (1·5)^{d}	6·3 (2·4)^{ab}
	Cl^{-}	8·9 (2·9)^{a}	9·3 (2·4)^{a}	5·9 (3·1)^{c}	6·8 (2·8)^{bcd}	6·9 (3·5)^{cd}	8·5 (4·1)^{abd}	8·3 (2·8)^{ab}
	SO_4^{2-}	29 (12)^{a}	29 (10)^{a}	16 (21)^{b}	10 (11)^{b}	7 (8)^{b}	7 (5)^{b}	21 (13)^{a}
Nutrients	N	1·5 (0·8)^{a}	1·6 (1·2)^{a}	0·3 (0·8)^{bc}	0·3 (0·4)^{c}	0·2 (0·4)^{c}	0·1 (0·0)^{c}	0·5 (0·6)^{b}
	P	0·02 (0·03)^{c}	0·03 (0·04)^{bc}	0·03 (0·16)^{c}	0·07 (0·43)	0·06 (0·19)^{ab}	0·13 (0·18)^{a}	0·07 (0·45)^{c}
	K^{+}	2·3 (1·0)^{a}	2·5 (1·4)^{a}	1·1 (1·2)^{c}	1·1 (1·0)^{c}	1·5 (1·4)^{bc}	1·3 (2·3)^{c}	2·1 (1·6)^{ab}

Superscript letters correspond to Table II.
EC in $\mu S\,cm^{-1}$, all other variables in $mg\,l^{-1}$ except pH.
N presented as TIN ($[NO_3^-] + [NH_4^+]$-N).
P presented as TIP ($[PO_4^{3-}]$-P).
Area (ha) is the sum of vegetation map polygon areas in which inundation water was sampled.
Columns with 'abcd' indicate variables are significantly different at $\alpha = 0{\cdot}05$ (data from Keizer *et al.*, 2014).
n = number of inundation water samples.

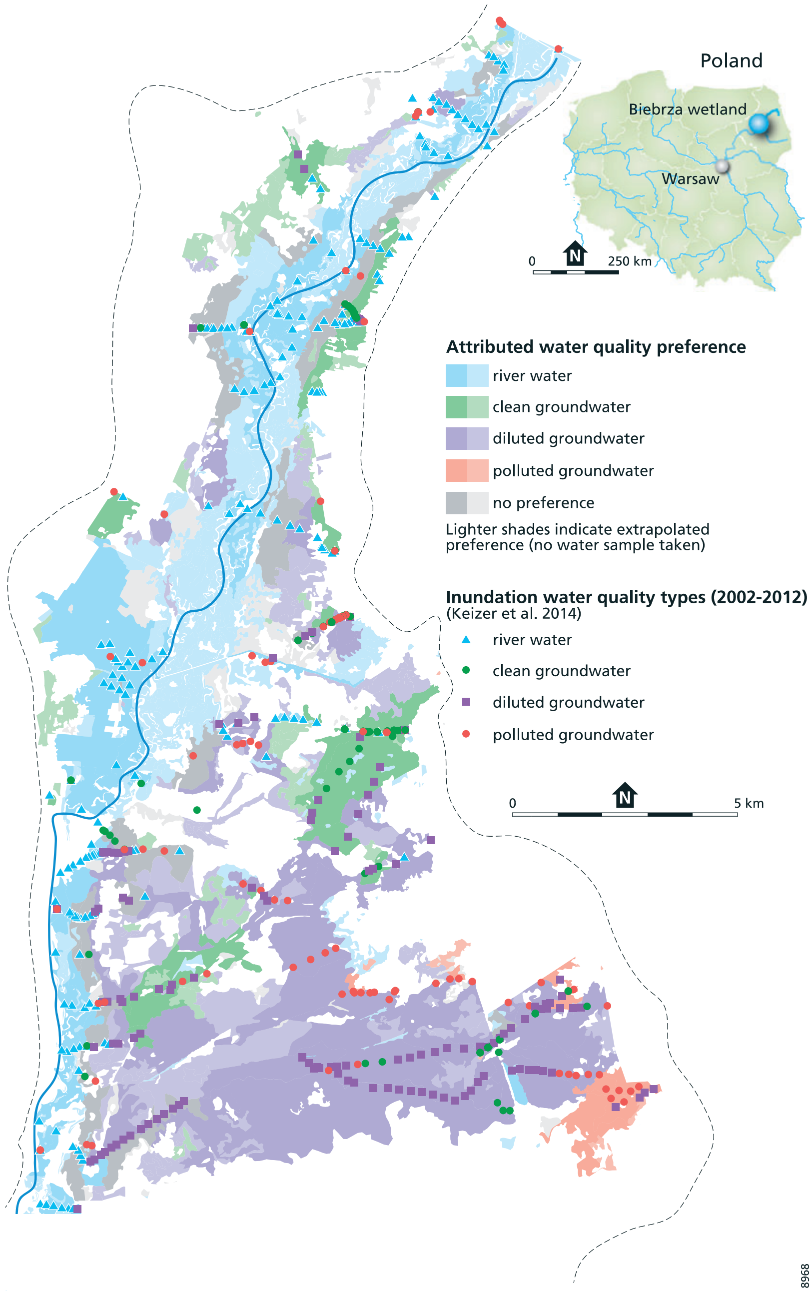

Figure 2. Verification of the match between observed water quality types at water sampling locations (points; Keizer *et al.*, 2014) and the spatial coverage of attributed water quality preference of vegetation communities (polygons) in the Biebrza Lower Basin.

diandra) are observed in the northern and central part at the edge of low populated dunes. West of the river this type occurs only locally.

iii Communities with attributed diluted groundwater preference are located intermediate between the zones where either groundwater seepage or river flooding are the dominant hydrological process. The relatively isolated position enables the influence of local precipitation and snowmelt to gain importance.

iv The community with attributed polluted groundwater preference *C. lasiocarpae* is found exclusively close to the valley margins in the south-eastern part where agricultural pollution on the adjacent moraine likely plays a steering role for vegetation development.

v The community with no attributed water quality preference *C. elatae* is found next to but on the outside the river water zone. *Molinion*/*Molinietum* is scattered over the floodplain, but mostly in the same longitudinal zone as *C. elatae*.

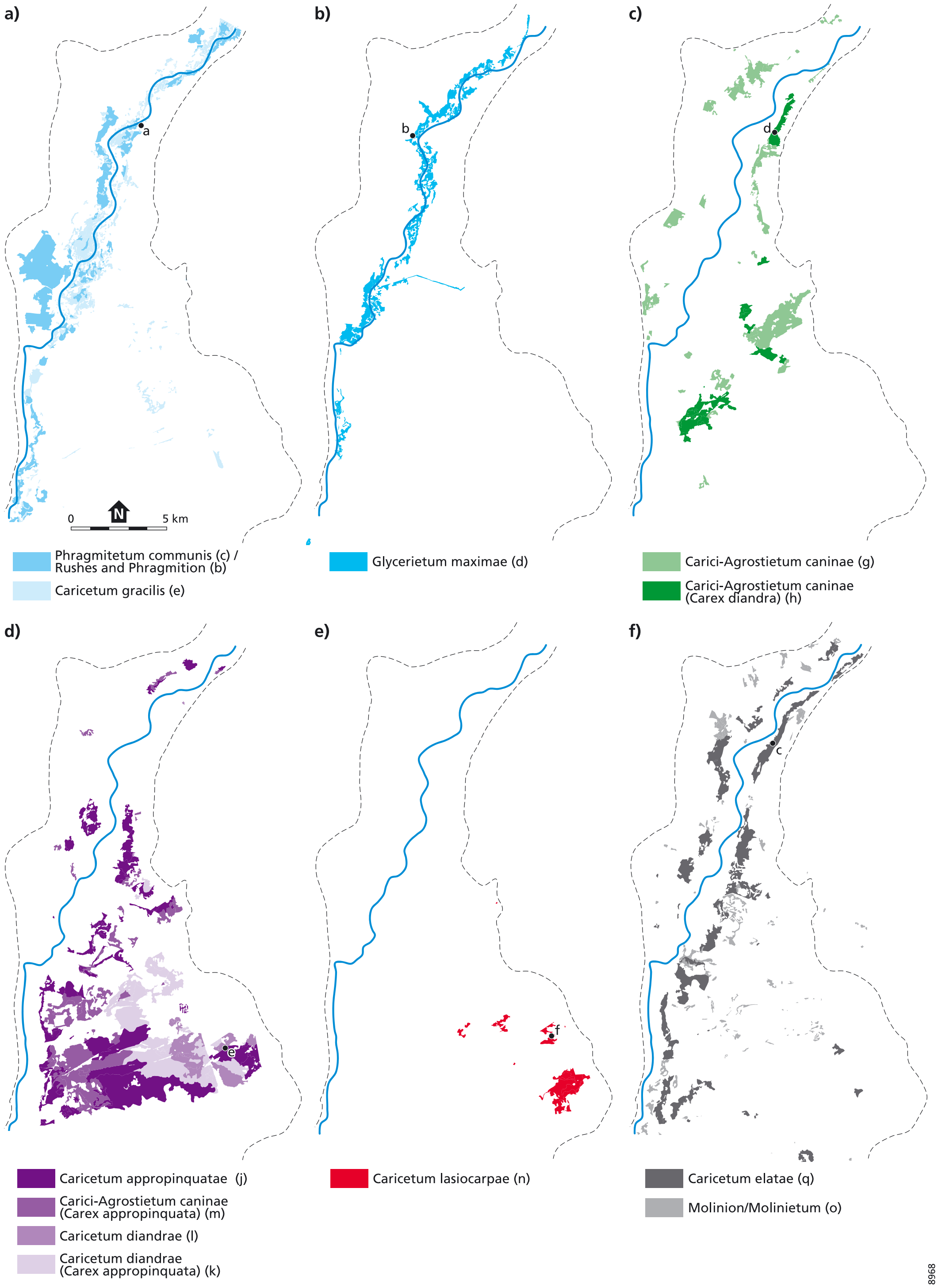

Figure 3. Distribution of the most common vegetation communities presented according to attributed water quality preference: (a) and (b) river water no preference, (c) clean groundwater, (d) diluted groundwater, (e) polluted groundwater and (f) no preference. Letters a–f indicate locations of photos in Figure 4.

Verification of the spatial distribution of the river water-attributed vegetation is further enhanced in Figure 5 by comparison with additional independent data from hydrodynamic modelling (50% flood probability; Grygoruk *et al.*, 2011) and inundation water samples taken in a year with average peak discharge (2002; Chormański *et al.* (2011).

Figure 6 finally presents a semi-3D ecohydrological map and 2D cross sections (cf., Keizer *et al.*, 2014) showing the spatial distribution of vegetation communities in relation to

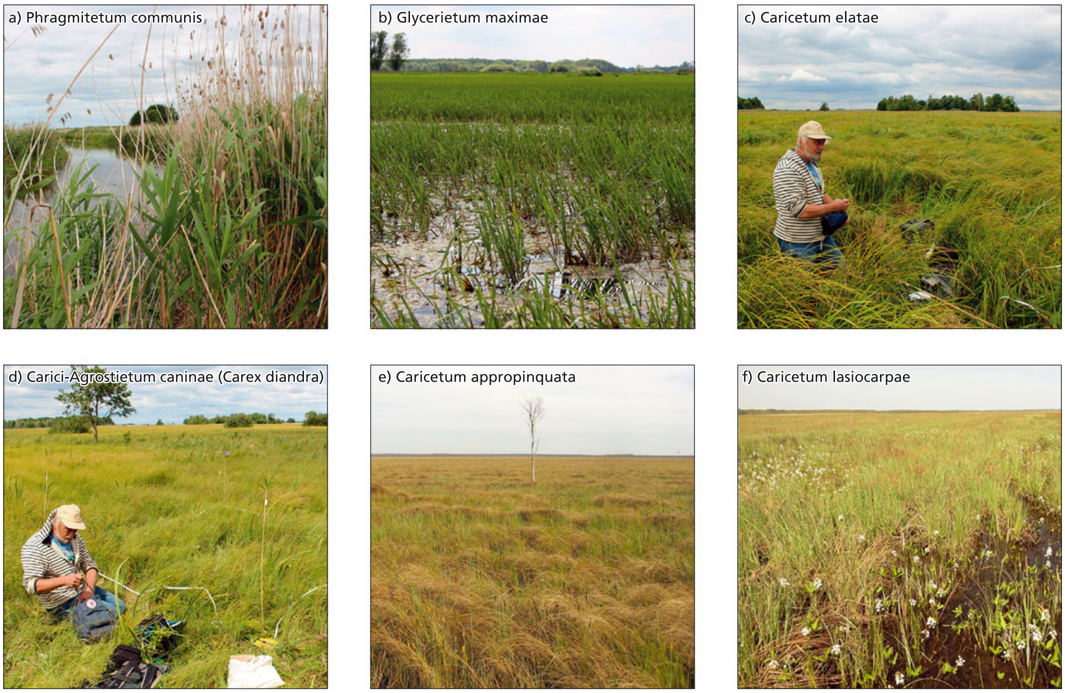

Figure 4. Vegetation communities (six out of the 17 analysed) in the Biebrza Lower Basin. For locations of the photos, see Figure 3.

topography and the main hydrological water sources and flow processes operating on the landscape scale.

DISCUSSION

Robustness of relations between water quality and vegetation communities

The spatial distribution of water quality types as determined from the 658 inundation water samples generally matches well with the spatial patterns in attributed water quality preference of the vegetation communities (Figure 2). However, we also observed some dissimilarities between both spatial patterns.

First, spatial water quality patterns may vary between years. This was especially noticed for locations adjacent to the river zone, where cluster membership of identical locations varied between years, most probably related to flooding magnitude and extent. Similarly, along the floodplain edges, where polluted or diluted groundwater was observed, variation between years may be related to the degree of dilution with rain and snowmelt water (Keizer *et al.*, 2014).

Second, within the zone of river water flooding also, some vegetation communities with a preference for groundwater are found (*Caricetum appropinquatae* in the south and central part and *Carici-Agrostietum caninae* and *Carici-Agrostietum caninae* (variety with *Carex diandra*) in the northern part; Figure 3). This indicates other factors besides inundation water quality also may play a role for the observed pattern of attributed water quality preference of the vegetation communities. For instance, groundwater table fluctuations may play a role, as De Mars *et al.* (1997) reported them to be >1·00 m near the river and <0·10 m near the valley edges. High dynamics in the river water zone result from flooding in spring followed by strongly lowered water tables because of the draining effect of low summer river water levels. Low groundwater tables allow for oxygen to enter the soil invoking mineralisation processes, and preventing, e.g. denitrification (Beumer *et al.*, 2008) and increasing phosphate availability (Hoffmann *et al.*, 2009; Griffioen, 2006). This increases nutrient availability resulting in higher production for the river water-preference communities (Figure 4). Wierda *et al.* (1997) found the highest groundwater level and fluctuations in groundwater level to be most determining for vegetation composition. Becker *et al.* (1999) concluded groundwater fluctuation to be the major environmental variable describing vegetation patterns in a groundwater-fed alluvial floodplain mire. The occurrence of groundwater-preferring communities within the river zone may be the result of local depressions unaffected by summer lowering of groundwater level preventing mineralisation and stimulating denitrification. However, it should be stressed that especially under conditions with high groundwater levels and little fluctuation, water quality is the most important determining factor (Wierda *et al.*, 1997).

Lastly, hydrochemistry could be vertically stratified during flooding, with nutrient-poor conditions in the waterlogged root zone and flooding with nutrient-rich river

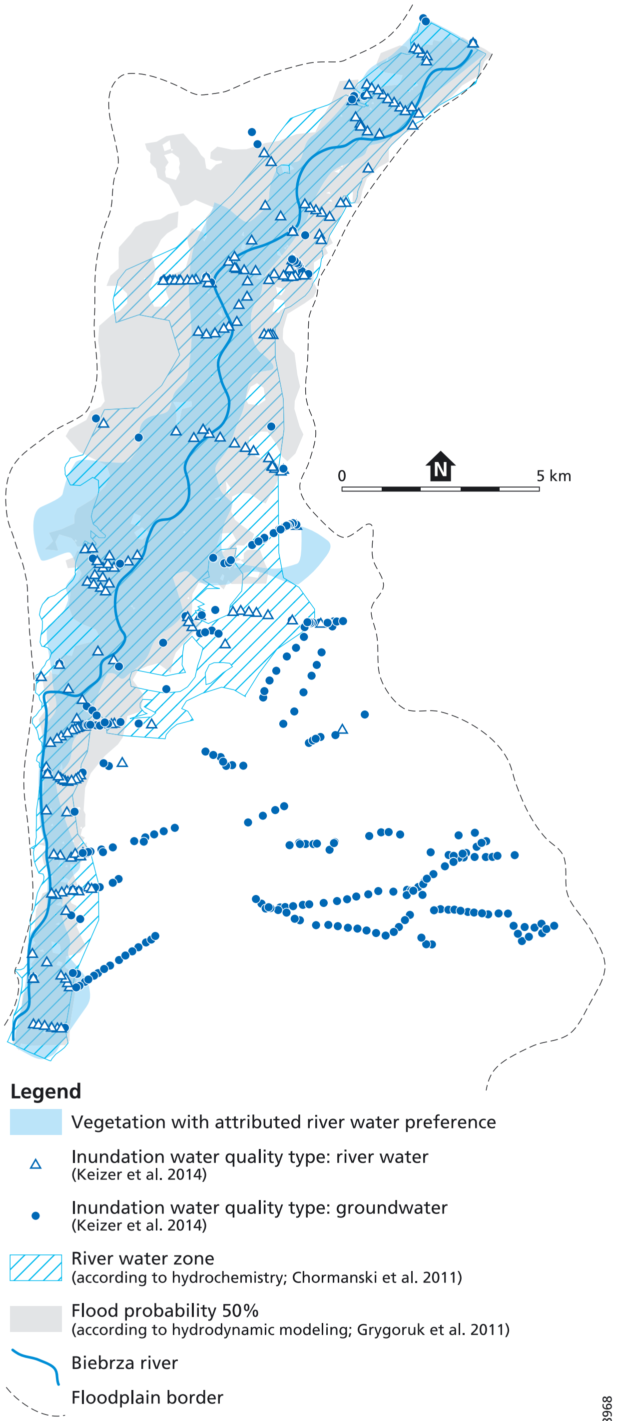

Figure 5. Comparison of spatial pattern in vegetation attributed to river water preference, with indices of river water presence: (a) inundation water quality (Keizer *et al.*, 2014: 2002–2012), (b) the river water zone as determined by inundation water quality in 2002 (Chormański *et al.*, 2011) and (c) the 50% river water flood probability (independent hydrodynamic modelling (Grygoruk *et al.*, 2011)).

water. This might explain the presence of groundwater-preferring vegetation communities, because they are subject to the nutrient-poor conditions in the root zone and not affected by high nutrient concentrations in the inundation water.

It is known that wetland age and succession stage also structures vegetation communities (Craft *et al.*, 2007). Wassen and Joosten (1996) presented a successional pathway model for *Caricetum diandrae* (low-growing rich fen) in the Biebrza Upper Basin, showing that only in the case of diminished groundwater feeding could the rich-fen system develop into another fen type. Large-scale lowering of the groundwater table by drainage elements is only observed in the north-western part outside the study area (National Park boundary). Therefore, we assume differences in wetland age and succession stage to play a minor role for the patterns in vegetation communities.

Inference of water quality properties from wetland vegetation communities

We successfully correlated vegetation communities to inundation water quality (82%; 14 out of 17 communities) for a floodplain containing the complete ecohydrological gradient from valley edge to river on a largely undisturbed, near-natural floodplain, with the main interacting hydrological forces of groundwater seepage, river flooding and drainage, and local precipitation all present (Table II). To our knowledge, this is one of the first studies to present such a rigorous analysis of ecohydrological relations between water quality properties and wetland vegetation, in contrast to previous studies limited to single transect or point observations (e.g. Wassen *et al.*, 2002; Schipper *et al.*, 2007), single or limited vegetation communities (e.g. Koczur and Nicia, 2013) or limited wetland types (e.g. Lukács *et al.*, 2009; Kłosowski and Jabłońska, 2008; Boyer and Wheeler, 1989).

We identified six communities with a preference for base-rich, nutrient-rich river water, three communities with a preference for base-rich, clean groundwater, four with a preference for diluted groundwater, one with a preference for polluted groundwater and three with no preference for any of the water quality types (Table II). We found similar concentrations of base cations in the studied communities (Table IV). We attribute this to (i) the dilution of base-rich groundwater with precipitation water (Keizer *et al.*, 2014) as we sampled surface inundation water and (ii) the enrichment of river water with groundwater. $[PO_4^{3-}]$-P concentrations in inundation water in the river water zone were found to be similar to those in the groundwater zone, all being low. This may be explained by the relatively undisturbed nature of the floodplain studied with low human interferences. Phosphate concentrations in groundwater and river water sources are generally low (Keizer *et al.*, 2014). Even when phosphate is present, it will be bound to iron or hydroxides when coming into contact with oxygen at the wetland surface. Nitrogen (and potassium)

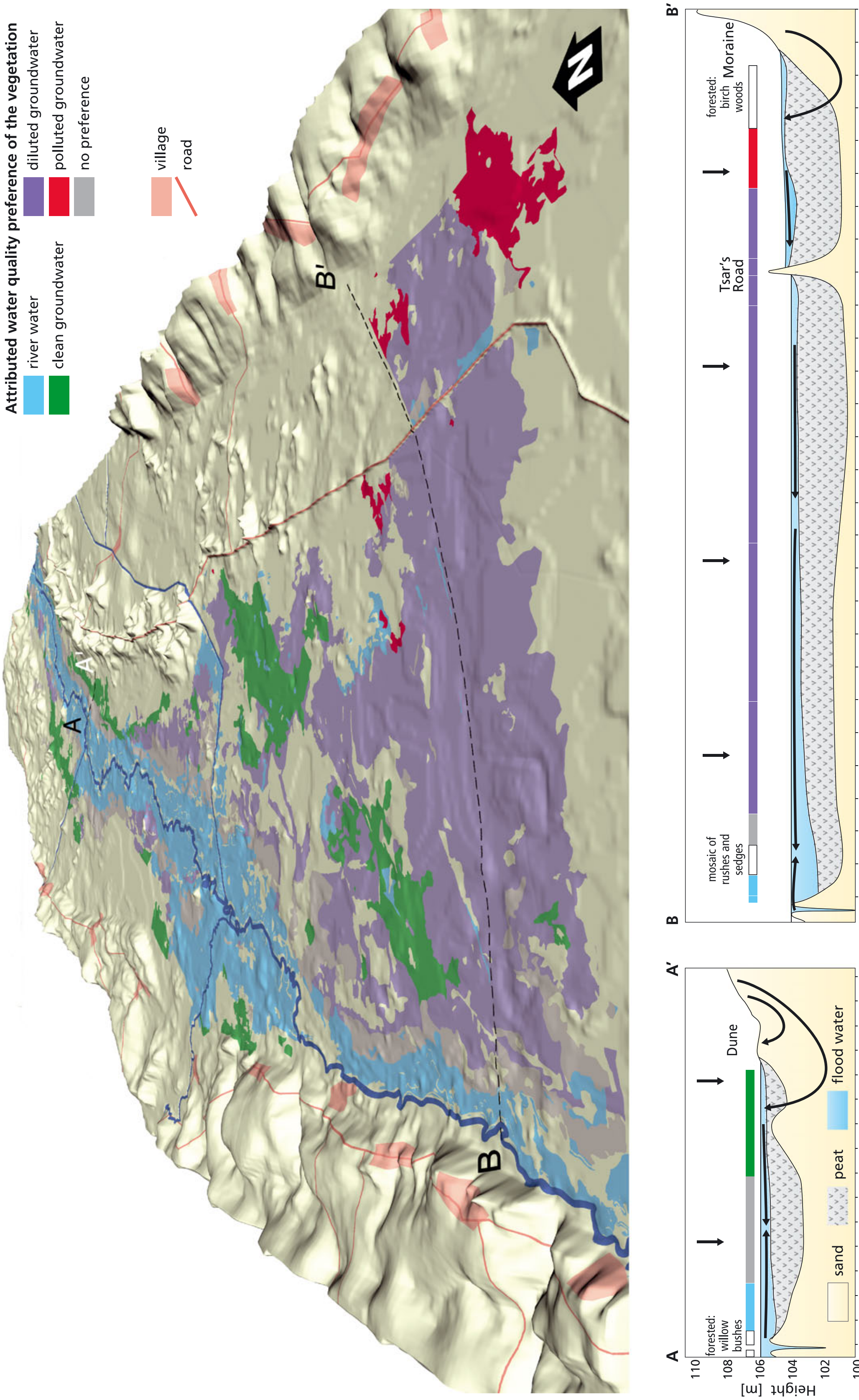

Figure 6. Landscape ecohydrological mapping showing how vegetation community distribution relates to hydrological flow processes. Upper panel: 3D diagram relates landscape geomorphology to vegetation distribution. Lower panel: cross sections (adapted from Keizer *et al.*, 2014) relate hydrological flow processes to river water flooding, groundwater discharge and precipitation (indicated by arrows).

concentrations on the other hand were higher in communities with river water preference, probably because of fertilizer and manure application by agriculture, or nitrogen leaching from drained peat upstream (cf., Daniels *et al.*, 2012). Additionally, the absence of denitrification in the oxic river water prevents breakdown of high nitrogen concentrations.

However, biogeochemical processes are also a function of geographical differences in climate, geology, topography, hydrology and soil type. When comparing water quality for three of the studied vegetation communities with other studies, variation was large indeed. *G. maximae* (Poland: this study, UK: Dawson and Szoszkiewicz, 1999 and Hungary: Lukács *et al.*, 2009, 2011) showed large variation in base-richness (expressed in EC: 176–655 $\mu S\,cm^{-1}$ and HCO_3^-: 176–281 $mg\,l^{-1}$) and nutrient availability (N: 0·12–1·50 $mg\,l^{-1}$). Rich fens with *Carex diandra* (Poland: this study, and the Netherlands: Wassen and Barendregt, 1992 and Bootsma and Wassen, 1996) showed large variation in base-richness (pH: 5·8–7·1 and Ca^{2+}: 11–54 $mg\,l^{-1}$) and nutrient-richness (N: 0·18–0·70 $mg\,l^{-1}$, P: 0·01–0·06 $mg\,l^{-1}$ and K^+: 0·60–4·20 $mg\,l^{-1}$). This shows our relations cannot be directly extrapolated to other wetlands in different climate and geological settings.

Nonetheless, despite spatial variance in clusters between years, and some unexpected occurrences, we were able to successfully attribute water quality preference to most of the vegetation communities. Also, the zone of vegetation with preference for river water adequately falls within the zone of river water flooding identified by Keizer *et al.* (2014) using hydrochemistry, and by Grygoruk *et al.* (2011) and others (Chormański *et al.*, 2009; Świątek *et al.*, 2008) using hydrodynamic modelling (Figure 5). This gives us confidence in the robustness of the ecohydrological relations between water quality and vegetation communities and enabled us to construct a process-based landscape ecohydrological map (Figure 6) describing the relations between water quality and vegetation communities at the landscape scale. Our findings demonstrate that including (hydrological) processes operating at the landscape level of the wetland is important to understand the emergence of vegetation patterns and predict the effect of changes in water quality because of natural or anthropogenic disturbances.

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