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Delineating the influence of water conditions and landscape on plant communities in eutrophic ditch networks

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Abstract Marshlands and floodplains are generally characterized by a long history of human occupation and management, with strong impacts on biodiversity. In these landscapes, ditch networks often represent the last or most significant aquatic habitat, and significantly contribute to regional biodiversity. To determine the drivers of biodiversity in ditch networks, especially the importance of the water regime, we monitored vegetation in ditches in 11 sites (independent blocks of ditch networks) of an Atlantic marshland (the Marais poitevin, France) over a 4-year period, and a panel of local environmental conditions and landscape characteristics. Large differences in the species richness and composition of ditch plant communities were observed among sites. The water regime had a predominant effect on all descriptors of ditch plant communities. High water levels combined with strong temporal variability, including drying-out periods, were found associated to the communities with the highest species richness. By contrast, water quality parameters did not influence plant communities across sites. Among landscape variables, woodland cover combined with high hedge cover along the ditches significantly influenced plant composition and species richness. These results are discussed in terms of management actions that may promote the diversity and composition of ditch plant communities and address conservation challenges.

Keywords Drying out · Environmental management · Species composition · Taxonomic diversity · Water level

Introduction

Together with ponds, networks of human-made ditches constitute one of the main open water bodies in heavily managed floodplains (Pierce et al. 2012). They are mainly used for agricultural purposes such as irrigation, drainage, but also drinking water and fencing for herds (Davies et al. 2008; Biggs et al. 2017). Moreover, ditches may provide a diversity of ecological functions, especially as to water quality and

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biodiversity. They mitigate water pollution (Castaldelli et al. 2015; Vymazal and Březinová 2018), in particular when they host a diversified aquatic vegetation (Gustafsson and Boström 2011). They also significantly contribute to the regional aquatic flora and fauna biodiversity (Armitage et al. 2003; Langheinrich et al. 2004; Chester and Robson 2013; Dorotovičová 2013; Whatley et al. 2014; Bubíková and Hrivnák 2018a) because they host specific species compared with other water bodies such as rivers or ponds (Williams et al. 2003; Davies et al. 2008).

Identifying the main drivers of ditch biodiversity is necessary to ensure the conservation of dich plant community diversity and maintain the ensuing ecological functions (Herzon and Helenius 2008; Dollinger et al. 2015). Differences in ditch biodiversity are expected to be mainly related to the variability of local environmental conditions (Milsom et al. 2004; Shaw et al. 2015; Meier et al. 2017), but may also reflect differences in landscape features (Favre-Bac et al. 2017; Teurlincx et al. 2018). Nutrient loads (Hinojosa-Garro et al. 2008; Bornette and Puijalon 2011) and water regime (Lacoul and Freedman 2006; Poff and Zimmerman 2010; Bornette and Puijalon 2011) are of prime importance, especially for the species richness and composition of plant communities. The water level is expected to screen plant species according to their tolerance to submergence and related light limitation (Blindow 1992). Variability in the water level may also impact the community pattern by limiting the establishment of submerged vegetation, especially when associated with strong flows and turbidity (Pierce et al. 2012), but can also benefit to submerged macrophyte diversity (van Geest et al. 2005). Drying-out periods, or periods of very low water levels, may lead to critical water regimes for vegetation (Leira and Cantonati 2008 and references therein; Cusell et al. 2015). For instance, they provide windows of opportunities for plant species (Bonis et al. 1995) that depend on the availability of propagules (Chester and Robson 2013). Furthermore, propagule dispersal (notably of water- and wind-borne propagules; (Twisk et al. 2003; Milsom et al. 2004; Rasran et al. 2018) is promoted by ditch connectivity (Favre-Bac et al. 2017; Teurlincx et al. 2018). Biotic factors, notably exotic species increasingly frequent in aquatic habitats, can also alter plant communities (Manchester and Bullock 2000; Mjelde et al. 2012; Souty-Grosset et al. 2016).

While the panel of possible drivers of plant communities is large, their respective significance remains largely undocumented (Chester and Robson 2013). As reported in other habitats (e.g. Bonan 1989), several drivers of ditch plant communities are likely interrelated. For instance, the chemical and physical conditions experienced by plants, as well as the abundance of exotic species, or ditch connectivity probably depend on the water regime (Meier et al. 2017). However, the majority of published studies is mainly focused on the effect of only one environmental factor (Raulings et al. 2010; Bornette and Puijalon 2011; Chester and Robson 2013). Hence the need to assess the relative importance of potential environmental—local and landscape—drivers and their joint influence to provide management guidelines for preserving and improving vegetation diversity in ditch networks.

Biodiversity conservation has been dramatically challenged in most fertile floodplains in the past decades as to the remaining water bodies, among which ditch networks. Concerns are mainly related to the intensification of agriculture and increased urbanization in watersheds (Dudgeon et al. 2006; Joosten 2009; Newbold et al. 2015). In practice, this has resulted in drastic changes in land use nearby ditches, water regimes and nutrient loads. The Marais poitevin—the second largest marshland in France—is no exception: it has been submitted to important changes over the last 50 years, with increased urbanization and the conversion of more than 50% of meadows into croplands (Duncan et al. 1999; Anonymous 2003; Godet and Thomas 2013). Along with land-use changes, ditch waters have become heavily eutrophic under the combined action of nutrient leaching from agricultural lands and increased sewage from the watershed. Marked changes in the water regime have also been observed: it is presently lower in winter and early spring and less variable in the course of the year than it was 50 years ago, while dredging has grown less frequent (see Duncan et al. (1999) and Anonymous (2003) for a more detailed description). However, environmental heterogeneity persists among localities. All these changes likely threaten biodiversity in ditches and the associated ecological functions (Vuori et al. 1998; Dudgeon et al. 2006).

We carried out our study in two steps. First, we characterized Marais poitevin ditch vegetation for species richness, diversity and composition over a 4-year period. We expected communities to be dominated by eutrophic species, with differences in the proportion of hydrophytes and amphibious species among sites (i.e. as a result of variations in environmental conditions). Second, we tried to identify the drivers of plant communities in the ditch networks by considering a large set of environmental variables. As all the ditches in the study area were largely eutrophic, the water regime was expected to be the main driver of ditch plant communities. Therefore, we predicted that (1) ditches characterized by a low water level would be dominated by amphibious species, while those with higher water levels would favor hydrophytes, (2) the occurrence of drying-out periods would favor amphibious species, (3) ditches characterized by highly variable water levels the year round would host diversified plant communities including both hydrophyte and amphibious species. We also expected (4) a negative relationship between the abundance and diversity of aquatic plants and the abundance of two biotic variables—macro-algae and red swamp crayfish (*Procambarus clarkii*). Macro-algae are indeed expected to compete with macrophytes for light and nutrients, while the red swamp crayfish—a widespread and harmful exotic species—is well known to consume and disturb aquatic vegetation (Rodriguez et al. 2003; Souty-Grosset et al. 2016). Finally, we expected that (5) ditches in landscapes with a high proportion of meadows would harbor a high plant diversity due to lower nutrient and sediment leaching. Our findings will be discussed in the light of plant community conservation perspectives and management strategies to meet the current and future challenges of threats in anthropized aquatic systems. The study was conducted in 11 sites (independent blocks of ditch networks, see below) distributed across the study area and representative of the range of possible water regime conditions. All sites were carefully characterized regarding environmental conditions, including within- and between-year variability. We paid special attention to water regime characterization, with continuous measurements of the water level and of its temporal variability, together with the occurrence and duration of drying-out periods.

Materials and methods

Study sites

The Marais poitevin is a *ca.* 102,000-ha large marshland located along the French Atlantic coast (46°30′-46°15′ N and 1°30′-0°35′ W, Fig. 1) characterized by intensive management of the water regime for flood control and agriculture (EPMP 2015). The Marais poitevin is however best known for its international importance for wildlife owing to its location along one of the main bird migration routes (Duncan et al. 1999). The climate is a warm Atlantic type characterized by rainfall greater than evapotranspiration in winter balanced by an almost equal deficit of 300 to 350 mm in summer. Flood peaks take place mostly in January–February and the system is particularly dry in summer, occasionally until autumn. An 8200-km long network of drainage ditches has been progressively set up since the middle Ages (EPMP 2015). The Marais poitevin has been divided into embanked blocks in which water management is controlled partly independently from the surrounding blocks, as a result of different water regulation directives and associated management committees. This leads to different local water regimes across blocks, thereafter called sites. The ditch vegetation was studied in 11 sites (300–365 ha) over 4 years (2015–2018). Sites were mainly occupied by meadows (from 48 to 100% of the area), croplands (0–42%) and woodlands (1–41%).

Vegetation monitoring

Ten sampling transects, representing 125-m long ditch stretches, were selected in each of the 11 sites. In each transect, 25 0.5 × 0.5 m quadrats were randomly chosen each year, avoiding areas close to the banks (> 1 m from the banks) to avoid sampling species having grown from the banks into the ditches. Sampling was performed once a year between mid-May and mid-June, when vegetation was well developed and no ditch had yet dried out. Monitoring consisted in (1) checking for the presence of vegetation in each quadrat by a single stroke of a rake in the whole water column, (2) identifying all plants to the species level following the taxonomic database taxRef v12.0 (Gargominy et al. 2018), and (3) visually assessing the plant species cover converted into six classes (0, < 5%, 5–25%, 26–50%, 51–75%, and >

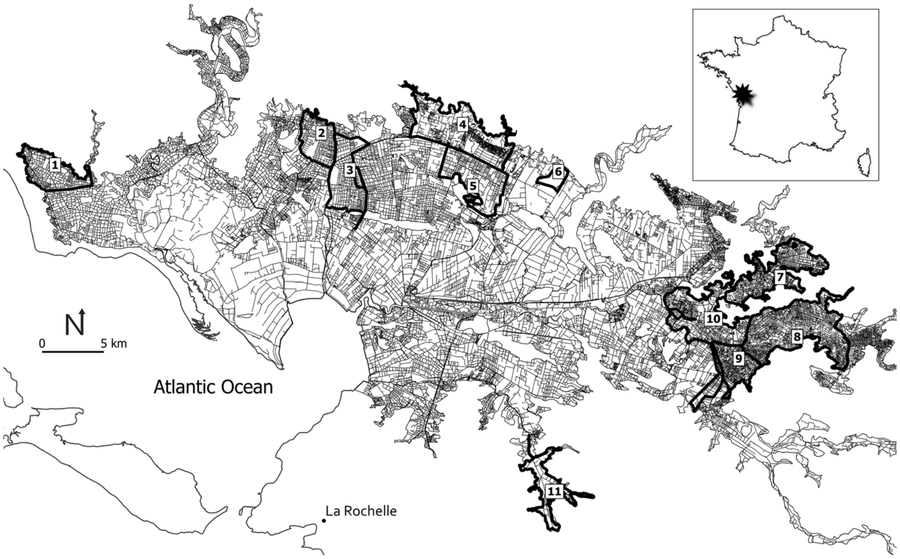

Fig. 1 Localization of the Marais poitevin. The 11 study sites (i.e. hydrological units) are delineated with bold lines. Sites were numbered from west to east

75%). *Elodea canadensis* and *E. nutalii* (both originating from North America) were both found and sometimes occurred in mixtures. As their relative proportions could not be reliably determined in the field, they were pooled and referred to as *Elodea spp*. Regarding algae, filamentous algae and Ulvaceae covers were combined and thereafter named macroalgae cover, while the charophyte cover was distinguished. Based on the Ellenberg F flooding index (Hill et al. 1999), plant species were subdivided into hydrophytes (either floating leaved or submerged rooted species, F = 11–13), and amphibious species including helophytes and non-helophytes.

Environmental conditions

Water regime

At each transect, the daily water level was derived from the values recorded by a limnigraph located in one representative major ditch of each site. These values were then corrected according to the altitude of the ditch bottom of each transect measured in situ with a graduated pole. Average monthly water levels were calculated, as well as coefficients of variation over two periods: December to February (‘CV winter’ thereafter) and March to May (‘CV spring’ thereafter). The measurement of elevation of the bottom of the ditches suffered some uncertainty, mainly because mud thickness varied at a fine spatial scale. Accordingly, ditches were considered dry when the daily water level was < 5 cm. Such a water level also corresponds to the exposure of a large fraction of hydrophyte biomass. Drying-out events can occur in summer and fall. Their duration, expressed in days, was calculated over the 12-month period prior to vegetation monitoring.

Water quality

To depict the water quality, we used data collected bimonthly by the Union des Marais de la Charente-Maritime (UNIMA) during the vegetation period (March to July) in one large representative drainage ditch of each site connected to all the sampling transects. Electrical water conductivity, pH and dissolved oxygen (expressed in % of saturation), were measured in situ in the top 30 cm of the water column using a portable electronic multi-parameter probe (WTW 3430, Thermo Fisher scientific Inc.). Ammonium, nitrite, nitrate, total nitrogen (Kjeldahl), orthophosphate and dissolved organic carbon contents were measured in laboratory, based on water samples collected in the top 30 cm of the water column. Chlorophyll a was measured by spectrophotometry after acetone extraction. Water column turbidity was not included in the analyses because it was highly related to dissolved organic carbon and chlorophyll a content (data not shown). Average values for all the water quality parameters were calculated for each site over the vegetation period.

Other ditch variables

Dredging can influence aquatic vegetation by removing the plant cover and altering the seed bank (Twisk et al. 2003; Milsom et al. 2004). Detailed information on dredging was not available for all the transects, so we used the thickness of the mud layer measured in each transect in 2015 as a proxy of the time elapsed since dredging because the mud layer is expected to increase with time after a dredging campaign (Botto et al. 2000). To consider a possible shading effect of the vegetation from hedges situated along the ditch banks, a hedge cover index was calculated for each sampled ditch bank and then summed. The hedge index, evaluated visually in situ in 2015, corresponded to hedge length (a semi-quantitative non-dimensional score varying from 1 to 5) multiplied by hedge width (score 1 to 3) and hedge height (score 1 to 3). Hedges were removed along a few transects in one site during the study period, therefore hedge cover index values were updated. Macro-algae cover (filamentous algae + Ulvaceae) was considered together with crayfish abundance as possible additional predictors of aquatic plant covers. Crayfish abundance was assessed annually in one representative ditch *per* site using 25 funnel traps deployed in a 250-m long stretch for 24 h in mid-June.

Landscape characteristics

The proportions of the major terrestrial land uses (meadows and crops) were measured in the whole area of each site using land-use maps provided by the Établissement Public du Marais Poitevin (EPMP 2015), built from the agricultural database of the Institut National de l’Information Géographique et Forestière (IGN) available at the scale of each agricultural plot (IGN 2016). Additionally, the proportion of woodlands in each site was measured using a Rapideye remote sensing image (May 2014, 7 × 7 m resolution following Rapinel et al. 2015). The length of the ditch network (expressed in km ha^{-1}) was used as a measure of the quantity of aquatic habitats and of the extent of connectivity among ditches. It was measured for each site using the IGN topographical database, version 2008 (EPMP 2015) using QGIS 3.1 (QGIS.org 2018).

Statistical analyses

Characterization of plant communities

Statistical analyses were performed at the site scale, using R 3.6.2 (R Core Team 2019).

Plant communities were described annually based on species richness (for all species together on the one hand and hydrophyte species only on the other hand), exponential of the Shannon index—the “number equivalent” of the Shannon index (Jost 2006)—and species cover (data from the 25 quadrats *per* transect were averaged, and the resulting data were once again averaged for the 10 transects assigned to each site). Then, an unscaled Principal Component Analysis (PCA) was performed on the plant community composition (cover data) over the four years using the vegan package (Oksanen et al. 2017), after a Hellinger transformation as recommended by Legendre and Gallagher (2001). This analysis mainly accounts for relatively abundant species. The scores on the first two components of the unscaled PCA (PCA1 and PCA2) were used to characterize plant community structure, together with the three descriptors mentioned above.

Evaluation of the effects of environmental conditions on plant community descriptors

Differences in environmental conditions across sites based on all combined variables over the study period were visualized using a PCA (vegan package). Generalized Linear Mixed Models (GLMMs, glmer from the lme4 package, Bates et al. 2015) were then used to examine the relationships between all descriptors of plant communities and the environmental characteristics of the 11 sites over the 4-year period. ‘Year’ was included as a random effect in the analyses. To avoid excessive collinearity between explanatory environmental variables (Dormann et al. 2013), we selected a limited set of variables using the variance inflation factor (VIF) procedure considering a correlation threshold of 0.7 (usdm package, Naimi 2017). Besides, a correlation matrix between all environmental variables was calculated (provided in Online Resource 1) including the relationships with the variables which were not implemented in the models. Models were run considering a Poisson error distribution for diversity indices, and a Gaussian error distribution for PCA scores. We tested all possible additive combinations of up to three variables from an initial set of 14 variables. Dredging and model averaging procedures were performed using the MuMin package (Bartoń 2016). Models were ranked by AICc, the Akaike information criterion corrected for small sample sizes (Burnham and Anderson 2002), and averaged estimates of the variables were calculated over a model selection with a cumulated weight of AICc of 0.95. The effect of an explanatory variable was considered significant when its estimate (i.e. the slope of the relation) was different from zero (i.e. when its 95% confidence interval excluded zero). The quality of the models was evaluated using r^2 values calculated for fixed effects for the global model (marginal r^2 using the r.squaredGLMM function of MuMin, Bartoń 2016).

Results

Characterization of plant communities

86 species were sampled over the 4-year period, and no significant difference was highlighted across years (see the complete list of species in Online Resource 2). No species was classified as rare or threatened at the regional or national scale. Furthermore, five non-native species were recorded (the floating hydrophytes *Azolla filiculoides* and *Lemna gibba*, and the submerged rooted species *Ludwigia peploides, E. canadensis* and *E. nutalii*). Only *L. peploides* is the object of uprooting campaigns in summer (i.e. after our vegetation monitoring). Total species richness ranged from 23 to 43 species depending on the site (Table 1). The site with the highest species richness exhibited the highest Shannon index (8.7 *vs.* 2.8 for the site with the lowest value) but an intermediate plant cover (14.2%, Table 1). On average, amphibious species largely dominated the species assemblages (67% of the total number of species) compared to hydrophytes (27.2% for submerged-rooted hydrophytes, and 5.8% for floating-leaved species, see details in hydrophyte richness in Table 1). The largest plant covers (32.5 and 49.1%) resulted from continuous mats of *Elodea spp., Stuckenia pectinata* or *Zannichelia obtusifolia.* Few sites were poorly vegetated (2–3% cover, Table 1). Unvegetated quadrats were present in all sites, sometimes even adjacent to densely covered quadrats. Species richness and total plant cover were not correlated ($r^2 = 0.04$, $P = 0.21$, Table 1), but hydrophyte richness and total plant cover were significantly correlated ($r^2 = 0.50$, $P < 0.001$).

The first two components of the PCA performed on the species composition of the communities (cover data) accounted for 39.4% of the total variance (Fig. 2a and b). Plant communities were plotted along PCA1 according to the proportion of amphibious *versus* hydrophyte species: positive PCA1 scores corresponded to communities dominated by amphibious species (*Carex elata*, *Phragmites australis*, *Agrostis stolonifera)* that formed a compact group with sites 7 to 11, and sites 4–5 only for 1 year, while negative PCA1 scores represented hydrophyte-dominated communities (including notably *Ceratophyllum demersum* or *Elodea spp.*). PCA2 mainly reflected differences between hydrophyte-dominated communities, dominated by either *C. demersum* (negative coordinates) or *S. pectinata* (positive coordinates, Fig. 2a and b). *C. demersum* was combined with *M. spicatum* (site 2), *Elodea spp*. (site 6) or *Potamogeton crispus* (site 4). Sites 1 and 3, and site 5 in 2015 to 2017, were characterized by the highest cover values of *S. pectinata,* and also high covers of *P. crispus.* By contrast, amphibious-species-dominated communities on the right of the ordination were little discriminated along PCA2 (Fig. 2a and b). Floating-leaved species also contributed to the differences in plant communities across sites, yet to a lesser extent.

Characterization of environmental conditions

The main significant differences in water level were first depicted by the water level in June, which was highly representative of the yearly water regime (Online Resource 1): water levels ranged between 0.18 and 0.87 m across sites in June (Table 2). Within-year fluctuations of the water level were only provided for two periods (winter and spring), but were highly correlated (Online Resource 1). Some sites exhibited large variations (coefficient of variation) every year (e.g. site 11; Table 2), others had much more stable water levels with coefficients of variation < 0.01 (Table 2; Fig. 3). The water regime was also characterized by drying events that occurred in all

Table 1 Biodiversity indices per site for all plant and hydrophyte species over the study period

Site	All species				Hydrophytes
	Cumulated richness	Annual average richness (range)	Average exp. Shannon	Average cover %	Annual average richness (range)
1	26	15.8 (15–18)	5.1	32.5	11.8 (11–14)
2	37	19.0 (14–26)	4.8	18.3	6 (3–8)
3	24	15.3 (2–17)	2.8	49.1	9.3 (6–11)
4	43	22.5 (16–28)	8.7	14.2	9.8 (7–13)
5	24	12.5 (9–16)	4.1	9.2	5.8 (5–7)
6	23	13.5 (10–17)	3.6	31.8	9.8 (8–12)
7	28	15.8 (12–21)	5.9	4.7	3.8 (2–6)
8	29	13.3 (8–19)	6.9	2.2	4.8 (2–8)
9	25	11.8 (8–17)	5.6	1.2	2.3 (0–4)
10	23	12.3 (10–18)	2.9	2.5	2 (1–3)
11	32	21.8 (18–24)	7.2	14.5	7 (5–8)

Cumulated richness over the 4 years, annual average richness range, annual means of the exponential of the Shannon index and of the total cover are given for all species, while only annual average species richness and its range are provided for hydrophytes

sites but one (site 6). Drying event duration varied substantially, from a few days (e.g. sites 1, 8 or 9) to more than 2 months in other sites (3, 5, 7, 11; Table 2; Fig. 3).

Water quality was typical of eutrophic and even hypertrophic systems (Table 2). Water pH differed little across sites. Differences in water conductivity were more pronounced, with the highest values in sites 3 and 5. Those sites were also characterized by higher chlorophyll a and organic carbon contents than the other sites, and discriminated along the first PCA component (Fig. 3). Mud depth ranged from 0.25 to 1.10 m, indicating large differences in dredging histories and sediment input into the ditches among sites. Macro-algae covers were highly variable among sites (from 0 to 50%). The maximum values were recorded in the most hypertrophic site (site 5; Table 2). Crayfish abundance greatly varied across sites and years (Table 2), and was correlated with the duration of drying events (Fig. 3; Online Resource 1).

Landscapes nearby ditches were overall dominated by meadows. However, sites 3 and 5 harbored a high proportion of crops, and sites 7–10 the highest proportion of woodlands (Table 2). The proportion of woodlands was correlated to the hedge cover along the ditch banks (Online Resource 1). Only site 11 was characterized by a low proportion of woodlands but a high hedge cover along ditches (Table 2). Lastly, the length of the ditch network varied up to fivefold across sites (from 40 to 200 m ha^{-1}, Table 2).

Effects of environmental characteristics on plant communities

The models fitted well with all plant community descriptors except the Shannon index (no convergence). At least one predictor related to the water regime was found significant for each plant community descriptor (Table 3). Total species richness was positively related to the water level, to drying event duration, and, to a lesser extent, to water level variability in winter (Table 3; Fig. 4a, b). Hydrophyte richness was driven by a combination of water level, water conductivity and mud depth showing positive effects, while it was negatively associated with the proportion of woodlands (Fig. 4c, d). Water level variability in winter did not affect hydrophyte richness.

Plant community composition, as described by PCA scores, was also associated with local and landscape environmental conditions (Fig. 2c). PCA1 scores and the water level were negatively related, indicating that amphibious-species-dominated communities occurred in sites with lower water levels. Such communities were also associated with shaded ditches (a high hedge cover index) and to sites

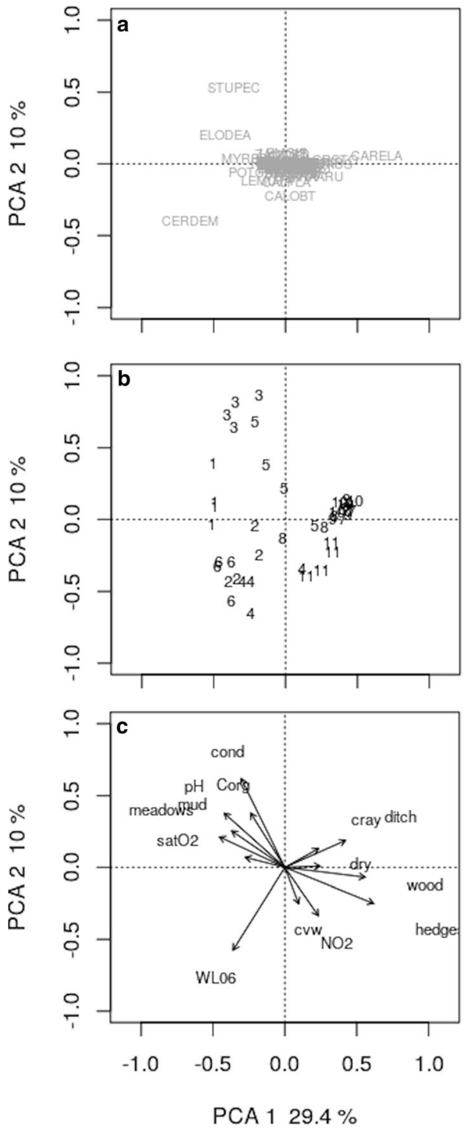

Fig. 2 Ordination of species cover data for all 11 sites and over the four years (unscaled PCA). **a** Species are indicated according to their scores on the first two components PCA1 and PCA2, with a six-letter code (three for genus names plus three for species names, see the list of species in Online Resource 2); **b** projection of the sites on the same ordination plan; **c** projection of the environmental variables

characterized by an increased proportion of woodlands (Fig. 4e). Conversely, PCA1 scores were negatively associated with water conductivity. Most of these environmental variables also influenced specific hydrophyte species covers (PCA2 scores). Positive PCA2 scores (corresponding to *S. pectinata*-dominated communities) were found mainly in localities with high water conductivity and a low water level, and were influenced by surrounding land uses (cropland and woodland), and mud thickness to a lesser extent (Table 3; Fig. 4f). Results were opposite for communities dominated by other hydrophytes, especially *C. demersum* (negative PCA2 scores). The structure of the plant communities was not related to the other water regime metrics (the duration of drying events or the coefficients of variation of the water level). Biotic variables (macro-algae or crayfish) did not significantly influence any of the plant community descriptors either. These relationships were consistent with the projection of the explanatory variables selected by the GLM on the PCA biplot, as shown in Fig. 2c.

Discussion

Ditch plant communities significantly differed across 11 Marais poitevin sites: some sites hosted a majority of strictly aquatic plants, while others were dominated by amphibious species. The water regime had a determining impact on plant communities, especially the water level and the duration of drying events, and so did some associations with landscape variables (woodland and cropland covers) to a lesser extent. By contrast, water quality and biotic variables (i.e. macro-algae and crayfish abundances) were poor predictors of ditch plant communities.

Role of the water regime

As expected, higher water levels corresponded to communities dominated by hydrophyte species and favored both hydrophyte and amphibious species richness. Regarding the timing of the water regime, no particular period of high water level was more determining than any other one for vegetation richness and composition because correlations between water levels were high at all periods (Online Resource 1).

Our results support the expectation that the water level is a strong predictor of most plant community descriptors in ditches (Shaw et al. 2015; Baláži and Hrivnák 2016; Bubíková and Hrivnák 2018b), as in lakes and wetlands (Cronk and Fennessy 2001). However, the influence of the water level found in the present study is somehow contradictory with studies reporting that high water levels may lead to

Table 2 Summary of the selection of non-collinear characteristics for each site over the 4-year period (range over the years or unique value when unchanged)

Environmental variables	Sites										
	1	2	3	4	5	6	7	8	9	10	11
Water regime											
Water level June (m)	0.52–0.59	0.45–0.76	0.31–0.37	0.73–0.87	0.18–0.26	0.64–0.81	0.34–0.43	0.45–0.49	0.36–0.39	0.25–0.34	0.40–0.63
CV winter water level (Dec–Feb)	0.04–0.06	0.05–0.11	0.02–0.10	0.04–0.14	0.01–0.08	0.02–0.09	0.01–0.10	0–0.07	0.01–0.13	0–0.14	0.11–0.23
Duration of drying events (d)	0–1	0–21	0–79	0–20	1–63	0	11–106	0–3	0–5	4–12	2–144
Water quality[a]											
Water conductivity (μS cm^{-1})	950–1422	733–1031	2734–3985	487–703	1505–2217	535–604	658–803	562–571	577–669	627–702	660–776
Chlorophyll (μg L^{-1})	37.3–148	24.4–57.2	65.3–278	8.3–235	279–1871	8.3–93.2	15.7–57.9	7.5–28.5	1.8–35.8	21.1–78.2	11.8–77
Nitrites (mg L^{-1})	0.3–0.8	2.9–12.3	0.7–4.1	17.6–53.7	0.5–0.8	3.7–27.3	5.4–36	11.7–29.7	8.4–23	4.3–18.8	14.5–35.3
Sat O_2 (%)	79–127	77–95	58–102	67–112	45–120	51–83	64–74	75–81	67–78	61–98	53–69
pH	8.3–8.8	8.1–8.3	8–8.5	7.5–7.8	7.9–8.5	7.5–7.7	7.6–7.7	7.8–7.9	7.6–7.8	7.7–7.9	7.4–7.8
Other variables											
Mud depth (m)	1.10	0.55	0.65	0.45	0.60	0.50	0.40	0.75	0.50	0.45	0.25
Hedge cover index[b]	0.4	1.2	0	35.9	3.1	66 > 17.4[c]	74.1	46.1	70.0	54.7	75.1
Macro-algae (%)	0–20	0.1–9.7	0.1–11.5	20–29	19–50	10.1–24.4	0.1–8.4	16–36.3	0.9–22.2	12.4–26.7	0.9–5.7
Crayfish abundance (n/24 h)	1–28	8–90	42–413	23–118	16–399	10–112	26–277	6–34	26–75	85–251	121–387
Landscape											
Proportion of crops (%)	0.1	0	33.5	11.9	42.4	15.7	3.9	3.3	1.2	25	3.8
Proportion of woodlands (%)	3.6	1.8	0.7	15.9	3.5	4.8	23.2	31.2	41.2	16.9	5.7
Ditch density (m ha^{-1})	116.8	141.6	86	67.5	117.1	39.3	166.6	194.7	215.4	138.3	44.5

Ditch density is correlated with woodlands % (r = 0.70, Online Resource 1) but still presented in the table as an important descriptor of the landscape of each site

[a] Average values from March, May and July

[b] Index ranging from 0 to 90

[c] Hedges were removed gradually between 2015 and 2018. No changes occurred in the other sites

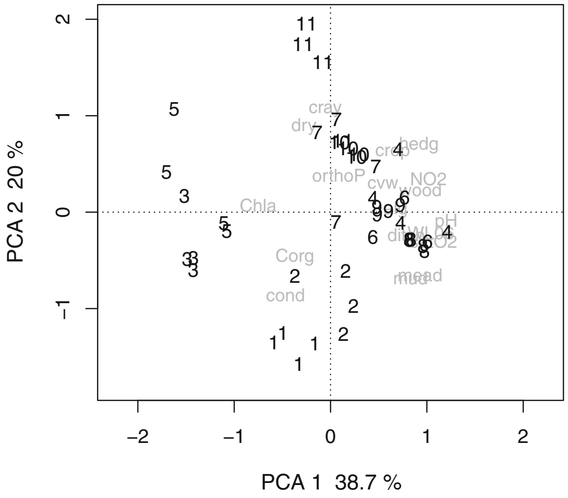

Fig. 3 Unweighted scaled PCA based on all environmental variables for all 11 sites, over four years. Sites are indicated according to their scores on the first two components PCA1 and PCA2 for each year and variable

stressful light-limited conditions and be detrimental to aquatic plant richness (Bornette and Puijalon 2011). Such a negative effect was not observed in our study, probably because the highest water levels still remained limited, with a maximum of 0.90 m in June. Investigating the effects of a larger range of water levels on aquatic plant richness using an experimental approach (Casanova and Brock 2000) is worth considering, all the more so in a climate change perspective (as discussed later).

Water level fluctuations appear as a crucial dimension of the water regime for aquatic vegetation (Altenfelder et al. 2016). We observed great water level variability in the ditches characterized by high water levels along the annual water cycle and combined with long drying events. Both drying duration and water level coefficients of variation promoted species-rich plant communities, with no impact on the relative abundances of dominant species. Water level variability can favor amphibious species (Coops et al. 2003; Howard and Wells 2009) and hydrophytes (Bonis et al. 1995; Riis and Hawes 2002; van Geest et al. 2005). These studies interpreted the effect of water level variability resulting from a limited abundance of dominant competitive species (Grime 1973; Goldberg 1987), together with opportunities for the establishment of poor competitive species (Sarneel et al. 2014). In the studied sites, total plant cover

Table 3 Results of GLMMs testing the influence of a set of uncorrelated environmental variables on the descriptors of plant communities in ditches (all species, except as specified)

Descriptor of plant communities	Environmental variable	Estimate (mean and 95% CI)		r^2
Total species richness	Water level June	0.13	[0.08, 0.25]	0.45
	Duration of drying events	0.11	[0.02, 0.21]	
	CV winter	0.12	[0.03, 0.21]	
Hydrophyte richness	Water level June	0.25	[0.05, 0.44]	0.61
	Water conductivity	0.23	[0.05, 0.41]	
	Woodlands	− 0.32	[− 0.53, − 0.12]	
	Mud depth	0.16	[0.02, 0.30]	
PCA1	Water level June	− 0.15	[− 0.21, 0.08]	0.87
	Woodlands	0.11	[0.03, 0.18]	
	Hedge index	0.22	[0.12, 0.32]	
	Water conductivity	− 0.08	[− 0.16, − 0.001]	
PCA2	Water level June	− 0.18	[− 0.24, − 0.12]	0.83
	Crops	− 0.08	[− 0.13, − 0.03]	
	Woodlands	0.07	[0.01, 0.13]	
	Water conductivity	0.20	[0.14, 0.27]	
	Mud depth	0.06	[0.04, 0.11]	

For the sake of simplicity, only significant variables from the model selections (estimates with a 95% confidence interval) are provided in the table. Marginal r^2 for the fixed effects of the global model is given for each descriptor of plant communities

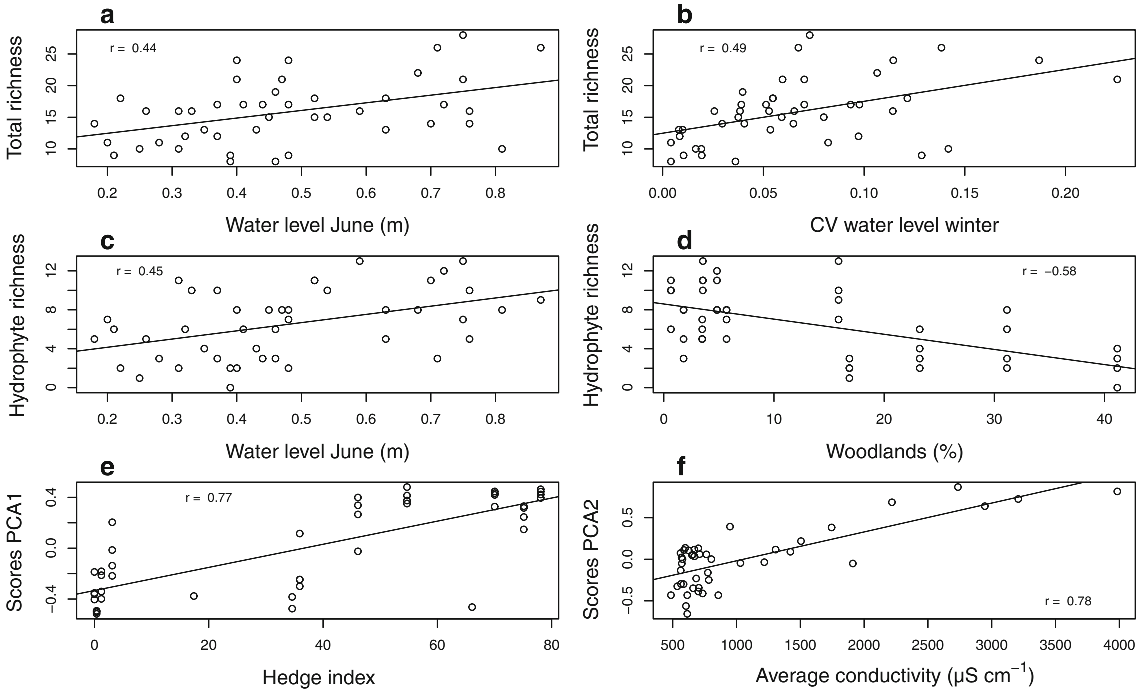

Fig. 4 Main two-way relationships between plant community descriptors and environmental variables of the ditches (also see Table 3) considering data from all 11 sites × 4 years

values were consistently lower than 50%. This suggests limited interspecific competition intensity, which in turn was probably not a strong limiting mechanism for local species richness.

Water fluctuations probably promoted species richness mainly in association with drying events. The summer and autumn drying-out periods observed in this study promoted amphibious species richness but not hydrophyte richness. Drying promotes the mineralization of organic components from sediment, and this increases nutrient availability and decreases the toxicity of long-waterlogged sediment for the next water cycle (Venterink et al. 2002). This effect may be particularly marked in eutrophic systems like those of the Marais poitevin. Overall, this specific effect of drying events is likely to counterbalance the survival stress induced on perennial hydrophyte species (Blindow 1992). We indeed observed long drying events (up to 144 days) without any detrimental impact on plant richness, as Riis and Hawes did (2002).

Land use effects

Contrary to our prediction, the meadow proportion was not a predictor of ditch plant communities. This can be explained by the fact that land uses were dominated by meadows in all sites ($>$ 50% cover), and also the eutrophic nature of ditch waters (e.g. chlorophyll a content mostly > 15 μg L^{-1}). All the plant species recorded in the ditches, especially the dominant ones, were typically nutrient-rich-tolerant species (Melzer 1999; Sondergaard et al. 2010). Overall, our results are in line with Baláži and Hrivnák (2016), who only found a limited effect of landscape variables on vegetation in ditches and canals in Slovakia compared to local environmental conditions. In our study, only the proportion of woodlands, slightly correlated to the hedge cover index along the ditches, was a significant predictor of hydrophyte richness and species composition. We notably highlighted a marked negative relationship between the proportion of woodlands and hydrophyte richness, and, ultimately, the occurrence of communities dominated by amphibious species in this land-use context. Wooded environments are known to negatively impact aquatic plant richness or plant cover in rivers and shallow lakes (Riis et al. 2001; Julian et al. 2011; Shaw et al. 2015), owing to a direct shading effect (Bornette and Puijalon 2011; Bubíková and Hrivnák 2018b). Confounding effects may exist between the effects of wooded contexts and other environmental variables on ditch plant communities. For example, the study sites characterized by a wooded landscape—unfavorable for hydrophyte species success and wind dispersal of seeds—were also characterized by a high ditch density that in turn can promote dispersal of aquatic plants by water (Favre-Bac et al. 2017). Whether dense ditch networks actually favored water-dispersed aquatic species (Sculthorpe 1967) is not known. This possible effect remained of a limited extent as it did not counterbalance the negative impact of hedge and woodland shading on hydrophyte richness.

Effects of other factors

We showed a positive correlation between hydrophyte richness, *S. pectinata*-dominated communities, and water conductivity, suggesting their good tolerance within the observed conductivity range. Water salinity is considered as a stressor for plant growth and can influence the species composition of aquatic habitats (Grillas et al. 1993; Hinojosa-Garro et al. 2008), but over a much broader range (up to 14 g L^{-1}) than in the present study. The thickness of the mud layer in the ditches, considered as a proxy for the time elapsed since the last dredging campaign, had a positive effect on hydrophyte richness and altered hydrophyte composition. This is contradictory with other results showing that mud removal by dredging enhanced submerged plant species richness (Twisk et al. 2003; Milsom et al. 2004), and that turbidity was detrimental to submerged plants (Akasaka et al. 2010). However, the observed mud thickness was only weakly related to water turbidity, and a moderate mud layer probably indicated that no recent dredging had disturbed plant communities. The absence of accurate data about dredging activities in our study sites prevents any clear conclusion on this factor.

Finally, it is worth observing that despite the known drastic impacts of red swamp crayfish on both the biomass and diversity of aquatic plant communities (Rodriguez et al. 2003), we found no such effect on the ditch vegetation. This can be interpreted by the fact that crayfish abundance fluctuated and never remained high in any given site over the years. Moreover, their abundance was positively correlated with drying event duration (Online Resource 1). This may blur their possible negative impacts because drying events have a positive (thus opposite) effect on plant diversity.

Towards management guidelines

Human-made wetlands such as ditches and canals may be the only remaining open-water bodies (along with ponds) in many large floodplains and agricultural landscapes (Armitage et al. 2003; Langheinrich et al. 2004; Davies et al. 2008; Chester and Robson 2013; Dorotovičová 2013; Meier et al. 2017; Bubíková and Hrivnák 2018a). In the current context of global wetland loss (Hu et al. 2017; Ramsar Convention on Wetlands 2018), it is critical to pay attention to such human-made aquatic habitats as possible alternatives to natural habitats, in view of their biodiversity and potential to support ecosystem services (Tscharntke et al. 2012; Hefting et al. 2013).

According to the assessment of ditch quality by Clarke (2015) on the basis of species richness, the ditches from the Marais poitevin are of poor to moderate quality, with 0–16 plant species along a 125 m long stretch of ditch, compared with good quality ditches (10–14 species *per* 20-m long stretch). Following this author and also Mountford and Arnold (2006), improving water quality is essential to enhance plant biodiversity in ditches. Moreover, naturally vegetated drainage ditches may contribute locally to nutrient removal from eutrophic waters (Vymazal and Březinová 2018). However, the eutrophic character of the water in our study area is probably typical of many marshlands surrounded by fertilized croplands, orchards or urbanized watersheds, with no short-term improvement of their trophic status to be expected. In such cases, the management of aquatic plant communities must be designed based on other environmental drivers than water quality. Our results highlights that both water levels and their annual fluctuations, and to a lesser extent the landscape composition, are key drivers to be considered for managing ditch plant communities.

Recommendations related to the water regime can be provided to enhance plant biodiversity in ditches. They will largely depend on the objectives that need to be clearly stated and prioritized. Favorable hydrological conditions vary substantially depending on whether species richness, species guilds (e.g. hydrophyte or amphibious), or some rare or heritage species are the desired targets. Species-rich communities of hydrophytes are expected in ditches when the water level is maintained sufficiently high in spring (> 70 cm in the present study) together with occasional summer drying events. This water level pattern better reflects the natural water level variations in line with climate conditions. In the near future, water management will need to integrate climate change perspectives (Horne et al. 2017) to meet current human and environmental requirements. With more frequent extreme climatic events (flooding and drying events), this global change perspective calls for enlarging the range of conditions to be considered when studying how biodiversity and ecological processes may be impacted and respond to changing environmental conditions.

The second family of drivers of plant biodiversity in ditches appears to be related to landscape composition, especially the proportion of woodlands and the hedge cover along ditches. Aquatic vegetation richness was reduced in ditches surrounded by trees, so that it is advisable to support regular hedge trimming by local managers. The proportion of woodlands in the studied sites also impacted ditch plant composition. Land use changes, or possible catastrophic events such as storms (e.g. the year 2000 storm along the Atlantic coast of France), the effects of the invasive pathogenic fungus *Hymenoscyphus fraxineus* or of the recently introduced ash borer (*Agrilus planipennis*) (Grosdidier et al. 2019; Orlova-Bienkowskaja et al. 2020) might cause dramatic changes in the woodland cover in the near future. The consequences of such changes on aquatic communities may not be predicted from the present situations because the investigated landscape range remains limited.

The high diversity of environmental conditions and the isolation that characterizes small water bodies compared to rivers and lakes probably explain their significance for local and regional biodiversity (Davies et al. 2008). Increasing the heterogeneity of environmental conditions regarding the water regime or landscape composition, both within and between sites, may promote the richness and diversity of plant communities in ditch networks (Armitage et al. 2003; Herzon and Helenius 2008). This could be achieved in the Marais poitevin thanks to the between-site heterogeneity of the water regime: water levels could be managed differently depending on each site. Within sites, topographical variation can generate a mosaic of water regimes and a diversity of micro-habitats favorable to a diversity of biological communities (Raulings et al. 2010).

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