Community Ecology (2025) 26:385–394
https://doi.org/10.1007/s42974-025-00250-9

ORIGINAL ARTICLE

Plant diversity and water quality of grassland ponds under different agri-environment schemes

Pauline Quoitin[1] · Grégory Mahy[2] · Julien Piqueray[1]

Received: 29 November 2024 / Accepted: 3 April 2025 / Published online: 25 April 2025

Abstract
Ponds are declining ecosystems of high importance for freshwater biodiversity. Promoting less intensive agricultural practices in pond catchments may be particularly effective at enhancing their biodiversity and is more feasible compared to larger freshwater habitats. This study aimed to determine whether ponds located in grasslands with lower management intensity, under agri-environment schemes (AES), exhibit better water quality, including lower nutrient content, and harbor specific plant communities that are richer in species compared to more intensively managed grasslands. A vegetation survey was conducted, and abiotic parameters were measured in 38 ponds located in grasslands under AES in Wallonia, southern Belgium. Four management intensities were considered, including three AES categories: 'MC4—Grassland with High Biological Value' ($n=10$), 'MB2—Natural Grassland' ($n=7$), 'MB9—Grassland in Forage Autonomy' ($n=10$), and grasslands without AES (none of these AES, $n=11$), representing the most intensive management. There was evidence that vegetation on pond banks in grasslands under MC4 or MB2 were richer in species and supported different plant communities compared to those under MB9 or without AES. Ponds exhibited variations in conductivity and dissolved oxygen concentration according to the type of AES. Additionally, high nitrate concentrations in water were more common under MB9 or in ponds without AES. However, the diversity of hydrophytes was not correlated with grassland management practices. The results suggest that AES promoting lower management intensity in surrounding grasslands, such as MC4 and MB2, may improve water quality and increase plant species richness in ponds. These AES also influenced the composition of plant species on pond banks, although they did not significantly affect hydrophyte species. While a pluriannual survey would be necessary to confirm these hypotheses, our findings support the promotion of grassland deintensification around ponds, particularly through AES.

Keywords Agriculture · Fertilization · Freshwater · Grassland management · Grazing · Plant communities

Introduction

Since the twentieth century, agriculture has undergone major changes through mechanization and the widespread use of pesticides and chemical fertilizers. As a result, agricultural yields have increased, but this has led to environmental problems, including the decline of many species and ecosystems that depend on agricultural management, such as grassland and arable-dependent species (Batáry et al., 2015). Natural or semi-natural habitats, such as semi-natural grasslands, have been destroyed or fragmented (Piqueray et al., 2011). Additionally, landscape elements such as hedgerows, ponds, and field margins have dramatically declined (Oertli et al., 2005; Robinson & Sutherland, 2002; Smith et al., 2022; Tscharntke et al., 2005).

Among these elements, ponds play a key role in freshwater biodiversity in agricultural landscapes. Farmland ponds may have a natural origin, such as sinkholes. However, most of them are human-made, initially for economic use (e.g., water reserves for livestock) and more recently for biodiversity conservation purposes (Hill et al., 2021; Oertli & Frossard, 2013), flow regulation, aesthetic value, and other ecosystem services they can provide (Oertli, 2018; Zamora-Marín et al., 2021). Their conservation is essential to preserve many plant and animal species that specifically need water bodies to survive

Julien Piqueray
jpiqueray@natagriwal.be

[1] Natagriwal ASBL, site de Gembloux. Passage des Déportés 2, 5030 Gembloux, Belgium

[2] Biodiversity and Landscape Unit, Gembloux Agro-Bio Tech, University of Liege, Passage des Déportés 2, 5030 Gembloux, Belgium

or reproduce (Oertli et al., 2005). Due to their high heterogeneity in species composition at the individual level, ponds contribute significantly to the regional biodiversity of macrophytes and macroinvertebrates (Davies et al., 2008a; Williams et al., 2004). Ponds shelter species-rich plant communities that may notably depend on their physical structure (e.g., area, depth) and water quality (Oertli & Frossard, 2013). Surface waters in agricultural landscapes are known to be highly polluted, notably by an increased load of nutrients due to fertilizer run-offs (Williams et al., 1997). Farming practices are therefore likely to play an important role in the ecological quality of ponds. It has been stated that promoting less intensive agricultural practices in a pond catchment area may be particularly effective at enhancing its biodiversity (Biggs et al., 2005; Davies et al., 2004). Due to the small catchment size, a pond's preservation status may primarily rely on local land-use (Novikmec et al., 2016; Přidalová et al., 2024), or even on activities in its immediate surroundings (Biggs et al., 2005; Davies et al., 2008b; Declerck et al., 2006). Therefore, even in landscapes where deintensification of agricultural practices on a large scale is not feasible, pond biodiversity may nevertheless be promoted through local actions (Céréghino et al., 2007).

This study aimed to determine if ponds' plant communities and water quality are related to the current management intensity of grasslands in their immediate surroundings. Studying the effect of pond management on biotic communities at local scale in different environmental settings, was identified as a key question for pond conservation by Hill et al. (2021). To this purpose, the agri-environment schemes (AES) in Wallonia (South Belgium) offer an opportunity to assess the effect of surrounding grassland management on pond biodiversity. AES are payments from the common agricultural policy (CAP) that aim at supporting environment-friendly practices in farms. In Wallonia, such a payment exists for maintaining existing or newly created ponds, with the condition that at least 75% of their perimeter must be fenced in case of grazing. On the other hand, several AES are dedicated to grassland management with a biodiversity conservation purpose, i.e., with a lowered management intensity. Ponds situated in such grasslands should therefore benefit from less intensive management in their surroundings, notably through a decreased nutrient load in their catchment.

We therefore make the hypotheses that ponds located in grasslands having the lowest management intensity should: (i) exhibit lesser evidence for eutrophication, (ii) harbor more diverse plant communities, (iii) have plant communities that are distinct from plant communities at the most intensive sites.

Methods

Study sites

Thirty-eight grasslands harboring ponds were selected in the Famenne region, Wallonia, Belgium. Famenne is a 15 km-wide Devonian shale belt running from southwest to northeast through Wallonia (Fig. 1). Grasslands were selected based on their management intensity, which corresponds to different types of agri-environmental schemes (AES). We considered that management intensity was lower in cases of fertilization restriction (either prohibition or limitation), restriction in mowing/grazing periods, or restriction in grazing intensity (Table 1). Four categories were therefore considered, from the least to the most intensive management: 'MC4—Grassland with High Biological Value' (10 grasslands, mean area ± SD: 3.8 ± 3.1 ha), 'MB2—Natural Grassland' (7 grasslands, mean area ± SD: 5.0 ± 5.8 ha), 'MB9—Grassland in Forage Autonomy' (10 grasslands, mean area ± SD: 5.6 ± 3.6 ha), and grasslands under none of these AES (without AES, 11 grasslands, mean area ± SD: 9.5 ± 5.9 ha).

Within the grasslands, selected ponds had to hold water during the survey period and have relatively good southern exposure or at least not be completely surrounded by trees. When several ponds fitting these criteria occurred in grasslands, one of them was randomly selected. Since the ponds were not connected to the hydrographic network, they received no permanent inflow. Based on recent and older orthophotos, we established that selected ponds were all at least 5 years old. Eighteen of them were already present in 1971 (i.e., on the oldest orthophoto available). These old ponds were mainly found in grasslands without AES (7 ponds) and in MB9 grasslands (6 ponds). On recent orthophotos, we observed evidence of maintenance work for most of these old ponds.

Data collection

The 38 study ponds were surveyed for vegetation from late May to late June 2018, at the peak of vegetation. Plant species occurrences were recorded within the water body and at the pond bank. The pond bank limit was visually determined based on vegetation physiognomy and topography (slope break). This roughly corresponds to the point where helophytes were not dominant in the plant community. Tracheophytes were listed and identified at the species level. Characeae were considered as a single taxon, as species within this family were not determined. Shrubs and trees were not included in the survey. Nomenclature follows Lambinon et al. (2004). The cover of each species

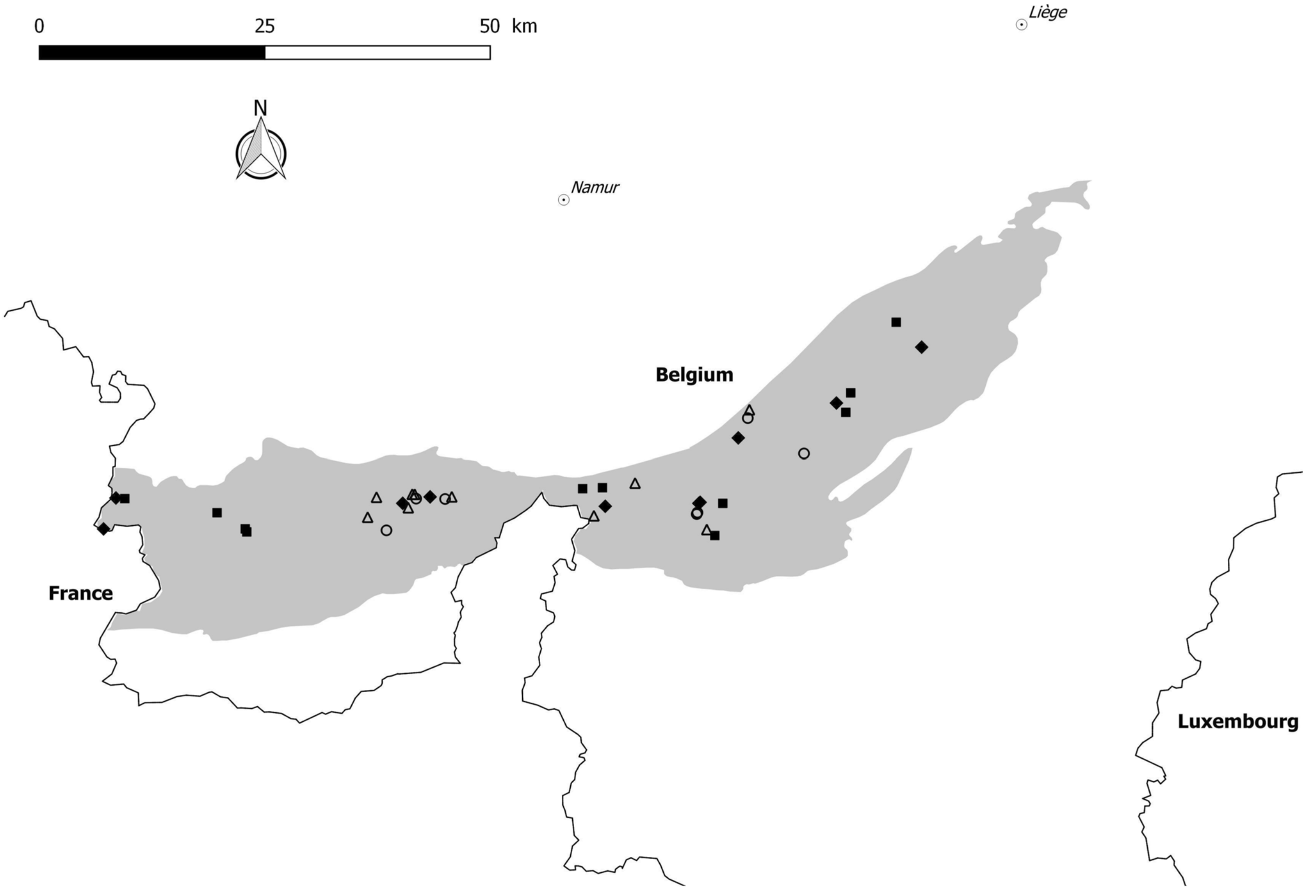

Fig. 1 Location of the 38 study ponds within the Famenne region (gray zone). Empty triangles: ponds in MC4, empty circles: ponds in MB2, filled diamonds: ponds in MB9, filled squares: ponds in grasslands without AES. Dotted circles are main cities

was estimated using the Braun-Blanquet (1932) scale of plant-cover abundance. To record submerged species, a rake was drawn from the center of the ponds toward their banks at four facing locations. Braun-Blanquet coefficients were attributed to submerged species according to their abundance in the rake and relative frequency among the four samplings. Species that were collected in the rake once or twice with low abundances received coefficient "+." Coefficient "1" was assigned to species that occurred either frequently with low abundances or once or twice with moderate abundances in the rake. Coefficient "2" was attributed to species that occurred frequently and were moderately abundant or to species that were highly abundant in the rake but occurred in only one sample. Coefficients "3", "4", and "5" were attributed to species that were found two, three, or four times in the rake with high abundances, respectively. Braun-Blanquet values were converted into van der Maarel (1979) values prior to analysis. The area surveyed was measured considering ponds as rectangles. Maximum water depth was measured using a rod equipped with a plumb line and a float. We evaluated shading by considering three shading classes: (i) "absent" when shrubs and trees were totally absent ($n=$ 11), (ii) "weak" when a few shrubs or trees were present (less than one third of the perimeter), never at the southern side of the pond ($n=$ 18), (iii) "significant" when shrubs or trees occupied more than one third of the pond perimeter, or some were present at the southern side of the pond ($n=$ 9). Farmers were interviewed to collect information on the grassland exploitation regime (grazing, cutting, or both) and the fertilization practices. Ponds' accessibility to livestock was observed in the field.

In early July 2018, water samples were collected in the morning at each of the 38 ponds to measure physicochemical parameters of the water. Samples were collected at the center of the ponds, at a depth between 0 and 20 cm. To minimize variation factors, all samples were taken within a 10-day period, in the morning, in the absence of rainfall, and avoiding densely vegetated zones. Although sampling conditions may still have differed between ponds, bias related to AES type was unlikely. The pH, conductivity, and dissolved oxygen of each water sample were directly measured in the field. The pH and conductivity were measured using a WTW® pH/Cond 3320 SET 2 multimeter. Dissolved oxygen and

Table 1 Specifications for each type of AES and actual grasslands management practices

AES type	Specifications	Actual management practices
MC4 (n = 10)	Preliminary diagnosis of the grassland by an AES advisor who provides management prescriptions (see Piqueray et al., 2016) Permanent grassland No intervention from the 1 st January to a date mentioned in the management prescriptions (generally 1 July) If case of mowing, forage removal is compulsory, and a 10% refuge zone must be maintained Spraying and fertilization forbidden Livestock at grazing cannot be supplied with additional fodder Integrated use of antihelminthics	8 mown grasslands, 1 grazed grassland, 1 grassland with mixed management* No grassland fertilization No pond accessible to livestock
MB2 (n = 7)	No management action from the 1 November to the 15 June Organic fertilization. Max. 1 annual spread between 16 June and 15 August Exploitation from the 16 June to the 31 October, either by grazing or by mowing with forage removal and with 5% of refuge zone maintained Livestock at grazing cannot be supplied with additional fodder No mineral fertilizer and no phytoparmaceutical products	4 grasslands with mixed management*, 3 mown grasslands 4 grasslands fertilized with organic fertilizers No pond accessible to livestock
MB9 (n = 10)	Livestock density at the farm level up to 1.4 LU/ha of land under grass and/or under fodder crops Permanent grasslands eligible to payment Organic fertilization only. Quantity limited to the manure produced in the farm Phytopharmaceutical products are forbidden in eligible grasslands	5 grazed grasslands, 3 grasslands under mixed management, 2 mown grasslands 6 fertilized grasslands, all with organic fertilizers 2 ponds accessible to livestock
Without AES (n = 11)	No constraint from AES specifications Other constraints from legislation concerning agriculture (e.g., EU Nitrate Directive)	9 grazed grasslands, 2 mown grasslands 10 fertilized grasslands, 6 with mineral fertilizers 5 ponds accessible to livestock

Actual management was assessed based on farmers' interviews. * Mixed management in MB2 and MC4 consisted in a delayed mowing (respectively after 15 June and 1 July), followed by grazing in the late summer

temperature were measured using a WTW® Oxi 340 oxygen meter equipped with a CellOX 325 probe. Nitrate and phosphate were measured using tube tests (Macherey–Nagel NANOCOLOR® Nitrate 8 and Macherey–Nagel NANOCOLOR® ortho- and total Phosphate 5). The detection limits were 1.3 mg/L NO3- and 0.5 mg/L PO43-. Such limits do not allow for a precise evaluation of water quality but rather to detect evidence of eutrophic conditions (Søndergaard et al., 2005). Values of dissolved oxygen concentration were transformed into oxygen saturation rates, based on water temperature, prior to analyses.

Data analysis

We first checked for some possible bias due to pond characteristics and environment, i.e., area, depth, age and shading, that were likely to have an impact on the pond species richness. For area, depth and age, we checked for existing correlations between these variable and pond species richness throughout our dataset using Pearson's correlation tests, and then for differences between our treatments by ANOVA. We computed ANOVAs to test for differences in species richness between shading classes, and then a Chi-square to verify for a possible uneven distribution of shading classes between treatments.

The ponds' plant diversity was described using the following indices: (1) Total species richness (SR_{total}); (2) species richness according to Raunkiaer's plant life-forms (Lambinon et al., 2004): hydrophytes (SR_{hydro}), helophytes (SR_{helo}), and terrestrial species (i.e., hemicryptophytes and geophytes) (SR_{terr}), and (3) the number of plant species that are protected in Wallonia (SR_{prot}). In addition, the mean Ellenberg's indicator value for nutrient status weighted by species cover (Ellenberg N) was computed for each pond as an indicator of eutrophication. To improve their normality and homoscedasticity, variables SR_{prot}, conductivity, and area were log-transformed. SR_{helo}, SR_{terr}, pH, and maximum depth were square root-transformed.

To test for differences in ponds' plant diversity indices and physicochemical parameters (excluding nitrate and phosphate) of the water between AES categories, we performed one-way ANOVAs using the ‘lm’ and ‘anova’ functions in R (R Core Team, 2018). In case of significant differences, post-hoc Tukey comparisons were performed using the R package “multcomp.” As many ponds had nitrate and phosphate concentrations below the detection limit, we could not estimate a proper mean and error for these parameters, especially in MB2 and MC4. We therefore considered exceeding the detection limit as the variable for analysis. We conducted a Chi-square test to determine if exceeding the detection limit (i.e., evidence of eutrophication) was dependent on AES.

To determine if the different AES were related to different plant communities, we used Ward’s clustering method (R function ‘hclust’) on the ponds’ Bray–Curtis distance matrix to create groups of ponds with similar plant compositions. The number of groups was determined based on partial R^2 (Carvalho et al., 2009). Subsequently, a chi-square test was used to assess if ponds in the same AES tended to be grouped together. To describe the variation in species composition and cover, principal coordinates analyses (PCoA) based on Bray–Curtis distances were performed using the R package “vegan.” To facilitate interpretation, environmental parameters (physicochemical, pond area, and depth) were added in PCoA diagrams based on their correlations to axes. Species were added based on their cover-weighted occurrence in ponds. To limit the number of species displayed in diagrams, we selected indicator species of the groups created by Ward’s clustering, using the Indval method (Dufrêne & Legendre, 1997). When available, we included the five species with the highest Indval for each group, with a p value lower than 0.05. Ward’s clustering and PCoA were performed on the whole plant dataset and separately according to plant life form (hydrophytes, helophytes, and terrestrial species).

Results

No differences were found in terms of species richness between the three pond shading classes, i.e., no shading, weak shading, and significant shading. We also found no significant correlation between pond age and species richness. We found a significant positive correlation between pond area and total species richness ($r = 0.42$, $P = 0.010$), as well as terrestrial species richness ($r = 0.35$, $P = 0.029$). There was also a significant positive correlation between pond depth and total species richness ($r = 0.34$, $P = 0.036$), as well as helophyte species richness ($r = 0.43$, $P = 0.007$).

Pond area ranged from 49.3 to 308 m^2. Ponds in MB2 tended to be smaller (96.1 ± 41.6 m^2) than those in other categories (143.0 ± 50.3 m^2, 146.1 ± 88.1 m^2, and 147.9 ± 82.6 m^2 for MC4, MB9, and no AES, respectively). However, this difference was not significant ($F_{[3,34]} = 0.94$, $P = 0.432$), allowing us to assume that pond area did not introduce a bias.

Pond depth ranged from 0.10 to 1.29 m. Ponds in MC4 (0.71 ± 0.35 m) and MB2 (0.70 ± 0.33 m) were deeper compared to those in MB9 (0.47 ± 0.38 m) and no AES (0.45 ± 0.21 m). Although the difference was not significant ($F_{[3,34]} = 1.85$, $P = 0.157$), we cannot completely rule out a potential bias for this variable, as the depth differences between treatments follow a similar pattern to species richness (see further results).

The actual management practices of the studied grasslands confirmed the existence of the expected gradient of management intensity. Grasslands in MC4 were not fertilized, whereas those in MB2 and MB9 were either not fertilized or received minimal fertilization, and those without AES were almost all fertilized, often with mineral fertilizers (Table 1). Grasslands in MC4 and MB2 were primarily under delayed mowing regimes, while those in MB9 and without AES were mainly grazed.

A total of 207 plant species were recorded during the survey, including 17 hydrophyte species, 59 helophyte species, and 131 terrestrial species. The species count for each AES type is provided in Table 2. Only four regionally protected species were found: *Centaurium erythraea*, *Dactylorhiza fuchsii*, *Oenanthe fistulosa*, and *Schoenoplectus lacustris*. Of these, three species were found in MC4 and two species in MB2, in all cases with low abundances (< 5% cover).

Total species richness of ponds differed between AES regimes ($P = 0.002$, Table 3). It was highest in ponds in MC4 and lowest in ponds in MB9 and without AES. MB2 had an intermediate value. Similar trends were observed for the number of protected species ($P = 0.005$), helophyte species richness ($P = 0.007$), and terrestrial species richness ($P = 0.037$, Table 3). Ellenberg N was higher for ponds without AES than for any AES type ($P = 0.024$). Overall, the ponds were circum-neutral to slightly alkaline and presented similar pH values across AES types. Ponds in MC4 presented higher values of oxygen saturation rate and lower values of conductivity than ponds without AES ($P = 0.037$ and $P = 0.014$, respectively, Table 3).

The detection limit for nitrate (1.3 mg/L NO_3^-) was exceeded in 6 ponds without AES (range: 1.4–31.5 mg/L),

Table 2 Species count, by plant life form for all the ponds in a same AES type

	MC4	MB2	MB9	Without AES
Hydrophytes	10	12	12	11
Helophytes	46	36	39	39
Terrestrial	92	75	86	74
Total	148	123	137	121

Table 3 Mean ± standard deviation of plant diversity indices and physicochemical parameters of ponds between four AES types

Variables	MC4	MB2	MB9	Without AES	P
SR_{total}	53.00 ± 9.87 ^{b}	43.14 ± 11.77^{ab}	35.90 ± 12.25^{a}	32.09 ± 14.05^{a}	**0.002**
SR_{prot}	0.60 ± 0.70^{b}	0.29 ± 0.49^{ab}	0.00 ± 0.00^{a}	0.00 ± 0.00^{a}	**0.005**
SR_{hydro}	2.40 ± 1.35	4.14 ± 1.35	2.80 ± 0.63	2.91 ± 1.64	0.069
SR_{helo}	16.40 ± 4.50^{b}	13.00 ± 5.20^{ab}	10.20 ± 4.34^{a}	9.09 ± 5.26^{a}	**0.007**
SR_{terr}	34.20 ± 11.02^{b}	26.00 ± 10.12^{ab}	22.90 ± 11.07^{ab}	20.09 ± 9.03^{a}	**0.037**
Ellenberg N	5.60 ± 0.52^{a}	5.57 ± 0.54^{a}	5.70 ± 0.48^{ab}	6.18 ± 0.41^{b}	**0.024**
pH	7.6 ± 0.5	7.5 ± 1.1	7.0 ± 0.4	7.2 ± 0.5	0.19
Oxygen saturation rate	0.734 ± 0.170^{b}	0.629 ± 0.155^{ab}	0.543 ± 0.403^{ab}	0.359 ± 0.306^{a}	**0.037**
Conductivity [μS/cm]	239.6 ± 132.0^{a}	342.0 ± 313.0^{ab}	306.2 ± 188.9^{ab}	548.7 ± 306.5^{b}	**0.014**

Multiple comparisons of means; Tukey's test: different letters indicate significant differences for $\alpha = 0.05$

6 ponds in MB9 (range: 1.3–19.4 mg/L), 1 pond in MB2 (1.7 mg/L), and no ponds in MC4 (*Chi-Sq* = 11.4; df = 3; $P = 0.010$). Concerning phosphate, the detection limit (0.5 mg/L PO_4^{3-}) was exceeded in 4 ponds without AES (range: 0.7–5.7 mg/L), 2 ponds in MB9 (range: 1.6–4.5 mg/L), and no ponds in MB2 and MC4 (*Chi-Sq* = 6.8; *df* = 3; $P = 0.078$).

PCoA based on the entire floristic dataset revealed that ponds in MC4 and MB2 tended to belong to the same Ward's clusters, as did ponds in MB9 and ponds without AES (Fig. 2a). These observations were confirmed by a Chi-square test, which showed that the distribution of AES types differed among Ward's clusters ($P = 0.015$). Following the Indval analysis, the Ward's clusters in which ponds in MC4 and MB2 were mostly present were characterized either by *Valeriana officinalis, Filipendula ulmaria, Scrophularia nodosa,* or by *Centaurea jacea, Carex flacca, Ranunculus acris* (Fig. 2e). Concerning ponds in MB9 and ponds without AES, some were characterized by *Plantago major, Matricaria recutita, Lythrum portula*, while others did not present characteristic species (Fig. 2e). The same trend in the distribution of AES types among Ward's clusters was observed in PCoAs based on helophyte species and terrestrial species datasets (Fig. 2b, c), confirmed by Chi-square tests ($P = 0.014$ and $P < 0.001$, respectively).

PCoA and Indval based on helophyte species showed that most ponds in MC4 and MB2 were characterized either by *Juncus inflexus, Epilobium parviflorum*, or by *Valeriana officinalis, Scirpus sylvaticus, Hypericum tetrapterum* (Fig. 2f). Concerning ponds in MB9 and ponds without AES, some were characterized by *Juncus effusus*, some by *Persicaria hydropiper*, others by *Glyceria fluitans* (Fig. 2f).

PCoA and Indval based on terrestrial species showed that most ponds in MC4 and MB2 were characterized either by species like *Scrophularia nodosa, Angelica sylvestris, Epilobium angustifolium*, or by species like *Anthoxanthum odoratum, Festuca pratensis, Lathyrus pratensis* (Fig. 2g). Most ponds in MB9 and without AES presented plant communities characterized by *Urtica dioica, Holcus lanatus,* or by species like *Polygonum aviculare, Plantago major, Lolium perenne* (Fig. 2g).

However, when considering hydrophyte species only, no general trend could be discerned from PCoA (Fig. 2d), and the Chi-square test did not reveal differences in the distribution of AES types among Ward's clusters. In PCoAs based on all plant species, helophyte species, and terrestrial species, the area of the chart showing higher values of depth and oxygen saturation and lower values of conductivity, nitrates, and phosphates concentrations grouped most of the ponds in MC4 and MB2 (Fig. 2a–c).

Discussion

Patterns in water physico-chemistry

Water physicochemistry varied between AES categories. The nitrate detection limit was exceeded more frequently in ponds located in grasslands under the most intensive management (MB9 and without AES). However, the sensitivity threshold of the tube tests was high, which may have hindered the expression of some variability, especially for phosphate. Almost all ponds in MB2 and MC4 were below the nitrate detection limit, i.e., 1.3 mg/L. None of them exceed the detection limit for phosphate (0.5 mg/L). This might indicate a good nutrient status in our ponds (Ministère de la Transition écologique et solidaire, 2019). However, nutrients were measured in the top 20 cm of pond water during the vegetation season. In these conditions, nutrient contents might be underestimated due to nutrient consumption by plants (Oertli & Frossard, 2013). It is also known that phosphorus content may be lower near the water surface due to a stratification along the water column (Gao et al., 2016).

Oxygen saturation rates tended to increase from ponds without AES to ponds in MC4. Interpretation of this highly variable parameter is challenging. Dissolved oxygen is known to decrease with organic matter input (Oertli & Frossard, 2013); this result may partly be due to increased

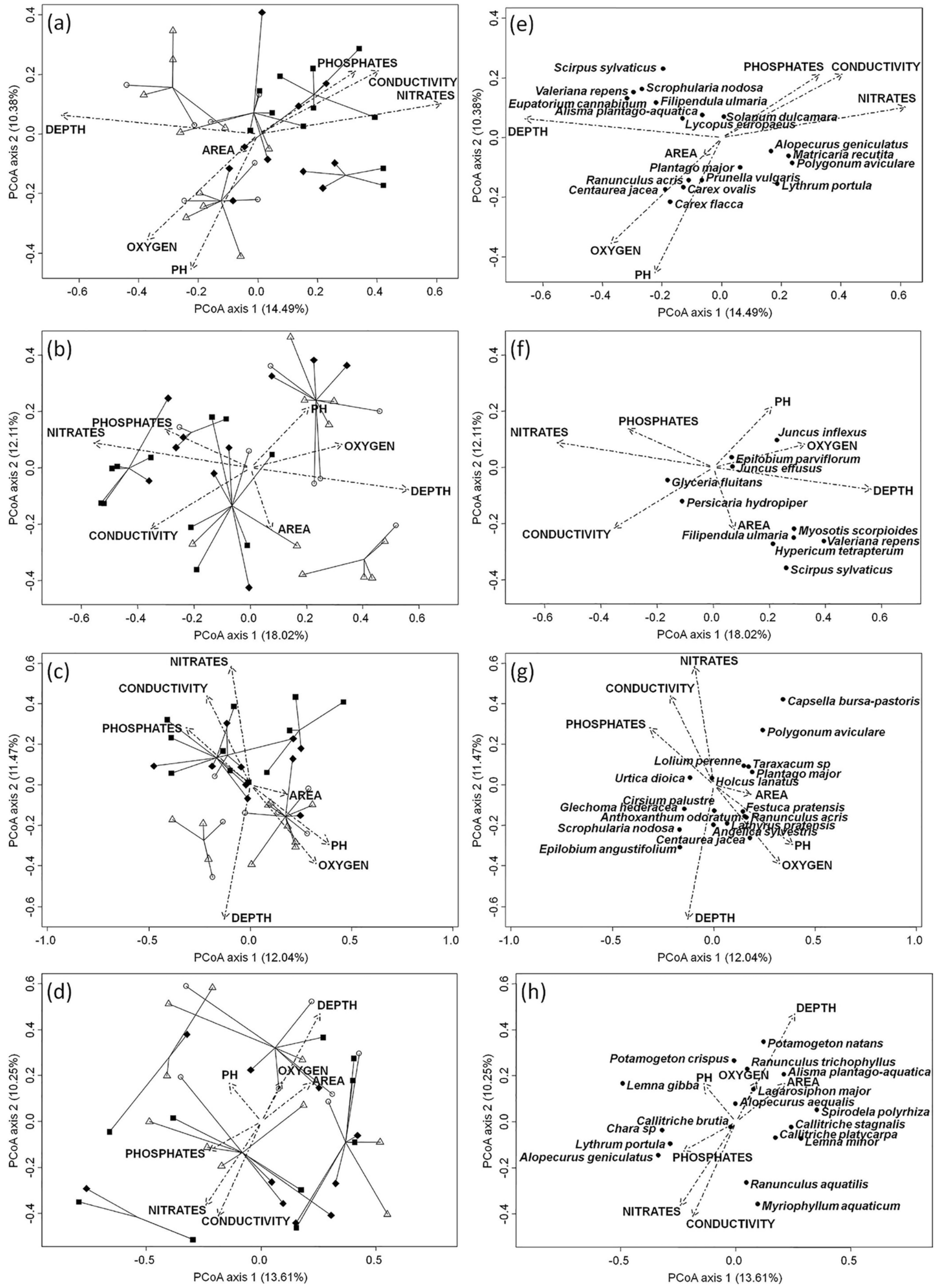

Fig. 2 PCoA of the 38 ponds, based on species cover data. Empty triangles: ponds in MC4, empty circles: ponds in MB2, filled diamonds: ponds in MB9, filled squares: ponds in grasslands without AES. Solid lines link ponds from the same Ward's cluster. Dotted arrows represent the correlation of the morphometric and physicochemical parameters to the PCoA axis. **a** Considering the entire plant dataset. **b** Considering helophytes species only. **c** Considering terrestrial species only. **d** Considering hydrophytes species only. Same PCoA-panels showing species position based on their cover in each pond (maximum five characteristic species per Ward's cluster are displayed). **e** Considering the entire plant dataset. **f** Considering helophytes species only. **g** Considering terrestrial species only. **h** Considering hydrophytes species only

coverage of *Glyceria fluitans*. Indeed, this species was more abundant in ponds in MB9 and without AES compared to MB2 and MC4 (results not shown), and it was dominant in several cases. Its increased coverage and accumulation likely caused increased oxygen consumption due to organic matter breakdown.

Additionally, water conductivity was higher in grasslands managed more intensively. This parameter is primarily influenced by geological substrate and pH (Bensettiti et al., 2002). However, these two factors did not vary significantly in this study. Conductivity may also correlate positively with dissolved solids concentration in water, which could explain its variation between AES categories and may result from higher organic matter accumulation. It was observed that most ponds without AES and some in MB9 were characterized by significant siltation, although the exact siltation rate was not precisely measured.

Furthermore, 7 out of the 38 studied ponds were accessible to livestock and all were in MB9 or without AES. Negative effects of cattle frequenting these ponds were previously assessed by Declerck et al. (2006), who reported that livestock increased water turbidity either directly through an increased load of suspended sediments or indirectly through urine and feces inputs contributing to pond eutrophication.

Patterns in plant communities and species richness

Diversity indices related to terrestrial and helophyte species (SR_{tot}, SR_{prot}, SR_{helo}, SR_{terr}) increased with lower management intensity of the surrounding grasslands. Ponds in MC4 and MB2 generally harbored richer species communities compared to ponds in MB9 and those without AES, often containing regionally protected species. Some ponds in MC4 and MB2 tended to host characteristic species of tall-herb mires such as *Valeriana repens* or *Filipendula ulmaria*, while others supported species typical of hay meadows like *Carex flacca* or *Centaurea jacea*. In contrast, ponds in MB9 and without AES were colonized by species indicative of trampled soils or silted ponds such as *Plantago major* or *Lythrum portula*. Other ponds in these categories predominantly harbored generalist species found in many ponds, such as *Glyceria fluitans*. These differences in species composition, like species richness, were primarily driven by terrestrial species and, to a lesser extent, by helophyte species.

AES such as MC4 and MB2 play a crucial role in maintaining diverse plant communities in grasslands (Cordier et al., 2025; Piqueray et al., 2016). Reduced fertilization particularly enhances grassland species richness (Hautier et al., 2009; Kleijn et al., 2009). Beyond their positive impact on water quality through buffer zones (Davies et al., 2008b), they contribute to preserve diverse semi-natural areas around ponds, which promote the establishment of species-rich vegetation on the pond banks. Moreover, this habitat diversity likely benefits pond animal diversity, especially invertebrates, as plants provide food, habitats, and fulfill other critical roles in their life cycles (Biggs et al., 2005).

Furthermore, damage associated with livestock access to ponds may partly explain the lower richness in helophyte species in MB9 and ponds without AES. As previously noted by Declerck et al. (2006), cattle reduce aquatic vegetation richness and complexity through bank encroachment and grazing.

In terms of biodiversity conservation strategy, the coexistence of ponds in MC4 or MB2 with those in MB9 or without AES is significant due to the beta-diversity of plant communities they support. However, their contribution to regional diversity (gamma diversity) is likely uneven. According to AES declarations, only 30% of grassland ponds are found in MC4 or MB2, compared to 70% in MB9 and without AES. This underscores the importance of promoting a mix of AES that protect ponds and those that promote less intensive grassland management such as MC4 or MB2. Also, the creation of ponds should be done as a priority in these grasslands where management is less intensive.

In contrast to terrestrial and helophyte species, hydrophytes did not exhibit richness and community patterns related to AES. This was despite differences in water parameters known to influence macrophyte species richness in ponds (Akasaka et al., 2010; Williams et al., 2020). The hydrophyte richness variation in our dataset ranged between 0 and 6 species. This was notably small and makes it challenging to observe contrasts in hydrophyte species diversity between AES types. Comparatively, Usio et al. (2017) and Svitok et al. (2018), respectively, found up to 22 and 24 hydrophytes per pond. This low variability suggests that other factors independent of management practices may have a greater influence on hydrophyte species. Many authors have noted that connectivity between ponds and other wetland types positively influences macrophyte diversity (Biggs et al., 2005; Bosiacka & Pieńkowski, 2012; Williams et al., 2004). Connectivity facilitates species dispersal, especially in heterogeneous habitat networks (Chisholm et al., 2011), enabling the natural establishment of a wide range of freshwater species (Davies et al., 2004). This factor appears particularly crucial for hydrophyte diversity (Svitok et al., 2018). However, large water bodies such as slow rivers or lakes, which serve as refuges and seed banks for many species, are scarce in the study region. Alongside connectivity, fluctuating water levels in many Famenne region ponds could explain hydrophyte distribution patterns. Famenne is characterized by impermeable clay soils, making it possible to maintain ponds that are not connected to the water table. But most of these ponds are likely to dry up in case of a summer with insufficient rainfall. This lack of permanency may be responsible for the low hydrophyte species richness in our ponds (Herault & Thoen, 2009).

Conclusion

This study reveals that management options in surrounding grasslands (averaging approximately 5 ha) are related to the water quality of ponds and the diversity of the vegetation on the pond banks. It can therefore be hypothesized that less intensive management practices have a favorable impact on plant diversity and water chemistry in ponds. However, further studies including diachronic analyses of plant communities would be necessary to fully assess the impact of farming practices. Indeed, our study lacked a true control group. Grasslands without agri-environment schemes (AES), despite representing the "business as usual," cannot serve as controls to assess the impacts of different AES options. In reality, it is likely that most grasslands under AES have not previously been intensively managed. This is especially true for MC4, where a diagnosis validating the "high biological value" based on vegetation is required to qualify for the scheme. Therefore, AES primarily contribute to maintaining less intensive practices and only secondarily promote the de-intensification of grasslands. However, our results rely on a small sample size, i.e., around 10 ponds per studied modality. This study should be considered preliminary and needs to be confirmed in other contexts and regions. In particular, such a small sample size did not allow us to distinguish between the components of agricultural intensification, i.e., fertilization, cattle access, and management (grazing or mowing), which tended to covary between treatments (see Table 2). Future studies will be needed to identify the actual driver of the observed differences in pond vegetation. Additionally, we cannot exclude the possibility that part of the results, notably regarding helophyte species richness, was biased by a greater water depth in MC4 and MB2 ponds. A higher depth may prevent ponds from completely drying up, which can influence their species richness (Herault & Thoen, 2009).

In Europe, AES are incentive tools provided by the second pillar of the common agricultural policy (CAP) to protect biodiversity and the environment in agricultural landscapes, benefiting from public funding that requires proof of their effectiveness. The results of this study are particularly valuable for improving AES efficiency as they highlight the positive effects of interactions between multiple AES. This study demonstrates that combining AES that protect ponds with AES promoting less intensive grassland management enhances the plant diversity on pond banks. Additionally, while reducing management intensity may be most effective at the catchment scale (Novikmec et al., 2016), this study shows that managing at the grassland level, which is easier to implement and organize as it involves a single owner, is a viable approach. However, grassland management alone may not suffice to enhance hydrophyte species richness. For this purpose, the creation of pond networks should be promoted through pond restoration and creation (Svitok et al., 2018).

Despite increasing awareness of their importance for freshwater biodiversity, ponds currently receive limited protection under existing conservation policies. Enhanced scientific understanding of ponds could support their better inclusion in international, national, and regional legislation (Hill et al., 2021). The results of this study could contribute to improving the qualitative inclusion of ponds in these policies.

Acknowledgements Natagriwal is a non-for-profit association funded by the Walloon government.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

Akasaka, M., Takamura, N., Mitsuhashi, H., & Kadono, Y. (2010). Effects of land use on aquatic macrophyte diversity and water quality of ponds. *Freshwater Biology, 55*, 909–922. https://doi.org/10.1111/j.1365-2427.2009.02334.x

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology, 29*, 1006–1016. https://doi.org/10.1111/cobi.12536

Bensettiti, F., Gaudillat, V., Haury, J. (2002). Cahiers d'habitats. *Natura* 2000. Connaissance et gestion des habitats et des espèces d'intérêt communautaire. Tome 3 - Habitats humides., MATE/MAP/ MNHN. Éd. La Documentation française. Paris

Biggs, J., Williams, P., Whitfield, M., et al. (2005). 15 years of pond assessment in Britain: Results and lessons learned from the work of Pond Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystem, 15*, 693–714. https://doi.org/10.1002/aqc.745

Bosiacka, B., & Pieńkowski, P. (2012). Do biogeographic parameters matter? Plant species richness and distribution of macrophytes in relation to area and isolation of ponds in NW Polish agricultural landscape. *Hydrobiologia, 689*, 79–90. https://doi.org/10.1007/s10750-011-0850-x

Braun-Blanquet, J. (1932). *Plant sociology: The study of plant communities*. McGraw-Hill Book Company Inc.

Carvalho, A. X. Y., Albuquerque, P. H. M., de Almeida Junior, G. R., & Guimaraes, R. D. (2009). Spatial hierarchical clustering. *Revista Brasileira De Biometria, 27*, 411–442.

Céréghino, R., Biggs, J., Oertli, B., & Declerck, S. (2007). The ecology of European ponds: Defining the characteristics of a neglected freshwater habitat. *Hydrobiologia, 597*, 1–6. https://doi.org/10.1007/s10750-007-9225-8

Chisholm, C., Lindo, Z., & Gonzalez, A. (2011). Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks. *Ecography, 34*, 415–424. https://doi.org/10.1111/j.1600-0587.2010.06588.x

Cordier, E., Rouxhet, S., Mahy, G., & Piqueray, J. (2025). The impact of activities within an agri-environment scheme on the habitat condition of hay meadows and its alignment with Natura 2000 objectives. *Journal for Nature Conservation, 84*, 126834. https://doi.org/10.1016/j.jnc.2025.126834

Davies, B. R., Biggs, J., Lee, J. T., & Thompson, S. (2004). Identifying optimum locations for new ponds. *Aquatic Conservation: Marine and Freshwater Ecosystems, 14*, 5–24. https://doi.org/10.1002/aqc.574

Davies, B. R., Biggs, J., Williams, P., et al. (2008a). Comparative biodiversity of aquatic habitats in the European agricultural landscape. *Agriculture, Ecosystems & Environment, 125*, 1–8. https://doi.org/10.1016/j.agee.2007.10.006

Davies, B. R., Biggs, J., Williams, P. J., et al. (2008b). A comparison of the catchment sizes of rivers, streams, ponds, ditches and lakes: Implications for protecting aquatic biodiversity in an agricultural landscape. *Hydrobiologia, 597*, 7–17. https://doi.org/10.1007/s10750-007-9227-6

Declerck, S., De Bie, T., Ercken, D., et al. (2006). Ecological characteristics of small farmland ponds: Associations with land use practices at multiple spatial scales. *Biological Conservation, 131*, 523–532. https://doi.org/10.1016/j.biocon.2006.02.024

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs, 67*, 345–366.

Gao, Y., Zhang, Z., Liu, X., et al. (2016). Seasonal and diurnal dynamics of physicochemical parameters and gas production in vertical water column of a eutrophic pond. *Ecological Engineering, 87*, 313–323. https://doi.org/10.1016/j.ecoleng.2015.12.007

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science, 324*, 636–638. https://doi.org/10.1126/science.1169640

Herault, B., & Thoen, D. (2009). How habitat area, local and regional factors shape plant assemblages in isolated closed depressions. *Acta Oecologica, 35*, 385–392. https://doi.org/10.1016/j.actao.2009.02.002

Hill, M. J., Greaves, H. M., Sayer, C. D., et al. (2021). Pond ecology and conservation: Research priorities and knowledge gaps. *Ecosphere, 12*, e03853. https://doi.org/10.1002/ecs2.3853

Kleijn, D., Kohler, F., Báldi, A., et al. (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proc R Soc B Biol Sci, 276*, 903–909. https://doi.org/10.1098/rspb.2008.1509

Lambinon, J., Delvosalle, L., & Duvigneaud, J. (2004). *Nouvelle flore de Belgique du Grand-Duché de Luxembourg, du Nord de la France et des régions voisines* (5th ed.). Jardin botanique national de Belgique.

Ministère de la Transition écologique et solidaire. (2019). Guide relatif à l'évaluation de l'état des eaux de surface continentales (cours d'eau, canaux, plans d'eau)

Novikmec, M., Hamerlík, L., Kočický, D., et al. (2016). Ponds and their catchments: Size relationships and influence of land use across multiple spatial scales. *Hydrobiologia, 774*, 155–166. https://doi.org/10.1007/s10750-015-2514-8

Oertli, B. (2018). Editorial: Freshwater biodiversity conservation: The role of artificial ponds in the 21st century. *Aquatic Conservation: Marine and Freshwater Ecosystems, 28*, 264–269. https://doi.org/10.1002/aqc.2902

Oertli, B., Biggs, J., Céréghino, R., et al. (2005). Conservation and monitoring of pond biodiversity: Introduction. *Aquatic Conservation: Marine and Freshwater Ecosystems, 15*, 535–540. https://doi.org/10.1002/aqc.752

Oertli, B., & Frossard, T. A. (2013). *Mares et étangs: Écologie, gestion, aménagement et valorisation*. PPUR.

Piqueray, J., Cristofoli, S., Bisteau, E., et al. (2011). Testing coexistence of extinction debt and colonization credit in fragmented calcareous grasslands with complex historical dynamics. *Landscape Ecology, 26*, 823–836.

Piqueray, J., Rouxhet, S., Hendrickx, S., & Mahy, G. (2016). Changes in the vegetation of hay meadows under an agri-environment scheme in South Belgium. *Conservation Evidence, 13*, 47–50.

Přidalová, M. S., Hamerlík, L., Novikmec, M., et al. (2024). Diversity and distribution of chironomids in Central European ponds. *Ecology and Evolution, 14*, e11354. https://doi.org/10.1002/ece3.11354

R Core Team. (2018). R: A language and environment for statistical computing—version 3.5.1

Robinson, R. A., & Sutherland, W. J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology, 39*, 157–176. https://doi.org/10.1046/j.1365-2664.2002.00695.x

Smith, L. P., Clarke, L. E., Weldon, L., & Robson, H. J. (2022). An evidence-based study mapping the decline in freshwater ponds in the Severn Vale catchment in the UK between 1900 and 2019. *Hydrobiologia, 849*, 4637–4649. https://doi.org/10.1007/s10750-022-05000-w

Søndergaard, M., Jeppesen, E., Jensen, J. P., & Amsinck, S. L. (2005). Water framework directive: Ecological classification of Danish lakes. *Journal of Applied Ecology, 42*, 616–629. https://doi.org/10.1111/j.1365-2664.2005.01040.x

Svitok, M., Novikmec, M., Hamerlík, L., et al. (2018). Test of the efficiency of environmental surrogates for the conservation prioritization of ponds based on macrophytes. *Ecological Indicators, 95*, 606–614. https://doi.org/10.1016/j.ecolind.2018.08.006

Tscharntke, T., Klein, A. M., Kruess, A., et al. (2005). Landscape perspectives on agricultural intensification and biodiversity—Ecosystem service management. *Ecology Letters, 8*, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Usio, N., Nakagawa, M., Aoki, T., et al. (2017). Effects of land use on trophic states and multi-taxonomic diversity in Japanese farm ponds. *Agriculture, Ecosystems & Environment, 247*, 205–215. https://doi.org/10.1016/j.agee.2017.06.043

van der Maarel, E. (1979). Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio, 39*, 97–114. https://doi.org/10.1007/BF00052021

Williams, P., Biggs, J., Corfield, A., et al. (1997). Designing new ponds for wildlife. *British Wildlife, 8*, 137–150.

Williams, P., Biggs, J., Stoate, C., et al. (2020). Nature based measures increase freshwater biodiversity in agricultural catchments. *Biological Conservation, 244*, 108515. https://doi.org/10.1016/j.biocon.2020.108515

Williams, P., Whitfield, M., Biggs, J., et al. (2004). Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation, 115*, 329–341. https://doi.org/10.1016/S0006-3207(03)00153-8

Zamora-Marín, J. M., Ilg, C., Demierre, E., et al. (2021). Contribution of artificial waterbodies to biodiversity: A glass half empty or half full? *Science of the Total Environment, 753*, 141987. https://doi.org/10.1016/j.scitotenv.2020.141987