Hydrobiologia
https://doi.org/10.1007/s10750-026-06203-1

POND BIODIVERSITY AND FUNCTIONS

Fish stock management as a driver of a nested community structure of macrophytes in fish pond systems

Léo Girard · Joël Robin · Soraya Rouifed · Vincent Tolon · Robby Wijns · Luc De Meester · Alexander Wezel · Pieter Lemmens

Received: 26 June 2025 / Revised: 10 March 2026 / Accepted: 19 March 2026
© The Author(s) 2026

Abstract Fish production in ponds has received less attention in the context of reconciliation between agricultural production and biodiversity conservation. These systems can contain remarkable biodiversity, including rich macrophyte communities. However, management intensification resulted in ecosystem and biodiversity deterioration. The present study capitalizes on two well-studied fish pond regions (Dombes, France, and Midden-Limburg, Belgium) to investigate how fish stock management type affects local and regional macrophyte community characteristics. We used data from macrophyte inventories in a set of ponds representing major management types. Our results reveal that fish stock management strongly affects local macrophyte richness and community composition. Management types with higher fish stock densities had lower local richness and the highest local diversity was found in ponds without fish stocking. Differences in community composition between management types within region were primarily determined by nestedness patterns. Communities in ponds with higher fish densities formed nested subsets of communities in ponds with lower fish densities. Our findings suggest that successfully combining fish production with biodiversity conservation, and enhancing macrophyte diversity in large anthropogenic fish pond systems, may be best achieved with a subset of ponds managed without fish stocking, while others are more intensively managed for fish farming.

Keywords Fish production · Aquatic plants · Fishpond · Biodiversity · Fish density

Guest Editors: Lena Fehlinger, Robert A. Briers, María Cuenca-Cambronero, Sandro Lanfranco & Dani Boix / Ponds for Biodiversity, Climate and People

L. Girard (✉) · J. Robin · S. Rouifed · V. Tolon · A. Wezel
Agroecology and Environment Research Unit, ISARA, Lyon, France
e-mail: legirard@isara.fr

R. Wijns · L. De Meester · P. Lemmens
Laboratory of Freshwater Ecology, Evolution and Conservation, KU Leuven, Louvain, Belgium

L. De Meester · P. Lemmens
Leibniz Institute Für Gewasserökologie Und Binnenfischerei (IGB), Berlin, Germany

L. De Meester
Institute of Biology, Freie Universität Berlin, Berlin, Germany

P. Lemmens
Research Institute for Nature and Forests (INBO), Brussels, Belgium

Introduction

Earth is increasingly characterized by anthropogenic landscapes that have been created to fulfill multiple human demands, including agricultural production (Stoate et al., 2001). Although the conversion

Published online: 29 April 2026

of natural land to human-dominated landscapes has contributed to major socio-economic development and food security (Van Zanten et al., 2014), it has become increasingly clear that agriculture detrimentally affects the ecological integrity and biodiversity of a variety of ecosystem types (Thomas et al., 2004). Agriculture is currently one of the most pervasive human activities on Earth (Rockström et al., 2009; Steffen et al., 2015), accounting for approximately 70% of terrestrial biodiversity loss (CBD, 2014). However, agricultural landscapes can also support a variety of organism groups (Waide et al., 1999; Queiroz et al., 2014; Eriksson, 2021) and are therefore increasingly targeted for biodiversity conservation in human-dominated landscapes (Andersen et al., 2004; Evans, 2012; Mueller & Maes, 2015). The central challenge is to maintain high agricultural production, while at the same time also preserving biodiversity. For this purpose, multiple public nature protection policies for agricultural landscapes, for example, Natura 2000, have been developed over the last 40 years (Andersen et al., 2004; Evans, 2012; Mueller & Maes, 2015). As a result, different types of agricultural production systems have been implemented with the specific aim to reconcile agriculture and biodiversity conservation.

Intensification of agricultural practices typically leads to spatial homogenization of habitats and their associated biotic communities (Jongman, 2002; Benton et al., 2003). Intensive agriculture also favors the dominance of generalist and opportunistic species (Buhk et al., 2017). Biodiversity conservation programs should therefore also explicitly consider among site variation and regional diversity (Ekroos et al., 2014). Management schemes that promote habitat diversification are therefore expected to enhance regional landscape scale biodiversity (Ekroos et al., 2014). It has been shown that practices such as crop diversification, agroforestry and intercropping have positive effects on biodiversity on agricultural land (Lichtenberg et al., 2017; Tamburini et al., 2020; Beillouin et al., 2021). For example, diversification of agricultural landscapes by combining grasslands, crops and semi-natural grass strips, can favor carabid diversity (Massaloux et al., 2020a, b).

While current efforts to promote biodiversity in agricultural landscapes largely focus on terrestrial systems (Priyadarshana et al., 2024), a large number of lentic freshwater systems are managed for purposes of commercial fish farming (Aubin et al., 2017). A key example is fish pond system that occurs not only in multiple European countries, including France, Belgium, Germany, Poland, Hungary, Austria, and Czech Republic (Aubin et al., 2017), but also in Central and South East Asia (Woynarovich et al., 2010). Such pond landscapes are characterized by a high density of ponds that are typically of anthropogenic origin and managed for purposes of fish farming (Adamek et al., 2015; Aubin et al., 2017). Many of these landscapes have a history of extensive fish farming that dates back to the Middle Ages, such as for example the fish ponds in the Dombes region (France) (Avocat, 1975; Sceau, 1980) that have been created by monastic communities (Sceau, 1980). Anthropogenic fish pond systems are increasingly recognized for their contribution to biodiversity (Broyer & Curtet, 2012; Lemmens et al., 2013; Robin et al., 2014; Rosset et al., 2014; Wezel et al., 2014; Vanacker et al., 2015). Multiple studies have shown that man-made fish ponds can act as surrogate habitats for species of which the natural habitat is lost (Zamora-Marín et al., 2021). Many fish ponds are currently characterized by relatively high levels of biodiversity and the occurrence of relatively high numbers of rare and protected species (Robin et al., 2014; Wezel et al., 2014), including macrophytes (Wezel et al., 2014), macroinvertebrates (Wezel et al., 2014), and birds (Kloskowski & Nieoczym, 2015; Broyer et al., 2018). Macrophytes play a pivotal role on pond ecosystem functioning (Carpenter & Lodge, 1986; Oertli & Frossard, 2013) and biodiversity (Jeppesen et al., 1997; Scheffer, 2004; Folke et al., 2004). They promote high water transparency by stabilizing pond sediments, increasing the sedimentation rate of particles, mediating food web interactions, as well as by suppressing phytoplankton through competition for resources and allelopathy (Scheffer, 2004; Oertli & Frossard, 2013). Macrophytes also promote biodiversity by enhancing physical habitat complexity, which increases niche availability and creates refuge habitat for prey against predation (Jeppesen et al., 1997; Scheffer, 2004; Folke et al., 2004; Declerck et al., 2005).

The ecological value and biodiversity in fish ponds are very responsive to human interference and management (Lemmens et al., 2013; Wezel et al., 2014; Kloskowski & Nieoczym, 2015; Broyer et al., 2018; Francová et al., 2019a, b; Francová

et al., 2021). Although fish pond management can vary between countries and regions (Aubin et al., 2017), key management actions include regular periodic pond drainage and fish stocking or harvesting practices (Horvath et al., 2002; Schlumberger and Girard, 2020) and can also involve the application of supplementary fish feeding and pond fertilization to increase fish biomass production (Horvath et al., 2002; Schlumberger & Girard, 2020). Fish are typically harvested by pond drainage that allows effective removal of the entire fish stock. After a periodic dry stand, the pond is refilled with water and restocked with fish. Fish stock management can directly and indirectly affect different aquatic organism groups (Lemmens et al., 2015; Francová et al., 2019a, b; Francová et al., 2021). Studies have shown that fish play an important role on the structure and dynamics of food webs in ponds and lakes (Kerfoot & Sih 1987; Carpenter & Kitchell 1996; Scheffer, 2004). Fish are efficient predators that can exert strong direct top-down effects on prey organisms (Jeppesen et al., 1997; Hansson et al., 2007). In addition, they can have profound indirect effects on the community characteristics of primary producers via trophic cascades (Carpenter et al., 1985; Carpenter & Kitchell, 1996; Jones & Sayer, 2003). Fish can also have profound effects on local pond conditions through resuspension of sediments, which enhances nutrient cycling, reduces light availability for submerged plants, and enhances internal eutrophication (Breukelaar et al., 1994; Weber & Brown, 2009; Kloskowski, 2011; Badiou & Goldsborough, 2015). In addition, fish can reduce submerged macrophytes directly by consumption and uprooting during foraging (Zambrano & Hinojosa, 1999; Badiou & Goldsborough, 2015). An earlier study on fish ponds by Francova et al. (2019a) has shown that fish density is a key driver of macrophyte diversity in fish ponds. In addition to fish stock management, pond drainage can have strong impact on different organism groups (Lemmens et al., 2015). For example, earlier studies have linked the presence of pioneer plant species in fish ponds to the regular periodic pond drainage regime (Lemmens et al., 2013; Fontanilles et al., 2023). There is currently an important paradox in fish pond management in Europe. Historically, traditional fish farming practices promoted biodiversity, whereas intensification of management practices over the latest decades has led to ecological degradation. Unfortunately, knowledge on how different management practices affect local and regional biodiversity remains relatively scarce.

The overall objective of the present study is to investigate how fish stock management affects macrophyte community characteristics at different spatial scales using two fish pond systems located in France and Belgium (Dombes and Midden-Limburg, respectively). Both regions share many similarities, but have a different fish stock management approach. While almost all ponds in the Dombes region are subjected to extensive fish farming (intermediate fish density), ponds in Midden-Limburg (Belgium) are managed in a much more differentiated way. This system includes ponds managed for commercial fish farming (higher fish density) and ponds that target biodiversity conservation and are kept free of fish. Using empirical data on key local environmental pond characteristics and macrophyte community characteristics, we specifically aimed to (1) assess the effect of fish stock management on local macrophyte richness and (2) explore to what extent fish stock management determines patterns of community nestedness and turnover at pond landscape scale.

We hypothesize that (i) pond management types with higher fish density have a lower local macrophyte taxon richness and that (ii) fish stock management type determines the patterns of variation in community composition and its components of nestedness and turnover. More specifically, we expect that macrophyte communities in ponds with higher fish densities form nested subsets of communities in ponds with lower fish densities.

Material and methods

Study area and study sites

We combined data from multiple ponds located in two important fish pond regions in Belgium (Midden-Limburg, 21 ponds) and France (Dombes, 17 fish ponds) that have been monitored in 2021 for local environmental pond characteristics and macrophyte community composition and diversity. Ponds were selected to represent the different fish stock management types within each region (Table 1). Pond management mainly relates to fish

Table 1 Description of five different fish stock management types with the number of ponds sampled within each category, the average surface area (ha) and the fish biomass harvested (kg.ha^{-1}.year^{-1}) at the end of the growth season

	NF (ML)	JF (ML)	IF (ML)	EF1 (D)	EF2 (D)
Number of investigated ponds	6	7	8	9	8
Mean surface (ha)	0.99	0.70	0.47	19.44	15.38
Fish biomass harvested (kg.ha^{-1}.year^{-1})	None	200–400	1200–1500	300–500	500–900

(NF (ML) = No Fish, JF (ML) = Juvenile Fish Farming, EF1 (D) = Extensive Fish Farming 1, EF2 (D) = Extensive Fish Farming 2, IF (ML) = Intensive Fish Farming). ML and D refer to management types applied in Midden-Limburg and Dombes, respectively

stock management by annual periodic pond drainage to harvest fish and subsequent restocking after refilling the ponds with water. Current fish farming practices in both regions largely target the cultivation of common carp (*Cyprinus carpio*, Linnaeus, 1758), although relatively small densities of other fish species can also be present as an accompaniment, including rudd (*Scardinius erythrophthalmus*, Linnaeus, 1758), roach (*Rutilus rutilus*, Linnaeus, 1758), tench (*Tinca tinca*, Linnaeus, 1758), pike (*Esox lucius*, Linnaeus, 1758), and pikeperch (*Sander lucioperca*, Linnaeus, 1758).

Both fish pond regions comprise a large number of shallow ponds (depth averaging between 80 and 100 cm) that have been created for purposes of fish farming. The Dombes regions comprises approximately 1 100 ponds (total area, 11 500 ha) that have been created during the Middle Ages within a wetland by monastic communities (Bernard & Lebreton, 2007). In contrast, the ponds in Midden-Limburg (total area 700 ha) are more recent and mainly result from iron and peat mining between 1850 and 1930 (Burny, 1999). A considerable number of additional ponds has been created in Midden-Limburg in the 1950s. Both regions are highly recognized for their strong contribution to biodiversity and have therefore been designated as Natura 2000 site. Despite their strong similarities (such as depth), the ponds in the two regions vary in size (Table 1). Ponds in Midden-Limburg are smaller, approximately one hectare, whereas ponds in Dombes average around ten hectares. These areas covering more than 5 hectares could be considered as small shallow lakes (Richardson et al., 2022), but we have chosen to retain the term "fish ponds" in this article in order to illustrate the primary function of these ecosystems (fish production).

The two regions also differ with respect to periodic temporal dry stand of ponds. Ponds in Dombes are left dry for an entire growth season after fish harvesting every four to five years. Ponds in Midden-Limburg are left dry for the winter period and are refilled with water in subsequent spring.

A key difference between the fish pond systems in the Dombes and Midden-Limburg lies in their fish stock management (Table 1). All fish ponds in the Dombes region are used for extensive fish farming and can be categorized into two major groups. The first extensive management type (EF1) includes ponds with the most extensive practice because it involves no additional feeding of fish and uses initial fish stocking densities of 100 kg.ha^{-1}. This management type typically results in a fish harvest of less than 500 kg.ha^{-1} at the end of the growth season. The second extensive management type in the Dombes (EF2) involves additional feeding of fish (grains or pellets, 50–150 kg.ha^{-1}.year^{-1}) and higher initial stocking densities (200 kg.ha^{-1}), resulting in a fish biomass harvested between 500 and 900 kg.ha^{-1}.year^{-1}. In the Dombes region, data on the total harvested biomass were collected by APPED, the local association of fish farmers for the promotion of pond fish.

In contrast, current pond management in Midden-Limburg can be categorized into three major types. Two management types, juvenile farming (JF) and intensive farming (IF), focus on commercial fish production, whereas the third management type consists of ponds managed without fish stocking for purposes of biodiversity conservation (NF). All ponds types are drained annually in autumn. Juvenile farming management (JF) targets the culture of Young of the Year (YOY) fish by stocking fish fry in early spring and harvesting them in autumn of the same year (biomass harvested: 200—400 kg.ha^{-1}). Intensive farming (IF) involves the stocking of one-year-old fish (Y1Y) and harvesting of two-year-old fish (Y2Y) at the end of the growth season (biomass harvested: 1200—1500 kg.ha^{-1}). Fish biomass production in intensive farming is enhanced by the supply

of additional fish feeds (pellets, circa 800 kg.ha^{-1}.year^{-1}). NF ponds are refilled in early spring with no fish stocking. Fine-mesh grids (2 mm) are installed on inlets during refilling to minimize fish immigration from small streams and rivulets. Despite these measures, earlier regional studies using fyke nets indicate that some NF ponds can contain very low densities of fish, mostly *Pseudorasbora parva* (Temminck & Schlegel, 1846), typically much lower than in other management types. Information on pond management was collected directly through exchanges with local fish farmers and through earlier scientific assessments (Lemmens et al., 2013, 2015).

Total nitrogen and phosphorus concentrations in water

Water samples for the analysis of total nitrogen (TN) and total phosphorus (TP) concentrations were collected mid-June in the deepest part of each pond (generally near the outlet) using a five-liter tube sampler (Van Dorn). The collected water was subsequently transferred into a plastic canister for transport and stored in a cold room at 4 °C prior to laboratory analysis.

TN and TP concentrations (in mg.l^{-1}) were determined from unfiltered water samples following standard Hach® procedures (HACH Company, Loveland, Colorado, USA, DR/2400 Spectrophotometer Procedure Manual, Hach Company, 2002). For both elements, the method involves the analysis by digestion, followed by absorbance reading using spectophotometry. TN was measured with nitrogen persulfate reagent powder (410 nm wavelength, HACH method 10,072) and TP with the method of PhosVer® 3 by using an acid persulfate (HACH method 8190).

Macrophytes

The macrophyte communities (submerged, floating, and emergent vegetation) were inventoried directly in the field in all studied ponds in both regions during the growth season (June–July) of 2021. Inventories were made across the different meso-habitats within each pond. In Belgium, the entire pond was surveyed until no additional species could be found. Since the ponds in France are considerably larger (17 ha on average), inventories were done in multiple quadrats (4 m^2) along different transects following the protocol described in Arthaud et al. (2013) and in Vanacker et al. (2015, 2016). Three parallel transects (one central and two intermediate) were established perpendicular to the pond dike and quadrats were laid out every 50 m. In addition to these three transects, the entire edge of the pond was surveyed, also using the method of quadrats. The total number of quadrats depended on the length of transects (related to pond size) and covered the different meso-habitats. The majority of specimens were identified directly in the field, although some were taken to the laboratory in plastic bags for more detailed inspection and confirmation of identification. Plants were collected by hand or by using a grapnel or garden rake at deeper spots.

All macrophytes were determined to species level, except for *Callitriche*, *Carex* (Linnaeus, 1753), *Glyceria* (Brown, 1810) and *Nitella* (Agardh, 1824), where genus-level identifications were used. The dataset provides information on the presence or absence of each taxon in each pond studied.

Statistical analysis

Macrophyte taxon richness was used as a measure of plant community diversity. Local richness (alpha diversity) was defined as the total number of taxa within an individual pond. Since the macrophyte communities in the Dombes region were assessed using quadrats because of the large pond size, local richness was estimated for each pond separately using a Jackknife extrapolation index, following recommendations made by Soukainen & Cardoso (2022) and Vanacker et al. (2016). This index (S_{Jackk}) was calculated based on the total number of species observed (S_0), the number of species returned only once (f_1), and the number of quadrats made (N).

$$S_{Jackk} = S_0 + f_1 * \frac{N}{N-1}$$

Jackknife extrapolation was not done for the ponds in Midden-Limburg because the entire pond surface has been surveyed until no additional species could be found.

We tested for significant differences in local richness between fish stock management types within each region using two separate Kruskal–Wallis

non-parametric test and Dunn post hoc tests for pairwise comparisons of management types within region.

Differences in community composition between fish stock management types and regions were investigated using a permutation multivariate analysis of variance (PERMANOVA, 'adonis2' function of 'vegan' package, 99,999 permutations) (Anderson, 2017) based on Sørensen distances. We chose Sørensen distances to focus on presence/absence data (Sørensen, 1948; Koleff et al., 2003) and because it can be partitioned into components of nestedness (BetaSNE) and spatial turnover (BetaSIM) (Baselga & Orme, 2012). Sørensen dissimilarity (distance matrix) was partitioned into components of turnover and nestedness using the 'beta.pair' function from the 'betapart' package (Baselga & Orme, 2012), and we subsequently tested with PERMANOVA whether differences in community composition between fish stock management types and regions reflect patterns of nestedness and turnover.

A complementary analysis of multivariate dispersion ('betadisper' function of the 'vegan' package; Oksanen, 2022) was used to test for significant differences in community dispersion (e.g., compositional variation as the average distance of each community to the centroid) among ponds between fish stock management types (i.e., centroids calculated based on the average community composition in each fish stock management type) (Anderson et al., 2006).

To confirm and improve robustness of the beta diversity partitioning, we investigated for both regions separately to what extent communities in species-poorer ponds formed nested subsets of communities in species-richer ponds, and how this relates to fish stock management type. For this purpose, we sorted the species by pond matrix based on species occurrences and local pond taxon richness. Subsequently, we tested whether this matrix is significantly nested by conducting a NODF analysis ('nestednodf' function in 'vegan package'; Oksanen, 2022) based on overlap and decreasing fill (Almeida-Neto et al., 2008). The significance of the nested pattern was determined by comparing the observed NODF value with those produced by null models ($n = 999$) following the PP algorithm (Ulrich & Gotelli, 2012) using the oecosimu function from the vegan package (Oksanen, 2022). The PP algorithm creates null matrices in which the rows and columns vary randomly, but the average row and column total in the generated matrices match those of the original matrix. This approach is especially suited for relatively small empirical surveys (Matthews et al., 2015). Finally, we formally tested whether patterns of nestedness relate to fish stock management types by testing for systematic differences in site rank scores (pond rank scores) between fish stock management types using Kruskal–Wallis tests following Cerini et al. (2020). The site rank scores in our NODF analyses were allocated in ascending order, with a lower rank score for species-richer sites compared to species-poorer sites.

All statistical analyses were conducted in R with the R Studio software (R Development Core Team, 2024). Graphical representations have been done with the ggplot2 package (Wickham, 2016).

Results

The investigated ponds in both regions had relatively high TN and TP concentrations (Table 2). We observed significant differences between fish stock management types within region for both TN and TP. In Midden-Limburg, and to a lesser extent for the Dombes region, management types with higher fish densities (respectively, IF and EF2) had higher

Table 2 Number of macrophyte taxa and TN/TP concentrations in the set of ponds from each fish stock management type (NF (ML) = No Fish, JF (ML) = Juvenile Fish Farming, EF1 (D) = Extensive Fish Farming 1, EF2 (D) = Extensive Fish Farming 2, IF (ML) = Intensive Fish Farming)

	NF (ML)	JF (ML)	IF (ML)	EF1 (D)	EF2 (D)
Total number of macrophyte taxa	69 (92%)	44 (59%)	22 (30%)	52 (81%)	39 (61%)
TN in $mg.l^{-1}$ (median and standard deviation)	1.10 (0.13)	1.30 (0.73)	2.15 (0.87)	2.72 (1.15)	3.56 (1.02)
TP in $mg.l^{-1}$ (median and standard deviation)	0.059 (0.025)	0.347 (0.855)	0.299 (0.164)	0.200 (0.076)	0.285 (0.084)

The percentage represents the fraction of species present in this group out of the total number of species in the respective studied region. ML and D refer to management types applied in Midden-Limburg and Dombes, respectively

TN and TP concentrations compared to those with lower fish densities (respectively, NF, JF, and EF1) (Kruskal–Wallis tests, TN: $P < 0.05$ and $P = 0.27$; TP: $P = 0.01$ and $P = 0.09$ for, respectively, Midden-Limburg and the Dombes region).

A total of 109 macrophyte taxa were observed over the entire set of 38 investigated ponds. From these, 55 and 54 taxa were classified as hydrophytes and helophytes, respectively. Thirty taxa were shared between both fish pond regions, whereas 34 and 45 taxa were unique to the Dombes and Midden-Limburg fish pond system, respectively. The total regional richness (gamma) was 75 taxa over 21 sites in Midden-Limburg and 64 taxa over 17 sites in the Dombes region.

The four most abundant species that occurred in both study regions and in all pond management types were *Phalaris arundinacea* (Linnaeus, 1753)(in 42% of the studied ponds), *Phragmites australis* (Steudel, 1841)(in 52% of the studied ponds), *Najas marina* (Linnaeus, 1753)(in 52% of the studied ponds), and *Lemna minor* (Linnaeus, 1753)(in 23% of the studied ponds). Ponds without fish (NF) jointly hosted 92% of the species observed in Midden-Limburg, whereas intensive fish farming (IF) contained only 30% of the species observed in this region (Table 2). In the Dombes, extensive management type 1 and 2 contained 81% (EF1) and 61% (EF2) of the species observed in the region, respectively (Table 2).

Macrophyte species richness

Local richness differed between management types within fish pond region. In both regions, pond management types with higher fish densities tended to have lower local macrophyte richness. In Midden-Limburg local taxon richness was significantly lower in ponds used for intensive fish farming (IF) and juvenile fish farming (JF) than in ponds without fish stocking (NF) (median richness 6, 9, and 31, respectively) (Kruskal–Wallis test, $H = 12.18$, 2 df, $P < 0.005$) (Fig. 1). In the Dombes region, local taxon richness in EF2 ponds tended to be lower than in EF1

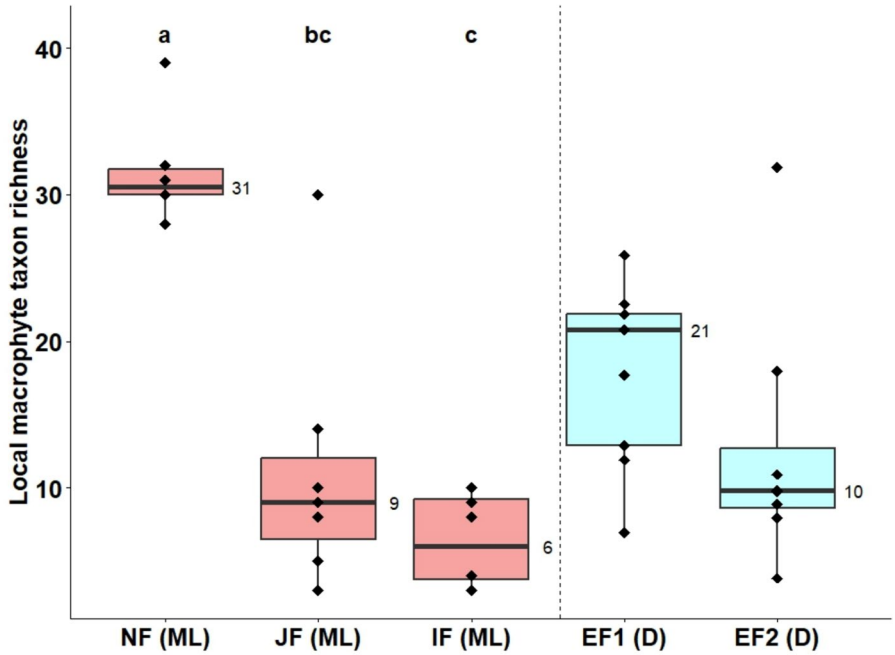

Fig. 1 Local macrophyte taxon richness for the different fish stock management types in both regions. NF = No Fish, JF = Juvenile Fish Farming, IF = Intensive Fish Farming, EF1 = Extensive Fish Farming 1, EF2 = Extensive Fish Farming 2. The lower and upper limits of the boxes correspond to the 1st and 3rd quartiles. Fish stock management types, within each region, that do not share letters are significantly different from each other (Dunn post-hoc test, $P < 0.05$). Management types from the Dombes (D) and Midden-Limburg (ML) region are shown in blue and red boxes, respectively. Values next to the boxplots, corresponding to the full line are medians for each fish stock management type

ponds, although the difference was not statistically significant (Mann–Whitney U test, U = 54, $P > 0.05$). A similar trend could be observed for total richness across ponds within management types, where the highest and lowest gamma richness were observed in the set of NF ponds and IF ponds, respectively (Table 2).

Beta diversity, turnover, and nestedness

PERMANOVA based on the entire set of ponds in both regions revealed that the variation in community composition was significantly determined by region ($R^2 = 0.21$, F = 10.8, $P < 0.005$) and fish stock management type ($R^2 = 0.14$, F = 2.5, $P < 0.005$). The first axis of the PCoA ordination clearly differentiates ponds located in Midden-Limburg from those located in the Dombes region (Fig. 2 panel A). The second axis of the ordination differentiates ponds based on fish stock management types and relates to a difference in fish stock density.

Community dispersion was considerably lower in the NF management type compared to other fish stock management types (ANOVA, F = 3.26, 4 df, $P < 0.05$; average distance to the class centroid of 0.29 for NF versus between 0.43 and 0.52 for other fish stock management types; Fig. 2 panel A).

Beta diversity partitioning considering all ponds in both regions revealed a relatively small turnover fraction (19.5% of compositional variation) and a rather large fraction of nestedness (80.5% of compositional variation) (Fig. 2). The turnover component was significantly determined by region (PERMANOVA $R^2 = 0.35$, F = 18.9, $P < 0.005$) and not by fish stock management type (PERMANOVA $R^2 = 0.03$, F = 0.6, $P > 0.05$) (Fig. 2 panel B). In contrast, the nestedness component was determined by fish stock management type (PERMANOVA $R^2 = 0.84$, F = 14.6, $P < 0.005$) and not by region (PERMANOVA $R^2 = -0.47$, F = − 24.7, $P > 0.05$) (Fig. 2 panel C). The majority of macrophyte taxa observed in ponds in Midden-Limburg were present in NF ponds (Table 2). Fish stock management types with high fish densities (IF) had lower local taxon community richness and hosted mostly generalist helophyte species also found in other fish stock management types, such as *Phragmites australis*,

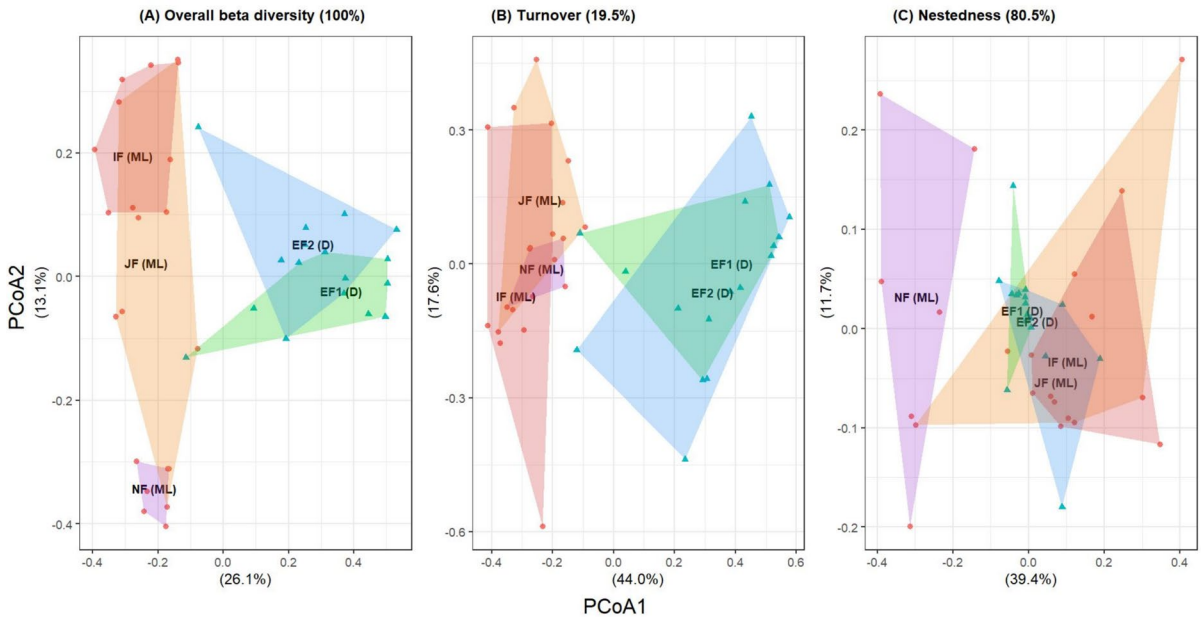

Fig. 2 PCoA ordination plot of overall beta diversity (**A**) and its components of turnover (**B**) and nestedness (**C**) with the individual ponds depicted as different symbols and colors based on the region where they are located (red points for Midden-Limburg and blue triangles for Dombes). Each fish stock management type is represented by a different color. The polygon limits of each type are defined by taking the extreme ponds. Percentages in titles and at axis level correspond to the fraction of turnover and nestedness in the compositional variation and to the part of variation explained by axes 1 and 2, respectively

Phalaris arundinacea (Linnaeus, 1753) and *Typha x glauca* hybrids.

The NODF analysis for both regions separately revealed a significant nested pattern in macrophyte community composition in ponds in Midden-Limburg (Observed NODF index = 47.6, mean null NODF = 28.4, z = 31.12, $P = 0.001$ (Fig. 3 panel A). Nestedness site rank scores of IF and JF ponds were significantly higher compared to those of NF ponds (Kruskal–Wallis test, $P < 0.01$), indicating that species-poorer communities in IF and JF ponds formed nested subsets of those in NF ponds (Fig. 3 panel B). A similar pattern of nestedness was observed in the set of ponds in the Dombes region (Observed NODF index = 27.9, mean null NODF = 22.4, z = 6.8, $P = 0.001$; Fig. 3 panel C), but the site rank scores did not significantly differ between both management types (Kruskal–Wallis test, $P > 0.05$; Fig. 3 panel D).

Discussion

The present study investigates the effect of fish stock management on macrophyte community richness and composition in two large fish pond systems that differ in their overall approach on how to combine fish farming with biodiversity conservation. Our results show that management types with higher fish stock densities were characterized by lower local macrophyte taxon richness and that macrophyte communities in ponds with higher fish density formed nested subsets of species-richer communities in ponds with lower fish density. The latter was especially the case in Midden-Limburg, where the different fish stock management types represent strong differences in fish density (from almost no fish to more than 1200 kg.ha^{-1}). Overall, our analyses reveal that the highest macrophyte richness is observed in ponds without fish stocking, and that ponds with fish farming do not strongly contribute to regional macrophyte richness. Our results suggest that pond management strategies that aim at the implementation of ponds without fish stocking is effective in maintaining high levels of regional macrophyte richness in anthropogenic fish pond regions.

The profound effect of fish stock management on local macrophyte richness in our study likely results largely from differences in fish stock density between management types. Within each of the two fish pond regions, fish stock management types with higher fish densities had systematically lower local macrophyte species richness compared to ponds with lower fish densities. This observation aligns with multiple studies showing that fish can strongly affect macrophyte abundance, community composition, and richness (Zambrano & Hinojosa, 1999; Goldsborough & Wrubleski, 2001; Badiou et al., 2011; Badiou & Goldsborough, 2015; Francová et al., 2019a, b). The negative effect of fish density on macrophyte richness in our study likely results from a combination of direct and indirect effects. Via trophic cascades, predation by fish on zooplankton can have profound indirect effects on the biomass and productivity of primary producers (Carpenter et al., 1985; Carpenter & Kitchell, 1996; Jones & Sayer, 2003). Benthic foraging can also promote internal eutrophication (Breukelaar et al., 1994; Weber & Brown, 2009; Kloskowski, 2011; Badiou & Goldsborough, 2015). Both factors reduce light availability in the water column and alter nutrient dynamics, which detrimentally affects macrophyte coverage, community composition, and richness through competition for light and resources (Scheffer, 2004; Bakker et al., 2013). Badiou & Goldsborough (2015) showed that common carp can mediate a transition from a clear macrophyte dominated state to a turbid state dominated by phytoplankton and low macrophyte species richness at fish biomasses below 600 kg.ha^{-1} (Badiou & Goldsborough, 2015). However, the critical fish density at which macrophytes are expected to disappear is likely context-dependent as it will vary with multiple factors, including pond morphology, size, nutrient status, and other environmental conditions. In addition to indirect effects, fish can also have important direct effects on macrophytes by consumption, as well as by uprooting and damaging vegetation during foraging in sediments (Zambrano & Hinojosa, 1999; Badiou & Goldsborough, 2015). Rather than being solely driven by fish density, the effect of fish on macrophytes likely also depends on the composition of the fish community. In particular, benthic species, such as common carp that dominated the fish communities in the ponds studied by us, are known to have a profound negative impact on water transparency and the establishment of macrophytes (Badiou et al., 2011; Badiou & Goldsborough, 2015; Francová et al., 2019a, b). In addition to fish

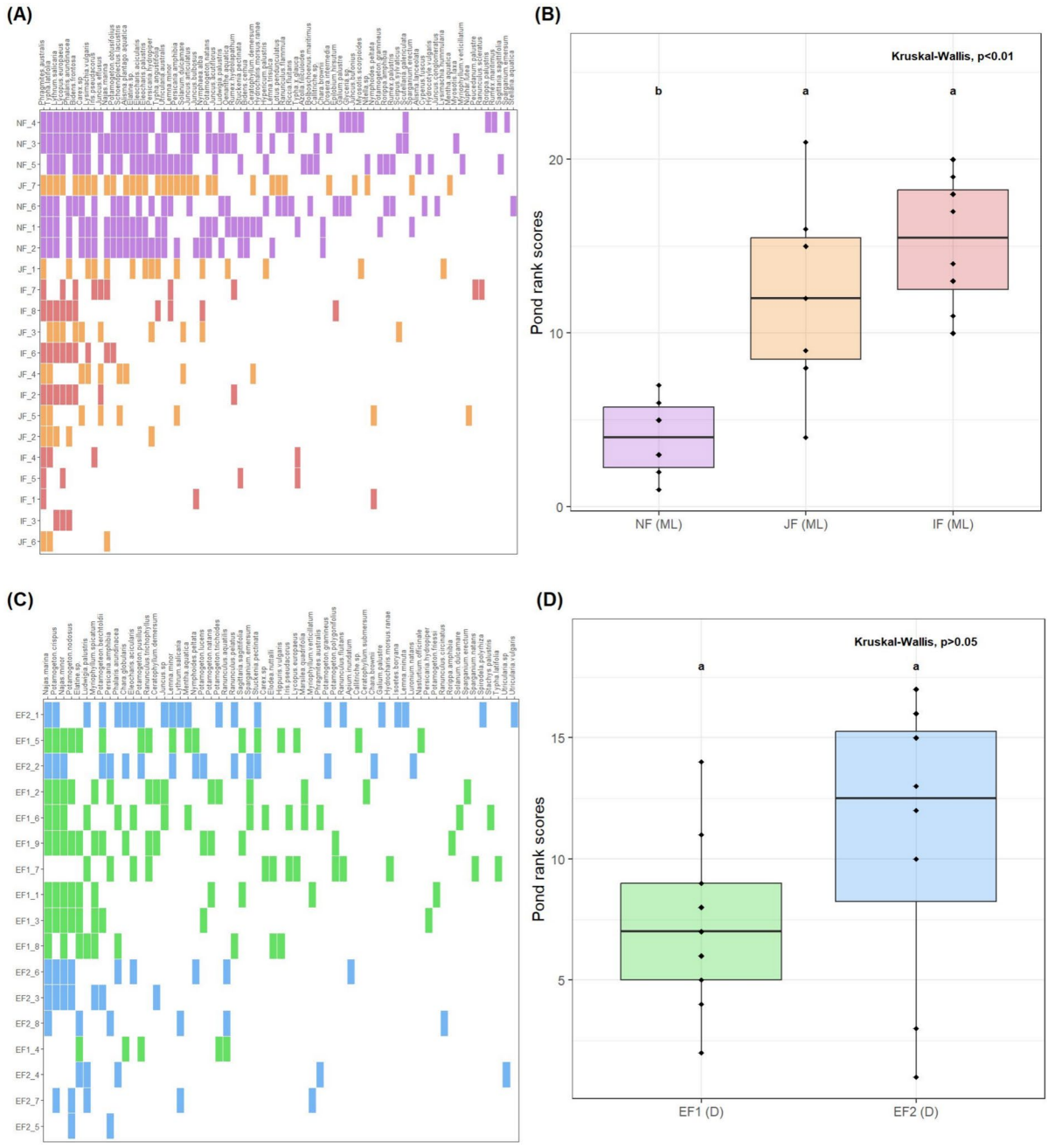

Fig. 3 Incidence plot and comparison of rank scores for ponds from the Midden-Limburg (**A** and **B**) and from the Dombes region (**C** and **D**). The rows and columns represent ponds and macrophyte taxa, respectively. Colored cells show the occurrences of individual taxa in the corresponding pond, and blank cells indicate that the taxon was not found in that pond. The boxplots (**B** and **D**) show the pond rank scores for the different fish stock management types. Fish stock management types that do not share letters are significantly different from each other (Dunn post hoc test, $p < 0.05$)

stock density, the use of additional feeds to enhance fish production might also have played a role on the observed differences in local richness between fish stock management types. Indeed, fish farming in Midden-Limburg and the Dombes region involves additional feeding of fish, which can increase nutrient concentrations in the water column and can thus affect macrophyte community characteristics. The

use of additional fish feed in the ponds studied by us might also explain the observed differences in nutrient concentrations between fish stock management types. This seems especially true in Midden-Limburg, where TN and TP concentrations in ponds without fish stocking (and thus without feeding) were considerably lower compared to ponds used for fish farming (JF and IF ponds), even though all ponds in the region obtain water from the same source stream.

The observed macrophyte species richness over the entire set of ponds in our study is well in line with observations from earlier studies in other European fish pond regions. For example, Francová et al. (2019b) recorded 27 macrophytes species in fish ponds in the Czech Republic that were characterized by fish densities around 1300 kg.ha^{-1}. Local macrophyte species richness in these ponds varied from 0 to 5, similar to our observations in ponds with the highest fish stock densities (IF). They also recorded from 3 to 20 macrophyte species in nursery ponds, with a somewhat lower fish density of around 800 kg.ha^{-1} (Francová et al., 2019b) Our findings are also in line with previous studies on other sets of fish ponds in the Dombes region (Broyer & Curtet, 2012; Wezel et al., 2014). Overall, the macrophyte species richness observed in fish pond regions is relatively high compared to findings for other types of ponds across Europe (Oertli et al., 2002; Søndergaard et al., 2005; Edvardsen & Okland, 2006; Davies et al., 2008). This observation likely stems from the active management of fish ponds with regular periodic drainage to harvest fish. Indeed, pond drainage has been shown to stimulate the development of aquatic vegetation and can stabilize the clear water state, especially in eutrophic systems (Lemmens et al., 2015). However, pond drainage can be ruled out as a factor determining variation in local macrophyte richness between management types in our study since all investigated ponds have been subjected to drainage for fish harvest every year. In the Dombes area, ponds are typically let dry for an entire growth season after 4 to 5 years of fish farming in addition to a short annual drainage to harvest fish. This particular practice is not applied in fish ponds from Midden-Limburg. Previous studies have shown that this drying-out for an entire production season significantly affects macrophyte richness in subsequent years (Fontanilles et al., 2023; Girard et al., 2023).

The ponds studied also hosted several rare or endangered plant species, such as *Marsilea quadrifolia* (Linnaeus, 1753), classified as vulnerable on the European IUCN list (Christenhusz et al., 2017; Corli et al., 2021), which was found in two studied ponds in the Dombes region. The presence of rare or endangered species in fish ponds, which are often eutrophic or even hypereutrophic, is in line with earlier observations (Robin et al., 2014; Wezel et al., 2014).

While our results are generally in line with earlier studies on macrophytes in fish pond regions, the observed low macrophyte richness in ponds used for juvenile fish farming in Midden-Limburg contradicts a previous study in the same region (Lemmens et al., 2013), which found that local richness in JF ponds was comparable to that in ponds without fish stocking (NF). Our study does not allow us to pinpoint the exact mechanism underlying this important difference, but one possible explanation is the intensification of juvenile fish farming over the past 10 years through the use of additional fish feed and the associated increase in nutrient concentrations. Alternatively, the JF ponds included in our study may have been used for intensive carp farming (IF) in the year prior to our sampling, which could have left a legacy effect on the current macrophyte community.

Our results show that variation in macrophyte community composition is strongly determined by fish stock management and by region. While differences between both regions largely correspond to patterns of community turnover, fish stock management and associated differences in fish stock densities within regions reflect a clear pattern of nestedness, especially in the Midden-Limburg pond system.

A key observation of our study is, however, that fish stock management types with higher fish stock densities form nested subsets of species-richer communities in ponds with lower fish densities. This was especially the case in Midden-Limburg, where ponds used for intensive fish farming, only hosted common, generalist species, most of which are emergent such as *Phragmites australis*, *Phalaris arundinacea,* and *Typha x glauca*. These emergent plant species grow mainly on the edges of ponds and are therefore less affected by turbidity and direct predation by fish (Oertli & Frossard, 2013). In ponds with high fish density we also found species with floating leaves, such as Nuphar lutea. Developing floating leaves is a strategy of aquatic plants enabling them

to capture light for photosynthesis without being affected by turbidity (Sculthorpe, 1967). Similarly, *Lemna minor* was common in ponds irrespective of fish management type. It is the most common duckweed species (Oertli & Frossard, 2013). Like other species of the *Lemna* genus, it readily colonizes environments with high nitrate levels and rich in organic matter (Francová et al., 2019b). It has a fast population growth rate when temperatures permit. This can be an efficient strategy to cope with fish predation (McNaughton, 1984).

In contrast, several submerged plant species, such as *Ceratophyllum demersum*, *Potamogeton gramineus*, *Myriophyllum verticillatum* (Linnaeus, 1753), and amphibious species, such as *Ludwigia palustris* (Elliot, 1817), only occurred in NF. While the overall trend for nestedness is very similar in the Dombes region, the pattern was less profound and non-significant, which likely is the result of the smaller difference in fish stock densities between both management types (EF1 and EF2). Interestingly, our results are in line with studies on terrestrial agricultural landscapes, where intensification of agricultural practices promotes the dominance of generalist species (Buhk et al., 2017) and a loss of species at landscape scale (Benton et al., 2003).

The observed community turnover between both regions likely results from several factors, including differences in regional species pool, pond morphology and size, or nutrient concentrations. Although many species are widely distributed, some species only occur in one region (Chambers et al., 2008). Ponds in the Dombes region are considerably larger than those in Midden-Limburg, which can affect environmental conditions relevant to macrophyte establishment and community composition, including wind exposure, wave-induced disturbance, sediment resuspension, and associated fauna. Our study does not allow us to identify the mechanism for the observed taxon turnover between regions.

Our findings have important implications for biodiversity conservation in large anthropogenic fish pond regions. Pond management types with higher fish density had lower local taxon richness than those with lower fish density, following a nested community structure in which species-poorer communities form subsets of species-richer communities. This pattern indicates that management types without fish stocking contribute more substantially to regional diversity, whereas the contribution of management types with fish stocking practices appears limited in terms of regional macrophyte richness. However, prolonged absence of dense fish stocking or restauration actions, to improve biodiversity, in shallow, eutrophic ponds, can promote the development of fast-growing eutrophic species or extensive emergent vegetation, typically dominated by E*lodea*, *Ceratophyllum*, *Typha* or *Phragmites*, which over time may undermine the establishment of species-rich submerged macrophyte communities (Hilt et al., 2018). Periodic cutting or removal of dense emergent vegetation may therefore be necessary to sustain high macrophyte diversity and maximize conservation value. In certain cases, the occasional introduction of high densities of fish, particularly common carp, may be employed to control dense emergent vegetation; however, such interventions should be infrequent, followed by a return to fishless management, and avoided in ponds serving as critical habitat for taxa susceptible to fish predation or hosting regionally rare and sensitive species.

Our results suggest that reconciling biodiversity conservation with fish farming at the landscape scale would benefit more from a land-sparing approach (Green et al., 2005), in which a subset of ponds in the region is managed without fish stocking, rather than a land-sharing/agroecological approach (HLPE, 2019), where all ponds are used for some form of extensive fish farming with intermediate fish densities. This approach is in line with the conclusions of a large number of studies on terrestrial agricultural schemes (Green et al., 2005; Ewers et al., 2009; Phalan et al., 2011; Law & Wilson, 2015; Kremen, 2015; Balmford et al., 2019). Nevertheless, there are risks associated with a land-sparing system. Ponds for intensive fish production are often characterized by intensive phytoplankton blooms, and more susceptible to cyanobacterial blooms (Lemmens et al., 2013). These blooms can be detrimental in many ways, not only to biodiversity and fish production (Havens, 2008), but also to human health (Kleinteich et al., 2012; Codd et al., 2016) and the recreational and many other services that ponds can provide (Kleinteich et al. 2012; Codd et al., 2016).

A limitation of our study is the focus on macrophytes. This taxa play a key role in pond ecosystem functioning and structure (Declerck et al. 2005), and is generally considered highly beneficial for the biodiversity of multiple other aquatic organism groups,

including amphibians, macroinvertebrates, zooplankton, and birds (Jeppesen et al., 1997; Scheffer, 2004; Folke et al., 2004). Diversification of fish farming practices, in addition to maintain a substantial number of ponds without fish stocking, may further enhance regional diversity across other taxonomic groups, including, for example, piscivorous birds (Kloskowski & Nieoczym, 2015; Broyer et al., 2018). Such approach resembles proposed schemes in terrestrial settings where land sharing and sparing are combined to promote habitat heterogeneity at the landscape scale (Benton et al., 2003; Butsic & Kuemmerle, 2015; Kremen, 2015).

In conclusion, our study demonstrates that pond and shallow lake management and associated fish stock density profoundly affect local macrophyte taxon richness. Ponds, managed with an annual drain, without fish stocking contributed most to regional macrophyte diversity. This management of ponds without fish can be linked to biomanipulation strategies, which are also used to reduce phytoplankton biomass and thus enable the development of macrophytes (Chen et al., 2025; Ren et al., 2022). The management of benthic fish allows reducing its indirect and direct effects on macrophytes (Li et al., 2023). Biodiversity conservation programs in anthropogenic fish pond systems may benefit from a land-sparing approach where a substantial number of ponds is actively managed without fish stocking to support biodiversity. Future research should explore whether this pattern holds true for other taxonomic groups and should adopt multi-disciplinary approaches that consider a broad range of ecosystem services and nature's contribution to people (NCP).

Acknowledgements We thank the fish pond owners and managers for providing access to their ponds and allowing us to sample them. We further thank the teams at Isara and KU Leuven for help with data collection. This research received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 869296 – The PONDERFUL Project. LDM also acknowledges a start-up budget from IGB, Biodiversa+ project TRANSPONDER, and KU Leuven research fund project C16/2023/003.

Author contributions Conceptualization: LG, PL, LDM, JR. Developing methods: LG, PL, LDM, JR, SR. Data analysis: LG, VT. Preparation of figures and tables: LG, VT, PL. Conducting the research, data interpretation, writing: LG, JR, SR, VT, RW, LDM, AW, PL.

Funding The funding was provided by Horizon 2020 Framework Programme.

Data availability Data are available from the authors upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by-nc-nd/4.0/.

References

Adamek, Z., M. Mossmer, & C. Bauer, 2015. Current issues and principles of common carp (Cyprinus Carpio) organic pond farming In Europe. An Overview.

Almeida-Neto, M., P. Guimarães, P. R. Guimarães, R. D. Loyola & W. Ulrich, 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117: 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x.

Andersen, E., D. Baldock, H. Bennett, G. Beaufoy, E. Bignal, F. Brouwer, B. Elbersen, G. Eiden, F. Godeschalk, G. Jones, D. McCracken, W. Nieuwenhuizen, M. van Eupen, S. Hennekens, & G. Zervas, 2004. Developing a high nature value farming area indicator. p. 75.

Anderson, M. J., K. E. Ellingsen & B. H. McArdle, 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9: 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x.

Anderson, M. J., 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). In Kenett, R. S., N. T. Longford, W. W. Piegorsch, & F. Ruggeri (eds) Wiley StatsRef: Statistics Reference Online. Wiley. pp. 1–15.

Arthaud, F., D. Vallod, J. Robin, A. Wezel & G. Bornette, 2013. Short-term succession of aquatic plant species richness along ecosystem productivity and dispersal gradients in shallow lakes. Journal of Vegetation Science

24: 148–156. https://doi.org/10.1111/j.1654-1103.2012.01436.x.
Aubin, J., J. Robin, A. Wezel, & M. Thomas, 2017. Agroecological management in fish pond systems. In Agroecological Practices for Sustainable Agriculture : Pinciples, Applications, and Making the Transition. World Scientific Europe Ltd.
Avocat, C., 1975. La Dombes, milieu naturel ou milieu en équilibre ? Introduction à une éco-géographie de l'espace dombiste. Revue De Géographie De Lyon 50: 35–58. https://doi.org/10.3406/geoca.1975.1666.
Badiou, P., L. G. Goldsborough, & D. Wrubleski, 2011. Impacts of the Common Carp on freshwater ecosystems: a review.
Badiou, P. H. J. & L. G. Goldsborough, 2015. Ecological impacts of an exotic benthivorous fish, the common carp (Cyprinus carpio L.), on water quality, sedimentation, and submerged macrophyte biomass in wetland mesocosms. Hydrobiologia 755: 107–121. https://doi.org/10.1007/s10750-015-2220-6.
Bakker, E. S., J. M. Sarneel, R. D. Gulati, Z. Liu & E. Van Donk, 2013. Restoring macrophyte diversity in shallow temperate lakes: biotic versus abiotic constraints. Hydrobiologia 710: 23–37. https://doi.org/10.1007/s10750-012-1142-9.
Balmford, B., R. E. Green, M. Onial, B. Phalan & A. Balmford, 2019. How imperfect can land sparing be before land sharing is more favourable for wild species? Journal of Applied Ecology 56: 73–84. https://doi.org/10.1111/1365-2664.13282.
Baselga, A. & C. D. L. Orme, 2012. betapart: an R package for the study of beta diversity. Methods in Ecology and Evolution 3: 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x.
Beillouin, D., T. Ben-Ari, E. Malézieux, V. Seufert & D. Makowski, 2021. Positive but variable effects of crop diversification on biodiversity and ecosystem services. Global Change Biology 27: 4697–4710. https://doi.org/10.1111/gcb.15747.
Benton, T. G., J. A. Vickery & J. D. Wilson, 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18: 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9.
Bernard, A., & P. Lebreton, 2007. Les oiseaux de la Dombes : une mise à jour.
Breukelaar, A. W., E. H. R. R. Lammens, J. G. P. K. Breteler & I. Tatrai, 1994. Effects of benthivorous bream (Abramis brama) and carp (Cyprinus carpio) on sediment resuspension and concentrations of nutrients and chlorophyll a. Freshwater Biology 32: 113–121. https://doi.org/10.1111/j.1365-2427.1994.tb00871.x.
Broyer, J. & L. Curtet, 2012. Biodiversity and fish farming intensification in French fishpond systems. Hydrobiologia 694: 205–218. https://doi.org/10.1007/s10750-012-1162-5.
Broyer, J., S. Richier, C. Renaud, B. Riotton-Roux & J.-Y. Vade, 2018. Consequences of fish farming demise for bird and odonate species richness in french fishponds. Revue D'écologie (La Terre Et La Vie) 73: 462–473. https://doi.org/10.3406/revec.2018.1950.
Buhk, C., M. Alt, M. J. Steinbauer, C. Beierkuhnlein, S. D. Warren & A. Jentsch, 2017. Homogenizing and diversifying effects of intensive agricultural land-use on plant species beta diversity in Central Europe — A call to adapt our conservation measures. Science of the Total Environment 576: 225–233. https://doi.org/10.1016/j.scitotenv.2016.10.106.
Burny, J., 1999. Bijdrage tot de historische ecologie van de Limburgse Kempen (1910-1950): tweehonderd gesprekken samengevat. Natuurhistorisch Genootschap in Limburg, Maastricht.
Butsic, V. & T. Kuemmerle, 2015. Using optimization methods to align food production and biodiversity conservation beyond land sharing and land sparing. Ecological Applications 25: 589–595. https://doi.org/10.1890/14-1927.1.
Carpenter, S. R. & D. M. Lodge, 1986. Effects of submersed macrophytes on ecosystem processes. Aquatic Botany 26: 341–370. https://doi.org/10.1016/0304-3770(86)90031-8.
CBD (Convention on Biological Diversity), 2014. Global Biodiversity Outlook 4. Montréal, Canada. p. 155.
Cerini, F., M. A. Bologna & L. Vignoli, 2020. Nestedness-patterns of Odonata assemblages in artificial and natural aquatic habitats reveal the potential role of drinking troughs for aquatic insect conservation. Journal of Insect Conservation 24: 421–429. https://doi.org/10.1007/s10841-020-00234-2.
Chambers, P. A., P. Lacoul, K. J. Murphy & S. M. Thomaz, 2008. Global diversity of aquatic macrophytes in freshwater. Hydrobiologia 595: 9–26. https://doi.org/10.1007/s10750-007-9154-6.
Chen, T., S. Feng, Y. Xie, K. Wang, X. Wang, J. Zhao & J. Zhang, 2025. Ecological trade-offs in shallow lake restoration: Assessing ecosystem responses to aquatic vegetation restoration and biomanipulation strategies against the background of fishing ban. Ecological Indicators 178: 113932. https://doi.org/10.1016/j.ecolind.2025.113932.
Christenhusz, M. J. M., M. F. Fay & M. W. Chase, 2017. Plants of the world: an illustrated encyclopedia of vascular plants, The University of Chicago Press, Richmond, Kew Publishing, Royal Botanic Gardens, Kew:
Codd, G. A., J. Meriluoto & J. S. Metcalf, 2016. Introduction: cyanobacteria, cyanotoxins, their human impact, and risk management. In Meriluoto, J., L. Spoof & G. A. Codd (eds), Handbook of Cyanobacterial Monitoring and Cyanotoxin Analysis. Wiley, New Jersey.
Corli, A., G. Rossi, S. Orsenigo & T. Abeli, 2021. Biological flora of central Europe: Marsilea quadrifolia L. Perspectives in Plant Ecology, Evolution and Systematics 53: 125641. https://doi.org/10.1016/j.ppees.2021.125641.
Davies, B., J. Biggs, P. Williams, M. Whitfield, P. Nicolet, D. Sear, S. Bray & S. Maund, 2008. 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.
Declerck, S., J. Vandekerkhove, L. Johansson, K. Muylaert, J. M. Conde-Porcuna, K. Van Der Gucht, C. Pérez-Martínez, T. Lauridsen, K. Schwenk, G. Zwart, W. Rommens, J. López-Ramos, E. Jeppesen, W. Vyverman, L. Brendonck & L. De Meester, 2005. Multi-group biodiversity in shallow lakes along gradients of phosphorus

and water plant cover. Ecology 86: 1905–1915. https://doi.org/10.1890/04-0373.

Edvardsen, A. & R. H. Økland, 2006. Variation in plant species richness in and adjacent to 64 ponds in SE Norwegian agricultural landscapes. Aquatic Botany 85: 79–91. https://doi.org/10.1016/j.aquabot.2006.01.014.

Ekroos, J., O. Olsson, M. Rundlöf, F. Wätzold & H. G. Smith, 2014. Optimizing agri-environment schemes for biodiversity, ecosystem services or both? Biological Conservation 172: 65–71. https://doi.org/10.1016/j.biocon.2014.02.013.

Eriksson, O., 2021. The importance of traditional agricultural landscapes for preventing species extinctions. Biodiversity and Conservation 30: 1341–1357. https://doi.org/10.1007/s10531-021-02145-3.

Evans, D., 2012. Building the European Union's Natura 2000 network. Nature Conservation 1: 11–26. https://doi.org/10.3897/natureconservation.1.1808.

Ewers, R. M., J. P. W. Scharlemann, A. Balmford & R. E. Green, 2009. Do increases in agricultural yield spare land for nature? Global Change Biology 15: 1716–1726. https://doi.org/10.1111/j.1365-2486.2009.01849.x.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson & C. S. Holling, 2004. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. Annual Review of Ecology, Evolution, and Systematics 35: 557–581. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711.

Fontanilles, A., J. Robin, S. Rouifed, M. Guerin, M. Vanacker, F. Arthaud, & A. Wezel, 2023. Disturbance and resilience of aquatic plant communities in fish ponds after temporary dry periods.

Francová, K., K. Šumberová, G. A. Janauer & Z. Adámek, 2019a. Effects of fish farming on macrophytes in temperate carp ponds. Aquaculture International 27: 413–436. https://doi.org/10.1007/s10499-018-0331-6.

Francová, K., K. Šumberová, A. Kučerová, M. Čtvrtlíková, M. Šorf, J. Borovec, B. Drozd, G. A. Janauer & J. Vrba, 2019b. Macrophyte assemblages in fishponds under different fish farming management. Aquatic Botany 159: 103131. https://doi.org/10.1016/j.aquabot.2019.103131.

Francová, K., K. Šumberová, A. Kučerová, M. Šorf, S. Grill, N. Exler & J. Vrba, 2021. Drivers of plant species composition of ecotonal vegetation in two fishpond management types. Wetlands Ecology and Management 29: 93–110. https://doi.org/10.1007/s11273-020-09770-9.

Girard, L., A. Wezel & J. Robin, 2023. Drying out fish ponds, for an entire growth season, as an agroecological practice: maintaining primary producers for fish production and biodiversity conservation. Open Research Europe. https://doi.org/10.12688/openreseurope.16363.1.

Goldsborough, L. G., & D. Wrubleski, 2001. The decline of Delta Marsh, an internationally significant wetland in south-central Manitoba.

Green, R. E., S. J. Cornell, J. P. W. Scharlemann & A. Balmford, 2005. Farming and the fate of wild nature. Science 307: 550–555. https://doi.org/10.1126/science.1106049.

Hansson, L.-A., A. Nicolle, J. Brodersen, P. Romare, P. Anders Nilsson, C. Brönmark & C. Skov, 2007. Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics. Limnology and Oceanography 52: 696–706. https://doi.org/10.4319/lo.2007.52.2.0696.

Havens, K. E., 2008. Cyanobacteria blooms: effects on aquatic ecosystems. 15.

Hilt, S., M. M. Alirangues Nuñez, E. S. Bakker, I. Blindow, T. A. Davidson, M. Gillefalk, L.-A. Hansson, J. H. Janse, A. B. G. Janssen, E. Jeppesen, T. Kabus, A. Kelly, J. Köhler, T. L. Lauridsen, W. M. Mooij, R. Noordhuis, G. Phillips, J. Rücker, H.-H. Schuster, M. Søndergaard, S. Teurlincx, K. Van De Weyer, E. Van Donk, A. Waterstraat, N. Willby & C. D. Sayer, 2018. Response of submerged macrophyte communities to external and internal restoration measures in north temperate shallow lakes. Frontiers in Plant Science 9: 194. https://doi.org/10.3389/fpls.2018.00194.

HLPE, 2019. HLPE Report #14 - Agroecological and other innovative approaches for sustainable agriculture and food systems that enhance food security and nutrition. 163.

Horvath, L., G. Tamas & C. Seagrave, 2002. Carp and Pond Fish Culture, Wiley:

Jeppesen, E., J. P. Jensen, M. Sondergaard, T. Lauridsen, L. J. Pedersen, & L. Jensen, 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. In Shallow Lakes '95.

Jones, J. I., & C. D. Sayer, 2003. Does the fish-invertebrates-periphyton cascade precipitate plant loss in shallow lakes? Ecology 84: 2155–2167. https://doi.org/10.1890/02-0422.

Jongman, R. H. G., 2002. Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. Landscape and Urban Planning 58: 211–221. https://doi.org/10.1016/S0169-2046(01)00222-5.

Kleinteich, J., S. A. Wood, F. C. Küpper, A. Camacho, A. Quesada, T. Frickey & D. R. Dietrich, 2012. Temperature-related changes in polar cyanobacterial mat diversity and toxin production. Nature Climate Change 2: 356–360. https://doi.org/10.1038/nclimate1418.

Kloskowski, J., 2011. Impact of common carp Cyprinus carpio on aquatic communities: direct trophic effects versus habitat deterioration. Fundamental and Applied Limnology 178: 245–255. https://doi.org/10.1127/1863-9135/2011/0178-0245.

Kloskowski, J., & M. Nieoczym, 2015. Management practices to enhance wildlife diversity of man-made fish ponds: the importance of the hydroperiod. Knowledge and Management of Aquatic Ecosystems : 34. https://doi.org/10.1051/kmae/2015032.

Koleff, P., K. J. Gaston & J. J. Lennon, 2003. Measuring beta diversity for presence–absence data. Journal of Animal Ecology 72: 367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x.

Kremen, C., 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation: reframing the land-sparing/land-sharing debate. Annals of the New York Academy of Sciences 1355: 52–76. https://doi.org/10.1111/nyas.12845.

Law, E. A. & K. A. Wilson, 2015. Providing context for the land-sharing and land-sparing debate: influence of context on land-use preferences. Conservation Letters 8: 404–413. https://doi.org/10.1111/conl.12168.

Lemmens, P., J. Mergeay, T. De Bie, J. Van Wichelen, L. De Meester & S. A. J. Declerck, 2013. How to maximally support local and regional biodiversity in applied conservation? Insights from Pond Management. Plos ONE 8: e72538. https://doi.org/10.1371/journal.pone.0072538.

Lemmens, P., J. Mergeay, J. Van Wichelen, L. De Meester & S. A. J. Declerck, 2015. The impact of conservation management on the community composition of multiple organism groups in eutrophic interconnected man-made ponds. PLOS ONE 10: e0139371. https://doi.org/10.1371/journal.pone.0139371.

Li, F., Z. Zuo, H. Zhao, W. Yu, H. Yu, D. Yu & C. Liu, 2023. Adaptive responses and transgenerational plasticity of a submerged plant to benthivorous fish disturbance. Ecology and Evolution 13(ece3): 10398. https://doi.org/10.1002/ece3.10398.

Lichtenberg, E. M., C. M. Kennedy, C. Kremen, P. Batáry, F. Berendse, R. Bommarco, N. A. Bosque-Pérez, L. G. Carvalheiro, W. E. Snyder, N. M. Williams, R. Winfree, B. K. Klatt, S. Åström, F. Benjamin, C. Brittain, R. Chaplin-Kramer, Y. Clough, B. Danforth, T. Diekötter, S. D. Eigenbrode, J. Ekroos, E. Elle, B. M. Freitas, Y. Fukuda, H. R. Gaines-Day, H. Grab, C. Gratton, A. Holzschuh, R. Isaacs, M. Isaia, S. Jha, D. Jonason, V. P. Jones, A. Klein, J. Krauss, D. K. Letourneau, S. Macfadyen, R. E. Mallinger, E. A. Martin, E. Martinez, J. Memmott, L. Morandin, L. Neame, M. Otieno, M. G. Park, L. Pfiffner, M. J. O. Pocock, C. Ponce, S. G. Potts, K. Poveda, M. Ramos, J. A. Rosenheim, M. Rundlöf, H. Sardiñas, M. E. Saunders, N. L. Schon, A. R. Sciligo, C. S. Sidhu, I. Steffan-Dewenter, T. Tscharntke, M. Veselý, W. W. Weisser, J. K. Wilson & D. W. Crowder, 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Global Change Biology 23: 4946–4957. https://doi.org/10.1111/gcb.13714.

Massaloux, D., B. Sarrazin, A. Roume, V. Tolon & A. Wezel, 2020a. Complementarity of grasslands and cereal fields ensures carabid regional diversity in French farmlands. Biodiversity and Conservation 29: 2861–2882. https://doi.org/10.1007/s10531-020-02002-9.

Massaloux, D., B. Sarrazin, A. Roume, V. Tolon & A. Wezel, 2020b. Landscape diversity and field border density enhance carabid diversity in adjacent grasslands and cereal fields. Landscape Ecology 35: 1857–1873. https://doi.org/10.1007/s10980-020-01063-z.

Matthews, T. J., H. E. W. Cottee-Jones & R. J. Whittaker, 2015. Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets. Diversity and Distributions 21: 392–404. https://doi.org/10.1111/ddi.12298.

McNaughton, S. J., 1984. Grazing lawns: animals in herds, plant form, and coevolution. The American Naturalist 124: 863–886. https://doi.org/10.1086/284321.

Mueller, A. & J. Maes, 2015. Arguments for biodiversity conservation in Natura 2000 sites: an analysis based on LIFE projects. Nature Conservation 12: 1–26. https://doi.org/10.3897/natureconservation.12.4848.

Oertli, B., D. A. Joye, E. Castella, R. Juge, D. Cambin & J.-B. Lachavanne, 2002. Does size matter? The relationship between pond area and biodiversity. Biological Conservation 104: 59–70. https://doi.org/10.1016/S0006-3207(01)00154-9.

Oertli, B., & P.-A. Frossard, 2013. Mares et étangs : Ecologie, conservation, gestion, valorisation. PPUR Presses polytechniques.

Oksanen, J., 2022. Vegan: ecological diversity.

Phalan, B., M. Onial, A. Balmford & R. E. Green, 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science 333: 1289–1291. https://doi.org/10.1126/science.1208742.

Priyadarshana, T. S., E. A. Martin, C. Sirami, B. A. Woodcock, E. Goodale, C. Martínez-Núñez, M. Lee, E. Pagani-Núñez, C. A. Raderschall, L. Brotons, A. Rege, A. Ouin, T. Tscharntke & E. M. Slade, 2024. Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: a global review and meta-analysis. Ecology Letters 27: e14412. https://doi.org/10.1111/ele.14412.

Queiroz, C., R. Beilin, C. Folke & R. Lindborg, 2014. Farmland abandonment: threat or opportunity for biodiversity conservation? A global review. Frontiers in Ecology and the Environment 12: 288–296. https://doi.org/10.1890/120348.

Ren, W., Z. Wen, Y. Cao, H. Wang, C. Yuan, X. Zhang, L. Ni, P. Xie, T. Cao, K. Li & E. Jeppesen, 2022. Cascading effects of benthic fish impede reinstatement of clear water conditions in lakes: a mesocosm study. Journal of Environmental Management 301: 113898. https://doi.org/10.1016/j.jenvman.2021.113898.

Richardson, D. C., M. A. Holgerson, M. J. Farragher, K. K. Hoffman, K. B. S. King, M. B. Alfonso, M. R. Andersen, K. S. Cheruveil, K. A. Coleman, M. J. Farruggia & R. L. Fernandez, K. L. Hondula, G. A. López Moreira Mazacotte, K. Paul, B. L. Peierls, J. S. Rabaey, S. Sadro, M. L. Sánchez, R. L. Smyth, & J. N. Sweetman, 2022. A functional definition to distinguish ponds from lakes and wetlands Abstract Scientific Reports 12(1) https://doi.org/10.1038/s41598-022-14569-0.

Robin, J., A. Wezel, G. Bornette, F. Arthaud, S. Angélibert, V. Rosset & B. Oertli, 2014. Biodiversity in eutrophicated shallow lakes: determination of tipping points and tools for monitoring. Hydrobiologia 723: 63–75. https://doi.org/10.1007/s10750-013-1678-3.

Rockström, J., W. Steffen, K. Noone, Å. Persson, F. S. I. Chapin, E. Lambin, T. M. Lenton, M. Scheffer, C. Folke, H. J. Schellnhuber, B. Nykvist, C. A. De Wit, T. Hughes, S. Van Der Leeuw, H. Rodhe, S. Sörlin, P. K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L. Karlberg, R. W. Corell, V. J. Fabry, J. Hansen, B. Walker, D. Liverman, K. Richardson, P. Crutzen & J. Foley, 2009. Planetary boundaries: exploring the safe operating space for humanity. Ecology and Society. 14: art32. https://doi.org/10.5751/ES-03180-140232.

Rosset, V., S. Angélibert, F. Arthaud, G. Bornette, J. Robin, A. Wezel, D. Vallod & B. Oertli, 2014. Is eutrophication really a major impairment for small waterbody

biodiversity? Journal of Applied Ecology 51: 415–425. https://doi.org/10.1111/1365-2664.12201.
Sceau, R., 1980. Les étangs de la Dombes, fondements socio-économiques d'un système hydraulique. Revue De Géographie De Lyon 55: 129–159. https://doi.org/10.3406/geoca.1980.1271.
Scheffer, M., 2004. Ecology of Shallow Lakes, Springer, Netherlands:
Schlumberger, O., & P. Girard, 2020. Memento de la pisciculture d'étang. Quae, Versailles.
Sculthorpe, C. D., 1967. The biology of aquatic vascular plants. London
Søndergaard, M., E. Jeppesen, J. Peder Jensen & S. Lildal Amsinck, 2005. Water framework directive: ecological classification of Danish lakes: water framework directive and Danish lakes. Journal of Applied Ecology 42: 616–629. https://doi.org/10.1111/j.1365-2664.2005.01040.x.
Sorensen, T. J., 1948. A Method of Establishing Groups of Equal Amplitude in Plant Sociology Based on Similarity of Species Content and Its Application to Analyses of the Vegetation on Danish Commons.
Soukainen, A., & P. Cardoso, 2022. Accuracy of non-parametric species richness estimators across taxa and regions. Ecology.
Steffen, W., K. Richardson, J. Rockström, S. E. Cornell, I. Fetzer, E. M. Bennett, R. Biggs, S. R. Carpenter, W. De Vries, C. A. De Wit, C. Folke, D. Gerten, J. Heinke, G. M. Mace, L. M. Persson, V. Ramanathan, B. Reyers & S. Sörlin, 2015. Planetary boundaries: guiding human development on a changing planet. Science 347: 1259855. https://doi.org/10.1126/science.1259855.
Stoate, C., N. D. Boatman, R. J. Borralho, C. R. Carvalho, G. R. de Snoo & P. Eden, 2001. Ecological impacts of arable intensification in Europe. Journal of Environmental Management 63: 337–365. https://doi.org/10.1006/jema.2001.0473.
Tamburini, G., R. Bommarco, T. C. Wanger, C. Kremen, M. G. A. Van Der Heijden, M. Liebman & S. Hallin, 2020. Agricultural diversification promotes multiple ecosystem services without compromising yield. Science Advances. 6: eaba1715. https://doi.org/10.1126/sciadv.aba1715.
Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. L. Phillips & S. E. Williams, 2004. Extinction risk from climate change. Nature 427: 145–148. https://doi.org/10.1038/nature02121.
Ulrich, W. & N. J. Gotelli, 2012. A null model algorithm for presence–absence matrices based on proportional resampling. Ecological Modelling 244: 20–27. https://doi.org/10.1016/j.ecolmodel.2012.06.030.
Van Zanten, B. T., P. H. Verburg, M. Espinosa, S. Gomez-y-Paloma, G. Galimberti, J. Kantelhardt, M. Kapfer, M. Lefebvre, R. Manrique, A. Piorr, M. Raggi, L. Schaller, S. Targetti, I. Zasada & D. Viaggi, 2014. European agricultural landscapes, common agricultural policy and ecosystem services: a review. Agronomy for Sustainable Development 34: 309–325. https://doi.org/10.1007/s13593-013-0183-4.
Vanacker, M., A. Wezel, V. Payet & J. Robin, 2015. Determining tipping points in aquatic ecosystems: the case of biodiversity and chlorophyll α relations in fish pond systems. Ecological Indicators 52: 184–193. https://doi.org/10.1016/j.ecolind.2014.12.011.
Vanacker, M., A. Wezel, F. Arthaud, M. Guérin & J. Robin, 2016. Determination of tipping points for aquatic plants and water quality parameters in fish pond systems: a multi-year approach. Ecological Indicators 64: 39–48. https://doi.org/10.1016/j.ecolind.2015.12.033.
Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday & R. Parmenter, 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257–300. https://doi.org/10.1146/annurev.ecolsys.30.1.257.
Weber, M. J. & M. L. Brown, 2009. Effects of common carp on aquatic ecosystems 80 years after "carp as a dominant": ecological insights for fisheries management. Reviews in Fisheries Science 17: 524–537. https://doi.org/10.1080/10641260903189243.
Wezel, A., B. Oertli, V. Rosset, F. Arthaud, B. Leroy, R. Smith, S. Angélibert, G. Bornette, D. Vallod & J. Robin, 2014. Biodiversity patterns of nutrient-rich fish ponds and implications for conservation. Limnology 15: 213–223. https://doi.org/10.1007/s10201-013-0419-7.
Wickham, H., 2016. ggplot2 : elegant graphics for dat analysis.
Woynarovich, A., T. Moth-Poulsen & A. Péteri, 2010. Carp polyculture in central and eastern Europe, the Caucasus and central Asia: a manual, Food and Agriculture Organization of the United Nations, Rome:
Zambrano, L. & D. Hinojosa, 1999. Direct and indirect effects of carp (Cyprinus carpio L.) on macrophyte and benthic communities in experimental shallow ponds in central Mexico. In Walz, N. & B. Nixdorf (eds), Shallow Lakes '98 Springer, Dordrecht: 131–138.
Zamora-Marín, J. M., C. Ilg, E. Demierre, N. Bonnet, A. Wezel, J. Robin, D.Vallod, J. F. Calvo, F. J. Oliva-Paterna & B. Oertli, 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.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.