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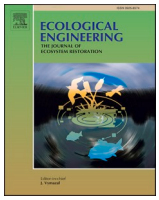

Environmental and spatial processes structuring macrophyte metacommunities in restored pondscapes

Van der Zon Karina Anna Elisabeth [a,*], Grac Corinne [a], Theissinger Kathrin [b,c], Paidere Jana [d], Brakovska Aija [d], Pupiņš Mihails [d], Škute Artūrs [d], Razafindralay Lydia [e], Georges Jean-Yves [c,f], Combroux Isabelle [a]

[a] Université de Strasbourg, CNRS, ENGEES, LIVE UMR 7362, F-67000 Strasbourg, France
[b] Rheinland-Pfälzische Technische Universität (RPTU) Kaiserslautern-Landau, Faculty of Biology, Ecology Department, Kaiserslautern, Germany
[c] Long Term Studies in Ecology and Evolution (SEE-Life) program of CNRS, Neu-Woerr, Lauterbourg & Neuburg am Rhein, F-67000 Strasbourg, France
[d] Institute of Life Sciences and Technologies, Daugavpils University, Daugavpils, Latvia
[e] Collectivité Européenne d'Alsace, Strasbourg, France
[f] Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

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ABSTRACT

Pond network creation can enhance freshwater biodiversity. However, environmental and spatial processes that structure macrophytes, a group central to pond ecology, need to be understood to improve pondscape design. Here, macrophyte communities were surveyed and environmental and spatial data were collected in two networks of man-made permanent ponds in western and northeastern Europe. Macrophyte diversity was high in the pond network in Latvia, and the relative cover of emergent, anchored submerged, anchored floating leaved and free-floating species varied among ponds. Diversity in the network on the French-German border in the former Rhine floodplain was low and consisted mainly of emergent plants and charophytes. The low diversity on the French-German site may result from the presence of the invasive calico crayfish (*Faxonius immunis*). Environmental variables, including water transparency, pH, chlorophyll-a concentration, as well as shade from surrounding trees and calico crayfish abundance (French-German site only), were correlated with abundances of macrophyte taxa. The variables were also correlated with macrophyte community metrics, including total macrophyte cover, taxonomic distinctness and the relative cover of submerged, emergent and free-floating life forms. Pond surface area and isolation had low contributions to the correlation between environmental variables and macrophyte community metrics. For the Latvian site only, macrophyte community similarity declined with geographic distance between ponds, but more importantly with differences in shade from surrounding trees and water transparency. A design of ponds with diverse environmental conditions and surroundings, as well as groups of ponds providing similar habitats, may be most effective for enhancement of macrophyte diversity at the pondscape scale.

1. Introduction

Wetland biodiversity decline is most importantly caused by habitat degradation and loss (Dudgeon et al., 2006; Kingsford et al., 2016), which can be considerable, as in Europe, where 71 % of wetland surface area *(sensu lato)* has been lost since 1900 (Davidson, 2014). To help mitigate biodiversity decline, wetland habitat restoration and creation have been recommended (Verhoeven, 2014). Emerging evidence shows that even the creation of small aquatic habitats can significantly enhance freshwater biodiversity (Williams et al., 2008). However, more research is needed to understand how ponds can contribute to biodiversity decline mitigation (Cuenca-Cambronero et al., 2023; Hill et al., 2021).

The term 'pond' refers to small (1 m^2 to 2–5 ha surface area), shallow (maximum depth of 5 m) standing waters that can be permanent or

* Corresponding author.
E-mail addresses: karina.vanderzon@live-cnrs.unistra.fr (V.Z. Karina Anna Elisabeth), corinne.grac@engees.unistra.fr (G. Corinne), kathrin.theissinger@rptu.de (T. Kathrin), jana.paidere@du.lv (P. Jana), aija.brakovska@du.lv (B. Aija), arturs.skute@du.lv (Š. Artūrs), lydia.razafindralay@alsace.eu (R. Lydia), jean-yves.georges@iphc.cnrs.fr (G. Jean-Yves), combroux@unistra.fr (C. Isabelle).

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temporary (with water at least 4 months per year) and natural or human-made (Biggs and Williams, 2024; Richardson et al., 2022). We reserve the term "restored pond" for ponds where a restorative intervention has been performed on the location of an existing or formerly existing pond, and the terms "man-made" and "created pond" for ponds that were made on locations where no known waterbody existed before (as in Cuenca-Cambronero et al., 2023). It should be noted that these terms are not synonymous with "constructed wetlands", which refers to systems in which macrophytes are planted during construction with the specific aim of water quality improvement (Vymazal, 2005).

Although individual natural, restored and man-made ponds can be exceptionally biodiverse (Biggs et al., 2005; Williams et al., 2004, 2008), their contribution to regional biodiversity should be studied at the scale of the "pondscape" (Hassall et al., 2012), which refers to a network of ponds and their surrounding terrestrial matrix (Boothby, 1997; Hill et al., 2021). Communities of different ponds within a pondscape are linked by dispersal of individuals and/or propagules, and thus function as a metacommunity (Céréghino et al., 2008; Fehlinger et al., 2023; Leibold et al., 2004). Following the metacommunity perspective (Heino et al., 2021; Leibold et al., 2004; Logue et al., 2011; Winegardner et al., 2012), both environmental processes at the local pond scale and spatial processes between ponds can interact and influence the composition and diversity of local pond communities withing a pondscape.

For effective design of pond networks it is important to understand how local environmental as well as spatial processes structure macrophyte metacommunities. Macrophytes are central to the functioning of pondscapes as they enhance water transparency, cycle nutrients, regulate sediment dynamics, and provide shelter, food and breeding habitat for other organism groups such as invertebrates, herpetofauna and birds (Capers et al., 2010; Carpenter and Lodge, 1986; Chambers et al., 2008). Locally, abiotic environmental filters (*sensu* Keddy, 1992), such as the availability of light, nutrients and bicarbonate, are known to structure macrophyte communities (Bornette and Puijalon, 2011; Lacoul and Freedman, 2006; Scheffer and Van Nes, 2007). They are therefore expected to influence the community composition, diversity and life forms of macrophytes in man-made ponds. Local biotic factors could also shape pond macrophyte communities by acting as filters, or by influencing abiotic filters. For example, algal growth or sediment resuspension by animals can increase water turbidity (Bakker et al., 2013). Depending on the species and abundance, crayfish can be a major biotic factor reducing macrophyte biomass and altering community composition, both by grazing and by resuspending sediment (Herrmann et al., 2022; Nyström et al., 1996; Twardochleb et al., 2013). Spatially, both the degree of isolation and the distance between ponds could influence macrophyte communities through dispersal limitation. Dispersal of sexual and vegetative macrophyte propagules was formerly assumed to be efficient, especially by water birds, but recent studies reported evidence suggesting that macrophyte dispersal can be limited, meaning that species present in the metacommunity do not reach suitable habitat patches often enough to establish a population, which influences macrophyte community composition and diversity (Capers et al., 2010; Gledhill et al., 2008; Lozada-Gobilard et al., 2019).

Despite the importance of macrophytes in pond network creation and restoration, for example to contribute to the mitigation of freshwater biodiversity decline, still few studies examined the processes shaping macrophyte communities in networks of ponds made for conservation purposes (Fleury and Strehler Perrin, 2004; Williams et al., 2008). Moreover, spatial factors that could influence the macrophyte metacommunities are seldom taken into account. To address this knowledge gap, we studied both environmental and spatial factors that could influence macrophyte metacommunities in two networks of permanent man-made ponds. Our study aimed to answer the following questions: 1*) How do abiotic and biotic conditions of man-made permanent ponds relate to macrophyte community composition, and to structural and functional macrophyte community metrics? 2) How does the land cover surrounding man-made permanent ponds relate to environmental variables in the ponds? 3) How do distances between man-made permanent ponds in a pond network, and differences in environmental conditions between the ponds, influence the dissimilarity of their macrophyte communities?*

We performed the same analyses for a western (France-Germany) and an northeastern (Latvia) European pondscape, to see if the responses to the research questions were similar for the two sites. To assess the influence of spatial factors, we included the distance to the nearest water body in the assessment of the correlation between environmental variables and macrophyte community composition and metrics. We also examined the influence of spatial distance, as well as differences in environmental conditions, on the macrophyte community dissimilarity between ponds. Accordingly, our study applies a metacommunity perspective to man-made pond networks and investigates factors known to shape macrophyte communities in this novel context, with the aim of informing pondscape design for freshwater biodiversity conservation.

2. Methods

2.1. Study sites

The two studied pond networks were made in already existing protected nature areas, with the aim to restore habitat for the European pond turtle *Emys orbicularis* (L., 1758), amphibians and other wetland dependent species. The ponds were colonised naturally and had not been planted. Study site Neu-Woerr is located in the continental biogeographical region (European Environment Agency, 2016) (Fig. 1a). The climate is semi-continental with an annual average (1981–2010) air temperature of 10.6 °C (1.8 °C in January, 19.4 °C in July) and precipitation of 883 mm (Météo-France, 2022). Potential evapotranspiration in the region can exceed annual precipitation (Météo-France, 2024).

Study site Neu-Woerr includes protected areas Naturschutzgebiet (NSG) Neuburger Altrhein in Germany, and Espace Naturel Sensible (ENS) Woerr in France (European Environment Agency, 2022) (Fig. 1b, c). The site is located in the floodplain of the Upper Rhine, which has been disconnected from the river by channelization works that started in the mid-19th century (Staentzel et al., 2018; Wantzen et al., 2022). The protected areas contain former agricultural fields, a former extraction pit, an anti-tank ditch from the second world war, oxbow lakes, woods and reedbeds that used to be harvested but are now becoming overgrown with willows. The site is bordered by corn fields and a gravel pit. Between 2011 and 2015, 19 ponds and three shallow extensions of larger water bodies were made in and adjacent to the protected areas. The ponds are connected to the groundwater of the Upper Rhine aquifer and can show large water level fluctuations ($>$ 1 m, L. Razafindralay, unpub. data). Parts of the area get flooded when the water level in the Rhine is high. Since 2013 the invasive calico crayfish *Faxonius immunis* (Hagen, 1870), which can drastically reduce macrophyte cover in ponds (Herrmann et al., 2022), is present in Neu-Woerr.

Study site Silene is boreal (Fig. 1a) and has a semi-continental climate with an average (1991–2020) annual air temperature of 6.6 °C (−4.1 °C in January and 18.1 °C in July) and average precipitation of 635 mm per year (Latvijas Vides, ģeoloģijas un meteoroloģijas centrs, 2022). After snowmelt in spring, many pools form which dry before summer (M. Pupiņš, pers. obs.). Silene is located within Silene Nature Park, southeast Latvia on the border with Belarus (Fig. 1d, e). The park contains lakes and bogs, and is dominated by coniferous and broad-leaved forests. In the past, wetlands have been drained for agricultural purposes and several farm ponds were dug. However, since the 1990's the region experiences agricultural decline, and meadows are becoming overgrown with woody plants (Vides Konsultāciju Birojs, 2019). In Silene, in total 26 ponds were made in 2006, 2013 and 2018, mainly in drained wetlands with former agricultural use, with some of them on locations of former farm ponds (Pupins et al., 2023). Crayfish are not known to occur in the Silene ponds.

In both study sites 13 man-made ponds that are permanent or only dry up in exceptionally dry years were selected (Table 1, Appendix A).

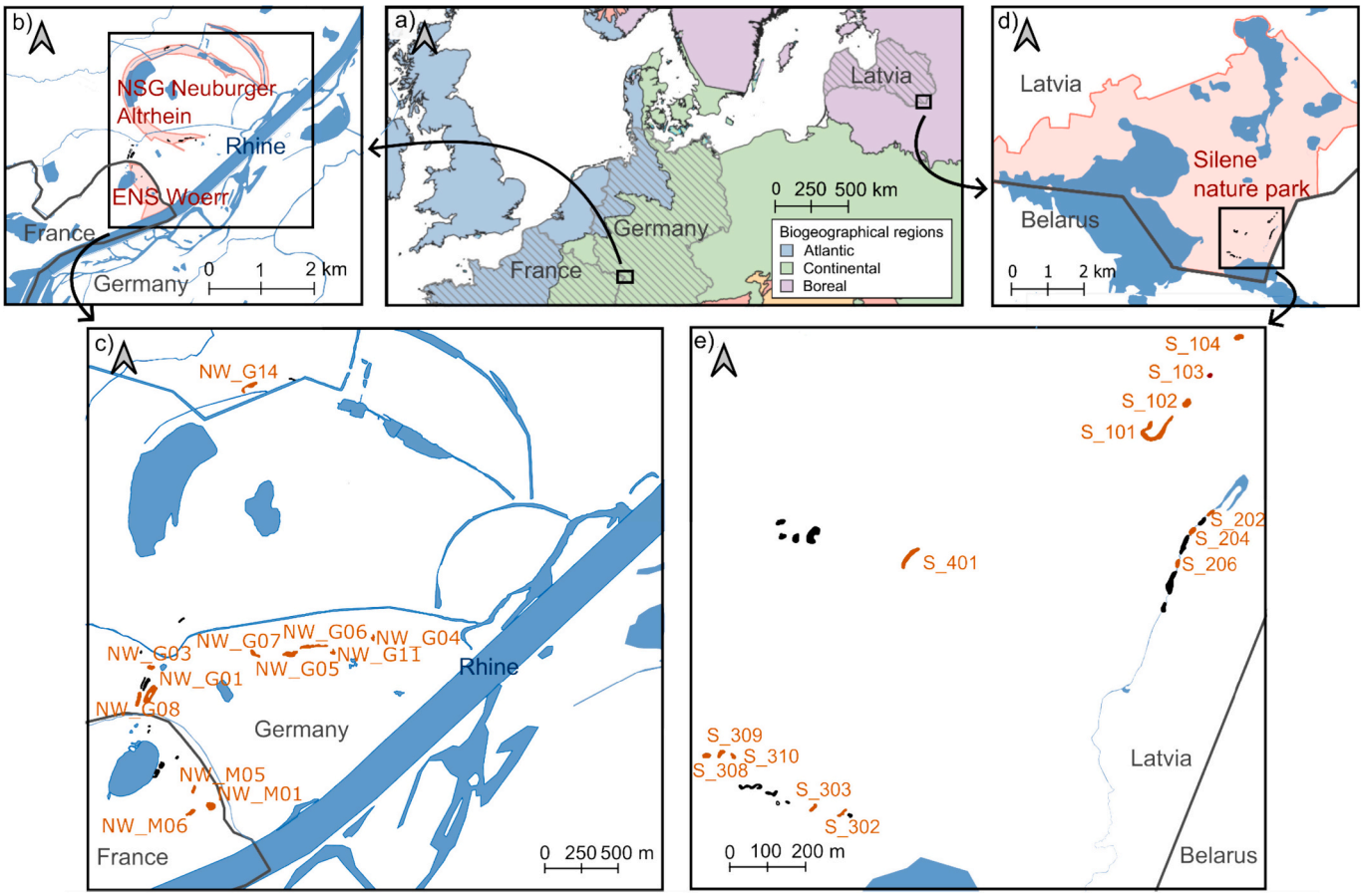

Fig. 1. a) Site locations within the continental (green) and boreal (violet) biogeographical regions of Europe, and within France, Germany and Latvia (hatched grey). b) Neu-Woerr and its connected protected areas Naturschutzgebiet (NSG) Neuburger Altrhein and Espace Naturel Sensible (ENS) Woerr (red). c) Studied Neu-Woerr ponds (orange). d) Silene nature park (red). e) Studied Silene ponds (orange). b-e) Borders are represented with black lines and waterbodies with dark blue polygons. Maps were made in QGIS 3.28 with data from the European Environment Agency (2016, 2022). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The ponds were chosen for our study to represent the widest range of pond macrophyte diversity in each site. In both sites, pond bases were generally sandy or silty, mixed with gravel for some Neu-Woerr ponds. A few Silene ponds had thick layers of oozy sediment. In a minority of studied ponds fish were observed: *Lepomis gibbosus* (L., 1758), *Proterorhinus semilunaris* (Heckel, 1837) (*cf.* Manné et al., 2013) and small cyprinidae in Neu-Woerr and *Percottus glennii* (Dybowski, 1877) (*cf.* Pupina et al., 2018) and *Tinca tinca* (L., 1758) in Silene.

2.2. Macrophyte surveys and metric calculations

Macrophyte surveys were performed in 2023, in June for Neu-Woerr and early July for Silene. In 2023, none of the studied ponds were flooded or dried up. Macrophyte surveys consisted in identifying all helophytes and hydrophytes growing in the usually wet area of the ponds. Bryophytes occurred at very low cover in some ponds and were not taken into account in the analyses. Taxonomy of the United States National Center for Biotechnology Information (NCBI) was used. For each pond, a map was drawn dividing the pond in sections with relatively homogeneous vegetation. The proportion of the surface area of the pond covered by each section was estimated, and within each section, the percentage cover of each macrophyte taxon was estimated visually. Based on this, the percentage cover of each taxon per pond was calculated.

The macrophyte percentage cover values were used to calculate multiple taxonomic and functional metrics (Table 2). Species richness is a focal metric in community ecology (Fleishman et al., 2006), but other metrics may capture different community responses to environmental variables (Beisel et al., 1998; García-Girón et al., 2019; Heino et al., 2005, 2007; Manzo et al., 2020). Therefore, we used multiple metrics to describe the macrophyte communities. As diversity metric we chose Hill Shannon diversity, which is the Shannon entropy expressed as effective number of species (Jost, 2006). For evenness we used "Simpson evenness", the index that is obtained by dividing the reciprocal of the Simpson concentration index by the number of taxa. Simpson evenness has the advantage over Pielou's evenness that it is independent of taxonomic richness, also for low taxonomic richness (Smith and Wilson, 1996). We calculated Warwick and Clarke's (1995) taxonomic distinctness, which is the average path length through a taxonomic tree connecting two randomly chosen individuals from different taxa. The path length weights given to two taxa belonging to the same genus, family, order and class, were respectively 20, 40, 60 and 80.

As functional metrics we used the total macrophyte cover and the relative cover of anchored emergent, anchored floating leaved, anchored submerged and free-floating life forms. Life form data was retrieved from books (Muller et al., 2021; Schou et al., 2023) and the Ecological Flora Database (Fitter and Peat, 1994) using the R package TR8 (Bocci, 2015). Species could be assigned to multiple life forms (Appendix B).

2.3. Environmental variable assessment

Assessment of local abiotic and biotic variables and estimation of land cover in the 5 m buffer around ponds was performed in the same

Table 1
Characteristics of studied Neu-Woerr (NW) and Silene (S) ponds. Codes refer to Fig. 1. Area is the surface area at the high water level.

Code	Latitude	Longitude	Area (m^2)	Year made	Original land occupation pond location
NW_G01	48.97708°	8.22260°	4640	2011/2012	Former gravel sieving platform
NW_G03	48.97874°	8.22285°	1010	2011/2012	Former gravel sieving platform
NW_G04	48.97964°	8.24374°	540	2011/2012	Location of former pond in reedbed and willow stand
NW_G05	48.97899°	8.23593°	2600	2011/2012	Willow and reed stands
NW_G06	48.97944°	8.23887°	2400	2011/2012	Willow and reed stands
NW_G07	48.97916°	8.23256°	1290	2011/2012	Willow and reed stands
NW_G08	48.97681°	8.22148°	2020	2013	Former gravel extraction platform
NW_G11	48.97892°	8.23992°	610	2013	Meadow on former agricultural field
NW_G14	48.99556°	8.23376°	2040	2013	Reedbed
NW_M01	48.96997°	8.22756°	2400	2011/2012	Reedbed
NW_M04	48.97511°	8.22232°	120	2011/2012	Forest
NW_M05	48.97106°	8.22607°	830	2015	Meadow on former corn field
NW_M06	48.96966°	8.22567°	1300	2015	Reedbed
S_101	55.69296°	26.78692°	1050	2013	Overgrown natural wetland
S_102	55.69361°	26.78832°	290	2018	Overgrown natural wetland
S_103	55.69425°	26.78933°	70	2018	Overgrown natural wetland
S_104	55.69513°	26.79063°	220	2018	Overgrown natural wetland with channel
S_202	55.69099°	26.78913°	110	2013	Wetland drainage channel
S_204	55.69058°	26.78833°	180	2013	Wetland drainage channel
S_206	55.68982°	26.78766°	150	2013	Wetland drainage channel
S_302	55.68420°	26.77315°	110	2013	Wetland drainage channel
S_303	55.68435°	26.77194°	130	2013	Wetland drainage channel
S_308	55.68569°	26.76755°	180	2018	Fallow meadow
S_309	55.68573°	26.76815°	170	2018	Fallow meadow
S_310	55.68565°	26.76867°	90	2018	Fallow meadow
S_401	55.69023°	26.77639°	530	2018	Natural wetland

time period as the macrophyte surveys. The percentage of the pond surface area that would be shaded at midday, as well as the contribution of reeds, willows and shrubs, high trees, wetlands and meadows to the land cover of the 5 m buffer around the pond were estimated. Water depth was measured at the deepest point in the pond and transparency was determined using a turbidity tube. To measure specific conductivity and pH, a WTW MultiLine 3630 IDS sonde was used in Neu-Woerr and an OTT Hydrolab DS5 sonde in Silene. For Silene, the portable sonde was used to measure chlorophyll-a concentrations, while for Neu-Woerr chlorophyll-a concentrations were measured in the laboratory using spectrophotometry following AFNOR standard NF T 90–117. Pond isolation, measured as the distance to the nearest waterbody, as well as spatial coordinates and the pond surface area at the high water level, were derived from digitized features based on Google Satellite maps in QGIS 3.28 using projections EPSG:2154 and EPSG:3059.

To estimate the abundance of calico crayfish in each Neu-Woerr pond, four littoral sweep net samples were taken in different meso-habitats (*sensu* Labat et al., 2022) and spread evenly along the pond margin. Samples covering 1 m^2 were taken by moving a 0.5 mm mesh size net with a rectangular 20 × 30 cm frame four times vigorously back and forth above the sediment with an amplitude of 1 m. Captured crayfish were identified and measured from rostrum to telson.

Table 2
Macrophyte metrics, with T the total number of taxa, p_i the relative cover of taxon i, w_{ij} the path length weight between taxa i and j, x_i the cover of taxon i, x_{em} the sum of the covers of emergent taxa, x_{fl} of anchored floating taxa, x_{su} of anchored submerged taxa, and x_{fr} of free-floating taxa.

Metric	Abbreviation	Formula	Reference
Taxonomic richness	Rich	Number of taxa	
Hill Shannon diversity	Shan	$e^{-\sum_{i=1}^{T} p_i ln(p_i)}$	Jost, 2006
Simpson evenness	Even	$\frac{1}{T\sum_{i=1}^{T} p_i^2}$	Smith and Wilson, 1996
Taxonomic distinctness	Dstar	$\frac{\sum\sum_{i<j} w_{ij} x_i x_j}{\sum\sum_{i<j} x_i x_j}$	Warwick and Clarke, 1995
Total cover	Cove	Total % of pond surface covered by macrophytes	
Relative cover emergent macrophytes	Emer	$\frac{x_{em}}{x_{em}+x_{fl}+x_{su}+x_{fr}}$	
Relative cover anchored floating macrophytes	Floa	$\frac{x_{fl}}{x_{em}+x_{fl}+x_{su}+x_{fr}}$	
Relative cover anchored submerged macrophytes	Subm	$\frac{x_{su}}{x_{em}+x_{fl}+x_{su}+x_{fr}}$	
Relative cover free-floating macrophytes	Free	$\frac{x_{fr}}{x_{em}+x_{fl}+x_{su}+x_{fr}}$	

2.4. Coinertia analyses

We performed coinertia analysis (CoIA) to investigate correlation between a) environmental variables and macrophyte metrics, b) environmental variables and macrophyte taxon abundance and c) land cover around ponds and environmental variables. Because of the small number of ponds sampled per network, it was not possible to perform redundancy analysis or canonical correspondence analysis. Instead, we chose CoIA, which can be used for datasets of many variables measured on few sites (Dolédec & Chessel, 1994; Dray et al., 2003). CoIA is most commonly used to relate environmental variables to community composition, but it is a flexible method that can relate any two datasets measured on the same entities (Borcard et al., 2011). It has been used to relate environmental variables to community metrics (Beisel et al., 1998).

CoIA requires appropriate initial ordinations of the datasets to be analysed (Borcard et al., 2011). We chose Principal Component Analysis (PCA) on the correlation matrix for the environmental variables and the metrics datasets. For the macrophyte abundance dataset, a transformation based PCA (Legendre and Gallagher, 2001) was performed. To this end, a Hellinger transformation of the percentage cover data was followed by covariance matrix PCA. This is equal to a Principal Coordinates Analysis of the Hellinger distance matrix (Legendre and De Cáceres, 2013). For each CoIA, an RV-coefficient, measuring the strength of the link between the two datasets on a scale from 0 to 1, was calculated (Robert and Escoufier, 1976), and its significance was evaluated using a Monte-Carlo test with 999 permutations. All CoIA's were performed for Neu-Woerr and Silene separately, because the two sites differed in terms of environmental variables (Appendix A), macrophyte communities (Appendix B), and invasive crayfish occurrence.

2.5. Community dissimilarity

To examine how geographic distance (G_{dis}) influences macrophyte community dissimilarity (C_{dis}) between ponds, we used non-linear regression as a first approach, and generalized dissimilarity modelling as a second approach. Generalized dissimilarity modelling allows the inclusion of differences between environmental conditions, besides geographic distance, as predictor variables (Ferrier et al., 2007). For both approaches we modelled the Bray-Curtis dissimilarity calculated on the log(x + 1) transformed percentage cover data (Borcard et al., 2011), but for the non-linear regression we expressed it as similarity ($C_{sim} = 1 - C_{dis}$). For the non-linear regression we fitted power functions of the form $C_{sim} = a \bullet G_{dis}^{-b}$, also referred to as log-log models (Nekola and McGill, 2014; Nekola and White, 1999; Soininen et al., 2007), to data from all pond pairs. We also tried exponential (log-linear) and linear models, but these fitted the data les well, as indicated by higher AIC values. From the power-law model, an initial C_{sim} at 10 m distance (C_{sim}_init) was calculated, as well as the halving distance (G_{dis}_half) at which C_{sim} had decayed to half the C_{sim}_init, using $G_{dis}\_half = 10 \bullet 2^{1/b}$. In order to investigate whether there was still decay of C_{sim} with G_{dis} for pond pairs separated by more than G_{dis}_half, a power function for the decay of C_{sim} with G_{dis} was also fitted on a reduced dataset with only pond pairs separated by more than G_{dis}_half.

We fitted generalized dissimilarity models (GDM) to identify both the contribution of G_{dis} and of environmental dissimilarities between ponds to C_{dis}. Generalized dissimilarity modelling is a matrix regression approach based on generalized linear modelling that accommodates for non-linearities in relationships between the predictor variables (G_{dis} and differences in environmental conditions) and C_{dis} (Ferrier et al., 2007). Following Mokany et al. (2022), we used three I-splines per predictor variable to model the Bray-Curtis macrophyte dissimilarity. The predictor variables assessed were G_{dis}, as well as differences between pond pairs in the percentage of the pond surface shaded by surrounding vegetation at midday, water depth, transparency, specific conductivity, pH, chlorophyll-a concentration, distance to the nearest waterbody, pond surface area, and for Neu-Woerr crayfish abundance. The significance of each predictor variable was tested with 999 permutations, and a backward selection procedure was used to keep only predictors with a *p*-value lower than 0.05. To check for correlation between the significant predictors, differences between pond pairs, in Euclidean geographic distance and in each environmental variable, were calculated, and Spearman correlation coefficients were evaluated. Furthermore, the importance of each of the remaining predictors for the predicted macrophyte community dissimilarity was evaluated as the sum of the three predicted I-spline coefficients (Mokany et al., 2022).

Data analysis and visualisation were performed in R version 4.4.0 with R studio 2023.06.0 using packages HillR, vegan, taxize, ade4, adegraphics, adespatial, gdm and the tidyverse.

3. Results

3.1. Macrophyte communities

In total, 81 macrophyte taxa were identified to the species level, of which 35 were detected in Neu-Woerr and 63 in Silene (Appendix B). Some *Carex* had neither flowers nor fruits at the time of sampling and were only identified to genus level. In Neu-Woerr, the most common species were *Phragmites australis*, *Veronica anagallis-aquatica* and *Juncus acutiflorus*, observed in respectively 100, 85 and 69 % of the ponds. In Silene, the most common species *Typha latifolia*, *Alisma plantago-aquatica*, *Carex acutiformis* and *Lemna minor*, were each recorded in 85 % of the ponds. In terms of conservation status, the species *Hippuris vulgaris*, observed in Neu-Woerr, is classified as Near Threatened on the French Red List, but as Least Concern on both the European and global Red Lists. *Sparganium natans*, occurring in Silene, is Near Threatened following the European Red List, and of Least Concern according to the global Red List (Bilz et al., 2011; Lansdown, 2014; UICN France et al., 2018). All vascular plant species were native to the location they were observed, except for *Acorus calamus*, found in Silene, which was introduced into Europe in the 16th century (Dykyjová, 1980; Schou et al., 2023; Royal Botanic Gardens, Kew, 2017).

Per pond, taxonomic richness (5 to 17 in Neu-Woerr, and 11 to 30 in Silene) and Hill Shannon diversity were lower in Neu-Woerr than in Silene (Appendix B). Furthermore, total macrophyte cover was on average 49 % in Neu-Woerr and 81 % in Silene (Fig. 2, Appendix B). Whereas Neu-Woerr ponds had almost no floating anchored and few free-floating plants, and their submerged vegetation consisted primarily of charophytes, the relative cover of different life forms in the Silene ponds varied among ponds.

3.2. Coinertia macrophytes, environmental variables and land cover

For both sites, CoIA showed significant correlations between local environmental variables and the macrophyte metrics (Fig. 3a, d), with a major contribution of light-influencing variables to the first coinertia axis (Fig. 3b, e). For Neu-Woerr, ponds with transparent water (Trans) were on the right side of the coinertia plane, whereas those with reduced light conditions, namely those shaded by surrounding trees (Shade) and those exhibiting relatively high chlorophyll-a concentrations (Chl-a), were on the left side of plane. Ponds with high crayfish abundance (Cray) were also on the left side of the plane. For Silene, ponds with reduced light conditions were on the right side, and those with relatively high pH and great depth on the left side of the plane.

For Neu-Woerr, the ponds with reduced light conditions and high crayfish abundance, on the left side on the coinertia plane, exhibited high relative cover of emergent species (Emer) (Fig. 3c). Ponds with enhanced light conditions, on the right side of the coinertia plane, were characterized by high relative cover of submerged plants (Subm), total cover (Cove) and taxonomic distinctness (Dstar). In Silene, ponds with reduced light conditions, on the right side of the coinertia plane, had high relative cover of free-floating macrophytes (Free) (Fig. 3f), while those with improved light conditions, as well as high pH and greater depth, where characterized by a high relative cover of submerged plants.

For both sites, surface area (Area) and distance to the nearest waterbody (DistNWb) had low contributions to the coinertia between the environmental variables and macrophyte metrics. For Neu-Woerr, pond age (Age) did not contribute to the coinertia and for Silene pond age had a small contribution to the first axis and a more important contribution to the second coinertia axis, but this axis only projected 20 % of the inertia. Specific conductivity (SpCond) also had a small contribution to the first axis for Silene, and contributed to the second axis for Neu-Woerr, but this axis only projected 19 % of the inertia. Taxonomic richness (Rich) contributed to the second axis in Neu-Woerr and only showed moderate contribution to the coinertia in Silene. Spearman rank correlations between taxonomic richness and the environmental variables studied were all lower than |0.6| and had *p*-values (Benjamini-Hochberg adjusted for multiple testing) higher than 0.05.

CoIA between macrophyte abundances and environmental variables showed high and significant correlations for both sites (Fig. 4a, d). For both sites, the first coinertia axis separated ponds with high light conditions (Trans) on the left from ponds with low light conditions (Shade, Chl-a) on the right side of the coinertia plane (Fig. 4b, e). For Neu-Woerr, crayfish abundance (Cray) and specific conductivity (SpCond) were with the low light conditions on the right side of the plane. This was also the case for depth, while for Silene depth was associated with improved light conditions, and with younger pondage.

For both sites, ponds with extensive *Chara* cover, of *Chara vulgaris* (CharVulg) in Neu-Woerr and *Chara globularis* (CharGlob) in Silene (Fig. 4c, f), had transparent water, and in Silene relatively high pH as well. In Silene, ponds with *Lemna minor* (LemnMino) were characterized by high shade from surrounding trees, high chlorophyll-a concentration, low transparency and low pH. In Neu-Woerr, *Eleocharis uniglumis*

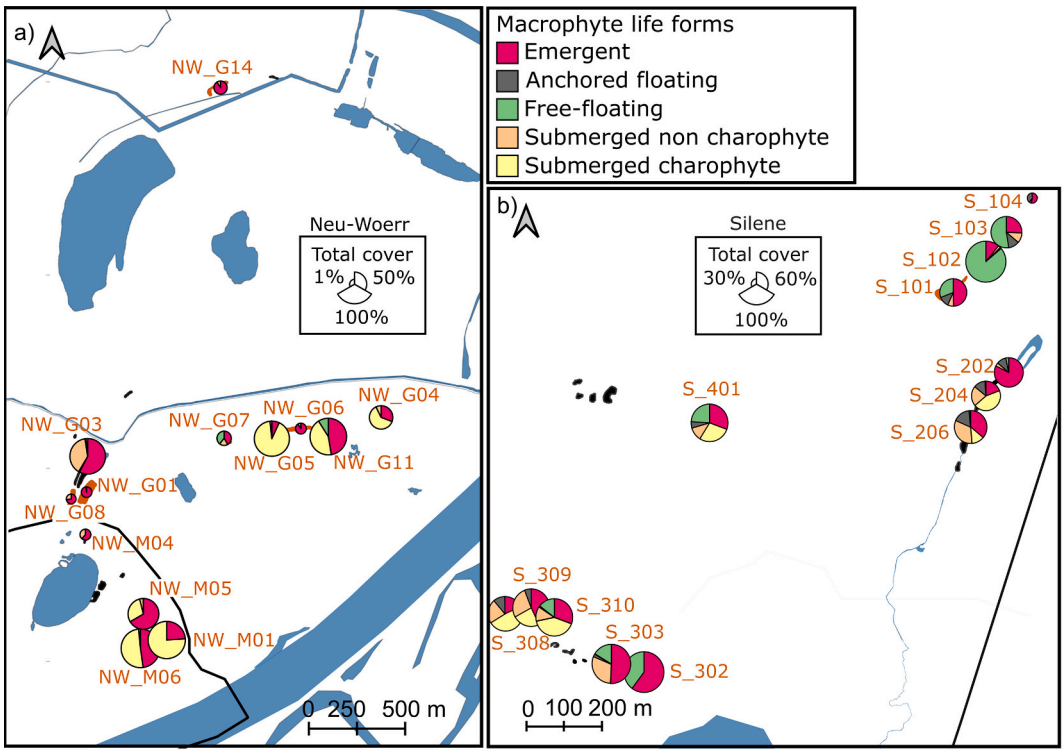

Fig. 2. Pond locations and pie charts showing the contributions of emergent, anchored floating, free-floating, submerged charophyte and submerged non-charophyte life forms to the total macrophyte cover of the ponds in a) Neu-Woerr and b) Silene. The radius of the pie chart indicates the total cover of macrophytes with the radius scales in the insert. Note that to improve readability different scales were used for the two sites.

(EleoUnig) and *Carex rostrata* (CareRost) only occurred in pond NW_G14, and *Ricciocarpos natans* (RiccNata) only in pond NW_G07, and both these ponds were characterized by high chlorophyll-a concentrations and specific conductivity.

For both sites, pond surface area only had a small contribution to the correlation between environmental variables and macrophyte taxon abundance. For Neu-Woerr, age did not contribute to the correlation, but for Silene age contributed to both axes. For both sites the distance to the nearest waterbody, and only for Silene specific conductivity, contributed mainly to the second coinertia axis. However, the second axes only projected 23 % and 17 % of the inertia for Neu-Woerr and Silene, respectively.

In both sites, ponds were surrounded by shrubs and willows, reeds, meadows and high trees. In Silene, four ponds bordered bogs as well (Appendix C). CoIA showed significant correlation between land cover in 5 m around ponds and selected environmental variables for Silene (RV coefficient = 0.56, $p = 0.001$), but not for Neu-Woerr (RV coefficient = 0.34, $p = 0.094$). In Silene, ponds surrounded by reeds and meadows were associated with relatively high pH and transparent water, whereas those surrounded by trees were more shaded and had higher chlorophyll-a concentrations (Appendix C).

3.3. Community dissimilarity

Power function models fitted on all pond pairs (Full), showed marginally non-significant decay of community similarity with geographic distance for Neu-Woerr, as indicated by the p-value of regression parameter b ($p = 0.064$), but highly significant decay for Silene ($p < 0.001$ for parameter b) (Fig. 5, Table 3). For Silene the halving distance (G_{dis}_half, the distance at which community similarity equals half its initial value at 10 m distance) was 300 m. Reduced models (Red), fitted only on pairs of ponds separated by more than G_{dis}_half, did not show a significant decay of community similarity with geographic distance. This indicates that excluding pairs of ponds separated by less than G_{dis}_half effectively removed the spatial correlation that was observed in Silene.

For Neu-Woerr, no generalized dissimilarity model (GDM) of the Bray-Curtis dissimilarity could be fitted, because none of the predictor variables were significant. For Silene, however, a GDM was fitted with as predictor variables the differences between ponds in shade from surrounding trees and water transparency (model $p < 0.001$, explained deviance = 45 %, Fig. 6). The Silene model did not include geographic distance between pond pairs as predictor variable. It had been excluded by the backward selection procedure, and would be marginally non-significant if added to the model (p would be 0.061). The pond pair differences in shade from surrounding trees and water transparency were not correlated (Spearman $\rho = 0.16$). Shade from surrounding trees was more important than water transparency for the community dissimilarity (C_{dis}), as indicated by the higher sum of the I-spline coefficients. The influence of shade on C_{dis} was larger between 0 and 50 % of the pond surface shaded, indicated by the steep slope of the I-spline curve in this range, than between 50 and 90 % shaded, where the slope was flatter. The influence of transparency on C_{dis} was most important between 70 and 120 cm transparency.

4. Discussion

To help inform the design of pondscapes for biodiversity conservation and restoration, we studied environmental variables and spatial processes that structure macrophyte communities in two pond networks in Europe with contrasting conditions. Ponds in the western European network Neu-Woerr had low macrophyte species richness, while those in northeastern European Silene had moderately high species richness compared to ponds studied in European surveys (Hassall et al., 2011; Oertli et al., 2002; Williams et al., 2008). In Neu-Woerr, macrophyte cover was low and consisted mainly of emergent and submerged charophyte life forms. In Silene, macrophyte cover was abundant and contributions of emergent, submerged, anchored floating and free-floating

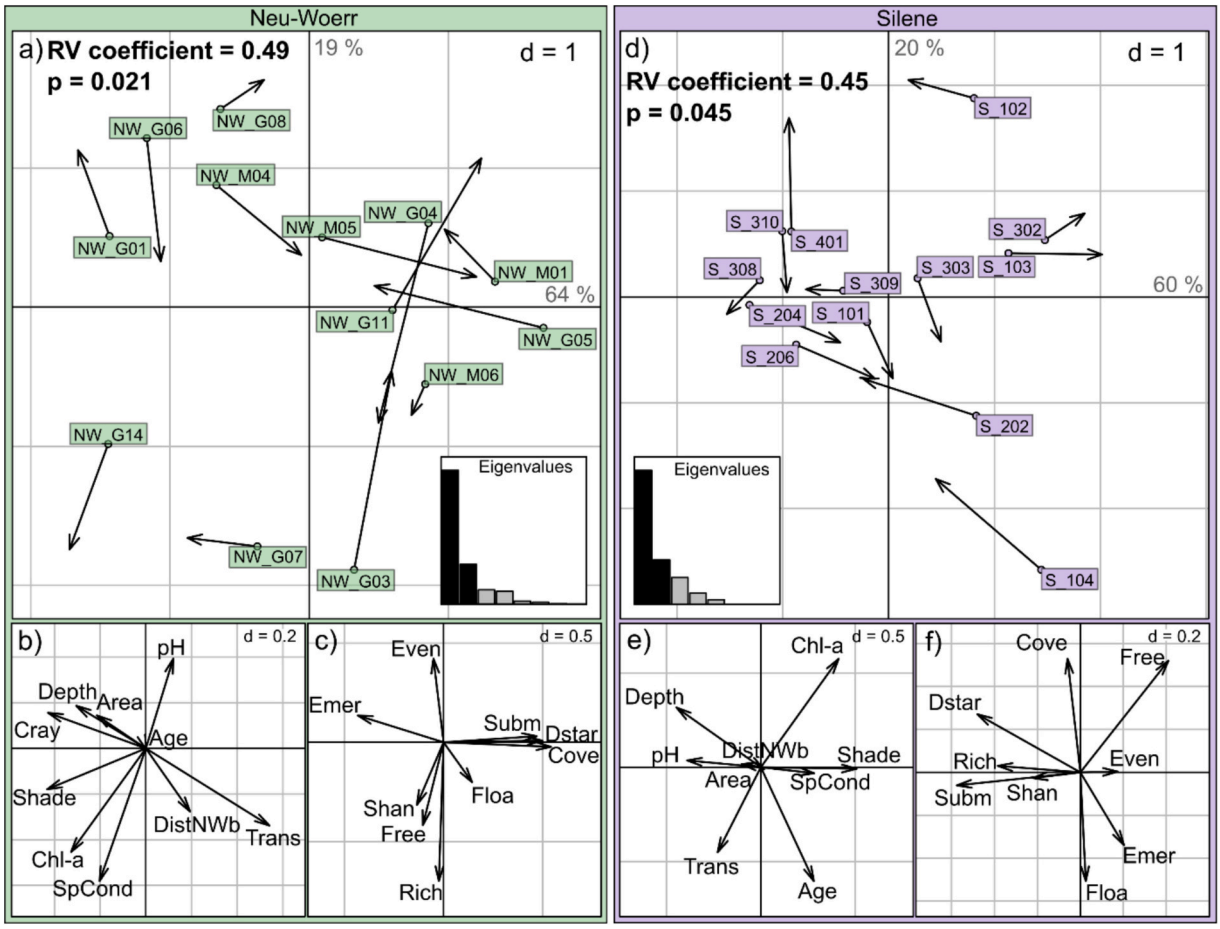

Fig. 3. CoIA environment – macrophyte metrics. a - c) Neu-Woerr. d - f) Silene. a, d) Positions of the ponds on the plane of the first two coinertia axes (% inertia projected by each axis in grey) according to the environmental variables (dots and labels) and according to macrophyte metrics (arrowheads). RV coefficients and p-values are in the top left corner in bold and the eigenvalue bar plots in the insets. b, e) Positions of environmental variables on the coinertia plane. c, f) Positions of the macrophyte metrics on the coinertia plane. For metric abbreviations see Table 2.

life forms to the total macrophyte cover varied among ponds. In both pond networks, taxon abundances and macrophyte metrics describing community structure and function were correlated with environmental variables. Varying responses of the different macrophyte metrics highlight the importance of evaluating multiple metrics. However, the metrics taxonomic distinctness and relative cover of submerged life forms provided similar information in our study, since they were both heavily influenced by the cover of charophytes.

4.1. Environmental correlates

Variables affecting light conditions were important for the macrophyte community composition and relative cover of different life forms, which is in line with literature (Bornette and Puijalon, 2011; Kautsky, 1988; Lacoul and Freedman, 2006). In Silene, ponds with clear water and no shading from trees exhibited high cover of submerged macrophytes, whereas ponds with turbid water and shading from trees were dominated by free-floating plants including *Lemnaceae*. Free-floating macrophytes have a competitive advantage over submerged macrophytes at low light conditions because their leaves are on top of the water surface (Scheffer et al., 2003). The dominance of *Lemnaceae* in shaded turbid ponds in Silene is probably due to a combination of low light conditions with an absence of wind and high nutrient levels, that comes together in ponds surrounded by trees. In windy conditions *Lemnaceae* are blown to the shore and cannot dominate (Sayer et al., 2012), but in shaded ponds surrounded by trees, which act as windbreaks, they can form mats. Unlike anchored macrophytes, *Lemnaceae* cannot take nutrients from the sediment but only from the water column, which is why they require high water nutrient levels (Scheffer et al., 2003). In Silene, ponds dominated by free-floating plants had high chlorophyll-a concentrations, indicating high nutrient levels, which was potentially related to historical farming activities, and maybe also to riparian trees. Our analysis on the correlation between the land cover in the 5 m buffer around ponds and in-pond environmental variables showed that ponds surrounded by willows, shrubs and high trees had high chlorophyll-a concentrations and low water transparency. Riparian trees and shrubs can contribute leaf litter to the ponds, which increases organic matter and nutrient concentrations (Sayer et al., 2012). The enhanced nutrient levels could allow *Lemnaceae* to take up sufficient nutrients and could stimulate algal growth, thus increasing chlorophyll-a concentrations and turbidity, which could give *Lemnaceae* a competitive advantage over submerged macrophytes.

In Neu-Woerr, ponds with low light conditions had low macrophyte cover of merely emergent life forms, whereas ponds with clear water and little tree shade had extensive beds of submerged charophytes. In Neu-Woerr, low light conditions were not only caused by algal biomass and tree shade, but also by calico crayfish. Calico crayfish resuspend sediment when digging, which causes turbidity, and they graze on macrophytes (Herrmann et al., 2022). Without macrophytes, algal growth increases, which adds to the turbidity (Scheffer and Van Nes, 2007). Turbidity, both from algal growth and sediment resuspended by crayfish, in turn impedes macrophytes from establishing. This positive feedback mechanism can maintain a pond in a crayfish induced turbid alternative stable state (Scheffer and Van Nes, 2007; Twardochleb et al.,

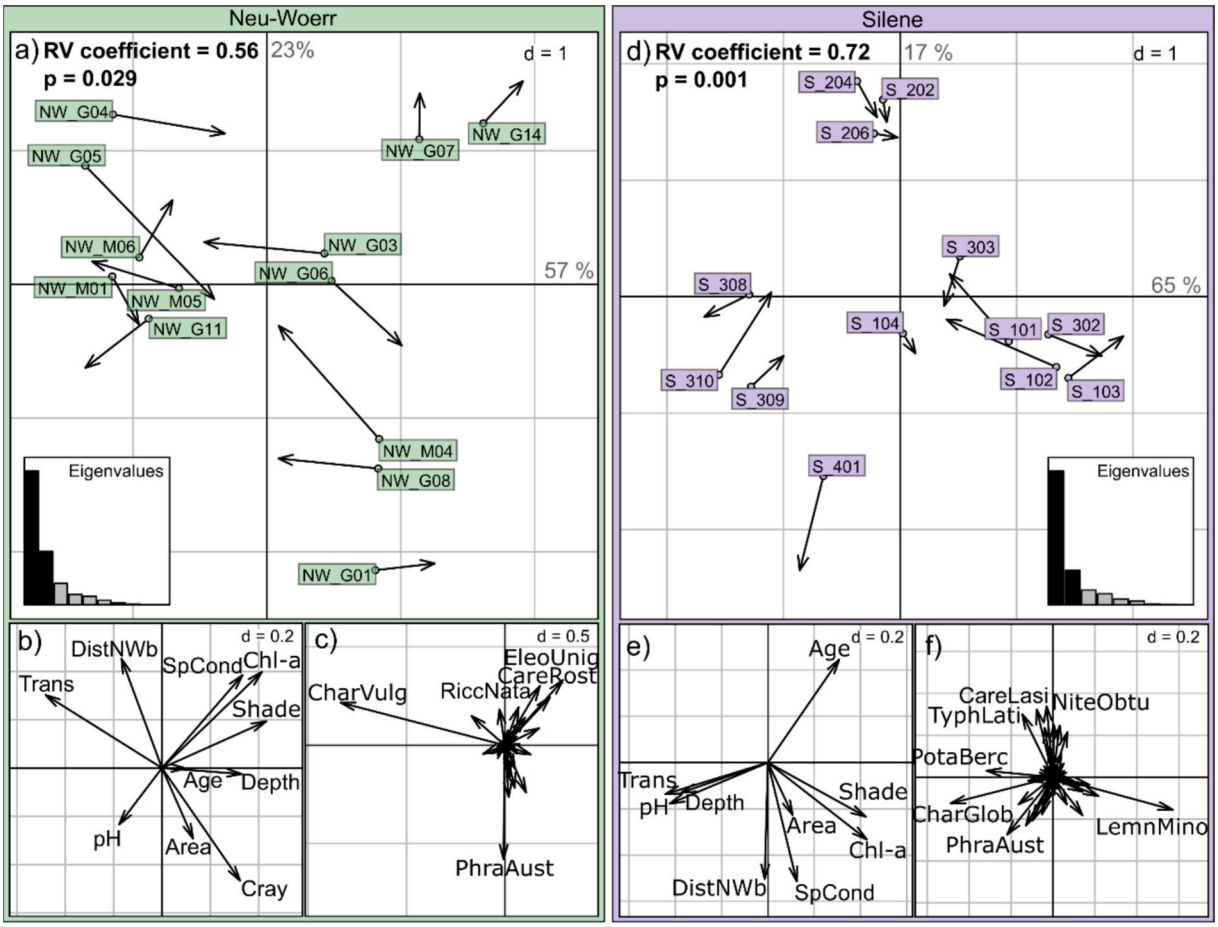

Fig. 4. CoIA environment – macrophyte taxa. a - c) Neu-Woerr. d - f) Silene. a, d) Positions of the ponds on the plane of the first two coinertia axes (% inertia projected by each axis in grey) according to the environmental variables (dots and labels) and according to taxon abundances (arrowheads). RV coefficients and *p*-values are in the top left corner in bold and the eigenvalues in the insets. b, e) Positions of environmental variables on the coinertia plane. c, f) Positions of the macrophyte taxa on the coinertia plane. For taxon name abbreviations see Table S2 (Appendix B).

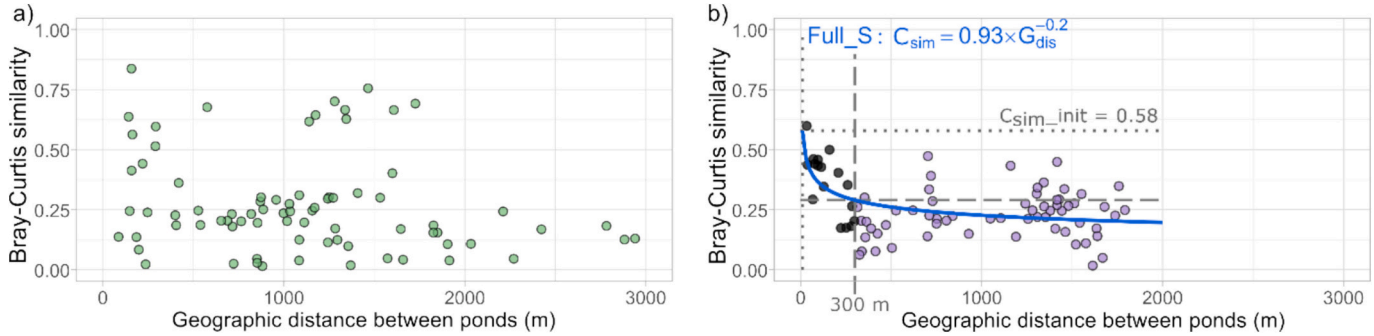

Fig. 5. Pairwise Bray-Curtis similarity between macrophyte communities as function of geographic distance between the ponds. a) Neu-Woerr. b) Silene with the power function fitted to all pairs of ponds and the regression equation (Full_S) in blue. Initial similarity (C_{sim}_init) is indicated with grey dotted lines and the halving distance (G_{dis}_half) with grey dashed lines. Pond pairs further apart from each other than the halving distance are presented in violet and pairs of ponds separated by less than the halving distance are in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2013). At the time of sampling, the cover of *Chara vulgaris* was quite extensive in Neu-Woerr. However, later in the season the charophyte populations collapsed and the water became turbid and devoid of macrophytes (K. van der Zon, pers. obs.). *Chara vulgaris* is a quick growing species that is resilient to disturbances (Bornette and Arens, 2002; Wade, 1990). It might be that the charophytes established in spring, when the crayfish activity was probably low. Calico crayfish hide in burrows during the winter and their eggs hatch in spring (Tack, 1941; Chucholl, 2012). At the time of sampling the crayfish activity was presumably not important enough to tip the ponds into a turbid state. Later in the season, however, increased crayfish activity could have induced the turbid state without charophytes.

In Silene, pH was positively correlated with relative cover of submerged life forms including *Chara globularis*. At high pH, inorganic carbon is primarily present in the form of bicarbonate. Charophytes can use bicarbonate more effectively for photosynthesis than angiosperm

Table 3
Regression parameters of full (Full) and reduced (Red) power functions describing decay of community similarity with geographic distance, following $C_{sim} = a \bullet G_{dis}^{b}$, for Neu-Woerr (_NW) and Silene (_S). Significance is indicated as *** for p < 0.001, ** for $p < 0.01$, * $p < 0.05$, and (n.s.) for $p > 0.05$.

Parameter	Full_NW	Full_S	Red_NW	Red_S
a	0.86 (n.s.)	0.92 ***	−0.02 (n.s.)	0.08 (n.s.)
b	0.17 (n.s.)	0.20 ***	0.08 (n.s.)	−0.15 (n.s.)

bicarbonate users. Consequently, at high pH charophytes have competitive advantage over angiosperms (Iversen et al., 2019; Maberly and Madsen, 2002; Sand-Jensen et al., 2021).

Surprisingly, whereas in Neu-Woerr pond depth seemed to be negatively correlated with charophyte cover, in Silene charophytes were relatively more abundant in deeper ponds. This contrasting outcome could be explained by the positive correlation between pond age and depth in Silene, a correlation that was absent for Neu-Woerr. It is possible that in Silene the older, ten year old, ponds already lost some depth to sedimentation, and some charophytes to succession. Succession rates depend on productivity (Hassall et al., 2012), and we expect succession to occur faster in the Silene ponds, which are characterized by extensive macrophyte cover, than in the Neu-Woerr ponds, which are disturbed by crayfish. In case of classical ecological succession, following an initial colonization phase, ponds reach a stage of maximum macrophyte diversity (Barnes, 1983; Fleury and Strehler Perrin, 2004). We expect that the older Silene ponds were at this stage. After the stage of maximum diversity ponds may become poorer in species, and richer in nutrients (Fleury and Strehler Perrin, 2004; Gee et al., 1997; Sayer et al., 2012; Williams et al., 2008). Furthermore, there may be an ongoing decrease in charophyte cover and increase in emergent vegetation cover with succession (Hassall et al., 2012; Van Geest et al., 2003). Additionally, in both studied networks, willow overgrowth will increase pond shading if unmanaged. As discussed above, this may increase the relative cover of emergent and free-floating life forms and decrease the relative cover of submerged macrophytes.

The contribution of pond surface area to the coinertia between environmental variables and macrophyte metrics was low for both sites. Some studies found macrophyte species richness to increase with pond surface area (Friday, 1987; García-Girón et al., 2019; Gee et al., 1997; Oertli et al., 2002) while others found no effect (Biggs et al., 2005; Edvardsen and Økland, 2006; Hassall et al., 2011; Linton and Goulder, 2000). Oertli et al. (2002) studied 80 Swiss ponds and concluded that there are more macrophyte species in several small ponds than in one large pond of the same total surface area. However, since some species only occurred in the smallest or largest ponds, the authors advise to create ponds of varying sizes when possible (Oertli et al., 2002).

Our analyses did not show effects of pond isolation, measured as distance to the nearest water body, on pond macrophyte community composition and metrics. This might be due to the fact that all studied ponds were quite close to other water bodies and because we only studied permanent ponds. The most isolated Silene pond was separated from the nearest water body by 240 m, and the most isolated Neu-Woerr pond by 170 m only. Linton and Goulder (2000) studied a pondscape with ponds separated from other water bodies by more than 500 m and did find pond macrophyte species richness to increase with the number of neighbouring water bodies. Lozada-Gobilard et al. (2019), studied kettle holes that (except for one) all had other water bodies within 500 m, and did not find an effect of isolation on macrophyte richness in permanent ponds. However, they did find a negative correlation between isolation and macrophyte species richness for ephemeral ponds, which might depend on nearby ponds for recolonization after disturbance (Lozada-Gobilard et al., 2019).

4.2. *Community dissimilarity as function of geographic distance and environmental dissimilarity*

In Silene, the power model fitted on all pond pairs showed significant decay in macrophyte community similarity with increasing geographic distance between ponds, while the power model fitted only on ponds separated by more than the halving distance (G_{dis}_half = 300 m) showed no decay of community similarity with geographic distance. From this we could derive that there was spatial correlation in the macrophyte community composition between ponds separated by less than 300 m in Silene. The generalized dissimilarity model for Silene, however, showed a marginally non-significant influence of geographic distance on community dissimilarity. This non-significance might be due to the relatively low number of ponds studied, or due to the selection strategy of ponds to study, which was aimed at capturing the largest macrophyte diversity possible. The generalized dissimilarity model did show significant effects of the difference in shade from surrounding trees and difference in water transparency on community dissimilarity, from which we derive that differences in environmental variables were more important than spatial distance in explaining beta diversity.

For Neu-Woerr, the power model showed marginally non-significant decay of community similarity with geographic distance. The non-significance may be explained by the high similarity in macrophyte community composition between two clusters of ponds that were separated by a relatively large distance of 1.1 to 1.7 km (Fig. 5a). We expect that pond pairs from these clusters have similar macrophyte communities because of similar hydrological regimes, an important factor influencing macrophyte community composition (Jeffries, 2008; Kautsky, 1988), which we unfortunately did not measure. The generalized dissimilarity model for Neu-Woerr did not show significant effects of geographic distance nor of any of the differences in environmental

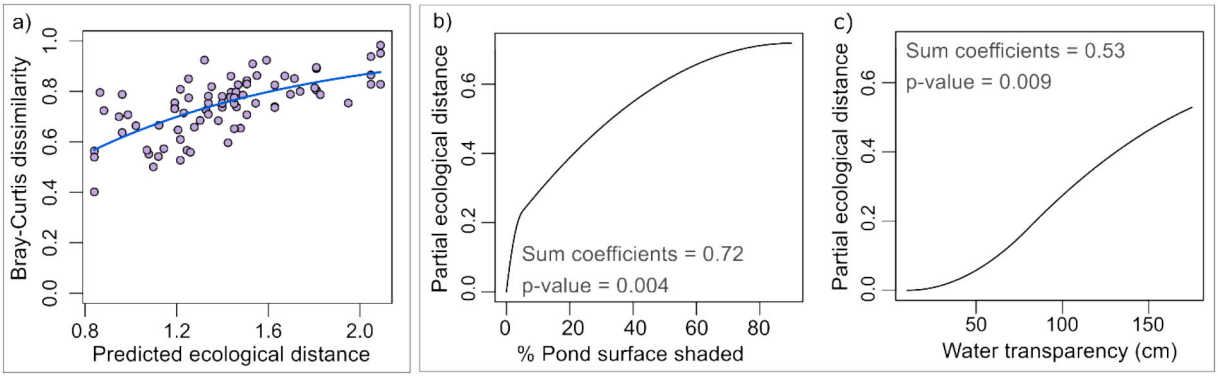

Fig. 6. Silene GDM. a) Observed Bray-Curtis dissimilarity as function of predicted ecological distance for each pair of ponds (points), and predicted Bray-Curtis dissimilarity as function of predicted ecological distance (line). b, c) I-spline functions for the predictor variables, with the slope indicating the rate of community composition change along the variable gradient, and in text the sum of coefficients, indicating the importance of the variable, and its significance.

variables on community dissimilarity. This non-significance may be due to the low number of ponds studied, short gradients, or unmeasured confounding variables. Besides hydrology, an unmeasured variable that could have influenced the Neu-Woerr macrophyte communities is pesticide runoff from the nearby agricultural activities (Ulrich et al., 2022). Furthermore, although crayfish abundance was measured, this was biased because we only captured juvenile crayfish. Crayfish abundance was measured by sweep netting at daytime along the pond edge, a technique that does not allow for the estimation of the number of adult crayfish, who live deeper in the pond and are only active at night (Tack, 1941). To estimate the abundance of both adult and juvenile crayfish, overnight trapping should be performed, for instance with artificial refuge traps (Green et al., 2018).

4.3. Pondscape design for target species

First of all, pond construction should not drain wetlands *(sensu stricto)* or destroy terrestrial habitats with valuable biodiversity. Furthermore, pondscape design should be adapted to the restoration or conservation goals of the planned network. A pond network that should host specific target species of conservation concern may have different requirements than a pond network aimed to increase freshwater biodiversity on a landscape scale in general.

One of the target species in our study sites was the European pond turtle *Emys orbicularis*. *Emys orbicularis* feeds on macrophytes and invertebrates associated with them, and uses macrophytes for hiding and basking (Lebboroni and Chelazzi, 1990; Thienpont et al., 2020). Ponds designed for *E. orbicularis* should have sufficient cover of submerged and anchored floating macrophytes, as well as a border of emergent vegetation, and should be exposed to sunlight (Bensettiti and Gaudillat, 2002). Based on our results on the scale of individual ponds, it can be advised that when a pond is made or restored for *E. orbicularis,* the abundance of crayfish species that have a large influence on macrophytes, and the percentage of the pond surface that is shaded by trees, should not be too high. This may require recurrent management of surrounding trees and placement of the pond on a site without crayfish species that have a large influence on macrophytes.

On the pondscape scale, the design for target species should consider the habitat requirements of the specific species at all life stages, and should, if relevant, not only include the aquatic but also the terrestrial habitat (Pupins et al., 2023; Rannap et al., 2020). Furthermore, the placement of ponds should depend on the locations of source populations and the dispersal abilities of the target species. If the species is not dispersing by air, dispersal corridors should be considered as well (Moor et al., 2024; Noel et al., 2006). Ponds made for the common spadefoot toad, *Pelobates fuscus* (Laurenti, 1768), another target species for the Neu-Woerr site, should for example be placed less than 500 m apart, because individuals from this species rarely disperse more than 500–1000 m from the pond they were born (Nyström et al., 2002).

4.4. Pondscape design to enhance regional biodiversity

To enhance regional diversity, one could aim to increase the alpha diversity of ponds, or the beta diversity between ponds, whereby an increase in beta diversity should not lead to a decrease in alpha diversity or *vice versa* (Socolar et al., 2016). Based on the two sites studied, it is hard to generalise on how to increase pond macrophyte alpha diversity. In our study, taxonomic richness did not contribute to the correlation between macrophyte community metrics and the environmental variables studied. Furthermore, although the ponds in Neu-Woerr and Silene were made for similar target species using similar methods, macrophyte diversity was lower in Neu-Woerr. The presence of calico crayfish may in part explain the low macrophyte richness and cover in Neu-Woerr. Other factors, such as the regional macrophyte species pool, anthropogenic pressures, pond use by mammals and macroecological aspects may also explain the difference in macrophyte diversity between the study sites. To disentangle the effects of these factors, studies on larger numbers of ponds should be performed. These should span different biogeographic regions, as there are still knowledge gaps on macrophyte macroecology, with for example contradictory results from studies on the relationship between latitude and diversity (Alahuhta et al., 2021).

Our results from Silene indicate that high macrophyte beta diversity may be obtained by creating ponds with varying levels of shade from surrounding trees and water transparency. Based on results from other studies, it can be expected that constructing both temporary and permanent ponds (Della Bella et al., 2008) of different sizes (Oertli et al., 2002) and at different points in time to attain different succession stages (Hassall et al., 2011) could enhance beta diversity as well. Pondscapes can be designed to include ponds of various ages, sizes, and levels of shade from surrounding trees. While it may be more complex to influence pond permanency and water transparency, pond placement may be informed by hydrological conditions, source water nutrient concentrations and the presence of bioengineering species.

Since pondscape design for high beta diversity should not come at the cost of decreased alpha diversity, and macrophyte metapopulations are probably more resilient when multiple suitable habitats are available within in a pondscape, it may be desirable to not only create ponds that differ in environmental conditions, but also ponds that provide similar habitats. When environmental conditions are spatially structured, a design of clusters of ponds that are close together but geographically isolated from other clusters may be optimal (Jeffries, 2008). Overall, pondscapes designed to include both ponds that differ in environmental conditions, as well as groups of ponds that provide similar conditions, may be most effective for enhancing macrophyte biodiversity on a regional scale.

CRediT authorship contribution statement

Van der Zon Karina Anna Elisabeth: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Grac Corinne:** Writing – review & editing, Supervision, Resources, Investigation, Data curation, Conceptualization. **Theissinger Kathrin:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Paidere Jana:** Writing – review & editing, Resources, Investigation. **Brakovska Aija:** Writing – review & editing, Resources, Investigation. **Pupiņš Mihails:** Resources. **Škute Artūrs:** Resources. **Razafindralay Lydia:** Resources. **Georges Jean-Yves:** Writing – review & editing, Project administration, Funding acquisition. **Combroux Isabelle:** Writing – review & editing, Supervision, Resources, Investigation, Funding acquisition, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT version GPT-4-turbo in order to correct errors in R code and rephrase sentences. After using this service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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Declaration of competing 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2025.107789.

Data availability

The macrophyte dataset is available on GBIF: https://doi.org/10.15468/qcqnub

References

Alahuhta, J., Lindholm, M., Baastrup-Spohr, L., García-Girón, J., Toivanen, M., Heino, J., Murphy, K., 2021. Macroecology of macrophytes in the freshwater realm: Patterns, mechanisms and implications. Aquatic Botany 168, 103325. https://doi.org/10.1016/j.aquabot.2020.103325.

Bakker, E.S., Sarneel, J.M., Gulati, R.D., Liu, Z., Van Donk, E., 2013. Restoring macrophyte diversity in shallow temperate lakes: Biotic versus abiotic constraints. Hydrobiologia 710 (1), 23–37. https://doi.org/10.1007/s10750-012-1142-9.

Barnes, L.E., 1983. The colonization of ball-clay ponds by macroinvertebrates and macrophytes. Freshw. Biol. 13 (6), 561–578. https://doi.org/10.1111/j.1365-2427.1983.tb00013.x.

Beisel, J.-N., Usseglio-Polatera, P., Thomas, S., Moreteau, J.-C., 1998. Stream Community Structure in Relation to Spatial Variation: The Influence of Mesohabitat Characteristics, 393, pp. 73–88.

Bensettiti, F., Gaudillat, V., 2002. Cahiers D'habitats Natura 2000. Connaissance et Gestion des Habitats et Des Espèces D'intérêt Communautaire. Tome 7 - Espèces Animales. La Documentation Française.

Biggs, J., Williams, P., 2024. Ponds, Pools and Puddles. Harper Collins Publishers.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Weatherby, A., 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. Aquat. Conserv. Mar. Freshwat. Ecosyst. 15 (6), 693–714. https://doi.org/10.1002/aqc.745.

Bilz, M., Kell, S.P., Maxted, N., Lansdown, R.V., 2011. European Red List of Vascular Plants. Publications Office of the European Union.

Bocci, G., 2015. TR8: an R package for easily retrieving plant species traits. Methods Ecol. Evol. 6 (3), 347–350. https://doi.org/10.1111/2041-210X.12327.

Boothby, J., 1997. Pond conservation: Towards a delineation of pondscape. Aquat. Conserv. Mar. Freshwat. Ecosyst. 7 (2), 127–132.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology in R. Springer.

Bornette, G., Arens, M.-F., 2002. Charophyte communities in cut-off river channels the role of connectivity. Aquat 73, 149–162.

Bornette, G., Puijalon, S., 2011. Response of aquatic plants to abiotic factors: A review. Aquat. Sci. 73 (1), 1–14. https://doi.org/10.1007/s00027-010-0162-7.

Capers, R.S., Selsky, R., Bugbee, G.J., 2010. The relative importance of local conditions and regional processes in structuring aquatic plant communities. Freshw. Biol. 55 (5), 952–966. https://doi.org/10.1111/j.1365-2427.2009.02328.x.

Carpenter, S.R., Lodge, D.M., 1986. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26, 341–370. https://doi.org/10.1016/0304-3770(86)90031-8.

Céréghino, R., Biggs, J., Oertli, B., Declerck, S., 2008. The ecology of European ponds: defining the characteristics of a neglected freshwater habitat. Hydrobiologia 597 (1), 1–6. https://doi.org/10.1007/s10750-007-9225-8.

Chambers, P.A., Lacoul, P., Murphy, S.M., Thomaz, S.M., 2008. Global diversity of aquatic macrophytes in freshwater. In: Freshwater Animal Divesrity Assessment. Springer, pp. 9–26.

Chucholl, C., 2012. Understanding invasion success: life-history traits and feeding habits of the alien crayfish *Orconectes immunis* (Decapoda, Astacida, Cambaridae). Knowl. Manag. Aquat. Ecosyst. 404 (4). https://doi.org/10.1051/kmae/2011082.

Cuenca-Cambronero, M., Blicharska, M., Perrin, J.-A., Davidson, T.A., Oertli, B., Lago, M., Beklioglu, M., Meerhoff, M., Arim, M., Teixeira, J., De Meester, L., Biggs, J., Robin, J., Martin, B., Greaves, H.M., Sayer, C.D., Lemmens, P., Boix, D., Mehner, T., Brucet, S., 2023. Challenges and opportunities in the use of ponds and pondscapes as nature-based Solutions. Hydrobiologia 850 (15), 3257–3271. https://doi.org/10.1007/s10750-023-05149-y.

Davidson, N.C., 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. Mar. Freshw. Res. 65 (10), 934. https://doi.org/10.1071/MF14173.

Della Bella, V., Bazzanti, M., Dowgiallo, M.G., Iberite, M., 2008. Macrophyte diversity and physico-chemical characteristics of Tyrrhenian coast ponds in Central Italy: implications for conservation. Hydrobiologia 597 (1), 85–95. https://doi.org/10.1007/s10750-007-9216-9.

Dolédec, S., Chessel, D., 1994. Co-inertia analysis: an alternative method for studying species–environment relationships. Freshwater Biology 31, 277–294. https://doi.org/10.1111/j.1365-2427.1994.tb01741.x.

Dray, S., Chessel, D., Thioulouse, J., 2003. Co-inertia analysis and the linking of ecolgical data tables. Ecology 84 (11), 3078–3089. https://doi.org/10.1890/03-0178.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. 81 (2), 163–182. https://doi.org/10.1017/S1464793105006950.

Dykyjová, D., 1980. Production ecology of *Acorus calamus*. Folia Geobotan. Phytotaxon. 15, 29–57. https://doi.org/10.1007/BF02853137.

Edvardsen, A., Økland, R.H., 2006. Variation in plant species richness in and adjacent to 64 ponds in SE Norwegian agricultural landscapes. Aquat. Bot. 85 (2), 79–91. https://doi.org/10.1016/j.aquabot.2006.01.015.

European Environment Agency, 2016. Biogeographical Regions, Europe 2016, ver. 1 [Data Set]. EER Geospatial Data Catalogue. https://www.eea.europa.eu/en/datahub/datahubitem-view/11db8d14-f167-4cd5-9205-95638dfd9618.

European Environment Agency, 2022. Natura 2000 End 2021 – Shapefile [Data set]. Natura 2000 – Spatial Data. https://www.eea.europa.eu/data-and-maps/data/natura-14/natura-2000-spatial-data.

Fehlinger, L., Misteli, B., Morant, D., Juvigny-Khenafou, N., Cunillera-Montcusí, D., Chaguaceda, F., Stamenković, O., Fahy, J., Kolář, V., Halabowski, D., Nash, L.N., Jakobsson, E., Nava, V., Tirozzi, P., Cordero, P.U., Mocq, J., Santamans, A.C., Zamora-Marín, J.M., Marle, P., Rimcheska, B., 2023. The ecological role of permanent ponds in Europe: a review of dietary linkages to terrestrial ecosystems via emerging insects. Inland Waters 13 (1), 30–46. https://doi.org/10.1080/20442041.2022.2111180.

Ferrier, S., Manion, G., Elith, J., Richardson, K., 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Divers. Distrib. 13 (3), 252–264. https://doi.org/10.1111/j.1472-4642.2007.00341.x.

Fitter, A.H., Peat, H.J., 1994. The ecological flora database. J. Ecol. 82 (2), 415. https://doi.org/10.2307/2261309.

Fleishman, E., Noss, R., Noon, R., 2006. Utility and limitations of species richness metrics for conservation planning. Ecol. Indic. 6 (3), 543–553. https://doi.org/10.1016/j.ecolind.2005.07.005.

Fleury, Z., Strehler Perrin, C., 2004. Colonisation par les végétaux de mares temporaires nouvellement creusées dans les marais de la Grande Cariçaie (lac de Neuchâtel, Suisse). Arch. Sci. 57, 105–112.

Friday, L.E., 1987. The diversity of macro invertebrate and macrophyte communities in ponds. Freshw. Biol. 18 (1), 87–104. https://doi.org/10.1111/j.1365-2427.1987.tb01297.x.

García-Girón, J., Fernández-Aláez, M., Fernández-Aláez, C., 2019. Redundant or complementary? Evaluation of different metrics as surrogates of macrophyte biodiversity patterns in Mediterranean ponds. Ecol. Indic. 101, 614–622. https://doi.org/10.1016/j.ecolind.2019.01.062.

Gee, J.H.R., Smith, B.D., Lee, K.M., Griffiths, S.W., 1997. The ecological basis of freshwater pond management for biodiversity. Aquat. Conserv. Mar. Freshwat. Ecosyst. 7 (2), 91–104.

Gledhill, D.G., James, P., Davies, D.H., 2008. Pond density as a determinant of aquatic species richness in an urban landscape. Landsc. Ecol. 23, 1219–1230. https://doi.org/10.1007/s10980-008-9292-x.

Green, N., Bentley, M., Stebbing, P., Andreou, D., Britton, R., 2018. Trapping for invasive crayfish: comparisons of efficacy and selectivity of baited traps *versus* novel artificial refuge traps. Knowl. Manag. Aquat. Ecosyst. 419, 15. https://doi.org/10.1051/kmae/2018007.

Hassall, C., Hollinshead, J., Hull, A., 2011. Environmental correlates of plant and invertebrate species richness in ponds. Biodivers. Conserv. 20 (13), 3189–3222. https://doi.org/10.1007/s10531-011-0142-9.

Hassall, C., Hollinshead, J., Hull, A., 2012. Temporal dynamics of aquatic communities and implications for pond conservation. Biodivers. Conserv. 21 (3), 829–852. https://doi.org/10.1007/s10531-011-0223-9.

Heino, J., Soininen, J., Lappalainen, J., Virtanen, R., 2005. The relationship between species richness and taxonomic distinctness in freshwater organisms. Limnol. Oceanogr. 50 (3), 978–986. https://doi.org/10.4319/lo.2005.50.3.0978.

Heino, J., Mykrä, H., Hämäläinen, H., Aroviita, J., Muotka, T., 2007. Responses of taxonomic distinctness and species diversity indices to anthropogenic impacts and natural environmental gradients in stream macroinvertebrates. Freshw. Biol. 52 (9), 1846–1861. https://doi.org/10.1111/j.1365-2427.2007.01801.x.

Heino, J., Alahuhta, J., Bini, L.M., Cai, Y., Heiskanen, A., Hellsten, S., Kortelainen, P., Kotamäki, N., Tolonen, K.T., Vihervaara, P., Vilmi, A., Angeler, D.G., 2021. Lakes in the era of global change: moving beyond single-lake thinking in maintaining biodiversity and ecosystem services. Biol. Rev. 96 (1), 89–106. https://doi.org/10.1111/brv.12647.

Herrmann, A., Grabow, K., Martens, A., 2022. The invasive crayfish *Faxonius immunis* causes the collapse of macroinvertebrate communities in central European ponds. Aquat. Ecol. 56 (3), 741–750. https://doi.org/10.1007/s10452-021-09935-5.

Hill, M.J., Greaves, H.M., Sayer, C.D., Hassall, C., Milin, M., Milner, V.S., Marazzi, L., Hall, R., Harper, L.R., Thornhill, I., Walton, R., Biggs, J., Ewald, N., Law, A.,

Willby, N., White, J.C., Briers, R.A., Mathers, K.L., Jeffries, M.J., Wood, P.J., 2021. Pond ecology and conservation: research priorities and knowledge gaps. Ecosphere 12 (12), e03853. https://doi.org/10.1002/ecs2.3853.
Iversen, L.L., Winkel, A., Baastrup-Spohr, L., Hinke, A.B., Alahuhta, J., Baattrup-Pedersen, A., Birk, S., Brodersen, P., Chambers, P.A., Ecke, F., Feldmann, T., Gebler, D., Heino, J., Jespersen, T.S., Moe, S.J., Riis, T., Sass, L., Vestergaard, O., Maberly, S.C., Pedersen, O., 2019. Catchment properties and the photosynthetic trait composition of freshwater plant communities. Science 366 (6467), 878–881. https://doi.org/10.1126/science.aay5945.
Jeffries, M., 2008. The spatial and temporal heterogeneity of macrophyte communities in thirty small, temporary ponds over a period of ten years. Ecography 31 (6), 765–775. https://doi.org/10.1111/j.0906-7590.2008.05487.x.
Jost, L., 2006. Entropy and diversity. Oikos 113 (2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x.
Kautsky, L., 1988. Life strategies of aquatic soft bottom macrophytes. Oikos 53 (1), 126. https://doi.org/10.2307/3565672.
Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. J. Veg. Sci. 3, 157–164. https://doi.org/10.2307/3235676.
Kingsford, R.T., Basset, A., Jackson, L., 2016. Wetlands: conservation's poor cousins. Aquat. Conserv. Mar. Freshwat. Ecosyst. 26 (5), 892–916. https://doi.org/10.1002/aqc.2709.
Lacoul, P., Freedman, B., 2006. Environmental influences on aquatic plants in freshwater ecosystems. Environ. Rev. 14 (2), 89–136. https://doi.org/10.1139/a06-001.
Lansdown, R.V., 2014. The IUCN Red List of Threatened Species. https://www.iucnredlist.org.
Latvijas Vides, Ģeoloģijas un Meteoroloģijas Centrs, 2022. Pašvaldību Klimatiskie Raksturojumi. Klimata portāls. https://klimats.meteo.lv/klimats_latvija/.
Lebboroni, M., Chelazzi, G., 1990. Activity Patterns of *Emys orbicularis* L. (Chelonia Emydidae) in Central Italy, 3, pp. 257–268. https://doi.org/10.1080/08927014.1991.9525373.
Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16 (8), 951–963. https://doi.org/10.1111/ele.12141.
Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129 (2), 271–280. https://doi.org/10.1007/s004420100716.
Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7 (7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x.
Linton, S., Goulder, R., 2000. Botanical conservation value related to origin and management of ponds. Aquat. Conserv. Mar. Freshwat. Ecosyst. 10 (2), 77–91.
Logue, J.B., Mouquet, N., Peter, H., Hillebrand, H., 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends Ecol. Evol. 26 (9), 482–491. https://doi.org/10.1016/j.tree.2011.04.009.
Lozada-Gobilard, S., Stang, S., Pirhofer-Walzl, K., Kalettka, T., Heinken, T., Schröder, B., Eccard, J., Joshi, J., 2019. Environmental filtering predicts plant-community trait distribution and diversity: kettle holes as models of meta-community systems. Ecol. Evol. 9 (4), 1898–1910. https://doi.org/10.1002/ece3.4883.
Maberly, S.C., Madsen, T.V., 2002. Freshwater angiosperm carbon concentrating mechanisms: processes and patterns. Funct. Plant Biol. 29 (3), 393. https://doi.org/10.1071/PP01187.
Manné, S., Poulet, N., Dembski, S., 2013. Colonisation of the Rhine basin by non-native gobiids: an update of the situation in France. Knowl. Manag. Aquat. Ecosyst. 411, 02. https://doi.org/10.1051/kmae/2013069.
Manzo, L.M., Grech, M.G., Epele, L.B., Kutschker, A.M., Miserendino, M.L., 2020. Macrophyte regional patterns, metrics assessment and ecological integrity of isolated ponds at Austral Patagonia (Argentina). Sci. Total Environ. 727, 138617. https://doi.org/10.1016/j.scitotenv.2020.138617.
Météo-France, 2022. Fiche Climatologique Wissembourg-PV (67). Statistiques 1981–2010 et Records.
Météo-France, 2024. Fiche Climatologique Strasbourg-Entzheim (67). Statistiques 1991–2020 et Records.
Mokany, K., Ware, C., Woolley, S.N.C., Ferrier, S., Fitzpatrick, M.C., 2022. A working guide to harnessing generalized dissimilarity modelling for biodiversity analysis and conservation assessment. Glob. Ecol. Biogeogr. 31 (4), 802–821. https://doi.org/10.1111/geb.13459.
Moor, H., Bergamini, A., Vorburger, C., Holderegger, R., Bühler, C., Bircher, N., Schmidt, B.R., 2024. Building pondscapes for amphibian metapopulations. Conserv. Biol. 38 (6), e14165. https://doi.org/10.1111/cobi.14281.
Muller, F., Ritz, C.M., Welk, E., Wesche, K., 2021. Rothmaler—Exkursionsflora von Deutschland. Springer.
Nekola, J.C., McGill, B.J., 2014. Scale dependency in the functional form of the distance decay relationship. Ecography 37, 309–320. https://doi.org/10.1111/j.1600-0587.2013.00407.x.
Nekola, J.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. J. Biogeogr. 26 (4), 867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.x.
Noel, F., Porcher, E., Moret, J., Machon, N., 2006. Connectivity, habitat heterogeneity, and population persistence in *Ranunculus nodiflorus*, an endangered species in France. New Phytol. 169 (1), 71–84. https://doi.org/10.1111/j.1469-8137.2005.01572.x.
Nyström, P., Brönmark, C., Granéli, W., 1996. Patterns in benthic food webs: a role for omnivorous crayfish? Freshw. Biol. 36 (3), 631–646. https://doi.org/10.1046/j.1365-2427.1996.d01-528.x.
Nyström, P., Birkedal, L., Dahlberg, C., Brönmark, C., 2002. The declining spadefoot toad *Pelobates fuscus*: calling site choice and conservation. Ecography 25 (4), 488–498. https://doi.org/10.1034/j.1600-0587.2002.250411.x.
Oertli, B., Joye, D.A., Castella, E., Juge, R., Cambin, D., Lachavanne, J.-B., 2002. Does size matter? The relationship between pond area and biodiversity. Biol. Conserv. 104 (1), 59–70. https://doi.org/10.1016/S0006-3207(01)00154-9.
Pupina, A., Pupins, M., Nekrasova, O., Tytar, V., Kozynenko, I., Marushchak, O., 2018. Species distribution modelling: *Bombina bombina* (Linnaeus, 1761) and its main invasive threat *Perccottus glenii* (Dybowski, 1877) in Latvia under global climate change. Environ. Res. Eng. Manag. 74 (4), 79–86. https://doi.org/10.5755/j01.erem.74.4.21093.
Pupins, M., Nekrasova, O., Tytar, V., Garkajs, A., Petrov, I., Morozova, A., Theissinger, K., Čeirāns, A., Skute, A., Georges, J.-Y., 2023. Geographically isolated wetlands as a reserve for the conservation of amphibian biodiversity at the edge of their range. Diversity 15 (3), 461. https://doi.org/10.3390/d15030461.
Rannap, R., Kaart, M.M., Kaart, T., Kill, K., Uuemaa, E., Mander, Ü., Kasak, K., 2020. Constructed wetlands as potential breeding sites for amphibians in agricultural landscapes: a case study. Ecol. Eng. 158, 106077. https://doi.org/10.1016/j.ecoleng.2020.106077.
Richardson, D.C., Holgerson, M.A., Farragher, M.J., Hoffman, K.K., King, K.B.S., Alfonso, M.B., Andersen, M.R., Cheruveil, K.S., Coleman, K.A., Farruggia, M.J., Fernandez, R.L., Hondula, K.L., López Moreira Mazacotte, G.A., Paul, K., Peierls, B. L., Rabaey, J.S., Sadro, S., Sánchez, M.L., Smyth, R.L., Sweetman, J.N., 2022. A functional definition to distinguish ponds from lakes and wetlands. Sci. Rep. 12 (1), 10472. https://doi.org/10.1038/s41598-022-14569-0.
Robert, P., Escoufier, Y., 1976. A unifying tool for linear multivariate statistical methods: the rv- coefficient. Appl. Stat. 25 (3), 257. https://doi.org/10.2307/2347233.
Royal Botanic Gardens, 2017. Kew Plants of the World Online. https://powo.science.kew.org. Accessed on 04 June 2025.
Sand-Jensen, K., Martinsen, K.T., Jakobsen, A.L., Sø, J.S., Madsen-Østerbye, M., Kjær, J. E., Kristensen, E., Kragh, T., 2021. Large pools and fluxes of carbon, calcium and phosphorus in dense charophyte stands in ponds. Sci. Total Environ. 765, 142792. https://doi.org/10.1016/j.scitotenv.2020.142792.
Sayer, C., Andrews, K., Shilland, E., Edmonds, N., Edmonds-Brown, R., Patmore, I., Emson, D., Axmacher, J., 2012. The role of pond management for biodiversity conservation in an agricultural landscape. Aquat. Conserv. Mar. Freshwat. Ecosyst. 22 (5), 626–638. https://doi.org/10.1002/aqc.2254.
Scheffer, M., Van Nes, E.H., 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. Hydrobiologia 584 (1), 455–466. https://doi.org/10.1007/s10750-007-0616-7.
Scheffer, M., Szabó, S., Gragnani, A., Van Nes, E.H., Rinaldi, S., Kautsky, N., Norberg, J., Roijackers, R.M.M., Franken, R.J.M., 2003. Floating plant dominance as a stable state. Proc. Natl. Acad. Sci. 100 (7), 4040–4045. https://doi.org/10.1073/pnas.0737918100.
Schou, J.C., Moeslund, B., Van de Weyer, K., Wiegleb, G., Lansdown, R.V., 2023. Aquatic Plants of Northern and Central Europe Including Britain and Ireland. Princeton Unvierstiy Press.
Smith, B., Wilson, J.B., 1996. A consumer's guide to evenness indices. Oikos 76 (1), 70. https://doi.org/10.2307/3545749.
Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation? Trends Ecol. Evol. 31 (1), 67–80. https://doi.org/10.1016/j.tree.2015.11.005.
Soininen, J., McDonald, R., Hillebrand, H., 2007. The distance decay of similarity in ecological communities. Ecography 30 (1), 3–12. https://doi.org/10.1111/j.0906-7590.2007.04817.x.
Staentzel, C., Arnaud, F., Combroux, I., Schmitt, L., Trémolières, M., Grac, C., Piégay, H., Barillier, A., Chardon, V., Beisel, J.-N., 2018. How do instream flow increase and gravel augmentation impact biological communities in large rivers: a case study on the Upper Rhine River. River Res. Appl. 34 (2), 153–164. https://doi.org/10.1002/rra.3237.
Tack, P.I., 1941. The life history and ecology of the crayfish *Cambarus immunis* hagen. Am. Midl. Nat. 25 (2), 420. https://doi.org/10.2307/2420785.
Thienpont, S., Barthe, L., Beau, F., Berthomieu, L., Hubert, S., Lerat, D., Marant, D., Miquet, A., Priol, P., Quesada, R., Razafindralay, L., Vermeer, J., 2020. Réintroduction et Renforcement de Populations Chez la Cistude d'Europe. Guide de Bonnes Pratiques. Société Herpétologique de France, p. 48.
Twardochleb, L.A., Olden, J.D., Larson, E.R., 2013. A global meta-analysis of the ecological impacts of nonnative crayfish. Freshw. Sci. 32 (4), 1367–1382. https://doi.org/10.1899/12-203.1.
UICN France, FCBN, AFB & MNHN, 2018. La Liste Rouge Des Espèces Menacées en France – Chapitre Flore Vasculaire de France Métropolitaine.
Ulrich, U., Lorenz, S., Hörmann, G., Stähler, M., Neubauer, L., Fohrer, N., 2022. Multiple pesticides in lentic small water bodies: Exposure, ecotoxicological risk, and contamination origin. Sci. Total Environ. 816, 151504. https://doi.org/10.1016/j.scitotenv.2021.151504.
Van Geest, G.J., Roozen, F.C.J.M., Coops, H., Roijackers, R.M.M., Buijse, A.D., Peeters, E. T.H.M., Scheffer, M., 2003. Vegetation abundance in lowland flood plan lakes determined by surface area, age and connectivity. Freshw. Biol. 48 (3), 440–454. https://doi.org/10.1046/j.1365-2427.2003.01022.x.
Verhoeven, J.T.A., 2014. Wetlands in Europe: Perspectives for restoration of a lost paradise. Ecol. Eng. 66, 6–9. https://doi.org/10.1016/j.ecoleng.2013.03.006.
Vides Konsultāciju Birojs, 2019. Silene Nature Park Nature Conservation Plan 2020 to 2032 [Dabas parka "Silene" dabas Aizsardzības Plāns 2020.-2032. Gadam]. Translated into English With DeepL pro.

Vymazal, J., 2005. Horizontal sub-surface flow and hybrid constructed wetlands systems for wastewater treatment. Ecol. Eng. 25 (5), 478–490. https://doi.org/10.1016/j.ecoleng.2005.07.010.

Wade, P.M., 1990. The colonisation of disturbed freshwater habitats by Characeae. Folia Geobotan. Phytotaxon. 25 (3), 275–278. https://doi.org/10.1007/BF02913027.

Wantzen, K.M., Uehlinger, U., Van Der Velde, G., Leuven, R.S.E.W., Schmitt, L., Beisel, J.-N., 2022. The Rhine River basin. In: Rivers of Europe. Elsevier, pp. 333–391. https://doi.org/10.1016/B978-0-08-102612-0.00010-9.

Warwick, R., Clarke, K., 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Mar. Ecol. Prog. Ser. 129, 301–305. https://doi.org/10.3354/meps129301.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., Sear, D., 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. Biol. Conserv. 115 (2), 329–341. https://doi.org/10.1016/S0006-3207(03)00153-8.

Williams, P., Whitfield, M., Biggs, J., 2008. How can we make new ponds biodiverse? A case study monitored over 7 years. Hydrobiologia 597 (1), 137–148. https://doi.org/10.1007/s10750-007-9224-9.

Winegardner, A.K., Jones, B.K., Ng, I.S.Y., Siqueira, T., Cottenie, K., 2012. The terminology of metacommunity ecology. Trends Ecol. Evol. 27 (5), 253–254. https://doi.org/10.1016/j.tree.2012.01.007.