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ADVANCES IN CLADOCERA RESEARCH

Cladoceran diversity build-up in newly created pondscapes

Bram Janssens · Robby Wijns · Maxime Fajgenblat · Pieter Lemmens · Thomas Neyens · Luc De Meester

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Abstract Pondscapes, networks of closely situated ponds within a landscape, can provide important habitat for freshwater biodiversity and are increasingly considered to be valuable elements in nature restoration. Understanding how communities build up in newly created pondscapes is important for improving pond creation as a restoration tool. This study aimed to identify the main drivers of cladoceran species richness build-up and species accumulation patterns in newly created pondscapes. A total of 26 newly created ponds across two newly established pondscapes were surveyed repeatedly ($n = 11$) for environmental pond variables and cladoceran community characteristics during the first three years after their creation. The study ponds varied in surface area, maximum depth and hydroperiod, ranging from permanent to temporary systems. In total, 16 cladoceran species colonized the ponds within three years. Consistent with previous research, *Daphnia obtusa* was the first species to colonize ponds in both pondscapes. Macrophyte establishment seems to be the most important local factor influencing species accumulation, with vegetated ponds showing faster accumulation, likely because later-arriving cladoceran taxa are associated with macrophytes. Our observations highlight the role of macrophyte establishment during early pond succession and offer insights for designing resilient pondscapes that support effective freshwater biodiversity build-up.

Keywords Cladocera · Colonization dynamics · Pondscapes · New habitat · Metacommunity ecology

Bram Janssens and Robby Wijns share first authorship.

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B. Janssens (✉) · R. Wijns · M. Fajgenblat · P. Lemmens · L. De Meester
Laboratory of Freshwater Ecology, Evolution and Conservation, KU Leuven, Louvain, Belgium
e-mail: bram.janssens@kuleuven.be

M. Fajgenblat · T. Neyens
Data Science Institute, I-BioStat, Hasselt University, Diepenbeek, Belgium

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

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

T. Neyens
Leuven Biostatistics and Statistical Bioinformatics Centre (L-BioStat), KU Leuven, Louvain, Belgium

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Introduction

Over the past decades, biodiversity loss and climate change have reached an alarming rate (Sayer et al., 2025). Nature-based Solutions (NbS) are increasingly promoted as crucial strategies to protect biodiversity, mitigate the effects of climate change and support ecosystem services and Nature's contribution to people (NCP) (Díaz et al., 2018; Keesstra et al., 2018; Mendes et al., 2020). The European Biodiversity Strategy for 2030 emphasizes the implementation of NbS to achieve its conservation goals (El Harrak & Lemaitre, 2023). Ponds harbour strong potential as NbS because they are ubiquitous globally and provide habitat for a variety of freshwater, riparian and terrestrial species that benefit from the presence of nearby water, including many rare and endemic species (Dudgeon et al., 2006; Strayer & Dudgeon, 2010). Moreover, they serve as vital stepping-stone habitats that facilitate the dispersal of a wide range of species (Juračka et al., 2019), provide a wide diversity in ecosystem services and NCP, including carbon storage and climate mitigation (Postel & Carpenter, 1997; Cuenca-Cambronero et al., 2023; Lynch et al., 2023), and are relatively easy to construct at a relatively low cost (Cuenca-Cambronero et al., 2023).

Pond ecosystems are vulnerable to anthropogenic stressors and are, due to their small size, largely overlooked by policymakers compared to larger aquatic systems such as large lakes and rivers (Bagella et al., 2016; Hill et al., 2021; Cuenca-Cambronero et al., 2023). As a result, these habitats are rapidly deteriorating, leading to steep declines in population sizes of their inhabitants and even the loss of the habitats themselves in recent decades (Dudgeon et al., 2006; Sayer et al., 2025). Both the reduction in quality and the reduction in their number have important impacts on biodiversity and landscape connectivity (Horváth et al., 2019). This highlights the urgent need for improved conservation measures targeting small water bodies (Biggs et al., 2016). To reach the full potential of ponds and pondscapes (networks of closely situated ponds in a landscape; Biggs et al., 2024; Bartrons et al., 2024) as NbS, increased know-how is needed on the management, restoration and creation of ponds and pondscapes.

Newly created ponds are typically non-equilibrium systems that display temporal variation in local environmental pond conditions (Williams et al., 2008; Coccia et al., 2016). Moreover, as early successional processes can have long-lasting effects on pond biodiversity and ecosystem functioning through priority effects and other legacy effects (De Meester et al., 2002; Chase, 2003), it is crucial to gain a deeper understanding of the processes at play in the early years upon pond creation.

Cladocerans are pivotal organisms in pond ecosystems (Leppänen, 2018; Ogorelec et al., 2021; Ebert, 2022) and are often used as study organisms in the context of metacommunity research (Cottenie & De Meester, 2003; Allen et al., 2011; Declerck et al., 2011; Gianuca et al., 2018). Cladocerans have been shown to rapidly colonize newly created ponds, and their presence may boost the establishment of other species groups (Louette & De Meester, 2005), for instance by altering local pond conditions through top-down control of phytoplankton, contributing to a clear water state (Luecke et al., 1990; Effler et al., 2015). They provide an important food source for planktivorous fish and various macroinvertebrates, making them a crucial link between primary producers and higher trophic levels (Sterner, 2009). Cladocerans are therefore attractive study organisms to identify important drivers during early pond succession, as their communities can build up rapidly in newly created habitats while still being shaped by dispersal limitation, connectivity and landscape structure (Louette & De Meester, 2005; Frisch et al., 2012; Juračka et al., 2016).

In this study, we capitalize on a unique opportunity provided by two newly created pondscapes to study the cladoceran species richness build-up in newly created ponds. These pondscapes were constructed as part of a large nature restoration project in Eastern Belgium, conducted by Foundation Elzéard [*Elzéard.org*]. The aim of this study is to assess to what degree species richness build-up is determined by pond identity, pondscape identity, macrophyte presence, hydroperiod and other environmental pond variables.

We expect the studied ponds to display strong temporal variation in environmental conditions and species composition during the first three years after their creation. We also expect that environmental conditions that are typical of newly created ponds, such as limited habitat structure and high turbidity, are important in shaping early species accumulation patterns. If community build-up is mainly determined by species' abilities to deal with the specific

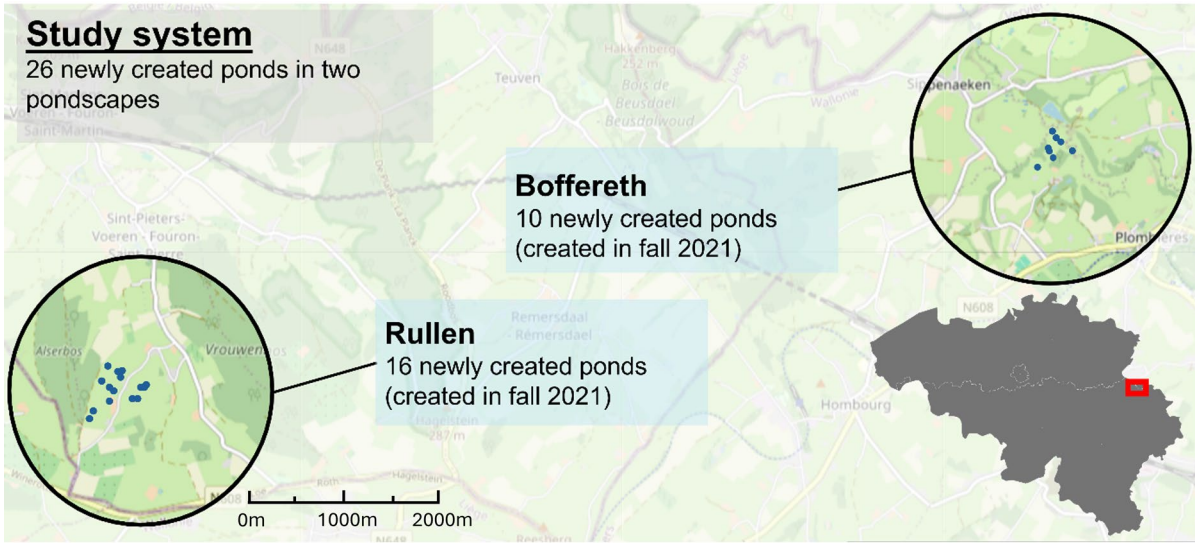


Fig. 1 Geographical location of the study system consisting of newly created ponds in two newly established pondscapes. The inset map (bottom right) shows where the study system is located in Belgium (red rectangle)

local conditions of early ponds or if they are driven by differences in dispersal capacity between species, we expect similar species accumulation curves across ponds within pondscapes. Between pondscapes, we expect species accumulation trajectories to differ if pondscapes differ in environmental conditions, in regional abundances of colonising species, or in the composition of the regional species pool. If variation in local conditions across ponds is important in determining species accumulation trajectories, we expect species accumulation curves to differ among ponds or pondscapes. Finally, if chance events linked to colonization events dominate the pattern, we expect highly diverging species accumulation curves that are not linked to local conditions (Louette & De Meester, 2005).

Materials and methods

Study site

Field sampling was conducted in 26 newly created ponds located in two newly established pondscapes situated in the East of Belgium: Rullen ($n = 16$, 50°43.5'N, 5°49.1'E) and Boffereth ($n = 10$, 50°44.8'N, 5°56.9'E) (Fig. 1). Each pondscape consisted exclusively of newly created ponds, with no previously existing ponds located between them. The Rullen pondscape covered approximately 17.2 ha, with a maximum distance of 850 m between ponds, whereas the Boffereth pondscape covered approximately 6.4 ha, with a maximum distance of 590 m between ponds. The two pondscapes were separated by approximately 9.5 km. Additional information on the distances of all studied ponds to the closest existing (i.e. older, not newly created) regional pond is given in supplementary information (Table S1.1).

Most ponds were created in November 2021, with the exception of one pond created in June 2022 (RUL16) and two ponds created in June 2023 (RUL1 & RUL2). During construction, the ponds were lined with a Dernoton® clay mixture and clay sourced from a local mine, precluding inoculation via dormant propagules in the local soil and allowing natural colonization. The ponds vary in surface area (2.4 to 27 m^2), depth (8 cm to 1.8 m) and hydroperiod, ranging from permanent ponds to ephemeral ponds that hold water only during the wettest seasons. More detailed information on these pond characteristics is given in Table S1. All ponds filled naturally through rainfall or groundwater seepage, with the exception of RUL3, 4, 5 and 6. These four ponds were manually filled using water from a local well, which we later found out contained *Daphnia obtusa* (Kurz, 1874), *Simocephalus vetulus* (O.F. Müller, 1776) and

Chydorus sphaericus (O.F. Müller, 1776). Given that these species may have been introduced into these ponds, data of these ponds were not included in the analyses presented here; a parallel analysis of the dataset including these four ponds is given in supplementary information (SI2).

Data collection

All ponds were monitored seasonally (four sampling campaigns a year: spring, summer, autumn and winter) to provide a temporally resolved picture of cladoceran diversity build-up over the first three years of the pondscapes' existence. The first sampling took place three to four months after pond creation. Given that we sampled all ponds during a three-year period (November 2021–November 2024) and that some ponds were constructed in the years following the initial creation of the pondscapes (notably: one pond in Rullen created in June 2022 and two ponds in Rullen created in June 2023), these ponds were monitored over a shorter period than three years. At each of the 11 sampling events, the cladoceran community was sampled by collecting a depth-integrated water sample using a tube sampler (length 1.2 m; diameter 75 mm) at several sampling locations situated on a wedge-shaped grid containing eight cells. Water from each location within each pond was pooled, and 30 L from the combined water was subsequently filtered through a 64-µm mesh filter. The zooplankton sample was preserved in glucose-saturated formaldehyde (4%) until further processing in the laboratory. During sampling, we paid special attention to prevent cross-contamination. Ponds were only entered when necessary, and most of them could be sampled directly from the bank due to the small size of the ponds. If entering the pond was nonetheless needed to get representative samples, waders were thoroughly rinsed (including the sole of the boots to prevent egg bank transfers between ponds) before entering a new pond. Between the sampling of different ponds, all equipment was thoroughly rinsed and disinfected with hydrogen peroxide (diluted 1:7) to prevent cross-contamination between the newly created ponds. For each pond sampled on a given day, we used a different cylindrically shaped mesh filter to concentrate the zooplankton.

Cladoceran specimens were identified to species level using a binocular stereoscope (Olympus SZX16) and identification keys of Amoros, (1984) and Flössner, (2000). We followed the same standardized counting protocol as De Bie et al., (2012). Before identifying cladocerans, formaldehyde was replaced with water. The entire sample was then examined using subsamples (1–10 mL, depending on the organic material present in the sample), which were transferred into a counting tray using a broad-mouthed micropipette, preventing cladocerans from floating at the surface. To maximize detection and to avoid underestimating species richness, the entire sample was thoroughly screened. This procedure ensured that all individuals present in the sample were considered, allowing us to compile an accurate estimation of cladoceran species richness data (presence/absence) for each pond and timepoint.

During each sampling occasion, a set of key local environmental pond variables was quantified using a depth-integrated water sample from different parts of the pond. Chlorophyll a (µg/L) and phycocyanin (RFU) concentrations were measured using a handheld fluorometer (Aquafluor, Turner Designs), taking the mean of three replicate measurements. Maximum pond depth was measured using a measuring stick. Water transparency was quantified using a modified Snellen tube consisting of a PVC pipe (diameter: 5.5 cm) and a vertically movable stick with a small Secchi disc at its lower end. The stick was lowered into the filled tube until the black-and-white cross on the disc was just visible, and transparency was recorded as the corresponding depth. Specific conductivity (mS/cm), pH and oxygen (mg/L) were measured directly in the pond using a HACH HQ 40d multimeter. To determine concentrations of TN and TP, expressed in milligrams per litre (mg/L), water samples were collected and frozen at − 20 °C for later analysis in the laboratory. Nutrient concentrations were measured after alkaline persulfate digestion (Koroleff, 1970) using a QuAAtro continuous flow analyser (Seal Analytical). The percentage of pond surface covered with emergent, submerged and floating vegetation was visually estimated to the nearest 5% during each sampling event.

Statistical analysis

A principal component analysis (PCA) was performed on scaled (standardized) data of local environmental pond variables (conductivity, chlorophyll a

concentration, phycocyanin concentration, maximum depth, surface area, TN and TP) to visualize the association between environmental variables, pondscape and time. The first two PCA axes were subsequently subjected to an orthogonal varimax rotation, and the resulting rotated components, referred to as RC1 and RC2, were used in subsequent analyses. A similar PCA analysis with varimax rotation was carried out for both pondscapes separately to visualize potential differences in environmental associations between the pondscapes. For the maximum depth and the surface area, the highest value measured over the entire sampling period was used. The PCA with varimax rotation was conducted using the principal function from the R package 'psych'.

We used linear mixed models to study how the rate of community build-up, during the first three years of a pond's existence, is modulated by pond identity, pondscape identity, macrophyte presence, hydroperiod and abiotic factors. We modelled the cumulative species richness, defined as the total number of observed species up to each sampling moment, as primary outcome to overcome imperfect species detection and seasonal variation in the observed instantaneous species richness. We modelled the cumulative species richness as a linear function of pond age (expressed in years) with an identity link function to approximate the rate of community build-up. Since the cumulative species richness of a pond is known to be zero at age zero, we omitted the model intercept and any other main effects other than pond age. Instead, we included pondscape identity (binary; Boffereth (0) and Rullen (1)), hydroperiod (fraction of sampling moments during which the pond was filled with water throughout the sampling period), macrophyte coverage (binary; defined as having reached > 25% emersed or submerged plant coverage at least once throughout the study period); this threshold was used because continuous cover estimates showed strong short-term variation related to water-level fluctuations and pond surface area, whereas exceeding 25% cover generally reflected persistent macrophyte establishment; two proxies of environmental pond conditions (standardized RC1 and RC2 coordinates extracted from the varimax-rotated PCA analysis, averaged over the entire study period per pond), and distance to an established pond (z-score standardized distance to the closest regional pond that existed before the pondscapes were created) as interaction terms with pond age, to estimate how these variables change the rate of community build-up. To account for unexplained pond-specific variation in the rate of community build-up, we included a pond-specific random slope for the effect of pond age. We fitted this model using the R package 'brms' (Bürkner, 2017), using cmdstan as the backend. The package relies on the probabilistic programming language Stan and performs Bayesian inference through a Hamiltonian Monte Carlo MCMC algorithm (Carpenter et al., 2017). We used weakly informative and mildly regularizing standard normal priors on all regression parameters, the random slope scale parameter and the residual error parameter. We used trace plots and the potential scale reduction factor to assess model convergence and used posterior predictive checks to ascertain goodness of fit (Gelman et al., 2013). We interpreted posterior probabilities using the following categories: no strong statistical support (< 70%), weak statistical support (70–80%), moderate statistical support (80–90%), strong statistical support (90–95%) and very strong statistical support (> 95%).

To evaluate the degree to which communities in species-poor ponds form nested subsets of communities in species-rich ponds, we conducted a NODF analysis (Nestedness metric based on Overlap and Decreasing Fill; Almeida-Neto et al., 2008) based on presence–absence data in the third year, using the nestednodf function from the package 'vegan' (Oksanen et al., 2013). To assess whether the observed nestedness was greater than expected by chance, we compared the observed NODF to a null distribution based on 1000 randomized matrices. Random matrices were generated using the permatfull function from the package 'vegan' (Oksanen et al., 2013), considering four null model algorithms: free row and column totals (most liberal approach), free row totals and fixed column totals, fixed row totals and free column totals and fixed row and column totals (most conservative approach). For each test, p-values were calculated as the proportion of randomized NODF values that were equal to or greater than the observed NODF.

All visualizations were created using the ggplot function from the R package 'ggplot2' (Wickham, 2011). All statistical analyses and visualizations were carried out in R (version 4.4.3) (R Core Team, 2025). All code and data to reproduce the analysis are archived in a permanent, DOI-assigned Zenodo

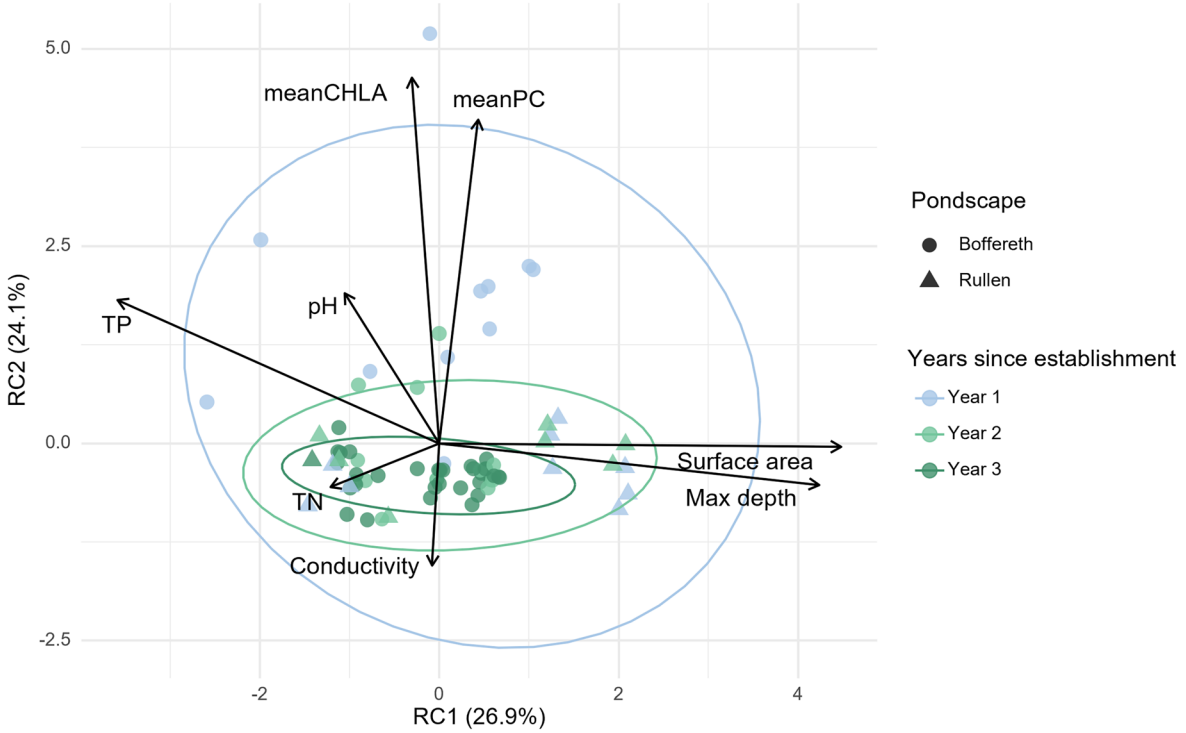


Fig. 2 Varimax-rotated PCA biplot based on environmental pond characteristics for each sampling moment, and maximum depth and surface area during the first three years of their existence. Different years are highlighted using different 95% confidence ellipses. Pondscapes are visualized by different symbols (Boffereth: circles; Rullen: triangles)

repository linked to the GitHub project: https://doi.org/10.5281/zenodo.20407444.

Results

Environmental properties of newly created ponds

The first and second axis of the PCA ordination based on standardized local environmental variables jointly explained 51.0% of the variation between ponds throughout the first three years (Fig. 2). The first rotated component (RC1; sum of squared loadings = 2.15) was primarily positively associated with maximum depth and surface area and negatively with TN and TP concentrations. The second rotated component (RC2; sum of squared loadings = 1.93) was predominantly positively associated with chlorophyll a concentration, phycocyanin concentration and pH, and negatively with conductivity. Separate ordinations for both pondscapes showed strong similarities in overall patterns between the pondscapes (e.g. the positive association between chlorophyll a concentration, phycocyanin concentration and pH—all associated with photosynthetic activity), but with a positive association between TP and TN in the Rullen pondscape, whereas they are rather negatively associated in the Boffereth pondscape (Supplementary Information, Fig. S1.1). Ponds exhibited the highest variability in their environmental conditions the first year after their creation, after which they converged into more stable and similar conditions.

Cladoceran species richness build-up

The mean cumulative species richness clearly increased in all ponds in both pondscapes during the first three years after pond creation. However, colonization was strongly constrained by hydroperiod: 15 of the 26 ponds never contained water for longer than three months, and no cladocerans were observed in these ponds throughout the study period. Species

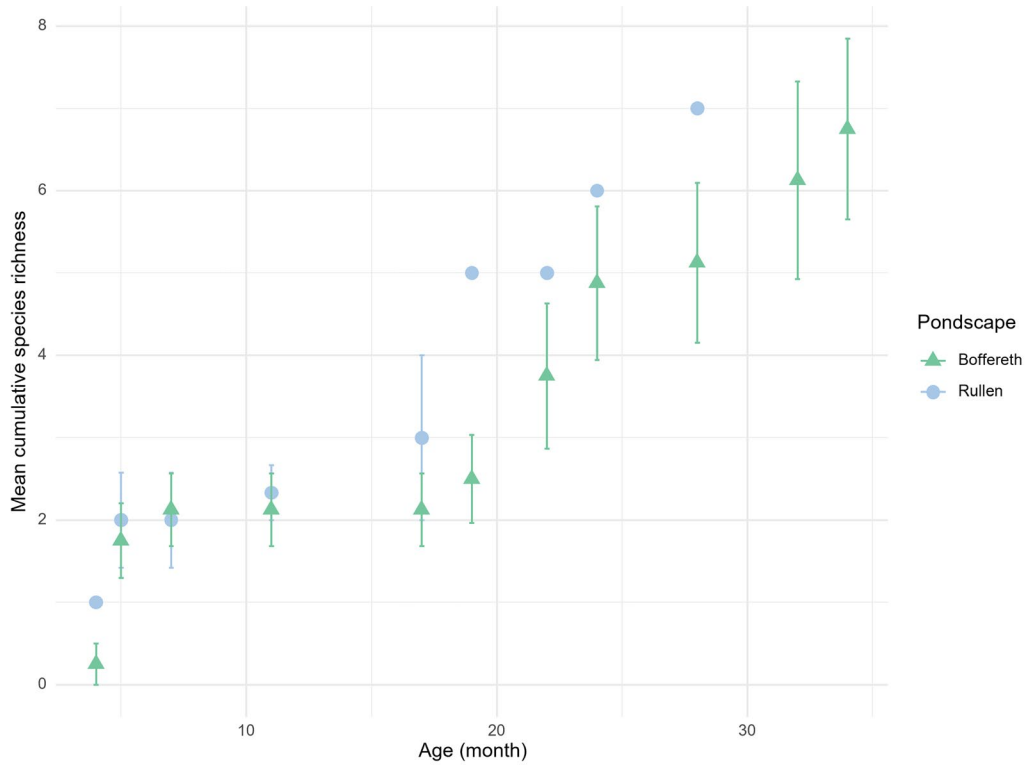
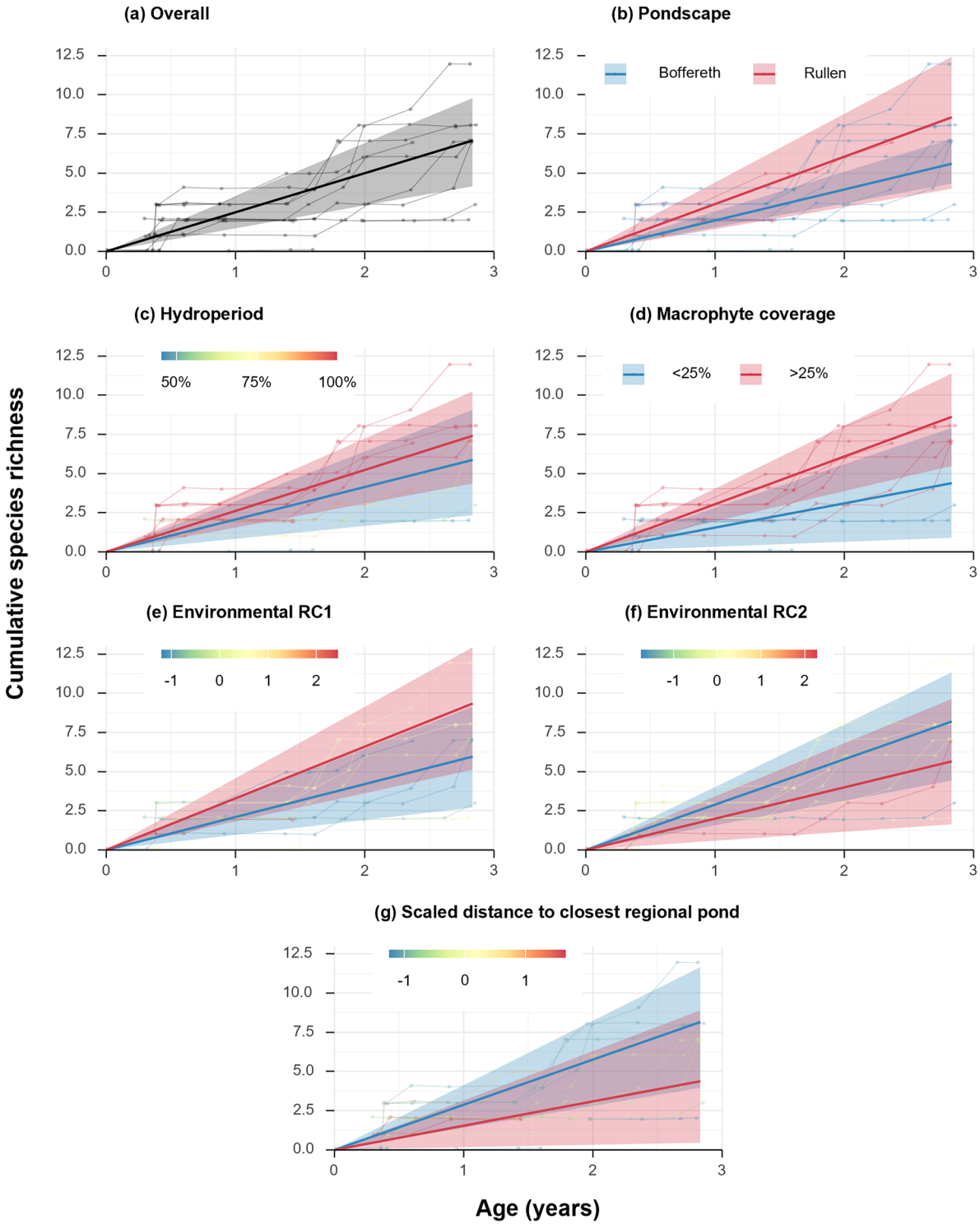


Fig. 3 Average cumulative species richness of cladocerans during the first three years after pond creation for each newly created pondscapes: Boffereth (green triangles) and Rullen (blue circles). Values are averaged across ponds per pondscapes. Error bars indicate the 95% standard error

accumulation rates were generally higher in Rullen compared to those in Boffereth (Fig. 3) and varied considerably between ponds within both pondscapes. When focusing on the overall accumulation patterns, we observed that, after an initial steep increase during the first months, species richness levelled off for nearly a year from month 7 onwards, to increase again in the second half of the second year after pond creation (Fig. 4). The pond BOF5 ultimately hosted the highest number of cladoceran species ($n = 12$) by the end of the three-year period.

Despite the observed difference in accumulation rate between ponds within pondscapes, we found moderate statistical support for a direct effect of pondscape identity per se, with 85.0% posterior probability of Rullen featuring a higher slope. An average pond (i.e. conditional on average characteristics, except for pondscape identity) in Rullen and Boffereth displays an estimated accumulation rate of 2.8 species per year (95% CrI [1.4; 3.9]) and 1.8 species per year (95% CrI [1.1; 2.6]), respectively (Fig. 4).

We found very strong statistical support that well-vegetated ponds feature higher accumulation rates than less-vegetated ponds (99.3% posterior probability of a positive effect). The average well-vegetated pond (highest recorded coverage of emersed or submerged macrophytes > 25%) displays an estimated accumulation rate of 2.7 species per year (95% CrI [1.3; 3.9]), while the average less-vegetated pond displays an estimated accumulation rate of 1.2 species per year (95% CrI [−0.3; 2.7]) (Fig. 4). This corresponds to a difference in accumulation rate of 1.5 species per year (95% CrI [0.3; 2.5]). We also found moderate statistical support for a positive effect of hydroperiod (88.8% posterior probability). The average pond containing water during all sampling moments displays an estimated accumulation rate of 2.2 species per year (95% CrI [0.8; 3.5]), while the average pond containing water during half of the



sampling moments displays an estimated accumulation rate of 1.7 species per year (95% CrI [0.5; 2.9]) (Fig. 4). This corresponds to an estimated difference

◂**Fig. 4** Estimated, conditional linear species accumulation trajectories as a function of pond age, all other conditions being held at the average value across the dataset. Individual points represent observed cumulative species richness data across ponds and time points, with points belonging to the same pond being joined by thin lines. Estimated linear species accumulation trajectories are shown using thick lines, with shaded areas representing 95% credible intervals. For continuous conditions (hydroperiod, environmental RC1, environmental RC2 and distance to regional pond), the trajectories for the lowest and highest observed values are visualized. **a** Estimated trajectory for the average pond; **b** estimated trajectory for the average pond in the pondscapes Boffereth and Rullen; **c** estimated trajectory for the average temporary and permanent pond, as defined by the pond with the lowest (45.4%) and highest (100%) observed hydroperiod, respectively, for visualization purposes; **d** estimated trajectory for the average pond with less and more than 25% macrophyte coverage; **e** estimated trajectory for the average pond with the lowest and highest observed value along the first rotated component (RC1) of the PCA on environmental variables; **f** estimated trajectory for the average pond with the lowest and highest observed value along the second rotated component (RC2) of the PCA on environmental variables; **g** estimated trajectory for the average pond with the lowest and highest distance to the closest regional pond

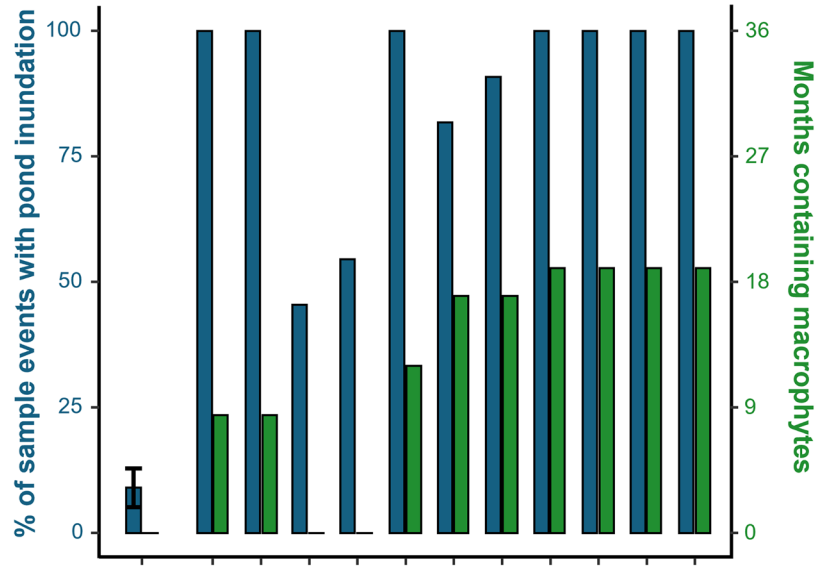
in accumulation rate of 0.5 species per year (95% CrI [−0.3; 1.3]).

We found the joint posterior distribution of macrophyte status and hydroperiod to be negatively associated, reflecting that macrophyte vegetation is, with moderately statistical support, better developed in ponds with longer hydroperiods than in ponds with shorter hydroperiods (Supplementary Information, Fig. S1.2). As a result of this collinearity, the model cannot fully disentangle the direct effects of macrophyte status and hydroperiod at a 95% certainty threshold. While we found very strong and moderate statistical support for the marginal effect of macrophytes and hydroperiod, respectively, the available data do not allow to fully isolate the effect of macrophyte status, leading to a more uncertain estimate and moderate statistical support. We found 88.1% posterior probability that both variables are directly related to the species accumulation rate, but only a 11.2% posterior probability for a pure effect of macrophytes (i.e. excluding the shared effect with hydroperiod), and a 0.7% posterior probability for a pure effect of hydroperiod (i.e. excluding the shared effect with macrophyte status; Supplementary Information, Fig. S1.2).

We found strong and moderate posterior support for an effect of local environmental conditions as summarized by the temporally averaged first and second rotated component coordinates, respectively. A one-standard-deviation increase in RC1, corresponding to larger and deeper ponds with lower TN and TP concentrations, was associated with an estimated increase in accumulation rate of 0.32 species per year (95% CrI [−0.11; 0.72]; 94.3% posterior probability of a positive effect), whereas a one-standard-deviation increase in RC2, corresponding to lower specific conductivity but higher pH, chlorophyll a and phycocyanin concentrations, was associated with an estimated decrease in accumulation rate of 0.22 species per year (95% CrI [−0.60; 0.21]; 88.1% posterior probability of a negative effect) (Fig. 4).

We found moderate posterior support for a positive effect of proximity to older regional ponds. Ponds close to an older regional pond showed an estimated accumulation rate that was 1.23 species per year higher than ponds farther away (95% CrI [−1.37; 3.44]; 83.9% posterior probability of a positive effect).

In terms of species composition, a clear nested pattern was observed during the last year of the study period, with species-poor ponds generally hosting a subset of the species present in species-rich ponds. Nestedness was highly significant under all considered null model schemes (observed NODF = 68.03; $p < 0.001$), except for the most conservative one ($p = 0.792$). In total, 16 cladoceran species colonized the newly created ponds during the study period. *Daphnia obtusa* Kurz, 1874 and *Chydorus sphaericus* (O.F. Müller, 1776) were by far the most widespread species, which colonized the vast majority of the ponds within the first three years of the pondscapes' existence (Fig. 5). *D. obtusa* emerged as the most successful colonizer, colonizing most ponds within the first six months after construction (Fig. 5). Nevertheless, colonization of *D. obtusa* in BOF7 was delayed until the third year, coinciding with a shift in local conditions, as this pond started retaining water for longer periods from that moment onwards (Janssens, pers. obs.). Overall, however, while being a successful colonizer, *D. obtusa* became less widespread as ponds became older, i.e. during the third year of the study period (Supplementary information Table S1.2). Other fast-dispersing species included *Bosmina longirostris* (O.F. Müller, 1785) and *Daphnia ambigua* (Scourfield, 1947), although their occurrences were



Species \ Pond	RUL7-15 & BOF8,10	RUL 1*	RUL 2*	BOF 7	BOF 9	RUL 16**	BOF 1	BOF 2	BOF 3	BOF 4	BOF 6	BOF 5	# Ponds with species
Daphnia obtusa Kurz, 1874		**3**	**3**	**24**	4	**2**	**5**	**5**	**7**	**5**	**5**	**5**	11
Chydorus sphaericus (O.F. Müller, 1776)		**14**	**5**	24	**35**	**5**	**32**	**32**	**24**	**5**	**5**	**5**	11
Simocephalus vetulus (O.F. Müller, 1776)						**5**	**24**	**28**	**24**	**7**	**19**	**24**	7
Daphnia pulex Leydig, 1860							22	5	7	22	5	22	6
Scapholeberis mucronata (O.F. Müller, 1776)						**29**		22	**19**	**22**		**19**	5
Peracantha truncata (O.F. Müller, 1785)							**35**	**32**	22	**22**		**32**	5
Pleuroxus aduncus (Jurine, 1820)						16	**35**	**32**			22	24	5
Alona guttata G.O. Sars, 1862							**35**				**24**	**32**	3
Picripleuroxus denticulatus (Birge, 1879)									**35**		22	**24**	3
Coronatella rectangula (G.O. Sars, 1862)						**16**					24		2
Bosmina longirostris (O.F. Müller, 1785)					4					5			2
Ceriodaphnia reticulata (Jurine, 1820)											**22**	**32**	2
Ceriodaphnia quadrangula (O.F. Müller, 1785)										**32**			1
Leydigia leydigi (Schödler, 1863)						**26**							1
Acroperus harpae (Baird, 1834)												**28**	1
Daphnia ambigua Scourfield, 1947												5	1
# Total species in pond	0	2	2	2	3	7	7	7	7	8	9	12	
# Species in third year	0	2	2	1	1	6	6	5	5	6	5	9	

Fig. 5 Upper: Barplot depicting the percentage of sampling moments that a given pond was inundated (blue) and the amount of months since creation that a pond contained any macrophytes (green). Lower: Month of first species detection in each newly created pond (ponds are ranked based upon their cumulative species richness). Species still present in the third year of a pond's existence are shown in bold. (*RUL1 and RUL2 were constructed in May 2023; **RUL16 in June 2022, these ponds were followed up until the pondscape was three years old, until they were 19 and 30 months old, respectively)

transient and typically observed only during a single sampling event.

In contrast to *D. obtusa*, *C. sphaericus* exhibited a more gradual colonization pattern, with most ponds only being colonized during their third year of existence. Despite its eventual widespread occurrence in the set of investigated ponds, its initial establishment was considerably slower compared to that of other cladoceran species. Also other chydorid species tended to colonize the ponds only in the last year. The increase in species richness

observed during the second and third year was indeed primarily driven by the arrival of chydorid species (genera: *Acroperus*, *Alona*, *Leydigia*, *Pleuroxus*, *Picripleuroxus*), in addition to *Simocephalus vetulus* (O.F. Müller, 1776) and *Ceriodaphnia* species. This increase in species richness was most pronounced in ponds that were more permanent and contained macrophytes (Fig. 5).

Discussion

Our results confirm earlier work from the same geographic region, showing that some species, notably *D. obtusa*, are fast in colonizing ponds and that chydorids are slower, even though some species such as *Chydorus sphaericus* eventually become widespread (Louette & De Meester, 2005). We also show that species accumulation trajectories differ among ponds and that the rate of species accumulation is higher in permanent ponds in which macrophytes establish.

The two most widespread species at the end of the study period (i.e. after three years) were *D. obtusa* and *C. sphaericus*. Both species were observed in eleven of the studied ponds. While the first observation of *D. obtusa* was in all but one pond within the first seven months of the ponds' existence, *C. sphaericus* was only observed in the second year or later in six out of eleven ponds. This observation is in line with Louette & De Meester, (2005), who also observed that *D. obtusa* was the dominant first colonizer in a different set of ponds in a different region, whereas chydorids colonized those ponds later in time. This contrasts with general surveys, where *D. obtusa* is not particularly common (Louette et al., 2007). This suggests a high dispersal ability, but it may also reflect a capacity of *D. obtusa* to deal with the unstable conditions typical for newly created ponds. Our data indeed show that the environmental characteristics of newly created ponds are highly variable in the first year of their existence and that conditions converge in the second and third year. If *D. obtusa* is better able than most other species to survive in very young ponds, then our observations might reflect establishment success rather than colonization dynamics. *D. obtusa* has a short generation time and reproduces quickly compared to many other *Daphnia* species (Milbrink et al., 2003), and this might contribute to his success as early colonizer. Notably, *D. obtusa* became less widespread in the third year of our study. As ponds age, environmental pond conditions stabilize and more species colonize the ponds, and *D. obtusa* seems to be less successful in maintaining detectable populations. *D. obtusa* was also a common early colonizer in newly created agricultural ponds in other regions in Belgium (Louette & De Meester, 2005; Louette et al., 2008), and in newly created ponds in Czech Republic studied by Juračka et al. (2016). This consistency across studies in different European regions suggests a general pattern, in which *D. obtusa* might be typical for temporary water bodies (Forró et al., 2003; Reynolds et al., 2004) and in more permanent systems might behave more like a so-called fugitive species that is very successful in early colonization and rapid population growth in young habitats and can occur in the landscape thanks to this effective dispersal even though it is weak in competition (Tilman et al., 1994).

There are a number of chydorid species, *Simocephalus vetulus* and *Scapholebreris mucronata* (O.F. Müller, 1776), that occurred in multiple ponds, but were only first observed in the second or third year of a pond's existence. This second wave of colonization coincided with the establishment of macrophytes in the ponds, which happened in month 18 or later. These species tend indeed to be either macrophyte-associated, such as chydorids (*Acroperus*, *Alona*, *Leydigia*, *Pleuroxus*, *Picripleuroxus*), *S. vetulus* and *Ceriodaphnia* spp. (Błędzki & Rybak, 2016), or prefer sheltered waters, typically provided by emergent or floating-leaved vegetation (the hyponeustic species *Scapholeberis mucronata*). This suggests that the association that we observed between the development of macrophytes and the rate of colonization of the ponds by zooplankton reflects a causal relationship, where the presence of macrophytes increases cladoceran richness by providing greater habitat complexity and niche availability (Declerck et al., 2007; Choi et al., 2014). This interpretation is in line with observations by Juračka et al., (2016), who showed that macrophyte cover was an important predictor of microcrustacean species richness in recently created ponds. Similarly, in a recent study by Peso et al., (2025), contrasting young and old ponds in survey data, it was observed that older ponds have higher species richness than younger ponds, but that the difference is especially striking in older ponds with a well-established vegetation of macrophytes. Given the strong correlation between macrophyte

establishment and hydroperiod, however, hydroperiod should also be considered when interpreting patterns of species accumulation. The positive association between RC1 and species accumulation is consistent with this interpretation, as higher RC1 values reflected larger and deeper ponds with lower TN and TP concentrations. Larger and deeper ponds are likely to retain water for longer periods, while lower nutrient concentrations favour the development of macrophytes and might themselves reflect the presence of macrophytes, given that macrophytes can absorb dissolved nutrients from the water column and reduce sediment resuspension and internal phosphorus loading. Earlier studies have also documented a central role of hydroperiod in structuring cladoceran communities (Coccia et al., 2024). Variation in hydroperiod of newly created ponds is therefore likely to, overtime, promote community divergence. This underscores the value of incorporating ponds with differing hydroperiod regimes within a pondscape in the context of nature restoration, as it can promote habitat heterogeneity and support freshwater biodiversity at the regional level.

In our study, macrophytes and hydroperiod are strongly collinear, which does not enable us to reliably assess their unique effects. Given that the later wave of colonization involved cladoceran species for which their association with macrophytes is very well documented, it seems logic to interpret our data as indicative of the importance of macrophytes, in line with the importance of well-developed macrophyte vegetation in determining the diversity of young ponds in earlier work (Peso et al., 2025). It is therefore difficult to derive strong guidelines on the importance of hydroperiod variation in nature restoration projects. Yet, given the unique species associated with temporary ponds (Williams, 1997; Céréghino et al., 2007), it is likely that the creation of variation in hydroperiod in the design of pondscapes will increase regional diversity of newly established pondscapes. In doing so, it will be crucial to consider climate warming in designing new pondscapes, given its important impact on pond hydroperiod (Brooks, 2009; Reid et al., 2019).

Spatial isolation showed moderate posterior support for an effect on species accumulation in our study, with the estimated slopes suggesting that ponds located closer to existing regional ponds accumulated species at a higher rate. A potential influence of distance aligns with expectations that dispersal from nearby source habitats can facilitate early community assembly, and earlier work indicated that regional species richness affects colonization dynamics (Louette & De Meester, 2005). It is also in line with studies showing that spatial context, connectivity and landscape structure can influence colonization rates and community assembly in newly created ponds (Frisch et al., 2012; Juračka et al., 2016). Given the limited number of ponds included in the present study, and the limited variation in the distance to the closest regional pond, our ability to detect an effect of distance was low.

Conclusion

Our results show that *D. obtusa* is a fast colonizing cladoceran species that successfully establishes in newly created ponds already in first few months after pond creation. After three years, its dominance declines when additional species arrive. This pattern suggests that *D. obtusa* thrives in unstable, early-succession pond conditions where it temporarily can be the dominant species, before other species such as *C. sphaericus* and *S. vetulus* become established. Our study also confirms that macrophyte presence is a key factor explaining variation in species richness build-up between pondscapes and among individual ponds, supporting the additional colonization by macrophyte-associated zooplankton taxa. Given the association between macrophyte establishment and hydroperiod, both habitat structure and pond permanence should be considered when interpreting early cladoceran community assembly. In addition to promoting conditions that favour macrophyte establishment, the presence of nearby older ponds might also be a factor that is worth considering when selecting or designing restoration sites, as these source habitats may facilitate colonization when newly created ponds lack an established propagule bank. The findings of our study highlight the role of macrophyte presence in shaping early freshwater community development during early pond succession, which offers valuable insights for designing effective pond creation supporting freshwater biodiversity.

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Data availability All code and data to reproduce the analysis are archived in a permanent, DOI-assigned Zenodo repository linked to the GitHub project: https://doi.org/10.5281/zenodo.20407444.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

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