Community assembly of cladoceran zooplankton in relation to pond age and the establishment of macrophytes and fish

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Abstract

1. A substantial body of research has assessed the relative importance of local and regional factors shaping ecological communities, often using lakes and ponds as model systems. However, little is known about how habitat age can help to explain current community structure. The present study investigates the effect of pond age on zooplankton community composition and diversity in farmland ponds.
2. We used a dataset of >100 morphologically similar farmland ponds of different ages (recent: 3 years; older: 4-15 years, and old: > 15 years) to analyse the extent to which the diversity and composition of current water flea assemblages (Crustacea; Anomopoda) reflect variation in pond age.
3. Young ponds had lower local species richness than old ponds and their communities were nested within those in ecologically similar old ponds. The presence of macrophytes enhanced local richness by promoting the establishment of additional species, while the presence of fish resulted in community turnover and lower local species richness compared to old ponds without fish.
4. Our results demonstrate that pond age is an important factor determining cladoceran species richness and community composition. Newly created ponds are rapidly colonized by regionally common species, while the colonization by regionally rare species was more restricted. In older ponds, effective species sorting occurred in response to changes in local environmental conditions associated with the establishment of macrophytes and fish.
5. These findings highlight the need for longer time perspectives in colonisation studies to understand patterns of community succession in newly created habitats.

Keywords: colonisation, species richness, community composition, nestedness, turnover

1. Introduction

Successful colonization of vacant habitat patches relies on the ability of species to reach the habitat and settle. The probability that a habitat patch is reached depends on the dispersal capacity and the regional abundance of the species (Catano et al., 2021), the degree of habitat connectivity (Tornero et al., 2016), and chance events (Talling, 1951; Cornell, 1992; Shurin, 2000). Once a species has arrived, it has to survive, grow and successfully reproduce for successive generations to persist. Successful colonization thus depends on the interaction of the ecological characteristics of the species with the abiotic and biotic properties of the habitat patch (Caley & Schluter, 1997; Shurin, 2000; Cottenie & De Meester, 2004; Kraft et al., 2015). Local and regional processes operate simultaneously (Loreau, 2000; Cottenie et al., 2005; Leibold & Chase, 2018), but the relative importance of regional factors is expected to decrease over time as community assembly progresses (Tilman et al., 1997; Mouquet et al., 2003; Alexander et al., 2012; Hessen et al., 2019).

Community assembly in new habitats can follow several non-mutually exclusive trajectories depending on the traits of colonizing species and on temporal changes in local biotic and abiotic properties of the focal habitat (Fig. 1). If early colonizing species are able to coexist with species that arrive later, local diversity may gradually increase over time and the species present in young habitats can form a nested subset of the species assemblage in older habitats (Fig. 1, scenario 1). Alternatively, if there is a trade-off between the dispersal ability of species and their competitive strength (Levins & Culver, 1971; Tilman, 1994), species that arrive later may replace early colonists via local competitive exclusion (Fig. 1, scenario 2). If this happens, the species composition of older habitats will differ from that of new habitats (species turnover), even when environmental conditions remain the same. Under this scenario, local diversity can decrease, stabilize or increase with time. Under a scenario of priority effects, the early colonizing species may reduce resource availability in the habitat and build up a numerical

advantage, leading to a reduced establishment success of subsequent immigrants (Fukami 2015). Such priority effects may be enforced by local adaptation of the resident populations of early colonist species (evolution-mediated priority effects; De Meester et al., 2002; De Meester et al 2016) (Fig. 1, scenario 3). In the case of strong priority effects, the community may remain relatively unchanged over time. Finally, it is possible that dispersal limitation is overall weak and that most species from the regional species pool are able to colonize the focal habitat patch in a relatively short period of time (Fig. 1, scenario 4). In this situation, local communities may still change over time due to species sorting when habitat conditions change (Alexander et al., 2012). Species sorting refers to the process where variation in local community composition results from differential responses of species to local abiotic and biotic factors (Leibold et al., 2004). A specific case of species sorting related to habitat age can be mediated by organism groups that have profound influence on the community of other organism groups and are dispersal limited themselves. Indeed, the establishment of foundational species (i.e. species with a disproportionate large impact on other species) or keystone species (i.e. species with a large impact on other species, even at very low densities) can change the environment in ways that alter the resident community and/or determine the establishment of later arrivals (Schoener & Spiller, 1996; Shurin, 2001; Shurin & Allen, 2001; Kikvidze, 2015). Macrophytes and fish are examples of foundational and keystone species, respectively, in lentic ecosystems. Both organism groups need time to successfully colonize newly created waterbodies (Kristensen et al., 2020; Sø Stage et al., 2020), but once they are present, they can have profound effects on the community of other organism groups (Kerfoot & Sih, 1987; Jeppesen et al., 1998).

Ponds are excellent model systems to empirically study patterns of species colonization because they have well-delineated habitat boundaries (De Meester et al., 2005). New ponds are also continuously being created for a variety of purposes (Oertli, 2018). Previous studies show that the majority of newly created ponds are colonized by zooplankton within the first months after

their creation (Cáceres & Soluk, 2002; Louette et al., 2008; Frisch et al., 2012, Hessen et al., 2019, Stehle et al., 2022). Other investigations show that local pond communities become more complex and increase in species richness over time (Alfonso et al., 2010; Miguel-Chinchilla et al., 2014). However, most studies on community assembly in newly created aquatic habitats focus on relatively short time scales (typically less than 4 years) (Cáceres & Soluk, 2002; Louette et al., 2008; Frisch et al., 2012), whereas studies considering longer time spans remain relatively limited (Sun et al., 2019; Damschen et al., 2019; Fu et al., 2021; Sferra et al., 2017). Such longer-term perspective is needed for understanding community assembly, as some of the patterns might develop only after longer time spans (Wolkovich, 2014).

The present study aims to increase our understanding of patterns of cladoceran zooplankton community composition and diversity along a pond age gradient using a space-for-time approach based on data from a large number of small ponds that differ in age (from 3 years to > 15 years). More specifically, we aim to (1) test for the effect of pond age on local taxon richness and community composition, (2) explore to which extent patterns of community assembly are related to dispersal limitation, and (3) investigate to which extent colonization of ponds by macrophytes or fish influence cladoceran community succession.

We hypothesized that communities in young ponds would differ considerably from those in old ponds due to the combined effects of dispersal limitation and changing environmental pond properties with increasing pond age. In the absence of profound changes in local habitat conditions with increasing pond age, we predict that early colonizers can co-exist with later arrivals and that communities in young ponds thus form nested subsets of those in environmentally similar old ponds. We also expect that communities in young ponds will be dominated by regionally abundant species because they are better represented in the regionally occurring propagule pool and thus have a higher chance of colonizing newly created habitat patches (Olmo et al., 2020). Furthermore, we hypothesized that the presence of macrophytes or

fish will be associated with profound differences in local community assembly. More specifically, we predicted that communities in old ponds without macrophytes would have lower local species richness and form nested subsets of communities in old ponds with macrophytes due to enhanced niche availability in the presence of macrophytes (Jeppesen et al., 1998). We expected that the presence of fish would promote community turnover from larger bodied taxa in ponds without fish towards communities dominated by smaller bodied taxa in ponds with fish as a result of positive size selective predation (Kerfoot & Sih, 1987; Lemmens et al., 2018). Finally, we hypothesized that the presence of macrophytes would weaken the impact of fish on zooplankton by providing shelter against predation (dos Santos et al., 2020). Differences in community composition between old ponds with and without fish were therefore expected to be less profound when macrophytes are present.

2. Materials and methods

2.1 Study sites and data collection

This study uses an extensive dataset on cladoceran zooplankton community composition and major local environmental habitat conditions of a large number of Belgian farmland ponds (n = 103) that belong to different age categories (< 3 years old [n = 10]; 4-15 years old [n = 72], and > 15 years old [n = 21]) (Fig. 2). The dataset combines previously published data from older ponds (Declerck et al., 2006) and unpublished data from newly created ponds, all collected in the same year (2004). The data from the older ponds were originally used by Declerck *et al.* (2006) to examine the effects of surrounding land use on pond characteristics. All the ponds are located in similar agricultural landscapes across different regions of Belgium, with surrounding land use largely dominated by meadows and pastures. Ponds were grouped into three age categories based on information from pond owners because the exact year of pond creation is not known for the majority of ponds. All investigated ponds are relatively small and shallow (mean summer size, 208 m^2 [range 12-3348m^2] and depth, 0.8m [range 0.2-1.6m])

149 and are assumed to permanently hold water. None of the ponds in this study had surface water
150 connections with other waterbodies, nor were they entirely overgrown by terrestrial vegetation.
151 To the best of our knowledge, the investigated ponds have not been subjected to management
152 or fish stocking prior to this investigation.

153 The zooplankton community was sampled once in all ponds during late spring 2004 (May-
154 June). At the same time, major local environmental pond characteristics (conductivity, pH,
155 water transparency, thickness of the sludge layer, water depth, pond size, coverage with aquatic
156 vegetation, the presence of fish, and concentration of total nitrogen, total phosphorus,
157 chlorophyll *a* and total suspended solids) were determined. Data collection followed the
158 procedures described by Declerck et al. (2006).

159 Quantitative sampling of the zooplankton community was performed by collecting depth-
160 integrated water samples using a tube sampler at eight randomly chosen locations within each
161 pond. Water samples from these locations (6 L) were pooled and a subsample the pooled sample
162 (40L) was filtered through a conical plankton net (64 µm mesh size). Zooplankton samples
163 were preserved with glucose saturated formaldehyde (4% concentration). In the laboratory,
164 cladoceran specimens were identified to species level following Flössner (2000) and counted
165 (a minimum of 200 individuals).

166 Conductivity and pH were measured *in situ* using standard electrodes (WTW multiline F meter,
167 Geotech). Water transparency was determined with a Snell's tube because pond depths were
168 shallow (Louette and De Meester, 2005). The thickness of the pond sludge layer was measured
169 as the mean from the profile of two sediment cores taken into the mineral substrate at the deepest
170 location of the pond. Water depth was measured with a measuring stick along two perpendicular
171 transects at distance intervals of 1m. Pond size was determined using areal pictures (Google
172 Earth). The percentage of pond surface covered with aquatic vegetation (submerged and

emergent combined) was visually estimated in the field. The presence of fish was assessed once in each pond by point sampling with electrofishing at eight locations.

Total nitrogen and total phosphorus concentrations, chlorophyll *a* concentration and the amount of suspended solids were quantified from depth integrating water samples taken with a tube-sampler in the open water zone. Water samples were stored at 4°C in the dark until further processing in the laboratory. Total nitrogen and total phosphorus concentrations were measured after alkaline persulfate digestion (Koroleff, 1970) using a Technicon Auto-analyser.

Chlorophyll *a* concentrations were quantified spectrophotometrically in the laboratory after methanol extraction (Tallings & Driver, 1963). The amount of total suspended solids in the water column (TSS) was determined gravimetrically by filtering a known volume of pond water over a preweighted glass fibre filter (Whatman GF/F).

2.2 Data analysis

We first tested the hypothesis that communities in young ponds differ from those in old ponds by testing for differences in local taxon richness and community composition between the three age categories of ponds (< 3 years old; 4-15 years old, and > 15 years old). We tested for differences in local richness between age categories using ANOVA with associated post-hoc Tukey HSD for unequal sample sizes. Prior to statistical analysis, local richness was rarified to a subsample of 200 individuals to correct for differences in the number of sampled specimens between different ponds. Differences in community composition between age categories were investigated through a permutational multivariate analysis of variance (PERMANOVA; 'adonis' function vegan) with 999 permutations (Anderson, 2017) based on Sørensen-distances (ß-sor) and applying Bonferroni correction for multiple pairwise comparisons. Sørensen-distance was chosen to focus on the presence/absence of taxa, rather than on their abundances (Sørensen, 1948; Koleff et al., 2003), and because it can be partitioned into turnover (BetaSIM) and nestedness (BetaSNE) (Baselga, 2010).

A complementary analysis of multivariate dispersion ('betadisper' function vegan, 999 permutations) was applied to test for significant differences in dispersion among ponds (e.g. compositional variation as the average distance of each community to the centroid) between age categories (i.e. centroids calculated based on the average community composition in each pond age category) (Anderson et al., 2006).

Aquatic vegetation was virtually absent in the entire set of young ponds (always less than 5% cover). Young ponds also lacked fish. In contrast, a subset of the older ponds (both 4-15 years old and >15 years old, n = 68)) contained macrophytes and/or fish (mostly small bodied species such as Ninespine stickleback [*Pungitius pungitius*]). Macrophytes and fish may strongly affect cladoceran community richness and composition (dos Santos et al., 2020; Deosti et al., 2021), and thus potentially confound the relationship between zooplankton community characteristics and pond age. In subsequent, more detailed comparisons of young and old ponds, we therefore considered key ecological pond characteristics. While all young ponds lacked fish and macrophytes, there was no significant difference in the occurrence of macrophytes and fish between the two categories of older ponds (4-15 years old and > 15 years old) (Chi² tests; $\chi^2(1) = 0.441$, $p = 0.5$ and $\chi^2(1) = 0.38$, $p = 0.535$ for macrophytes and fish, respectively). In the set of older ponds (4-15 years and > 15 years old combined), we distinguished four categories of ponds based on the presence of macrophytes and fish; (1) ponds with no macrophytes and no fish (NM/NF, n = 25); (2) ponds with no macrophytes and with fish (NM/F, n = 20); (3) ponds with macrophytes (>25 % cover) and no fish (M/NF, n = 27); and (4) ponds with both macrophytes and fish (M/F, n = 21).

To test for the effect of pond age on community assembly independently of the presence of macrophytes and fish, we compared the young ponds (all of which lacked macrophytes and fish) with the corresponding category of old ponds with no macrophytes and no fish (NM/NF). More specifically, we formally tested for differences in richness and community composition

between both categories of ponds with an independent t-test and through PERMANOVA based on Sørensen dissimilarity (999 permutations), respectively. In addition, we tested for significant differences in community variation within both pond categories using an analysis of multivariate dispersion (Anderson et al., 2006). Subsequently, we partitioned variation in Sørensen dissimilarity into components of turnover (BetaSIM) and nestedness (BetaSNE) following Baselga (2010) using the 'beta.multi' function from the 'betapart' package (Baselga and Orme, 2012), and tested with PERMANOVA whether differences in community composition between young and similar old ponds reflect patterns of turnover and nestedness.

A priori we tested for systematic overall differences in local environmental ponds conditions between both pond categories using PERMANOVA (999 permutations) based on Euclidean distances for normalized environmental variables and performed separate independent t-tests for individual environmental variables. Except for pH, all environmental variables were transformed using log(x+1) prior to any statistical analysis.

Complementary to the partitioning of beta diversity, we investigated the extent to which species richer communities formed nested subsets of species richer communities by sorting the taxon-by-pond matrix based on the local richness in individual ponds, and subsequently testing whether this matrix was significantly nested using the NODF nestedness metric based on overlap and decreasing fill (nestednodf) (Almeida-Neto et al., 2007).The significance of the nested pattern was determined by comparing the observed NODF value with those produced by null models (n=999) following the PP algorithm (Ulrich & Gotelli, 2012). The PP-algorithm creates null matrices by randomizing row and column while preserving the average row and column from the original matrix. This approach provides higher statistical power to detect nested matrices and is especially suited for relatively small-scale surveys (Matthews et al., 2015). Subsequently, we tested the hypothesis that early colonizers can co-exist with later colonizing species by assessing whether communities in young ponds form nested subsets of

248 communities in old ponds. For this purpose, we tested the extent to which the rank site scores
249 of young ponds are systematically lower than the site rank scores of old ponds with no
250 macrophytes and no fish (NM/NF) using a Mann-Whitney-Wilcoxon test (rank sum). The site
251 rank scores in our NODF analysis were allocated in descending order by assigning higher rank
252 scores to species-richer sites than to species poorer-sites (Cerini et al., 2020 and Coccia et al.,
253 2016). In addition, we examined the extent to which communities in young ponds are composed
254 of regionally abundant species by correlating the species rank scores obtained from the NODF
255 analysis to the regional occurrence of individual cladoceran species in Flanders, as reported by
256 Louette et al., 2007 (Table S2.2). This correlation was assessed using a Spearman rank
257 correlation coefficient.

258 The effect of the presence of macrophytes and fish on local cladoceran community richness and
259 community composition was investigated by considering only the different categories of old
260 ponds (NM/NF, M/NF, NM/F, M/F). We first tested for the effect of macrophytes, fish, and their
261 interaction on local cladoceran richness using two-way ANOVA and associated Tukey HSD for
262 unequal sample sizes. Similarly, we conducted a two-way PERMANOVA to test for the effect
263 of macrophytes, fish and their interaction on the variation in Sørensen community dissimilarity
264 (Beta), and on patterns of turnover (BetaSIM) and nestedness (BetaSNE). Model significance
265 was assessed using 999 permutations. Variation in community dispersion in relation
266 macrophytes and fish was investigated using a complementary betadisper analysis. The effect
267 of macrophytes and fish on communities in old ponds was further investigated using multiple
268 separate NODF analyses as outlined above.

269 Since all young ponds were located in the north of Belgium (Flanders) and old ponds were
270 distributed across the country, we repeated the above mentioned analyses on the effect of pond
271 age using a subset of ponds only located in Flanders to ensure that the effects of pond age were
272 not spatially confounded (see Supplementary information S1).

All statistical analyses were conducted in R (version 3.5.3) using the packages betapart (function beta.multi), vegan (functions: adonis, betadisper, decostand, vegdist), pairwiseAdonis (function pairwise.adonis) and ggplot2 (function ggplot). The NODF analyses were done in the online tool Ned (https://ecosoft.alwaysdata.net/).

3. Results

A total of 46 cladoceran species were identified over the entire set of ponds. The three most frequently detected species were *Chydorus sphaericus*, *Simocephalus vetulus* and *Daphnia obtusa* (occurring in 94%, 83%, and 40% of the ponds, respectively). These species also occurred in the majority of young ponds (occurring in 100%, 60%, and 60% of the young ponds, respectively). Some species, such as *Alona guttata*, *Ceriodaphnia laticaudata*, and *Graptoleberis testudinaria,* were exclusively found in older ponds (4 years or older). The species observed over the entire set of young ponds accounted for 26% of the total number of species encountered in this study. None of the cladoceran species observed were exclusively restricted to young ponds.

The first set of exploratory analyses based on the three age categories of ponds revealed a significantly lower local species richness in young ponds compared to both categories of old ponds (4-15 years and >15 years old) (ANOVA, $F_{(2,100)} = 11.74$, $p < 0.001$) (Tukey HSD, $p < 0.001$ for both pairs) (Fig. 3). There was no significant difference in local richness between 4-15 years old ponds and ponds older than 15 years (Tukey HSD, $p = 0.290$). Similarly, PERMANOVA revealed significant differences in community composition between young ponds and the two categories of old ponds (4-15 years and > 15 years old) (pseudo-F = 2.76, $p = 0.001$) (post-hoc comparison; $p = 0.003$ for both pairs), but not between two categories of old ponds (post-hoc comparison; $p = 1.000$). Community dispersion was significantly lower in young ponds compared to both categories of older ponds (betadisper F = 20.23, $p < 0.001$) (post-hoc comparison; $p < 0.001$ for both pairs). There was no systematic difference in

298 community dispersion between the two categories of old ponds (post-hoc comparison; p =
299 0.809).

300 Young ponds had a significantly lower local richness than the corresponding category of old
301 ponds with no macrophytes and no fish (NM/NF) (T-test, $t(32.7) = -5.94$, $p < 0.001$). We
302 observed significant differences in community composition between young ponds and old
303 NM/NF ponds (Table 1). This pattern was significantly determined by nestedness, but not by
304 turnover (Table 1). Community dispersion was lower among young ponds compared to among
305 old ponds with no macrophytes and no fish (betadisper $F = 12.23$, $p = 0.001$). The
306 complementary NODF analysis revealed a significant nested pattern (NODF index = 46, $z =$
307 12.02, $p < 0.001$; Fig. 4A) with nestedness site rank scores of old ponds with no macrophytes
308 and no fish being significantly higher than those of young ponds (Mann-Whitney- Wilcoxon
309 (rank sum) test, $w = 31$, $p < 0.001$; Fig. 4B). In addition, species nestedness rank scores were
310 positively related to regional abundance of individual species (Spearman, $r = 0.43$, $p = 0.014$
311 (Fig. S2.1), indicating that the species most frequently observed in young ponds were also
312 regionally more common.

313 Young ponds and the corresponding category of old ponds with no macrophytes and no fish
314 (NM/NF), differed from each other with respect to eutrophication related variables
315 (PERMANOVA, pseudo-F= 3.34, p = 0.001). Separate t-tests confirmed that TN, TP, and sludge
316 depth were significantly lower in young ponds compared to the corresponding category of old
317 ponds. Old ponds with no macrophytes and fish were also characterized by lower water
318 transparency, shallower depth and smaller size compared to young ponds (Table S2.1).
319 Statistical analyses based on the subset of ponds only located in Flanders revealed overall very
320 similar results (see Supplementary information S1).

321 The presence of macrophytes and fish each were significantly associated with local cladoceran
322 richness in older ponds (Two-way ANOVA, $F_{(1,89)} = 10.53$, $p = 0.001$ and $F_{(1,89)} = 4.21$, $p =$

0.043 for macrophytes and fish, respectively), but there was no significant interaction effect between both factors ($F_{(1,89)}$ = 0.001, p = 0.980). Local richness was systematically higher in old ponds with macrophytes compared to old ponds without macrophytes and in old ponds with no fish compared to old ponds with fish (Fig. S2.2).

PERMANOVA analysis revealed a significant association between the presence of macrophytes and fish and the variation in community composition among the set of old ponds (Table 2). There was no significant macrophyte-fish interaction effect. The presence of macrophytes was associated with a significant turnover and nestedness component, while the presence of fish was only associated with turnover (Table 2). Community dispersion was higher in the NM/F category (0.48) compared to the other categories of old ponds (NM/NF, M/NF, M/F = < 0.41) ($F_{(3,89)}$ = 5.89, p = 0.001). An additional NODF analysis revealed significant nestedness patterns across the entire set of old ponds (NODF = 41.31, Z-score = 21.59, p = 0.001; Fig. 5A). The site rank scores of old ponds without macrophytes were systematically lower than the site rank scores of old ponds with macrophytes (Mann-Whitney-Wilcoxon (rank sum) test, w = 519, p = 0.0006) (Fig. 5B).

4. Discussion

We used a comparative study of young and old ponds to empirically assess the effect of pond age on variation in cladoceran community characteristics and relate patterns of community assembly to colonization by macrophytes and fish. Our results show that young ponds hosted multiple regionally common species. Young ponds had a lower local species richness compared to old ponds. Variation in community composition between young and ecologically similar old ponds was largely determined by patterns of nestedness. Old ponds with no macrophytes had a lower local richness compared to old ponds with macrophytes following a nested pattern. The presence of macrophytes also contributed to community turnover. The presence of fish was associated with lower local zooplankton richness and community turnover.

348 The observation that all young ponds in our study hosted multiple cladoceran species shows
349 that newly created ponds can be colonized relatively rapidly by species from the regional
350 species pool. This finding is in line with earlier empirical colonization studies (Frisch, 2007;
351 Louette, 2008; Stehle et al., 2022) and suggests that dispersal rates for zooplankton can be
352 relatively high (Louette & De Meester, 2005). However, the lower species richness in young
353 ponds compared to that in ecologically similar old ponds (no macrophytes and no fish) reveals
354 that communities in young ponds were not yet saturated with species within a period of three
355 years after their creation. This observation may hint towards the importance of dispersal
356 limitation for at least some species from the regional species pool, although unmeasured local
357 abiotic and biotic differences between the two pond age categories may also have played a role.
358 Young ponds and old ponds with no macrophytes and no fish (old NM/NF) differed from each
359 other with respect to nutrient concentrations (TN and TP), sludge layer thickness, water
360 transparency, pond size and water depth. This corroborates earlier investigations on the effect
361 of pond age on local environmental conditions (Hassall et al., 2012; Johansson et al, 2019).
362 Although nutrient concentrations determine the potential primary production in freshwater
363 systems (Chase & Ryberg, 2004; Elser et al., 2007; Carpenter et al., 2016) and can thus affect
364 zooplankton community composition and richness (Hoffmann & Dodson, 2005; Rogalski et al.,
365 2017; Storch & Okie, 2019), it is unlikely that these differences explain the observed variation
366 in community richness between young and old ponds. The ponds in our study, including the
367 category of young ponds, can be classified as eutrophic to hypertrophic (mean TN
368 concentrations young: 3.62 mg N L^{-1}; old: 5.26 mg N L^{-1} and mean TP concentrations young:
369 2.39 mg P L^{-1}; old: 4.08 mg P L^{-1}). Most empirical and experimental studies report unimodal or
370 negative diversity-productivity relations in zooplankton communities (Beisner et al., 2003;
371 Hoffmann & Dodson, 2005; Declerck et al., 2007; Šorf et al., 2015; Beklioğlu et al., 2020). It
372 is therefore unlikely that the observed positive association between richness and pond age in

373 our study resulted from higher resource availability in older ponds. Similarly, the higher
374 richness in old ponds compared to young ponds is unlikely to be linked to the larger size and
375 deeper depth of young ponds. Extensive research on species-area relationships (see review in
376 Rosenzweig 1995) shows that species richness within a taxonomic group tends to increase with
377 increasing habitat size (Preston 1960; Brose 2001; Oertli et al., 2002). Therefore, the positive
378 association between richness and ponds age is unlikely to result from differences in habitat size
379 between young and old ponds. The fact that communities in young ponds formed nested subsets
380 of those in ecologically similar old ponds suggests that early colonizing species can co-occur
381 with later colonizers. Earlier studies show that such co-occurrence patterns can result from
382 multiple non-exclusive processes (Diamond, 1975; Gilpin & Diamond, 1982; Ulrich, 2004;
383 Bell, 2005; Heino, 2013), including low interspecific competition and environmental niche
384 differentiation (Pantel et al., 2022). Our data do not allow to pinpoint the precise mechanism
385 behind the observed co-occurrence patterns between early and later colonizing species.

386 The negative relationship between the species nestedness rank and the regional abundance of
387 individual species revealed that communities in young ponds mainly comprised regionally
388 common species. Indeed, cladoceran communities in young ponds in our study were dominated
389 by regionally common species such as *Chydorus sphaericus, Daphnia obtusa* and
390 *Simocephalus vetulus*, whereas multiple regionally less common species (including *Alonella*
391 *nana*, *Moina macropa* and *Daphnia curvirostris*) only occurred in older ponds, and ponds that
392 are ecologically similar to the young ponds because they lack fish and macrophytes. Dispersal
393 limitation for regionally rare species is one potential explanation for this pattern. Zooplankton
394 are passive dispersers that rely on abiotic and biotic dispersal vectors (Allen 2007). None of the
395 ponds in our study were directly connected by surface water to other waterbodies. Colonization
396 therefore had to occur overland through dispersal of dormant stages (i.e. ephippia) (Panov et
397 al., 2004) by wind (Caceres and Soluk, 2002; Cohen et al., 2003; Vanschoenwinkel et al., 2008a;

Altermatt & Ebert, 2010) or biotic vectors such as amphibians (Bohonak and Whiteman, 1999), birds (Figuerola and Green, 2002; Green and Figuerola, 2005) or mammals (Vanschoenwinkel et al., 2008b; Vanschoenwinkel et al., 2011). Information on interspecific variation in dispersal capacity among cladocerans is relatively scarce (Cohen and Shurin 2003; Allen 2007, Pinceel et al., 2016), but low propagule density reduces dispersal rates (Vanschoenwinkel et al., 2008c; Chase et al., 2023). Regionally common species might be better colonizers for two possible reasons. Firstly, because they are regionally abundant, they may contribute more dormant eggs to the regional species pool increasing the probability that some will end up in a new pond (Chase et al., 2023). Secondly, it might be that the morphology of the dormant eggs of these species facilitate dispersal (e.g. hooks on ephippia of *Daphnia magna*) by increasing the likelihood of attachment to animal vectors or to be picked up by wind (Pinceel et al., 2016). The first explanation seems most likely given that the three rapidly colonizing species of young ponds in our study do not have ephippia with obvious traits that promote dispersal ability. Another explanation for the negative relationship between the species nestedness ranks and the regional abundance of individual species is that unmeasured local environmental conditions acted as environmental filters preventing the establishment of regionally rare species, even if their propagules effectively reached young ponds.

The observed larger variation in community composition in old ponds with no macrophytes and no fish compared to that in young ponds may suggest that the additional gradual colonization of older ponds by regionally less common species follows a more stochastic pattern (Jenkins and Buikema, 1998). However, this observation might also be the result of historical contingency (Fukami, 2015), including priority effects (Ward and Thornton, 2000; Fukami et al., 2005). Alternatively, this observation might be a purely statistical result arising from the smaller number of young ponds compared to the number of ecologically similar old ponds (n=10 and 25, respectively).

Our study shows that community assembly is not only directly affected by habitat age, but is also determined by the establishment of foundational or keystone species. Cladoceran communities in old ponds were strongly affected by the presence of macrophytes and fish. Both organism groups only occurred in old ponds, suggesting that they need time themselves to establish in newly created habitats. Once they are present, they exert a strong impact on community richness and composition. The observed higher local richness in old ponds with macrophytes compared to old ponds with no macrophytes is well in line with earlier studies showing the positive effect of macrophytes on the diversity of multiple aquatic organism groups, by promoting physical habitat complexity, enhancing niche availability, and providing refuges for prey against predation (Jeppesen. et al., 1998; Akhurst, 2017; Law et al., 2019; dos Santos, 2020). In addition, the presence of macrophytes may also have attracted water-associated birds (Özgencil et al., 2020), which could, in turn, have contributed to the colonization of ponds by cladoceran (Hessen et al., 2019; Moreno et al., 2019; Green et al., 2023).

Our finding that communities in old ponds with no macrophytes formed nested subsets of communities in old ponds with macrophytes suggests that the presence of macrophytes allows the establishment of additional species, most likely through enhanced niche availability (Law et al., 2019). The observed effect of macrophytes on community turnover might be related to changes in resource availability, such as phytoplankton biomass and size structure (Leibold, 1999), or structural changes (e.g. hard surfaces for browsers) once macrophytes are established. In old ponds, the presence of fish had a negative effect on local cladoceran richness and affected community composition largely by community turnover. These observations corroborate earlier studies showing that fishes are indeed highly effective visual predators that can exert strong top-down effects on their prey community by positive size-selective predation (Kerfoot & Shia, 1987; Stefanoudis, 2017). Our finding that fish and macrophytes determine community

448 structure in old ponds suggests that dispersal rates are sufficiently high for a considerable
449 number of species from the regional species pool to allow effective species sorting under
450 changing environmental conditions associated to the age-linked colonization of macrophytes
451 and fish.

452 While our study provides valuable insights into patterns of community assembly in newly
453 created habitats, there are also some limitations. Firstly, we used a space-for-time approach in
454 which a large number of ponds from different age categories were sampled once. Such an
455 approach does not capture temporal community dynamics, and thus prevents us from assessing
456 the role of priority effects or stochastic contingencies on community succession. Secondly, we
457 cannot entirely exclude potential collinearity between pond age and unmeasured environmental
458 pond properties affecting community structure. However, we believe that the interpretation of
459 our results is robust as we assessed a variety of physical, chemical and morphometric pond
460 variables (>10 variables in total) that well represent the major ecological gradients in the type
461 of ponds investigated (Declerck et al., 2006; De Bie et al. 2012) and that have previously been
462 used to study cladoceran niche width (Pantel et al., 2022).

463 Using a space-for-time approach based on extensive data from a large number of small ponds
464 that differ in age, our investigation highlights the pivotal importance of pond age in shaping the
465 composition and richness of zooplankton communities. Our findings indicate that the
466 colonization of newly created ponds by zooplankton follows a two-step trajectory. Initial
467 colonization of newly created ponds is marked by the establishment of regionally common
468 species, while the colonization by regionally rare species is more restricted, likely reflecting
469 dispersal limitation. Subsequently, age-associated establishment of ponds by macrophytes and
470 fish affects cladoceran community composition and richness by altering local environmental
471 pond conditions. This finding highlights the need for longer time perspectives in pond

colonisation studies to fully understand the process of community succession in newly created ponds.

Author contribution statement

Conceptualisation and development of methods: MP, LDM, PL, TDB, SD. Data analysis: MP, PL, BV, data interpretation: MP, LDM, PL, BV, SD. Preparation of figures and tables: MP, LDM, PL. Conducting the research and writing: MP, LDM, TDB, BV, GL, LB, KM, SD, PL.

Acknowledgments

This study was supported by the PONDERFUL project (Grand No. H2020-LC-CLA-2019-2), funded by the European Union (H2020), by a KU Leuven Research Council grant (C16/23/003) and by a National Science Fund Flanders grant (FWO GOA3M24).

Conflict of interest statement

The authors declare no conflict of interests.

Data availability statement

Data analysed in this work are available from the authors upon reasonable request.

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FIGURES

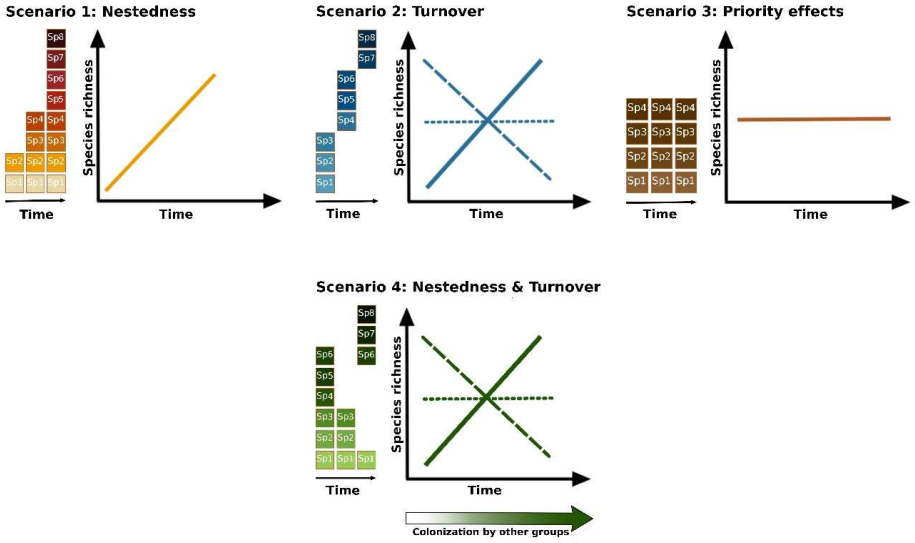


Figure 1. Illustration showing different non-mutually exclusive trajectories of community assembly in new habitats: (1) coexistence of early and later arriving species (nestedness), (2) replacement of early by later arriving species (turnover), (3) early species dominance leading to priority effects, and (4) community changes due to environmental change and colonization by other organism groups. Real-life scenarios may involve a mix of these trajectories.

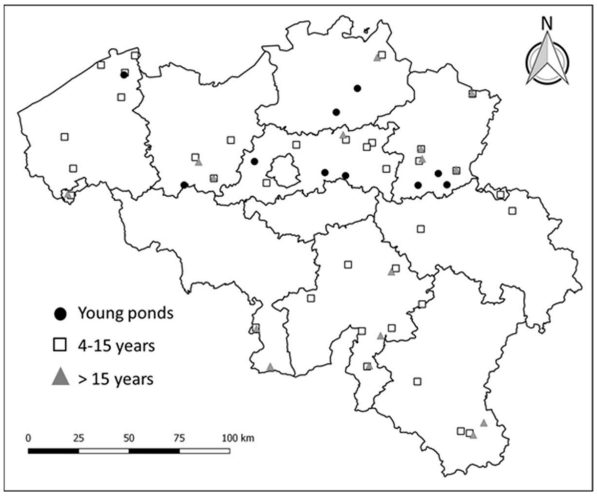
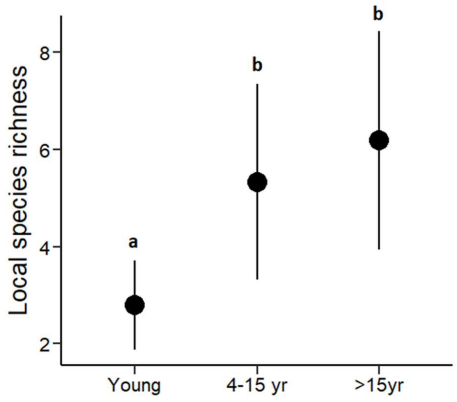


Figure 2. Map of Belgium with the geographical location of the investigated ponds (n = 103) from the three different age categories.



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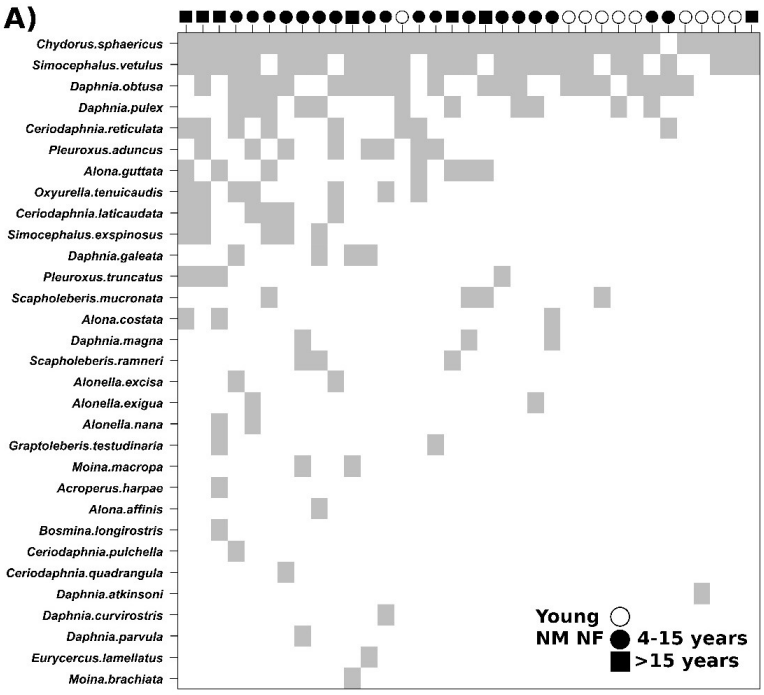
507 **Figure 3.** Mean local species richness for each category of pond age (young, > 4 years and >
508 15 years). Error bars denote the standard error to the mean. Pond age categories without letters
509 (a, b) in common differ significantly from each other.



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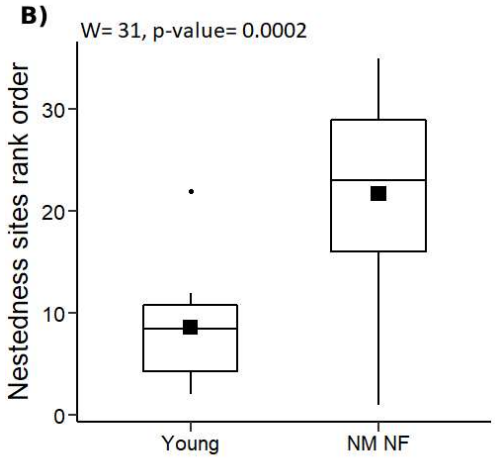

512

513 **Figure 4.** A) Taxon by pond matrix arranged according to maximum nestedness for young
514 ponds and older ponds without fish and macrophytes (NM/NF) (visualized in white and
515 respectively). Grey cells represent the occurrences of individual species in the corresponding
516 site. B) Boxplot showing the nestedness site rank order for young and the category NM NF.
517 Boxes represent interquartile range; central bar represents the median, black square represent
518 the mean, upper and lower whiskers represent scores outside the middle 50%.

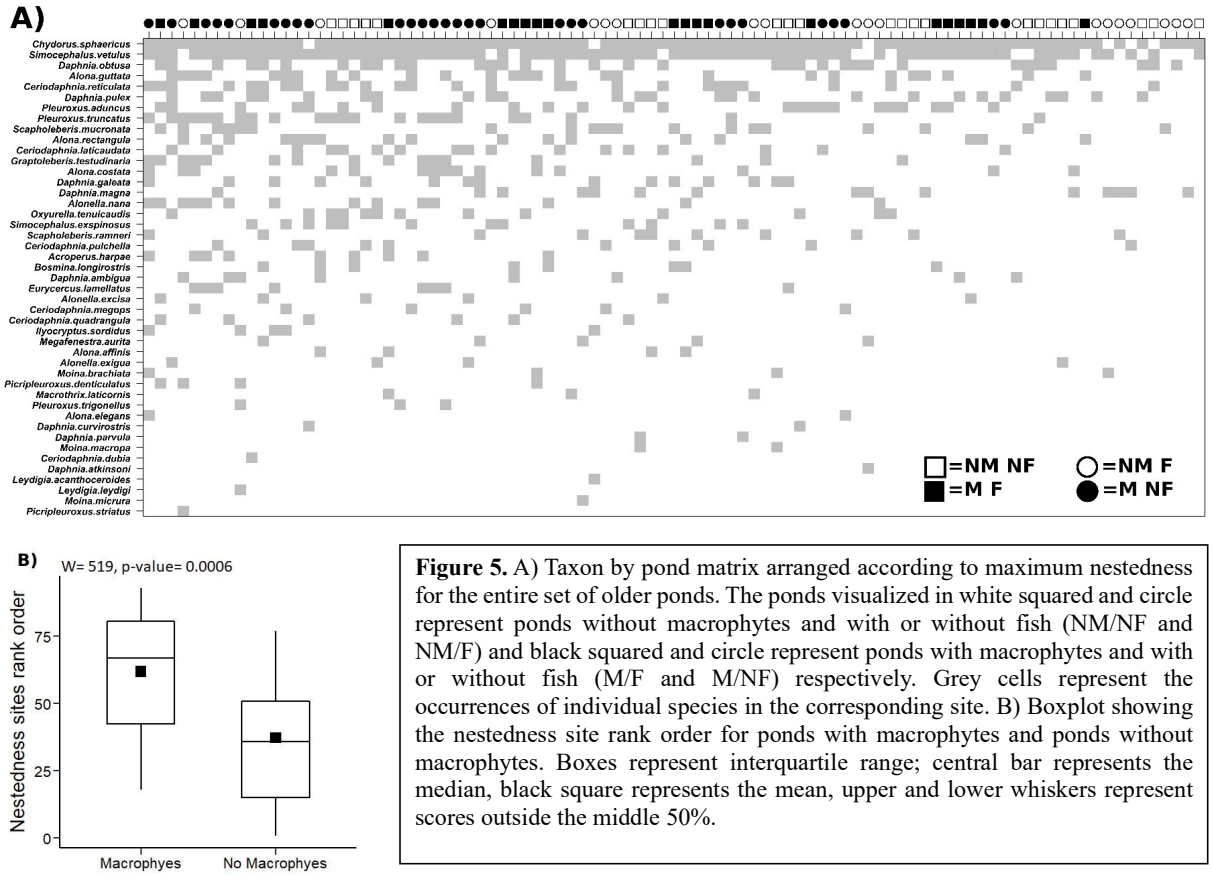

Figure 5. A) Taxon by pond matrix arranged according to maximum nestedness for the entire set of older ponds. The ponds visualized in white squared and circle represent ponds without macrophytes and with or without fish (NM/NF and NM/F) and black squared and circle represent ponds with macrophytes and with or without fish (M/F and M/NF) respectively. Grey cells represent the occurrences of individual species in the corresponding site. B) Boxplot showing the nestedness site rank order for ponds with macrophytes and ponds without macrophytes. Boxes represent interquartile range; central bar represents the median, black square represents the mean, upper and lower whiskers represent scores outside the middle 50%.

Table 1. Results of PERMANOVA analyses testing for the effect of ponds age on variation in community composition and its components of nestedness and turnover by comparing young ponds with ecologically similar old ponds (NM/NF).

	df	SS	R^2	F	P-value
community variation (BetaS)					
young vs old NM/NF	1	0.496	0.092	3.343	**0.005**
residual	33	4.896	0.908		
total	34	5.392	1.000		
community variation (BetaSIM)					
young vs old NM/NF	1	-0.253	-0.084	-2.568	1.000
residual	33	3.253	1.084		
total	34	3.000	1.000		
community variation (BetaSNE)					
young vs old NM/NF	1	0.475	0.440	26.005	**0.001**
residual	33	0.603	0.559		
total	34	1.078	1.000		

Table 2. Results of PERMANOVA analyses testing for the effect of macrophytes, fish and their interaction on variation in community composition and its components of nestedness and turnover in the set of old ponds.

	df	SS	R^2	F	p-value
community variation (BetaS)					
macrophytes	1	0.813	0.042	4.220	**0.001**
fish	1	0.711	0.037	3.690	**0.002**
macrophytes * fish	1	0.342	0.018	1.776	0.081
residual	89	17.151	0.901		
total	92	19.018	1.000		
community variation (BetaSIM)					
macrophytes	1	0.512	0.037	3.758	**0.003**
fish	1	0.609	0.045	4.464	**0.002**
macrophytes * fish	1	0.263	0.019	1.929	0.115
residual	89	12.143	0.897		
total	92	13.528	1.000		
community variation (BetaSNE)					
macrophytes	1	0.126	0.091	8.951	**0.001**
fish	1	-0.016	-0.011	-1.151	0.875
macrophytes * fish	1	0.019	0.014	1.401	0.383
residual	89	1.257	0.906		
total	92	1.386	1.000		

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