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Influence of a new fishpond design on invertebrate community biodiversity and secondary production

Marc Roucaute[1,*], Joël Aubin[1], Sarah Nahon[2] and Christophe Jaeger[1]

[1] UMR SAS, INRAE, Institut Agro, 35000 Rennes, France
[2] UMR MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, INRAE, Sète, France

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Abstract – The aim of this study was to compare the impact of three aquaculture production systems on the biodiversity and productivity of aquatic invertebrates. We compared two conventional fishpond designs (extensive and semi-intensive) with a new design combining a semi-intensive carp polyculture fishpond with a planted lagoon, called coupled semi-intensive design. All fishponds were stocked with the same proportions of common carp, roach, and Eurasian perch. Fish density was double in coupled semi-intensive and semi-intensive ponds compared to extensive ponds for which no formulated feed was provided. Benthic macroinvertebrates were sampled in May and September. Zooplankton was sampled monthly from May to November. For benthic macroinvertebrates, community taxonomic richness, biomass, production, and mean individual dry mass were higher in lagoons than in the coupled semi-intensive, semi-intensive and extensive fishponds. Zooplankton production was highest in extensive fishponds and lowest in coupled semi-intensive ponds. Zooplankton production peaked in summer and was lower than benthic macroinvertebrates production in May and September. *Asellus aquaticus*, whose production was higher in September than May, was the dominant macroinvertebrate in lagoons, but was almost absent from all fishponds. *Bosmina longirostris*, the most productive plankton taxon, especially in extensive fishponds, reached peak production in July and August. Our study highlighted the functional role of a shallow, fishless, planted lagoon linked to the fishpond for biodiversity and production of benthic macroinvertebrates and zooplankton.

Keywords: Integrated Multi-Trophic Aquaculture / fish polyculture / benthos / zooplankton / pond / benthic macroinvertebrates

1 Introduction

The demand for food from aquatic sources continues to increase (FAO, 2024). The proportion of food provided by aquaculture has increased as wild fish stocks continue to decline. While aquaculture may reduce pressure on aquatic ecosystems, it also presents environmental threats, especially degradation of water quality and consumption of resources to feed fish. Consequently, effort has been invested in developing new aquaculture approaches that would alleviate these pressures on ecosystems.

At the same time, pond ecosystems are threatened in agricultural landscapes (Oertli *et al.*, 2005a) and often overlooked in environmental conservation policies. In the European Union (EU), the Water Framework Directive, which intends to restore all continental water bodies to good ecological status, considers only standing waterbodies larger than 50 ha (European commission, 2003). However, smaller ponds are more common and also provide most freshwater biodiversity (Davies *et al.*, 2008). Well-designed and managed artificial ponds, such as fishponds used in aquaculture, can provide shelter for certain threatened species at the landscape scale and serve as reservoirs for neighboring natural systems (Oertli, 2018; Vanacker *et al.*, 2015; Zamora-Marín *et al.*, 2021).

Considering invertebrate communities (i.e. benthic macroinvertebrates and zooplankton) in the context of a fishpond system is particularly relevant for three reasons: their role as indicators of ecosystem quality, their ecological functions, and their role as a potential food source for the fish reared in ponds. For more than a century, the biodiversity of invertebrate communities has been considered a valuable bioassessment tool for determining the ecological status of freshwater ecosystems (Metcalfe, 1989). Invertebrates exhibit a wide range of sensitivities to multiple disturbances (Mondy, *et al.*, 2012)

*Corresponding author: marc.roucaute@inrae.fr

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and also have high functional diversity, which makes them key actors in ecosystems (Covich *et al.*, 1999; Tachet *et al.*, 2010; Vrba *et al.* (2023)). In the context of aquaculture, this functional diversity is especially important because invertebrates can use many food resources within a pond, especially decaying organic matter or living plants and phytoplankton. They break down and assimilate this organic matter, and their biomass becomes a food resource for fish. Zooplankton forms the basis of the diet of many freshwater juvenile fish (Geiger, 1983; Kloskowski, 2011; Ptatscheck *et al.*, 2020) and macroinvertebrates are often consumed by fish in later stages (Declerck, *et al.*, 2002; Garcia-Berthou, 2001; Gile *et al.*, 1990, Kloskowski, 2011). This contribution to the food web and energy flow in ponds is best assessed by quantifying invertebrates' secondary production (i.e., their production of biomass over time) (Benke, 2010; Dolbeth *et al.*, 2012). Although many studies have explored the secondary production of aquatic ecosystems, they mostly focused on rivers, streams or marine environments while lakes and wetlands received little attention (Benke, 2010). Most of these studies focused on macroinvertebrates, while freshwater zooplankton production has been poorly studied.

Oertli (2018) showed that fishponds tend to have lower invertebrate biodiversity than natural ponds and Lemmens *et al.* (2013) found that different management practices resulted in contrasting results for biodiversity. In the latter study, extensive fishponds (initial fish stock around 40 kg ha^{-1}) used to rear young fish or for recreational purposes, had higher plant and invertebrate biodiversity than ponds used for intensive carp farming (initial fish stock around 100 kg ha^{-1} and feed input of 1400 kg ha^{-1} year^{-1}). Fishpond management practices aiming at improving fish production through stimulation of trophic chains, such as feeding, liming, manuring, and fertilization have led to the eutrophication of many fishponds throughout Europe (Francová *et al.*, 2019). Eutrophication can alter the trophic structure of ponds and the contribution of plankton to fish diet (Vrba *et al.* (2023)). However, extensive fishponds are by definition far less productive than intensive ones and the trade-off between production and biodiversity may not be economically acceptable for aquaculture. Interestingly, Broyer and Curtet, 2011 showed that the biodiversity and biomass of invertebrates in intensive fishponds in three French regions were positively influenced by emergent shore vegetation and pond macrophyte cover. Nieoczym *et al.* (2023) showed that while all invertebrate taxa were not similarly affected by the presence of fish, the diversity in shore plant habitat tended to be higher than in open water. While important macrophyte development may occur in fishponds, depending on fish species reared, plant coverage can be seriously altered or destroyed by direct consumption or bioturbation of the pond bottom (Francová *et al.*, 2019). Beside individual pond design and management, Wezel *et al.* (2014) have shown the importance to consider the contribution of ponds to biodiversity at the larger scale. Lemmens *et al.* (2013) also observed that the diversity of pond management at the landscape level may favor regional biodiversity.

In this study, we explored the invertebrate biodiversity hosted by an aquaculture facility and the potential contribution of invertebrates' secondary production to food resources for fish, during an aquaculture experiment testing different pond designs. We especially tested the influence of different fishpond designs on invertebrate biodiversity and secondary production. Analyzing the experimental results for fish, Jaeger *et al.* (2021) showed that fish production (per total surface unit) in a coupled system (fed semi-intensive fishpond coupled with a fishless shallow planted lagoon) was twice as high as that in an extensive pond but slightly lower than in a semi-intensive pond, probably due to nutrient catchment in the planted lagoon. Water quality was better in the coupled system than in the semi-intensive pond, with no major phytoplankton bloom. We hypothesized that the fishless planted lagoon would have higher invertebrate biodiversity and secondary production than both the semi-intensive and extensive ponds, with the coupled system having a high level of fish production and good environmental performance.

2 Materials and methods

2.1 Experimental design

The study was conducted March-December 2016 in eight 500 m^2 ponds, with a mean depth of 80 cm, located at the U3E-INRAE experimental facility (Rennes, France, 48°07'13" N, 1°47'33" W). Ponds were earthen, manmade, rectangular shaped (20 × 25 m) with steep slopes and flat bottoms. The facility is located along the Flume River from which water is pumped into a reservoir used to fill the ponds through a pipe network arriving at the extremity of each pond. At the other extremity, another pipe allows to empty the ponds and harvest the fish. No liming or fertilization was applied. Formulated fish feed was the only element introduced in some ponds.

Three fishpond designs, one consisting of two coupled ponds, were tested in duplicates. The experimental setting is presented and summarized in Figure 1 (see also Jaeger *et al.*, 2021 for details). The small number of replicates (two) was due to pond availability and the desire to study identical systems with the same surface area, water input, and history to reduce confounding factors. The first pond design was an extensive fishpond (EXT) stocked with a fish assemblage of common carp (*Cyprinus carpio*), roach (*Rutilus rutilus*), and perch (*Perca fluviatilis*), with no feed supply. The second design, a semi-intensive fishpond (SI), had the same fish assemblage, but at twice the density and with feed supply (2440 kg ha^{-1}). Continuous pumping circulated the water within the fishpond. The third design was a coupled semi-intensive system (CSI). For this, a fishpond (CSIF) with fish assemblage and feed management similar to those of the SI design was coupled with a lagoon (LAG) of similar surface to the CSIF pond. One pipe was connected to a pump that circulated water continuously from the LAG to the CSIF. Coarse screens placed on the pump restricted animal exchanges between LAG and CSIF. Another pipe circulated water via gravity from CSIF to LAG. A net covered the pipe opening in CSIF to prevent fish from entering LAG. LAG ponds were planted with macrophytes (*Nasturtium officinale, Nuphar lutea, Glyceria aquatic, Ceratophyllum demersum* and *Pontederia cordata*), received no fish and were kept at shallower depth (30 cm) than the fishponds. The water level in all ponds was kept constant during the experiment by regular inputs of water from the neighboring Flume River. Fish were introduced four weeks after the ponds were filled. See Jaeger *et al.* (2021) for more details about the aquaculture systems, fish production, and water quality results.

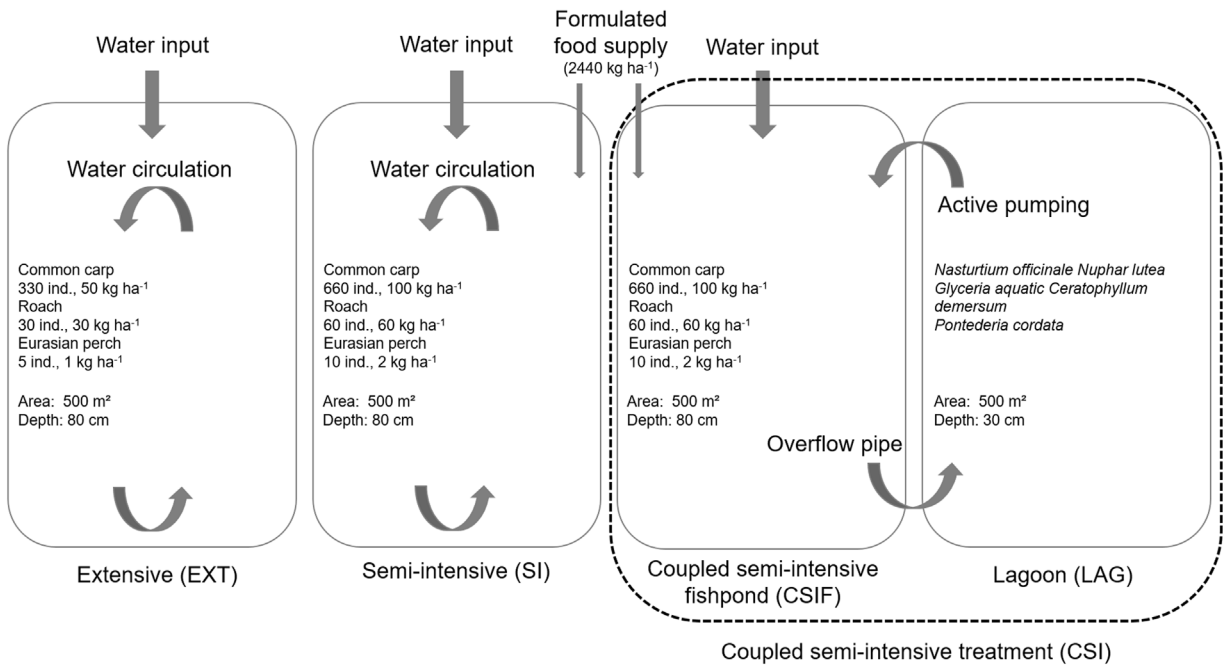

Fig. 1. Main characteristics of each pond design with the list of introduced species (with densities of specimen and mass per ha for fishes), surface and depth, with large grey arrows representing water circulation and small grey arrows formulated food supply.

2.2 Macroinvertebrate and zooplankton sampling and laboratory processing

Invertebrate sampling started after leaving a time lapse of six weeks for fish to settle in the ponds. Benthic macroinvertebrates (BMI) were sampled in spring (May 17) and late summer (September 6) according to a PLOCH-derived protocol (Oertli *et al.*, 2005b). The choice of the two sampling dates was based on previous experiments in pond mesocosms in the same area (Auber *et al.*, 2011; Bayona *et al.*, 2015; Caquet *et al.*, 2007). In these studies, BMI abundances and biomasses in May and September were very close to the annual mean while displaying contrasted community composition. Sampling only twice allowed to limit pond disturbance. On each sampling date, six sub-samples were collected in each pond using a 25 × 20 cm net sampler with 500 µm mesh: two sub-samples were collected along the shoreline and four offshore. The sampler was swept for 30 seconds along a 1 m band of substrate, resulting in a sub-sample of ca. 0.25 m^2 (100 × 25 cm band). The sub-sample was then transferred into a 1 L high-density polyethylene bottle and preserved in 70% ethanol for later analysis.

Zooplankton (ZPK), which has a higher turnover than BMI (Bayona *et al.*, 2014, 2015), was sampled seven times during the experiment with the protocol used in previous pond experiments (Hanson *et al.*, 2007; Roucaute and Quemeneur, 2007). A tube sampler (6.3 cm in diameter) was used to collect water from the entire water column, from 20 cm above the pond bottom, up to the water surface. It was operated from a small boat that moved slowly across the pond. At least four subsamples were collected and grouped in a gauged bucket; up to 6.5 L were collected per pond. The water was then filtered in a sieve with 32 µm mesh. Sieve contents were transferred into a polypropylene vial with a rose Bengal stain and preserved with a neutralized solution of formalin (4% final concentration).

In the laboratory, BMI and ZPK samples were rinsed in a sieve column of decreasing mesh size (which decreased by half with each sieve) ranging from 8 mm to 0.5 mm and from 1 mm to 40 µm, respectively, as described in previous studies (Bayona *et al.*, 2014; 2015; Stephenson *et al.*, 2007). Animals in each sieve were sorted, identified to the lowest practical taxonomic level, usually genus, using taxonomic handbooks for French fauna (Amoros, 1984; Pourriot and Francez,1986; Tachet *et al.*, 2010) and counted. When the abundance in a sieve was high (hundreds or more animals), it was subsampled using a Motoda (1959) splitting box according to the French procedure for aquatic invertebrate laboratory processing (AFNOR, XP T90 388, 2010). The subsampling procedure is detailed in Supplementary material 1. Invertebrates were observed under a stereomicroscope (Nikon® SMZ800N) with a maximum magnification of 80×.

2.3 Biodiversity analysis

The biodiversity of BMI and ZPK was analyzed separately to compare EXT, SI, CSIF-LAG pond designs. For each pond, taxonomic lists for all subsamples at all sampling dates were combined to calculate the annual α-diversity ($D_{\alpha\ \mathrm{year}}$). We also determined the ɣ-diversity (D_γ) combining the taxonomic lists of all ponds at all dates. The idea is that ponds are often not isolated. If different treatments (pond designs) result in different species compositions, alpha diversity may be low or look similar between ponds, while gamma diversity at the larger scale of a group of ponds may be higher (Lemmens et al., 2013; Wezel et al., 2014). Based on Jost (2007), diversity was expressed as Hill numbers of order 0, 1, and 2 (^{0}D, ^{1}D and

^{2}D, respectively). They correspond to taxonomic richness, Shannon diversity (exponential of Shannon entropy index), and Simpson diversity (inverse Simpson concentration index), respectively (Supplementary material 2).

Observed diversity ($_{obs}$D) may be subject to sampling bias, especially when densities differ greatly. We thus applied the interpolation-extrapolation approach developed by Chao *et al.* (2014) to compare Hill numbers between ponds based on a standardized sample size ($_{sam}$D). Chao *et al.* (2014) recommend caution when estimating ^{0}D based on extrapolations that are more than twice as large as the sample abundance. Thus, we standardized the estimates of diversity indices using a sample size that was twice as large as that of the pond with the lowest abundance (EXT2 for BMI: 5394 individuals). Estimates of biodiversity indices for other ponds were thus interpolated or extrapolated to a standardized sample size of 10,788 individuals. We used the same sample size for ZPK interpolation-extrapolation to standardize to the same sampling effort. The estimates were calculated using the Estimate D function of the iNEXT package (Hsieh et al., 2016) of the R software (R Core Team, 2020). All statistical analysis were performed using R software with the BiodiversityR package (Kindt and Coe, 2005), which is based on the Rcmdr graphical user interface (Fox and Bouchet-Valat, 2020) and uses the vegan package (Oksanen et al., 2019) for most statistical analysis. For univariate diversity indices ($_{sam}{}^{0}D_{\alpha}$, $_{sam}{}^{1}D_{\alpha}$, $_{sam}{}^{2}D_{\alpha}$), we tested effects among pond designs (EXT, SI, CSIF-LAG being tested as two different pond designs). All estimates were tested individually for normality using a Shapiro-Wilk test, and for homoscedasticity using Bartlett's test. Data that did not meet prior assumptions were log transformed. When normality and homoscedasticity were confirmed, variables (or log-transformed variables) were tested using one-way ANOVA followed by Tukey post-hoc tests.

2.4 Quantitative metrics: density, biomass, secondary production, biomass turnover, and individual biomass

Quantitative metrics of BMI and ZPK were analyzed separately. Raw abundances of BMI and ZPK measured at each sampling date were converted into density, expressed in number of individuals per m^{2}. For BMI, the individuals counted in each sub-sample were weighted by the area of the habitat sampled. The 25 cm band along the pond perimeter was considered the shoreline zone, while the rest of the area was considered offshore. All six weighted abundances of BMI subsamples were used to compute the mean pond density at a given date. For ZPK, abundance was first expressed as density per liter and then, using the mean pond depth, converted into density per m^{2}.

A single BMI and ZPK annual mean was then computed for each quantitative metric for each pond combining all sampling dates: density, expressed in number of individual per m^{2}, biomass (B), expressed in mg of dry mass per m^{2}, secondary production (P), expressed in g DM m^{-2} year^{-1}, biomass turnover (P:B ratio), expressed in year^{-1} and mean individual biomass (B: density ratio), expressed in mg dry mass. B and P were estimated using the fast sieving approach developed by Stephenson *et al.* (2007), which has been applied in previous studies (Bayona *et al.*, 2014; 2015), as summarized below. The fish community has been analyzed in details in Jaeger *et al.* (2021), but to ease comparison with invertebrate's biomass and production, fish yield originally expressed in kg fresh mass ha^{-1}, were converted into g DM m^{-2} using a conversion factor of 5 (Cresson et al., 2017).

2.4.1 Biomass estimation

Samples of mixed freshwater invertebrates were rinsed in the sieve column. Then, samples of all encountered taxa in each sieve were measured individually for total length to the nearest 0.05 mm under a stereomicroscope using an ocular micrometer. Mean individual size was obtained for each taxon in each sieve. Using allometric relations from the literature (Bayona *et al.*, 2015; Benke et al., 1999; EPA, 2003), sizes were converted into individual dry mass (DM). The abundance of each taxon (N) for a given sieve was multiplied by its corresponding individual DM to estimate the biomass in that size class. The sum of all sieves and taxa biomasses corresponded to the sample community biomass.

2.4.2 Secondary production estimation

Secondary production was calculated using empirical models to estimate individual daily growth rates. For BMI we used equations from the literature based on individual DM and water temperature (Morin and Dumont, 1994), and these two factors plus chlorophyll *a* concentration for ZPK (Zhou *et al.*, 2010). Equations from Morin and Dumont 1994, were chosen because they allowed us to separate the main insect orders which represent the more diversified and abundant taxa in pond communities and the main food resource for fish (Kloskowski, 2011). The error generated by the application of a general model for insect larvae to other taxa was negligible compared to the order of magnitude in production differences (Tagliapietra *et al.*, 2007). For each sieve and taxon, the growth rate was based on the previously estimated individual DM.

Secondary production was estimated for each month separately. For BMI secondary production estimation, we used the observed community structure in May for March, April, and May and that in September for September, October, and November, and the mean composition of May and September for June, July, and August. We used the same method to estimate secondary production of ZPK for March and April, using the community structure observed in May. Monthly mean water temperature was calculated from the temperature recorded weekly in each pond at the beginning of the afternoon.

Chlorophyll *a* concentrations to calculate ZPK secondary production were measured monthly (synchronized with invertebrate sampling) using the Lorenzen (1967) method. A second measurement of total chlorophyll *a*, described by Jaeger *et al.* (2021), was performed using a phytoPAM® probe (WALZ Co., Germany). We used a regression model to estimate chlorophyll *a* concentrations in November when the Lorenzen method was not used. The model formula was : $\text{Chl } a_{\text{Lorenzen}} = 5.349 \times \text{total Chl}_{\text{PhytoPAM}} - 33.348$.

The individual daily growth rate for each taxon in each sieve was applied to the corresponding biomass estimate. We

then summed the resulting production estimates of all taxa in all sieves within a given sample to represent the daily secondary production (P_{day}), which was then multiplied by the number of days of the corresponding month. The sum of all monthly production estimates was used to compute the total secondary production during the experiment (P_{year}).

For all quantitative metrics (density, B, P, P:B, B:density), we tested the effect of pond design on ponds (EXT, SI, CSIF-LAG being tested separately by pond). Prior to performing an analysis of variance (ANOVA), all metrics were tested individually for normality using a Shapiro-Wilk test, and then for homoscedasticity using Bartlett's test. Data that did not meet these conditions were log transformed. When normality and homoscedasticity were confirmed, metrics variables (or log-transformed metrics) were tested using one-way ANOVA followed by Tukey post-hoc tests for pairwise comparisons of ponds.

2.5 Multivariate analysis

A distance-based multivariate approach was used to assess differences in the contribution of BMI and ZPK taxa to secondary production. That is, to explore if the production was driven by the same taxa for different ponds designs. Differences in community composition of BMI and ZPK were analyzed using non-metric dimensional scaling (NMDS) based on Bray-Curtis distances. Dissimilarity matrices were calculated using untransformed P_{day}. The Bray-Curtis distance is sensitive to zero counts, which reduces the dissimilarity between samples both lacking the same taxa and may reduce the ability of the analysis to detect differences. Moreover, it may give too much weight to the many common taxa with low P_{day} whose signal may mask the one of the most productive ones. To improve the analysis, we therefore discarded the least productive taxa, including only those that represented at least 1% of P_{day} on a given sampling date (all ponds combined). The BMI dataset was thus reduced to 23 taxa (from 122), and the ZPK dataset to 21 taxa (from 58).

NMDS ordination was carried out based on the Bray-Curtis dissimilarity matrix calculated with the Braypart function of the Betapart package (Baselga and Orme, 2012). The dissimilarity among designs, dates, and their interaction was tested using permutational analysis of variance (PERMANOVA), with the sampling date set as strata, using the adonis function of the vegan package (Anderson, 2001). When overall effects were significant, effects of pond design and date were further explored using pairwise comparisons performed with the "pairwise Adonis" package (Martinez Arbizu, 2020). This package performs PERMANOVA on subsets of the data using the vegan adonis function associated with a Holm correction for multiple comparison tests. If effects of the pond design date interaction in the overall analysis were significant, pairwise comparisons of pond types also considered the effect of date to explore different temporal patterns of production.

The contribution of taxa to dissimilarities was analyzed to identify key taxa that contributed most to differences in secondary production patterns between designs or dates. It was tested using the SIMPER procedure (Clarke, 1993), which is based on a permutation approach, using the SIMPER function of the vegan package. We then further explored the production pattern of taxa that contributed significantly to dissimilarity and represented at least 10% of one pairwise dissimilarity (between pond designs or dates). We analyzed the production pattern of these taxa over time in more detail to identify effects of date or design using GLMs with negative binomial distributions. Effects of design, date, and their interaction were tested using Type II ANOVA followed by Tukey post-hoc tests to compare, date by date, the effect of pond design.

3 Results

3.1 Biodiversity

Overall we sampled 96800 BMI belonging to 116 taxa from 64 families (Supplementary material 3). Most of them were insects (69 taxa). More than a million ZPK belonging to 42 taxa were sampled (Supplementary material 3). They mainly consisted of micro-crustaceans (13 taxa) and rotifers (19 taxa). BMI ^{0}D differed significantly among the four pond types (Tab. 1, ANOVA, $F = 40.36$, $df_{treatment} = 3$, $df_{error} = 4$, $p = 0.002$). The LAG ponds in the CSI design had significantly higher taxonomic richness than all other pond types, while EXT ponds had significantly lower taxonomic richness than SI ponds. CSIF ponds in the CSI design did not differ significantly from EXT or SI fishponds. In constrast, BMI ^{1}D and ^{2}D did not differ significantly among the four pond types (Tab. 1, ANOVA, $F = 5.939$, $df_{treatment} = 3$, $df_{error} = 4$, $p = 0.059$ and $F = 2.712$, $df_{treatment} = 3$, $df_{error} = 4$, $p = 0.18$, respectively). Similarly, ZPK ^{0}D, ^{1}D, and ^{2}D did not differ significantly among the four pond types (Tab. 2, ANOVA, $F = 1.838$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.280$; $F = 0.458$, $df_{design = 3,\ dferror} = 4$, $p = 0.726$; and $F = 0.299$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.825$, respectively).

3.2 Density, biomass, production, turnover, and individual biomass

3.2.1 Benthic macroinvertebrates

Benthic macroinvertebrate density did not differ significantly among the four ponds types (Tab. 3, ANOVA, $F = 4.257$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.098$); for raw abundances see Supplementary material 5. Biomass was significantly higher in LAG ponds than in CSIF, SI or EXT ponds, which did not differ from each other (Tab. 3, ANOVA, $F = 28.48$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.004$). P_{year} was significantly higher in LAG ponds compared to CSIF and EXT ponds, but did not differ significantly from SI ponds, while SI did not differ significantly from CSIF or EXT ponds (Tab. 3, ANOVA, $F = 19.33$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.008$). The P:B ratio in LAG ponds was significantly lower than that of EXT ponds (Tab. 3, ANOVA, $F = 7.015$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.045$) and the B:density ratio of LAG ponds was significantly higher than those of the other pond types (Tab. 3, ANOVA, $F = 33$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.003$).

3.2.2 Zooplankton

Zooplankton density did not differ significantly among pond designs (Tab. 3, ANOVA, $F = 4.439$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.920$). In contrast, B was significantly higher in EXT ponds than in CSIF ponds (Tab. 3, ANOVA, $F = 9.75$, $df_{treatment} = 3$, $df_{error} = 4$, $p = 0.026$). ZPK P_{year} was highest in

Table 1. Estimate of benthic macroinvertebrate taxonomic diversity (D) by pond type. The exponent number is the q order 0, 1, or 2, which corresponds to the richness, exponential of the Shannon entropy index, and the inverse Simpson concentration index, respectively. Obs and sam indices correspond to estimates based on observed or standardized samples, respectively. May, Sept, and year indices correspond to estimates based on May or September sampling and the sum of both, respectively. Alpha (α) and gamma (γ) indices correspond to pond/pond design and overall facility-level diversity estimates, respectively. Mean $_{sam}{}^{0}D_{\alpha\ year}$ is shown ± 1 standard error (SE). Numbers in parentheses indicate family richness. Letters in exponent show significantly different groups of pond designs after Tukey post-hoc tests.

Pond	Design	$_{obs}{}^{0}D_{\alpha\ May}$	$_{obs}{}^{0}D_{\alpha\ Sept}$	$_{obs}{}^{0}D_{\alpha\ year}$	$_{sam}{}^{0}D_{\alpha\ year}$	Mean ± SE $_{sam}{}^{0}D_{\alpha\ year}$	$_{obs}{}^{0}D_{\gamma\ year}$	$_{sam}{}^{0}D_{\gamma\ year}$	$_{obs}{}^{1}D_{\alpha\ year}$	$_{sam}{}^{1}D_{\alpha\ year}$	Mean ± SE $_{sam}{}^{1}D_{\alpha\ year}$	$_{obs}{}^{1}D_{\gamma\ year}$	$_{sam}{}^{1}D_{\gamma\ year}$	$_{obs}{}^{2}D_{\alpha\ year}$	$_{sam}{}^{2}D_{\alpha\ year}$	Mean ± SE $_{sam}{}^{2}D_{\alpha\ year}$	$_{obs}{}^{2}D_{\gamma\ year}$	$_{sam}{}^{2}D_{\gamma\ year}$
EXT1	EXT	35 (20)	15 (9)	36	37.1	38.3±1.2[a]			9.8	9.8	7.5±2.3			6.5	6.5	4.8±1.7		
EXT2		24 (16)	23 (18)	37	39.5	5.2			5.2					3.1	3.1			
SI1	SI	51 (31)	31 (20)	59	58.0				12.4	12.4				8	8			
SI2		47 (32)	30 (22)	55	57.3	57.6±0.4[b]			12	12	12.2±0.2			7.4	7.4	7.7±0.3		
CSIF1	CSI	38 (27)	29 (17)	49	52.8				8.4	8.4				5.4	5.4			
CSIF2		44 (30)	29 (19)	50	47.0	49.9±2.9[ab]	116	87.4	5.9	5.9	7.2±1.2	18	17.9	3.8	3.8	4.6±0.8	12	12
LAG1	CSI	57 (35)	55 (36)	80	72.5				13.7	13.6				7.6	7.6			
LAG2		44 (25)	56 (41)	70	67.1	69.8±2.7[c]			18	18	15.8±2.2			12.8	12.8	10.2±2.6		
CSIF1 +LAG1		67 (42)	60 (40)	88	76.7				14.3	14.3				9	9			
CSIF2 +LAG2	CSI	59 (36)	62 (45)	81	71.5	74.1±2.6[c]			14.7	14.6	14.5±0.2			9.2	9.2	9.1±0.1		

EXT1: extensive pond replicate number 1; SI: semi-intensive; CSIF: coupled semi-intensive; LAG: lagoon.

EXT ponds and lowest in CSIF ponds, while LAG and SI ponds did not differ (Tab. 3, ANOVA, $F = 239.9$, $df_{treatment} = 3$, $df_{error} = 4$, $p < 0.001$). The P:B ratio did not differ significantly among designs (Tab. 3, ANOVA, $F = 1.341$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.400$). In contrast, the B:density ratio, which was log transformed before analysis, differed significantly among designs (Tab. 3, ANOVA, $F = 30.34$, $df_{design} = 3$, $df_{error} = 4$, $p = 0.003$), being significantly higher in LAG ponds.

All significant differences among pond types for biodiversity, density, biomass, production, turnover, and individual biomass both for benthic macroinvertebrate and zooplankton have been summarized in Table 4.

3.2.3 Fish production

SI ponds had the highest fish production, with 49.56 and 46.48 g DM m^{-2} for SI1 an SI2 respectively (Tab. 5), slightly above CSIF, with 41.04 and 40.76 g DM m^{-2} for CSIF1 and CSIF2 respectively. EXT ponds were the least productive with 11.6 and 12.02 g DM m^{-2} for EXT1 and EXT2 respectively. Statistical analyses are explained in Jaeger *et al.* (2021).

3.3 Multivariate analysis of daily community secondary production

3.3.1 Benthic macroinvertebrates

For benthic macroinvertebrates, NMDS showed differences between pond designs and dates (Fig. 2). Analysis of the distance matrix confirmed the significance of both factors and their interaction (PERMANOVA, $F = 2.17$, $df_{design} = 3$, $p = 0.006$; $F = 3.81$, $df_{date} = 1$, $p < 0.011$; and $F = 1.8$, $df_{interaction} = 3$, $p = 0.022$, respectively). Pairwise comparisons revealed that LAG ponds differed significantly from all other pond types. SI and EXT ponds also differed significantly from each other, but not from CSIF. Date had a significant effect in all pairwise comparisons, except for CSIF and SI ponds. An interaction between pond design and date was identified only for LAG and EXT, indicating that their BMI communities had different seasonal trajectories.

SIMPER analysis revealed that *Asellus aquaticus* and *Physa* sp. were the only taxa that significantly contributed more than 10% of dissimilarity between designs. They were more productive in LAG ponds compared to all fishponds (Suplementary material 6). Only the subfamily Orthocladiinae contributed significantly more than 10% to dissimilarity between dates (14.5%).

3.3.2 Zooplankton

For zooplankton, NMDS showed an effect of design and date (Fig. 3). Analysis of the distance matrix confirmed a significant effect of both factors and their interaction (PERMANOVA, $F = 7.6$, $df_{design} = 3$, $p < 0.001$; $F = 2.51$, $df_{date} = 6$, $p < 0.001$; and $F = 1.39$, $df_{interaction} = 18$, $p = 0.012$, respectively). Pairwise comparisons revealed significant effects of design and date on the dissimilarity for each pair of ponds. Comparisons between SI and LAG or EXT ponds revealed a significant design date interaction. Pairwise comparisons for all dates revealed a significant dissimilarity between them, except between June and September, which did not differ significantly from November. Pond type significantly

Table 2. Estimate of zooplankton taxonomic diversity (D) by pond type (two replicates). The exponent number is the q order 0, 1 or 2, which corresponds to richness, exponential of the Shannon entropy index, and inverse Simpson concentration index, respectively. Obs and sam indices correspond to estimates based on observed or standardized samples, respectively. Year indices correspond to estimates based on the sum of all sampling dates. Alpha (α) and gamma (γ) indices correspond to pond and overall facility-level diversity estimates, respectively. Mean $_{sam<sup>}{}^{\circ}D_{\alpha\ year}$ is shown as ± 1 standard error (SE).

Pond	Design	$_{obs}{}^{0}D_{\alpha\ year}$	$_{sam}{}^{0}D_{\alpha\ year}$	Mean ± SE	$_{sam}{}^{0}D_{\alpha\ year}$	$_{obs}{}^{0}D_{\gamma\ year}$	$_{sam}{}^{0}D_{\gamma\ year}$	$_{obs}{}^{1}D_{\alpha\ year}$	$_{sam}{}^{1}D_{\alpha\ year}$	Mean ± SE	$_{sam}{}^{1}D_{\alpha\ year}$	$_{obs}{}^{1}D_{\gamma\ year}$	$_{sam}{}^{1}D_{\gamma\ year}$	$_{obs}{}^{2}D_{\alpha\ year}$	$_{sam}{}^{2}D_{\alpha\ year}$	Mean ± SE	$_{sam}{}^{2}D_{\alpha\ year}$	$_{obs}{}^{2}D_{\gamma\ year}$	$_{sam}{}^{2}D_{\gamma\ year}$
EXT1	EXT	27	25.5	23.2 ± 2.3				6.5	6.5	5.8 ± 0.5				4.3	4.3	3.9 ± 0.5			
EXT2		25	20.8	5				5						3.4	3.4				
SI1	SI	32	24.5	25.5 ± 1				4.3	4.3	4.8 ± 0.4				2.6	2.6	3.1 ± 0.5			
SI2		31	26.6					5.2	5.2					3.6	3.6				
CSIF1	CSI	31	25.7	27 ± 1.4	42	34		5.6	5.6	6 ± 0.4	7.7	7.7		3.6	3.6	4.1 ± 0.5			
CSIF2		29	28.4					6.4	6.3					4.7	4.7				
LAG1	CSI	34	28.9	27.9 ± 1				6.7	6.7	5.5 ± 1.3				4.9	4.9	3.5 ± 1.4		5	5
LAG2		29	26.9					4.2	4.2					2.1	2.1				
CSIF1 + LAG1	CSI	37	29.7	30.8 ± 1.1				7.7	7.7	7.3 ± 0.4				5.6	5.6	4.8 ± 0.8			
CSIF2 + LAG2		36	32.0					7	7					4.1	4.1				

EXT: extensive fishpond; SI: semi-intensive fishpond; CSIF: coupled semi-intensive fishpond; LAG: lagoon.

Table 3. Benthic macroinvertebrate and zooplankton community mean (across replicates) quantitative metrics ± 1 standard error (SE). N is the mean density per sampling date expressed in individuals per m^2; B is the mean community biomass per sampling date expressed in mg of dry mass per m^2; P is the annual secondary production $g.m^{-2}.y^{-1}$; P:B is the turnover ratio of biomass per year; and B:N is the mean individual dry mass expressed in μg.

Pond type	Mean density ± SE (ind m^{-2})	Mean B ± SE ($mg.m^{-2}$)	Mean P_{year} ± SE ($g.m^{-2}.y^{-1}$)	Mean P:B ratio ± SE (y^{-1})	Mean B:density ratio ± SE (μg)
Benthic macroinvertebrates					
EXT	2313 ± 283	228 ± 26^{a}	3.6 ± 0.1^{a}	16.1 ± 1.6^{b}	98.736 ± 0.946^{a}
SI	3373 ± 329	478 ± 106^{a}	5.6 ± 0.66^{ab}	12.1 ± 1.3^{ab}	139.994 ± 17.799^{a}
CSIF	3289 ± 1590	245 ± 54^{a}	3.4 ± 1.2^{a}	13.6 ± 1.8^{ab}	86.640 ± 25.450^{a}
LAG	6694 ± 847	1920 ± 290^{b}	14.5 ± 2^{b}	7.5 ± 0.1^{a}	285.889 ± 7.189^{b}
Zooplankton					
EXT	$2.40 \pm 0.10 \times 10^{6}$	559 ± 19^{b}	49 ± 0.84^{c}	88 ± 4.4	0.233 ± 0.002^{bc}
SI	$2.35 \pm 0.82 \times 10^{6}$	272 ± 2^{ab}	20.87 ± 1.18^{b}	76.6 ± 3.8	0.132 ± 0.047^{ab}
CSIF	$0.95 \pm 0.39 \times 10^{6}$	60 ± 33^{a}	3.7 ± 1.3^{a}	70.4 ± 16.7	0.060 ± 0.010^{a}
LAG	$0.52 \pm 0.11 \times 10^{6}$	379 ± 128^{ab}	19.3 ± 1.5^{b}	55.8 ± 14.9	0.710 ± 0.095^{c}

EXT: extensive fishpond; SI: semi-intensive fishpond; CSIF: coupled semi-intensive fishpond; LAG: lagoon
Letter groups indicate significant differences between designs (ANOVA, $p < 0.05$).

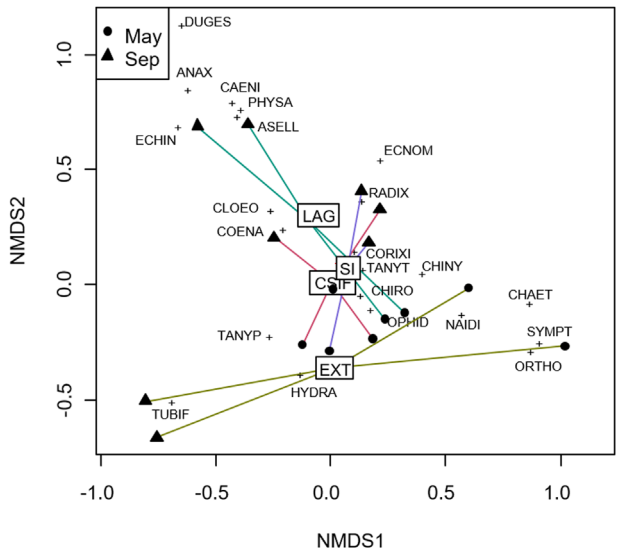

Fig. 2. Two-dimensional plot of non-metric dimensional scaling (NMDS) of the dissimilarity matrix (Bray Curtis distance) of daily secondary production of benthic macroinvertebrate taxa (Stress = 0.12). Rectangles are the center of gravity of each pond type (EXT extensive, SI semi-intensive, CSIF coupled semi-intensive, LAG lagoon) and are connected to the corresponding pond community/date combinations. Circles are communities in May, while triangles are communities in September. Crosses are projections of the taxa on the NMDS plot. Taxa codes: ANAX *Anax imperator*, ASELL *Asellus aquaticus*, CAENI *Caenis sp*., CHAET *Chaetogaster* sp., CHINY Chironomidae Nymphs, CHIRO Chironomini, CLOEO *Cloeon dipterum*, COENA Coenagrionidae, CORIXI Corixinae, DUGES *Dugesia tigrina*, ECHIN *Echinogammarus berilloni*, ECNOM *Ecnomus tenellus*, HYDRA *Hydra sp*., NAIDI "other" Naididae, OPHID *Ophidonaïs serpentina*, ORTHO Orthocladiinae, PHYSA *Physa sp.a*, RADIX *Radix peregra*, SYMPT *Sympetrum* sp., TANYP Tanypodinae, TUBIF "other" Tubificidae.

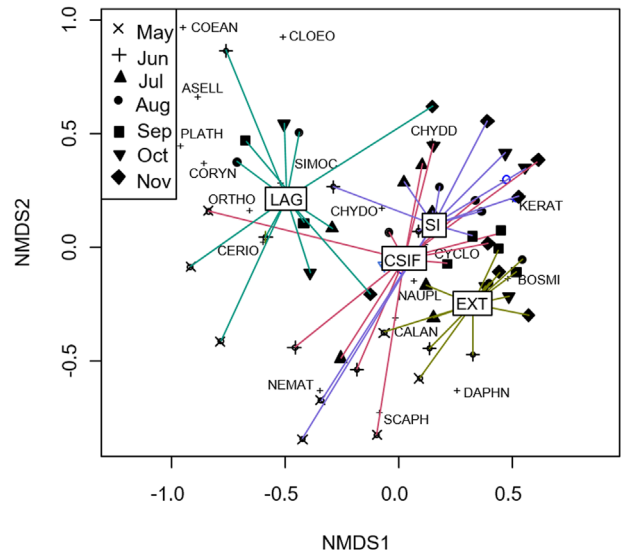

Fig. 3. Two-dimensional plot of non-metric dimensional scaling (NMDS) of the dissimilarity matrix (Bray Curtis distance) of daily secondary production of zooplankton taxa (Stress = 0.22). Rectangles are the center of gravity of each pond type (EXT extensive, SI semi-intensive, CSIF coupled semi-intensive, LAG lagoon) and are connected to the corresponding pond community/date combinations, identified by sampling date. Small crosses are projections of the taxa on the NMDS plot. Taxa codes: ASELL *Asellus aquaticus*, BOSMI *Bosmina longirostris*, CALAN Calanida, CERIO *Ceriodaphnia* sp., CLOEON *Cloeon dipterum*, CHYDD "other" Chydoridae, CHYDO *Chydorus* sp., COENA Coeanagrionidae, CORY Corynoneurinae, CYCLO Cyclopoida, DAPHN *Daphnia* sp., KERAT *Keratella* sp., NAUPL copepod nauplii, NEMAT Nematoda, ORTHO Orthocladiinae, SCAPH *Scapholeberis mucronata*, SIMOC *Simocephalus vetulus*.

influenced the dissimilarity between all pairs of dates. A significant interaction between date and pond type was observed between May and all other sampling dates, except June and November; between July and August; and between August and both October and November.

SIMPER analysis identified three taxa that contributed significantly to dissimilarities between designs ($p < 0.05$) and represented at least 10%: *Ceriodaphnia* sp.; *Keratella* sp. and *Bosmina longisrostris* (Supplementary material 6 for more details). Four taxa contributed significantly to dissimilarities between dates ($p < 0.05$) and represented at least 10%: *Ceriodiaphnia* sp.; *Keratella* sp.; *Bosmina longirostris* and adult copepods of the order Cyclopoida.

3.4 Daily secondary production of key taxa

Pond design and date had a significant effect on P_{day} of all BMI key taxa, except for the Chironomini tribe for design and *Physa* sp. for date (Tab. 6). The design-date interaction was only significant for *Keratella* sp.. P_{day} of *A. aquaticus* was higher in September than in May (Fig. 4a). Tukey pairwise comparisons identified no significant differences between ponds types. In contrast, P_{day} of Orthocladiinae was higher in May than in September (Fig. 4b). P_{day} of EXT ponds in May was significantly higher than that of all other designs. No differences among designs were observed in September. Tukey pairwise comparisons of pond designs for *Physa* sp. identified no significant differences between dates (Fig. 4c). We also fitted a GLM to P_{day} of the Chironomini tribe, which although not a significant contributor to dissimilarity between designs or dates, was the second-most productive BMI taxon, lying between *A. aquaticus* and Orthocladiinae (Fig. 4d). The P_{day} of Chironomini was higher in May than in September.

According to GLM, pond design and date had a significant effect on all ZPK key taxa (Tab. 6). A significant design-date interaction was observed only for *Keratella sp.*

Pairwise differences between designs at each date for P_{day} of the order Cyclopoida revealed that this taxon was less productive in CSIF ponds than in other ponds throughout the experiment (Fig. 5a). LAG and EXT ponds were the most productive, except in May and November, when no differences were detected, and in June, when P_{day} of EXT ponds was highest. SI ponds were also one of the most productive for the Cyclopoida group from June to September. P_{day} of *Ceriodaphnia* sp. was higher in LAG ponds than in all other ponds in May, August, and September (Fig. 5b). In July, EXT ponds were the most productive for this taxon. In contrast, *B. longirostris* was the least productive in LAG ponds throughout the experiment (Fig. 5c). P_{day} of EXT ponds was the

Table 4. Summary of significantly different diversity and quantitative metrics for benthic macroinvertebrates and zooplankton among pond types. ${}_{sam<sup>}{}^{\circ}D_{\alpha\ year}$ is the annual alpha taxonomic richness based on a standardized sample size; density is the mean density of individuals per m^2 per sampling date; B is the mean community dry biomass per m^2 per sampling; P is the annual secondary production per m^2 ; P:B is the turnover ratio of biomass per year; and B:N is the mean individual dry mass. Symbols are as follows: (+++) significantly higher than the other three pond types, (++) significantly higher than two other pond types, (+) significantly higher than one other pond type, (–-) significantly lower than the other three pond types, (–) significantly lower than two other pond types, and (−) significantly lower than one other pond type. Symbols for EXT and SI correspond to their comparison to CSIF and LAG ponds.

	Benthic macroinvertebrates						Zooplankton		
Comparison	${}_{sam}{}^{0}D_{\alpha\ year}$	Density	B	P	P:B	B:density	B	P	B:density
EXT	–		–	–	+	–	+	+++	+
SI	+/–		–	–		–		+/–	–
CSIF- EXT/SI	–		–	–		–	–	–-	–
LAG- EXT/SI	++		+++	+++	–	+++		+/–	++

Table 5. Wet biomass of each fish species harvested in each fishpond design (in kg per pond), their initial stock in brackets (kg per pond), and fish yield at the end of the experiment (kg ha^{-1}). Total dry biomass per m^2 was estimated based on a conversion factor of 5 (i.e., 1 g of dry mass per 5 g of wet mass) to compare it more easily to that of invertebrates (Cresson, 2017). Adapted from Jaeger et al. (2021).

Pond	Common carp (kg)	Roach (kg)	Eurasian perch (kg)	Total wet biomass (kg ha^{-1})	Total dry biomass (g m^{-2})
EXT1	21.83 (2.5)	6.90 (1.12)	4.67 (0.05)	580	11.60
EXT2	26.06 (2.5)	3.56 (1.12)	0.42 (0.05)	601	12.02
SI1	115.68 (5)	6.78 (2.25)	1.26 (0.1)	2478	49.56
SI2	110.70 (5)	4.86 (2.25)	0.65 (0.1)	2324	46.48
CSIF1	96.10 (5)	6.18 (2.25)	0.32 (0.1)	2052	41.04
CSIF2	93.77 (5)	7.48 (2.25)	0.66 (0.1)	2038	40.76

highest throughout the experiment, except in November, when no difference was detected. P_{day} of *B. longirostris* in SI ponds was also among the highest from July to October. CSIF ponds were among the most productive ponds in September. For *Keratella* sp., LAG and CSIF ponds were the least productive throughout the experiment (Fig. 5d). P_{day} of *Keratella* sp. was the highest in EXT ponds in August and October and in SI ponds in July and November.

4 Discussion

Although all experimental ponds were similar in size and age, filled at the same time with water from the same river, and located next to each other, the pond designs led to significantly different invertebrate communities (Tab. 4). This finding agrees with results of Jaeger *et al.* (2021) observed for fish production and water quality, which were similar in the two fishponds with the same design but differed among designs. This highlights the influence that pond management practices have on the invertebrate compartment.

4.1 Comparing local biodiversity to those of other studies

Comparisons among studies are often difficult due to differences in sampling protocols, taxonomic resolutions and densities, which may influence estimates of taxonomic richness. For example, Nieoczym *et al.* (2023) used a bottle-funnel type sampler, focused the study on macroinvertebrates from only three groups (hydracarina, coleoptera and heteroptera) and only collected around 1000 animals. Therefore, comparisons with other studies are restricted to the few ones encompassing the whole community and should be considered with caution. BMI taxonomic richness (${}_{obs}{}^{\circ}D\gamma$ = 116) was representative of the local pondscape: 103 BMI taxa had been identified in a 2012 survey of 11 ponds around Rennes sampled using the same protocol (M. Roucaute, unpublished) (Supplementary material 7). Ponds in this previous survey contained 21–47 taxa (${}_{obs}{}^{\circ}D\alpha$), while ponds in the present study contained 24–57 taxa in May and 15–56 taxa in September. Comparing results with studies with similar taxonomic resolution showed that the observed ${}_{obs}{}^{\circ}D\gamma$ of 116 was higher than that of the datasets of Bayona *et al.* (2015) or Lagadic *et al.* (2016) who reported 65 and 115 taxa respectively. Cereghino *et al.* (2012) reported higher γ taxonomic richness: 145 taxa in 52 ponds in the Atlantic region of Europe. This result may have been due to the larger number of ponds sampled in their study and the wider geographical area considered, which extended from Belgium to Spain, including the British Isles. Hassal *et al.* (2011) also found a higher γ taxonomic richness, but their study included 425 ponds in the UK and animals were identified at the species level. Comparisons based on family richness indicate that our

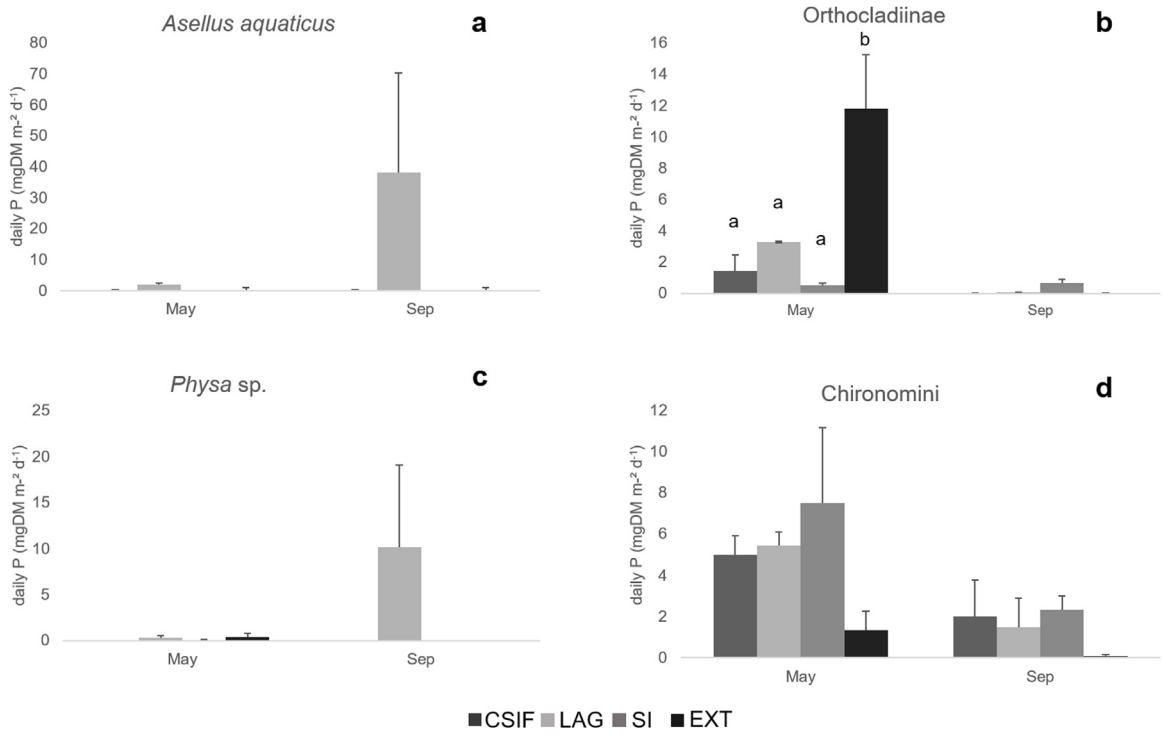

Fig. 4. Mean daily secondary production (mg of dry mass m^{-2} d^{-1}) of the benthic macroinvertebrate taxa that contributed most to community dissimilarities. EXT extensive, SI semi-intensive, CSIF coupled semi-intensive, LAG lagoon. Error bars indicate ±1 standard deviation. Letters show significantly different groups of pond types (treatments) after Tukey post-hoc tests for a given date.

Table 6. Results of ANOVA for major contributing BMI and ZPK taxa based on GLM outcomes. Effect of pond type, sampling date and their interactions are given with *F* as the Fisher score, df the degree of freedom and P-value for the risk of type I error.

	Pond type			Sampling date			Interaction		
Taxon	*F*	df	*p*-value	*F*	df	*p*-value	*F*	df	*p*-value
A. aquaticus	22.479	3	<0.001	11.189	1	0.01	0.305	3	0.821
Orthocladiinae	10.128	3	0.004	37.688	1	<0.001	2.59	3	0.125
Physa sp.	7.646	3	0.01	3.796	1	0.087	1.934	3	0.202
Chironomi tribe	2.503	3	0.133	7.64	1	0.024	0.158	3	0.921
Cyclopoida	18	3	<0.001	9.5	6	<0.001	1.497	18	0.165
Ceriodaphnia sp.	22.635	3	<0.001	6.872	6	<0.001	1.794	18	0.080
B. longirostris	35.428	3	<0.001	6.936	6	<0.001	1.027	18	0.463
Keratella sp.	27.417	3	<0.001	12.071	6	<0.001	2.472	18	0.015

experimental pond facility had higher biodiversity than that observed in most other studies. With 64 identified BMI families in the present study, this is more than in the datasets of Broyer and Curtet (2011), Lemmens *et al.* (2015) or Wezel *et al.* (2014), who observed respectively 59, 33 and 48 families respectively. Thus, in our context, neighboring ponds with different management practices may have favored ɣ −biodiversity to an extent similar to that found by Wezel *et al.* (2014) at the regional scale for fishponds in another French region. Considering only individual ponds, LAG ponds were richer than most ponds described in the literature. Only Davies *et al.* (2008) and Hassal *et al.* (2011) observed some ponds that hosted more taxa, but they identified communities to the species level, which we did not do. When comparing richness at the family level, LAG ponds were the richest. This contradicts the observation of Zamora-Marín *et al.* (2021) who, while showing that artificial ponds may positively contribute to regional biodiversity, found lower α diversity than in natural ponds. For example, in the present study artificial ponds hosted higher biodiversity than those surveyed by Lagadic *et al.* (2016), which were located mostly in natural protected areas under the EU Natura 2000 convention.

4.2 Influence of pond design on invertebrate biodiversity

LAG ponds had the highest family richness: 41 families in a single pond sampling event (Supplementary material 7). This supports our hypothesis that this type of pond promotes biodiversity, even when continuously receiving wastewater

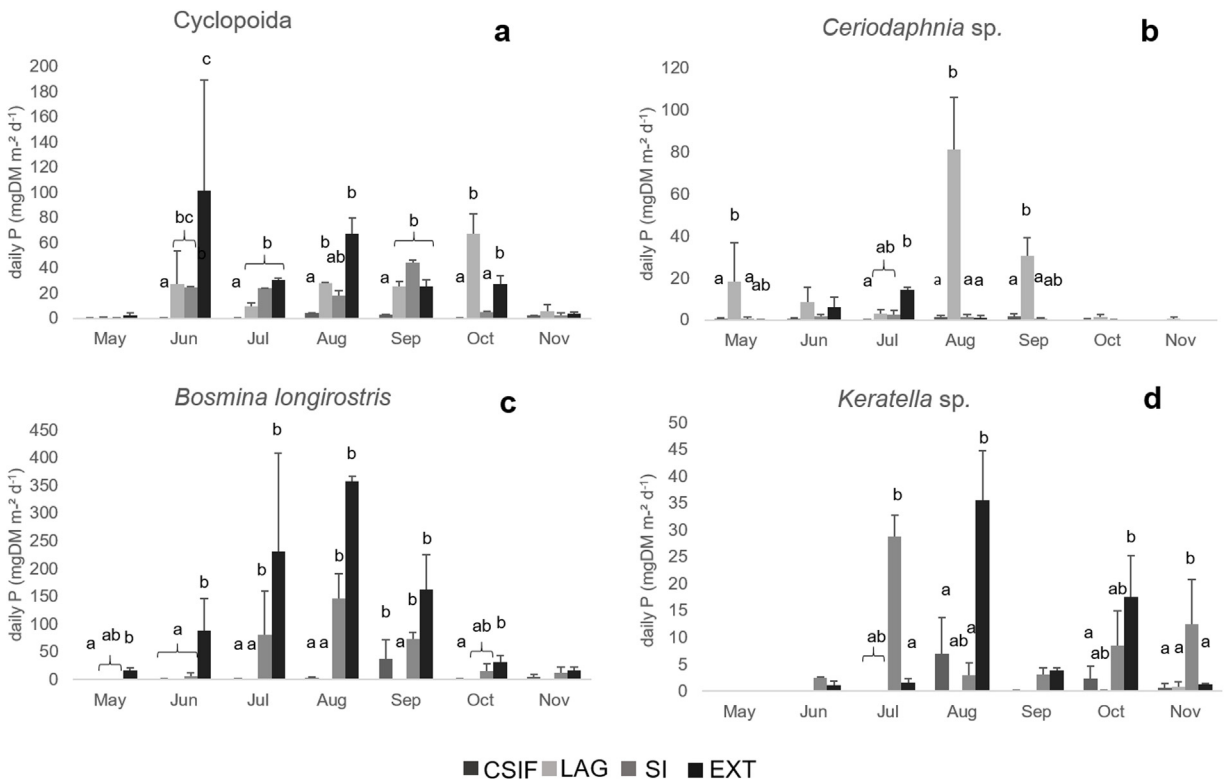

Fig. 5. Mean daily secondary production (mg of dry mass m^{-2} d^{-1}) of zooplankton taxa that contributed most to community dissimilarities. Error bars indicate ±1 standard deviation. Letters show significantly different groups of pond designs after Tukey post-hoc tests for a given date.

from a semi-intensive fishpond. Coupling a semi-intensive fishpond with a lagoon resulted in a CSI pair with a richer BMI community than those in SI and EXT ponds (Tab. 4). However, this biodiversity was concentrated in the LAG ponds, with an annual mean richness of 69.8 taxa based on a standardized sample, while the CSIF ponds had fewer (49.9 taxa) (Tab. 1). Nevertheless, CSIF ponds had a slightly different community than LAG ponds, which resulted in an overall higher estimated BMI richness (${}_{sam}{}^{0}D_{\alpha}$) of 74.1 taxa for the CSI design (Tab. 1). Similarly, the overall BMI richness of the whole facility (${}_{sam}{}^{\circ}D\gamma$) consisted of 87.4 taxa in a standardized sample, which was higher than that in the CSI design alone. This indicates that the other fishpond designs also had unique fauna that resulted in a rich BMI community at the scale of the experimental facility. These findings are in accordance with our hypothesis and the observations of Lemmens *et al.* (2013) and the suggestions of Oertli (2018) and Zamora-Marín *et al.* (2021) for improving pond biodiversity: the diversity of practices in neighboring ponds allows for a higher γ biodiversity.

A variety of interacting factors may have contributed to the identified differences and the generally high biodiversity observed in our experiment. One potential factor was the diversity of habitats, especially in LAG ponds. While we did not quantify macrophyte development precisely, our observations differed greatly among ponds. LAG ponds were nearly completely covered by plants. Plant community composition also differed between the two lagoons. LAG1 was covered mainly by *Nymphoides peltata,* which appeared spontaneously during the experiment. In contrast, as expected, LAG2 had patches of the different species planted at the beginning of the experiment. This last lagoon was the poorest one, which is in contradiction with the findings of Hassal *et al.* (2011) who detected a positive correlation between macroinvertebrates and plants species richness. The fact that taxa such as *A. aquaticus* and *Physa* sp., which feed on decaying macrophytes, were found nearly exclusively in LAG ponds (Figs. 4a and 4c), especially in September, confirms the influence of the macrophyte habitat on community composition. The reduced plant development in fishponds may be due to burrowing activity from fish which may uproot plants and create high turbidity (Francová *et al.*, 2019). The SI ponds were the only fishponds with patches of vegetation. The BMI diversity in SI ponds was slightly lower than that in LAG ponds and greater than in EXT ponds (Tab. 4), while fish density was high (Tab. 5), which suggests a positive influence of the macrophyte habitat. These observations are similar to those of Oertli (2018), who identified factors that resulted in high biodiversity in artificial ponds. He stressed the major role of the shallowest parts of the ponds, as well as that of macrophyte coverage. This also agrees with Broyer and Curtet, 2011 and Nieoczym et al., 2023 who stressed the positive influence of emergent plant cover on invertebrate biodiversity. However, the lack of quantification in our study did not allow us to precisely confirm this correlation.

Since BMI richness was lower in all fishpond types than in LAG ponds with no fish, the difference in pond biodiversity may also have been due to fish predation on invertebrates. This interpretation is supported by the results of Lemmens *et al.* (2015), who observed that the presence of fish decreased both

BMI and ZPK community richness in ponds. EXT ponds, which had the lowest fish density, also had the lowest BMI richness (Tab. 4), probably because no formulated feed was supplied, and fish fed only on natural resources. In contrast, fish in SI and CSIF ponds, which had high fish density, fed on pellets, which probably reduced the amount of fish predation on invertebrates. This is in contradiction to Lemmens *et al.* (2013) who observed a more negative impact of intensive carp farming compared to low intensity practices; these are similar to SI and EXT designs respectively. However, this agrees with results of Nahon *et al.* (2020), who showed in the same experiment that carp in semi-intensive ponds relied mainly on artificial feed rather than pond resources. Therefore, the lower BMI richness in CSIF ponds was more likely due to the lack of plant habitat. In contrast, ZPK taxa richness in the present study did not change due to the presence of fish, which differs slightly from results of Lemmens *et al.* (2015) or Vrba *et al.* (2023). However, the smaller size of ZPK in all fishponds compared to LAG ponds suggests a predation effect by fish, which is in accordance with Kloskowski (2011) who observed a reduction of the proportion of large cladocerans in the presence of carps. Our results also differ slightly from those of Robin *et al.* (2014), who identified that chlorophyll *a* concentrations in spring had a major influence on biodiversity in ponds. While our ponds remained below the chlorophyll *a* thresholds reported by Robin *et al.* (2014) in spring (Jaeger *et al.*, 2021), BMI richness differed greatly in our study, with EXT ponds having the lowest. Moreover, in summer, chlorophyll *a* concentrations peaked in SI ponds, up to nearly 350 μg l^{-1}, but SI ponds still had higher BMI taxonomic richness than EXT ponds.

4.3 Influence of pond management on invertebrate community secondary production

As for biodiversity, comparisons between studies for secondary production may be difficult due to different methodological choices. We based our BMI estimations of annual production on the empirical model for insect larvae from another study. However Tagliapietra *et al.* (2007) observations showed that the application of different models, including some developed for rivers and lakes to some brackish water samples from Venice Lagoon (i.e., with a completely different fauna) all correctly separated the most and least productive sites. Moreover, for each site, the ratio of secondary production estimations between the highest and lowest was no more than two. This ratio is lower than the one we observed between the different pond designs and values reported in the literature. Comparing secondary production among studies (Supplementary material 8), that of BMI found in our study can be considered low for fishponds (at least 2.5 g DM m^{-2}.$year^{-1}$) and high for LAG ponds (at most 16.4 g DM m^{-2}.$year^{-1}$). However, our ponds were not as productive as those of Oertli (1993), who reported annual production of up to 64.6 g DM m^{-2}.$year^{-1}$ in a pond in a Swiss forest. For ZPK, Lemke and Benke, 2009 reported secondary production of 8.4–12.6 g DM m^{-2}.$year^{-1}$ along the shore of an eutrophic lake. This production was lower than that observed in EXT ponds (49 g DM m^{-2}.$year^{-1}$) and, to a lesser extent, in SI (20.9 g DM m^{-2}.$year^{-1}$) and LAG ponds (19.3 g DM m^{-2}.$year^{-1}$). In contrast, production was much lower in CSIF ponds (3.7 g DM m^{-2}.$year^{-1}$). Fish yield in EXT ponds (11.81 g DM m^{-2} $year^{-1}$) was around one fifth that of cumulative BMI and ZPK production (52.6 g DM m^{-2}.$year^{-1}$) (Tab. 5). In contrast, fish yield in SI and CSIF ponds (48.02 and 40.9 g DM m^{-2} $year^{-1}$, respectively) was higher than cumulative BMI and ZPK production (26.5 and 7.1 g DM m^{-2} $year^{-1}$, respectively). When considering the amount of food supplied in these fishponds (244 g DM m^{-2} $year^{-1}$), fish yield was around one fifth that of cumulative food supply and invertebrate production in SI and one sixth of that in CSIF ponds.

The differences in quantitative metrics of the ponds' invertebrate communities were similar to those of biodiversity composition, with BMI contributing more to secondary production in LAG ponds than in CSIF and EXT, with SI ponds in-between. BMI and ZPK were larger in LAG ponds than in other pond types. The BMI in LAG ponds also had a lower turnover (P:B ratio) than in EXT, as expected for larger species. But this result is quite different from the observations of Riera *et al.* (1991). In their study, while abundance, biomass and production of tubifids in fishless enclosures was higher than in the rest of the carp populated pond, the P:B ratio was the same, suggesting a lack of size selection by fish. In our study, the size structure of BMI and ZPK was affected, with an apparent higher pressure on large-sized animals. This is consistent with results of other studies that indicated smaller ZPK in the presence of fish (Geiger, 1983). Indeed, EXT ponds had the highest ZPK production, mainly due to the small Cladocera *B. longirostris*.

In EXT ponds, ZPK was probably subject to fish predation, as indicated by the fish production that was nearly twice as high as BMI production (Tab. 5). The difference between ZPK and fish production, the former nearly five times as high as the latter, was of the same order of magnitude as the difference between fish production and food supply in semi-intensive fishponds. Therefore, contrary to observations from Vrba *et al.* (2023), not only did we not observe a top-down effect of fish predation on ZPK production, but ZPK production was probably an important limiting factor of fish production, as suggested by models presented by Aubin *et al.*, 2021. Interestingly, most ZPK production occurred in summer (Fig. 5), by which time fish had already grown and should have relied less on small prey preferred by juvenile fish (Kloskowski, 2011 ; Ptatscheck *et al.*, 2020). This is a completely different pattern of production than the one observed in Kloskowski (2011), where ZPK biomass was not different between May and July, and in Vrba et al. (2023), where ZPK abundance peaked in April and May and was much lower in summer in most ponds. The high turnover of ZPK could have compensated for fish predation. Jaeger *et al.* (2021) also observed high chlorophyll *a* concentrations in summer in SI and EXT ponds, which could explain the high ZPK production. Fish predation on BMI also decreased predatory pressure on ZPK: LAG ponds contained more predators from BMI taxa than the fishponds did. These hypotheses agree with the diet composition of these fish estimated by the balance of biomass in the trophic niches of the ponds using Ecopath modeling (Aubin *et al.*, 2021).

In SI ponds, the input of pellets enriched the nutrients in the systems and resulted in high primary production and turbidity (Jaeger *et al.*, 2021). This supported production of ZPK similar to that in certain natural eutrophic systems. This phenomenon

did not happen in CSIF ponds, which had the lowest ZPK production. The water circulating through LAG ponds helped to deplete their nutrient concentrations, a major food resource for phytoplankton, which likely explains the low primary production in CSIF ponds observed by Jaeger *et al.* (2021). In contrast, the water from CSIF ponds sustained the development of macrophytes (100% of LAG was covered by plants on the surface and underwater), which created a habitat and food source for BMI. Thus, coupling a lagoon with a fishpond benefited the trophic chain in the lagoons rather than in the fishponds. While allowing an improvement of invertebrates productivity and biodiversity in the first it reduced the fish production efficiency in the second : CSIF ponds produced significantly less fish biomass than SI ponds which had both the same initial stocking and feed and which even had a poorer water quality (Jaeger *et al.*, 2021).

4.4 Temporal changes

Analysis of overall daily community production reflected the community pattern described above and highlighted dynamics of taxa contributions to secondary production. The pond design-date interaction observed in the overall dissimilarity test seems to have been due to the contrast between LAG ponds, which contained many taxa that were more productive in September, and the fishponds, which contained taxa that were more productive in May. The production of most BMI taxa decreased in September in the fishponds, especially in EXT and SI ponds. This is in accordance with the previous observations on the whole community production and reinforces the hypothesis of a visible top-down effect of fish predation on BMI. The production of these ponds relied mainly on ZPK taxa, which are productive in the summer. LAG ponds benefited from more consistent production throughout the experiment: several BMI taxa were more productive in September (*A. aquaticus, Physa* sp.), which compensated for the decrease in production of other taxa (Chironomini, Orthocladiinae). LAG ponds also benefited from ZPK production in summer, but not for the same taxa as in the fishponds (*Ceriodaphnia* sp.). CSIF ponds were the least productive pond type for all key taxa.

All these observations confirm the interest of secondary production estimates for the assessment of the food resources available for fish in aquaculture experiments. An analysis of abundance alone would have made big animals negligible (e.g. odonata, large hemipterans or crayfishes) and make numerous smaller ones dominate the analysis (e.g. ZPK density is thousands times higher than BMI, but annual P is just tens times higher). Secondary production integrates the biomass produced by each compartment over time and gives a better idea of the resource available for fishes during their whole development (ZPK biomass at a given time may look negligible compared to BMI, but considering their high turnover, they contribute much more in the end to secondary production). Our methodological compromise to stick to the two chosen sampling dates for BMI, based on past experiments, has provided representative estimates of annual production. However, it was probably insufficient to follow the precise seasonal changes in production patterns, considering the shifts in fish diet over time. More sampling dates should be considered in future studies on fishpond BMI production.

5 Conclusions

Agro-ecological aquaculture systems should be developed to rely more on natural productivity. Aquatic invertebrates could serve as a major nutrient source for reared species, especially fish, and as an indicator of the quality and diversity of the aquatic ecosystem. The ZPK compartment is highly relevant due to its potential for high productivity. Many practices already aim at improving its production (Francová *et al.*, 2019). In our experiment, it benefited indirectly from the availability of nutrients in the water column for phytoplankton. However, high production occurred mainly in the summer, while according to Kloskowski (2011) carp diet tends to shift from ZPK to BMI in summer, whatever the size of the fish. BMI has the advantage to exhibit a good production both in May and September. Several BMI taxa could contribute to fish diets, especially in spring, when ZPK production is not optimal, and in late summer and autumn for large fish that rely on larger preys. However, fish predation on BMI reduced its production greatly, since BMI turnover is not high enough to compensate for predation. Therefore, future developments of systems of integrated multi-trophic aquaculture should also promote BMI production by regulating its availability to fish and support early production of ZPK.

In conclusion, we were able to apply lessons learned from empirical observations regarding factors that positively influence invertebrate communities in fishponds (Oertli, 2018). The aquaculture system design we tested confirms the positive influence of a fishless shallow planted lagoon on biodiversity in an aquaculture facility. However, while it allowed for intensive fish production, the economical relevance of the system has not been explored (i.e. balance of costs/benefits). More generally, the study demonstrated that inland pond aquaculture can become hotspots of aquatic biodiversity if they provide habitats for invertebrates and protect them from over-predation by fish, while maintaining high levels of fish production.

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Data availability statement

The data that support the findings of this study are available from the corresponding author, M Roucaute, on request.

Supplementary material

Supplemental 1. Detail of laboratory subsampling of the most abundant taxa

Supplemental 2. Remarks on the different biodiversity estimates

Supplemental 3. Number of benthic macroinvertebrate taxa identified in each pond in the experiment

Supplemental 4. Number of zooplankton taxa identified in each pond in the experiment by major taxonomic group.

Supplemental 5. Table of BMI raw abundances

Supplemental 6. Details of SIMPER dissimilarity analysis

Supplemental 7. Comparison of taxonomic richness of benthic macroinvertebrates in ponds and lakes. Richness values are means or ranges (in parentheses) at the pond level or total number of taxa at the group or study level. Taxonomic richness corresponds to the maximum taxonomic resolution in the study (often the genus).

Supplemental 8. Comparison of biomass (B) and secondary production (P) of benthic macroinvertebrate (BMI) and zooplankton (ZPK) in studies of ponds and lakes.

The Supplementary Material is available at https://www.alr-journal.org/10.1051/alr/2024013/olm.

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