Functional response of the aquatic and semiaquatic macroinvertebrate communities to the temporality of temporary ponds in the department of Magdalena, Colombia

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Research Article

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Abstract

Temporary or stationary wetlands (Ponds) are bodies of shallow water that experience periodic droughts and an irregular flood cycle throughout the year. Although these wetlands are widely distributed in the Colombian territory, there have been few studies on their ecology. The aim of this research is to determine the effects of hydroperiod on the functional diversity of aquatic and semiaquatic macroinvertebrates in five temporary ponds in the department of Magdalena (Colombia). The samplings were performed during the hydroperiods of filling and drying phase. Samples were collected from all the microhabitats present (coastal, sediment, and lacustrine). Correlation analyses were performed between the traits and sites in the two hydroperiods, and a multidimensional and comparative analysis of functional diversity was performed, where indices of distance, richness, and functional dispersion were calculated in each hydroperiod. Statistical differences in functional replacement were found for only one of the ponds; however, the other ponds showed a similar trend. These results fit the functional turnover ecological hypothesis in that the response of the aquatic and semiaquatic macroinvertebrate communities was associated with the hydroperiod of the ponds based on the habitat "templet" theory.

Introduction

Wetlands are strategic ecosystems that provide ecosystem services such as water regulation, nutrient retention and export, terrestrial biomass decomposition, and biodiversity reservoirs (Dudley 2006; Betancur et al. 2016; Flórez et al. 2016). Among these ecosystems, temporary wetlands, also known as temporary or stationary ponds, are natural water bodies that experience periodic droughts, with an interannual irregular flood cycle that depends on the topography and soil composition soil (Dudley, 2006; Camacho, et al. 2009). Water level changes are rapid, and the duration of the hydroperiod is variable, which determines the establishment of very specific biota characterized by adaptations, dispersal mechanisms, or life histories that allow survival during periods of drought (Dudley, 2006; Camacho, et al. 2009). For example, monocylic diaptomids (Copepoda) rapidly develop after the flood phase, brachiopods (anostraceans, notostraceans and conchostraceans) have diapausal eggs that resist drought, and coleopterans, dipterans, hemipterans and odonates have broad dispersal strategies (Dudley, 2006; Camacho, et al. 2009;Óliveros-Villanueva, et al. 2011; Abraham, et al. 2021).

Among the faunal groups found in temporary ponds, aquatic macroinvertebrates are the most abundant and diverse (Dudley, 2006; Domínguez and Fernández, 2009). These communities have been widely studied due to their sensitivity to natural and anthropic environmental changes (Castellanos, 2009; Walteros et al. 2016). Many of the studies on aquatic macroinvertebrate communities have evaluated biological diversity from the perspective of community richness and abundance. However, in recent years, studies on these organisms have changed their focus to a functional approach, considering them an important component of biodiversity and recognizing the variety of ways they interact with resources and their environment (Bonada, et al. 2007; Salgado-Negrete and Paz 2015; Motta-Díaz, et al. 2017). This approach uses the components of functional biodiversity to determine the functioning of an ecosystem (Tilman, 2001; Bonada, et al. 2007; Bazzanti, et al. 2012). One form of measurement is through functional traits, which are morphological, physiological and/or ecological characteristics of organisms that affect their growth, reproduction, and survival (Mammola, et al. 2021).

On the other hand, temporary ponds are very exposed to anthropic activities, such as livestock rearing, agriculture, transportation, and construction. These actions alter pond geomorphology and consequently physicochemical and biological conditions (Gobierno de Aragon, 2010). In addition, these ecosystems are considered climate change indicators due to their sensitivity to changes in hydroperiods (Waterkeyn et al. 2009). In Colombia, it has been estimated that temporary wetlands cover more than 17 million hectares, which, together with the few scientific studies on these ecosystems, represents a challenge when generating policies and management actions (Flórez, et al. 2016.).

The present study aims to understand the effects of temporality on the functional diversity of aquatic macroinvertebrates in the temporary ponds in the central and southern parts of the department of Magdalena, Colombia. In addition, it was expected that the transition between these wetlands filling with water and completely drying would eliminate available habitat and modify the physicochemical conditions of the water, generating an environmental filter effect that favours the species that are best adapted to drought.

Materials And Methods

Study area: Samples were collected from five temporary ponds in the department of Magdalena: three were in the central zone (P1, P2, and P3) of the department, and two were in the southern zone (P4 and P5) (Fig. 1). The soil around the charcas is used for grazing cattle, except in P4, where the soil is used for farming. The climate regime in the central zone is bimodal, with two dry seasons (a strong one between December and March and a mild one between June and July) and two rainy seasons (one mild between April and May and a strong one between August and November). However, in the southern zone of Magdalena, the climatic regime is monomodal, with a well-marked dry season between December and March and continuous rains between April and November (IDEAM 2021).

Sampling: Sampling was carried out during the period when the pond water level increased - filling phase (November 2020), and sampling also occurred during the period when the water level decreased - drying phase (February 2021). At each visit, three replicates of sediment from the center of the water body and three replicates from the limnetic and coastal zones were obtained. The sediment was collected approximately in the limnetic zone with an Ekman dredge (866 cm²). In the littoral and limnetic zones, a 2 m transect parallel to the line shore was established, in which were to collect the macroinvertebrate using a type D manual net (net opening: 250 μm). Subsequently, a linear sweep was performed in the littoral zone, while a zigzag sweep was conducted in the limnetic zone within a 2 m² area (Roldán & Ramírez, 2008). The samples were deposited in high-density plastic bags previously labelled and preserved in 96% ethanol. In the laboratory, all samples were separated manually. The sediment samples were passed through a 300 μm sieve. The macroinvertebrates were preserved in 70% ethanol and identified in the Carl Seizz Stermi 508 stereoscope based on taxonomic keys and reference documents (Merritt, Cummins & Berg, 2008; Domínguez & Fernández, 2009; Springer, Ramírez, & Hanzon, 2010; Ramírez, 2010).
Environmental variables

Physical and chemical variables, such as dissolved oxygen concentration (mg/L $O_2$), temperature (°C), acidity (pH), total dissolved solids (mg/L), turbidity (formazin nephelometric units - FNU), and conductivity (µS/cm), were measured in situ using Hanna H19829 multiparameter equipment. In addition, water samples were collected in plastic bottles, which were stored in a plastic refrigerator at 4°C and transported to the laboratory where nitrite concentrations (mg/L $NO_2$) were measured using the 1.00609.0001 cuvette test, and orthophosphates (mg/L $PO_4$-P) with the Merk test 1.14842.0001, whose readings were performed by the photometric method using the Spectroquant® Move 100.

Data analysis

To determine the characteristic physicochemical variables in each hydroperiod, a principal component analysis (PCA) was performed after transforming the data to log $(x) + 1$. Then, the multicollinearity of the variables was quantified through the variance inflation factor (VIF), taking as a critical value a VIF > 20, which allowed detecting high multicollinearity in turbidity (VIF = 31.57), conductivity (VIF = 42.44), orthophosphates (VIF = 23.22), and dissolved oxygen (VIF = 23.26); the last two variables were conserved in the analysis given their importance in explaining the biological processes of the ecosystem, and conductivity and turbidity were removed. Additionally, a state of eutrophication was assigned based on the values of $PO_4$-P following the categorization of Moreno-Franco (2010).

The functional traits of the organisms were selected based on their possible relationship with the temporality of the ecosystem and environmental variables considering the approaches of Beche et al. (2006), Bonada et al. (2007), and Motta et al. (2017). In total, there were 63 attributes of 12 functional traits, grouped into four categories: three traits related to the life cycle, one reproductive trait, five behavioural and physiological traits, and three morphological traits (Appendix 1). Each taxon was assigned a score by attribute according to the fuzzy method and taking into account that some taxa can have more than one attribute; this process consisted of assigning each attribute a value between 0 and 3, where 0: no affinity, the taxon had no affinity with the trait modality; 1: weak affinity, a weak affinity was previously observed or mentioned in the literature, but it was not observed in recent data; 2: moderate affinity, a moderately strong affinity was observed; and 3: strong affinity, where a close relationship with the attribute was evidenced (Chevenet et al. 1994; Diaz Rojas et al., 2020).

The representativeness of the samplings was estimated by the sample coverage (°C) taking into account the abundance and richness data using the iNEXT statistical package (Hsieh et al. 2016; Chao et al. 2014). Subsequently, the graphic hypothesis proposed by Boersma et al. (2016) was evaluated, performing a nonmetric multidimensional scaling analysis (nMDS) using the Gower distance to describe the functional diversity of each community in a “multidimensional functional space” with two axes. Next, as metrics of the communities, the indices for each replica were estimated: functional distance -FDist (Boersma et al. 2016), functional richness - FRic (Villéger et al. 2008), and functional dispersion-FDis (Laliberté and Legendre, 2014). The FDist involved applying the Markov Chain Monte Carlo (MCMC) algorithm between the functional centroids of each hydroperiod. Next, the Welch’s t-test was applied (Welch, 1947) for FRic and FDisp to detect significant differences between the two hydroperiods. Subsequently, to evaluate the association between the different categories of the traits with season and temporality, a fuzzy correspondence analysis (FCA) was performed. Finally, to identify relationships between traits and environmental variables, canonical correspondence analysis (CCA) was performed between functional traits, sampling stations, and physicochemical variables.

All analyses were performed in R Studio 4.1.0. To perform the PCA, the FactoMineR package was used; the functional analyses were developed with FD; the MCMC was executed with MCMCglmm; for the FCA, the ade4 was used; and for the ACC and the NMDS, the VEGAN package was used (R Core Team, 2021).

Results

Temporality and environmental variables

The PCA showed temporal variation in the physicochemical variables in (Fig. 2). In component 1, P5A and P3A (A = filling phase) were associated with the highest values of orthophosphates. P3R (R = drying phase) and P1A were associated with higher oxygen and temperature values. In component 2, in comparison to the other points, P2A and P4A had higher pH values. In addition, P1R was associated with higher values of total dissolved solids and nitrates (Table 1).

Tabla 1. Environmental variables in the temporary ponds. TDS: Total dissolved solids; $PO_4$-P: orthophosphates; $O_2$: dissolved oxygen; $NO_2$: Nitrates. P: Pond, A: Filling phase; R: Drying phase. Ho: Holigotrophic; Me: Mesootrophic; Hi: Hipertrophic; Eu: Eutrophic.
Of the variables, orthophosphates, dissolved oxygen, and temperature best explained the temporal variation in ponds 1, 3 and 5. The ponds 3 and 5 had the highest values of dissolved oxygen at 2.8 and 1.7 mg/day and the lowest concentrations of orthophosphates (0.1 and 0.13 mg/L PO$_4$-P, respectively) during the drying phase. In contrast, in pond 1, the maximum values of dissolved oxygen (2.5 mg/L O$_2$) and temperature (°C) were observed during the filling phase.

In addition, pond 1 showed a higher concentration of nitrites (4.4 mg/L, during filling phase) and total dissolved solids (1104 mg/L, during drying phase).

### Effect of temporality on functional diversity

The aquatic macroinvertebrate communities consisted of 55 genera, grouped into 34 families and 12 orders. The sample coverage in each pond was between 0.95 and 0.98 (2), which indicated that the samples were representative at each site and in the two climatic periods. Thus, the probability of finding a new individual of a different taxon in any of the ponds was less than 5% (Table 2).

#### Table 2
Sample coverage from aquatic macroinvertebrate in the temporary ponds. SC = Sample coverage; SC.LCL, SC.UCL = lower and upper confidence limits for the expected sample coverage

<table>
<thead>
<tr>
<th>Pond</th>
<th>Filling phase</th>
<th>Drying phase</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SC</td>
<td>SC.LCL</td>
</tr>
<tr>
<td>1</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>2</td>
<td>0.96</td>
<td>0.94</td>
</tr>
<tr>
<td>3</td>
<td>0.99</td>
<td>0.97</td>
</tr>
<tr>
<td>4</td>
<td>0.97</td>
<td>0.95</td>
</tr>
<tr>
<td>5</td>
<td>0.97</td>
<td>0.95</td>
</tr>
</tbody>
</table>

#### Table 3
Functional distance index (FDist) of temporary ponds from Magdalena. MCMC: Markov chain Monte Carlo.

<table>
<thead>
<tr>
<th>Pond</th>
<th>MCMC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
</tr>
<tr>
<td>1</td>
<td>-0.017</td>
</tr>
<tr>
<td>2</td>
<td>-0.018</td>
</tr>
<tr>
<td>3</td>
<td>-0.015</td>
</tr>
<tr>
<td>4</td>
<td>-0.023</td>
</tr>
<tr>
<td>5</td>
<td>-0.057</td>
</tr>
</tbody>
</table>
Table 4
Functional richness index (FRic) of temporary ponds from Magdalena Department. t = T Statistic; df = degrees of freedom.

<table>
<thead>
<tr>
<th>Pond</th>
<th>FRic</th>
<th>Welch t test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Filling phase</td>
<td>Drying phase</td>
</tr>
<tr>
<td>1</td>
<td>12,4</td>
<td>16,0</td>
</tr>
<tr>
<td>2</td>
<td>9,6</td>
<td>20,0</td>
</tr>
<tr>
<td>3</td>
<td>9,0</td>
<td>16,5</td>
</tr>
<tr>
<td>4</td>
<td>15,9</td>
<td>13,0</td>
</tr>
<tr>
<td>5</td>
<td>9,0</td>
<td>13,2</td>
</tr>
</tbody>
</table>

Table 5
Functional dispersion index (FDisp) of temporary ponds from Magdalena. t = T Statistic; df = degrees of freedom.

<table>
<thead>
<tr>
<th>Pond</th>
<th>FDisp</th>
<th>Welch t test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Filling phase</td>
<td>Drying phase</td>
</tr>
<tr>
<td>1</td>
<td>0,16</td>
<td>0,15</td>
</tr>
<tr>
<td>2</td>
<td>0,16</td>
<td>0,16</td>
</tr>
<tr>
<td>3</td>
<td>0,15</td>
<td>0,16</td>
</tr>
<tr>
<td>4</td>
<td>0,16</td>
<td>0,16</td>
</tr>
<tr>
<td>5</td>
<td>0,15</td>
<td>0,13</td>
</tr>
</tbody>
</table>

The FDist analysis allowed the detection of a change in the displacement of the functional centroid of the aquatic macroinvertebrates in pond 4. This was explained by the absence of zero in the credible interval in the MCMC (Table 3). This pond presented 13 taxa shared over the two hydroperiods, 10 exclusive taxa in the filling phase (7 Coleoptera, 1 Lepidoptera, 1 Rhynchobdela, and 1 Decapoda), and 10 exclusive taxa in the drying phase (4 Coleoptera, 3 Odonata, 2 Diptera, 1 Basommatophora, and 1 Diplostraca -Cyclestheria).

In the nMDS graphical models, some changes were observed in the functional volume at the following sites: in pond 1, Cyclestheria (Diplostraca) and Clamidoteca (Ostracoda) were found during the filling phase, while Pomacea (Architaenioglossa) and Ora (Coleoptera) were present during the drying phase, generating an increase in functional volume. In pond 2, Chironomus (Diptera), Tabanus (Diptera), and Ora are reported during drying phase, which promoted an increase in functional richness in this period (Fig. 3). In addition, the nMDS showed the change in abundance of some taxa between the two hydroperiods. However, the Welch's t-test of the indices of FRic and FDisp did not show differences between the hydroperiods (P > 0.05) for any of the ponds (Tables 4 and 5).

Functional traits and temporality
The FCA of the life cycle traits showed a temporal change in pond 3, where the filling phase was associated with multivoltine organisms (c3) and a decrease in univoltine organisms (c2) (Fig. 4). Ponds 1 and 4 were characterized by the presence of univoltine organisms, and ponds 2 and 5 were characterized by multivoltine organisms in the two hydroperiods.

Regarding reproductive traits, organisms with endophytic eggs (d8) and isolated cemented eggs (d3) dominated in ponds 1 and 4 during the filling phase. During the drying phase, in pond 1, the organisms with cemented nested eggs (d4) were the most representative, and in pond 6, the organisms with eggs were in free clutches (d5).

The traits associated with behaviour and physiological aspects showed temporal variation in pond 4. During the filling phase, predators (g6) that feed on macroinvertebrates (h7), with cutaneous respiration (e1) and habitat preference of macrophytes, dominated. During the period of drying phase, complete swimmers (f3) with gill respiration (e2) were more abundant. The pond 5 presented the highest number of filter feeders (g2) in the filling phase and organisms that breathe through specialized structures such as plastron (e4) in the drying phase. Regarding the morphological traits, it was observed that the organisms without body armour (j3) were mainly associated with pond 4 in the drying phase, and those with cylindrical bodies (l3) dominated in pond 5 in the filling phase.

Canonical correspondence analysis (CCA)
According to the CCA, the morphological life cycle traits did not show associations with environmental variables. However, the attributes of asexual and ovoviviparous reproduction were associated with dissolved oxygen and water temperature. Regarding the behavioural traits and physiological aspects, a dominance of organisms that feed on coarse detritus (h3) with high concentrations of nitrates was observed, while those that feed on sediment particles (h1) were associated with high values of total dissolved solids.

Discussion
Our results partially supported our hypothesis. Although most stations did not show significant changes, in the nMDS, there was a tendency to separate the abundance of each hydroperiod in the multidimensional functional space. In fact, one of the stations (pond 4) showed evidence of an environmental filter effect (habitat "templet") on the functional diversity of the macroinvertebrate community. In this way, in pond 4, a greater abundance of predatory organisms and reproduction by endophytic eggs were observed in the filling phase, and these attributes were typical of the most abundant groups in this period, such as coleopterans, odonates and Hemiptera; however, in the drying phase, a greater abundance of organisms without body shielding (Diptera) was observed. These results support a "functional rotation" effect induced by pond hydroperiod, which is common in ecological succession processes (Boersma et al. 2016). Similarly, these findings are consistent with those of Southwood (1988) and the theory of habitat "templet", in which the habitat acts as a filter that allows the persistence of functional traits that best adjust to the environmental conditions that occur independently of the number of species.

Pond 4 was smaller (0.03 ha) and was completely exposed to solar radiation, so the environmental filter had an early effect on its community (Dudley, 2006). In addition, the climatic effects on the functional diversity of the other ponds were not significant because by being larger, the impact of the climate on the ponds was smaller, and therefore, the filter effect would have been reflected in a period after that evaluated in this study. However, it is necessary to evaluate the relationship of the physical variables associated with the hydroperiod (such as area, depth, and soil type) to verify this trend. The variables that best explained the differentiation of the ponds with respect to the hydroperiod in the PCA were orthophosphates, whose values at the sites oscillated between the ranges corresponding to mesotrophic and hypertrophic systems (Moreno-Franco et al. 2010), except for pond 1, which presented characteristic values of oligotrophic systems. The values of orthophosphates could be an effect of the presence of livestock (ponds 2, 3 and 5) and agriculture in the surrounding area (pond 4), given that these areas contain many products with high concentrations of macronutrients that promote eutrophication and anoxia in temporary ponds (Gobierno de Aragon 2010). However, the CCA did not show an association of any of the traits used with orthophosphates, which suggests that this variable did not have an effect related to temporality on the functional diversity of the aquatic macroinvertebrates.

The low variability observed in the metrics of functional diversity with respect to the hydrological periods in most of the ponds studied shows that the functional diversity is relatively resistant to the temporality of the bodies of water conferring stability to the ecosystem, as has been verified in temporary lotic systems (Haybach et al. 2004; Bonada et al. 2007). Culioli et al. (2006) noted that when a temporary pond in the region of Corsica (France) reaches a maximum fill level, the structure of the aquatic macroinvertebrate community is stabilized and mainly dominated by predators such as odonates and coleopterans and remains in that state until the drying phase, when most predators begin to leave the pond. The FCA showed that there was no significant effect of temporal variability on the traits related to life cycles in most ponds, except for pond 3, where a change in the multivoltine to univoltine attribute was observed between the filling and drying phase. This result coincides with what is expected in tropical ecosystems, where the minimal variation in temperature and light conditions causes continuous periods of growth and reproduction in aquatic macroinvertebrates generating overlapping generations of both univoltine and multivoltine organisms (Jackson & Sweeney, 1995). However, in tropical temporary lotic systems, voltinism is an important functional trait of the variability in the functional diversity of aquatic macroinvertebrates during the different seasons because it is a trait sensitive to niche availability (Motta-Díaz et al. 2017; Jackson & Sweeney, 1995; Huryn, et al. 2008). Batzer and Wissinger (1996) warned that there are aspects of wetland insect ecology that should be reevaluated since much of the information originates from lotic ecosystems. However, Layton and Voshell (1991) evaluated the colonization of aquatic macroinvertebrates in experimental temporary wetlands in Virginia (United States) during the four main seasons and considered voltinism an important factor affecting the structure of communities. These wetlands were oligotrophic without fish and low levels of nutrients and organic matter. Therefore, we recommend that the ecological aspects of aquatic and semiaquatic macroinvertebrate communities in temporary wetlands continue to be evaluated in the tropics, where environmental and climatic conditions are different from those in temperate zones.

Declarations

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Competing Interests: The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval: The capture of macroinvertebrates and the sampling was done with the permission of the national environmental licensing authority of Colombia in the resolution number 1293.

Data Availability: The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

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**Figures**

![Figure 1](image.png)

**Figure 1**

Location of the temporary ponds in the Magdalena department (Colombia)
Figure 2

Principal component analysis (PCA) of the environmental variables and temporary ponds. TDS: Total dissolved solids; PO₄-P: orthophosphates; O₂: dissolved oxygen; NO₂: Nitrites. P: Pond, A: Filling phase, R: Drying phase.
Figure 3

Non-metric multidimensional scaling (nMDS) of the temporal variation of the functional diversity. Each circle is a taxon and the size is proportional to its abundance. Blue circle: ascent waters. Red circle: relegation waters.
Figure 4

Fuzzy correspondence analysis (FCA) of the functional traits and temporary ponds. P: pond, A: Filling phase; R: Drying phase. **A. Lifecycle:** 1) **aquatic stage:** egg (a1), larvae and/or pupa (a2), and adult (a3); 2) **resistance forms:** statoblast (b1), gemula (b2), cocoon (b3), cells against dehydration (b4), and diapause or dormancy (b5); 3) **voltinism:** semivoltine (c1), univoltine (c2), and multivoltine (c3). **B. Reproductive:** ovovivipara (d1), isolated free eggs (d2), isolated eggs, segmented (d3), segmented nested eggs (d4), free nested eggs (d5), vegetation nested eggs (d6), terrestrial nested eggs (d7), endophytic eggs (d8), and asexual reproduction (d9). **C. Behavioural and physiological:** 1) **breathing:** cutaneous (e1), gills (e2), plastron (e3), aerial (e4), and respiratory pigments (e5); 2) **locomotion:** flyer (f1), surface swimmer (f2), all swimmer (f3), walker (f4), epibenthic burrower (f5), endobenthic burrower (f6), and temporarily fixed to the substrate (f7); 3) **feeding:** collector (g1), filter (g2), fragmenter (g3), scraper (g4), piercer (g5), and predator (g6); 4) **food:** sediment particles (h1), fine debris (h2), coarse debris (h3), microphytes (h4), macrophytes (h5), microinvertebrates (h6), macroinvertebrates (h7), vertebrates (h8), and dead animals (h9); 5) **habitat preference:** sediment (i1), leaf litter (i2), macrophytes (i3), rocks (i4), branches (i5), and water surface (i6). **D. Morphological:** 1) **body armour:** sclerotized body (j1), strong case/shell (j2), and without adaptation (j3); 2) **maximum size:** <2.5 mm (k1), 2.5-5 mm (k2), 5-10 mm (k3), 11-20 mm (k4), 21-40 mm (k5), and 41-80 mm (k6); 3) **body shape:** streamlined (l1), flattened (l2), cylindrical (l3), and spherical (l4).
Figure 5

Canonical correspondence analysis (CCA) between functional traits, environmental variables, and temporary ponds. TDS: Total dissolved solids; PO$_4$-P: Orthophosphates; O$_2$: Dissolved oxygen; NO$_2$: Nitrites. P: pond, A: Filling phase; R: Drying phase. **A. Lifecycle:** 1) aquatic stage: egg (a1), larvae and/or pupa (a2), and adult (a3); 2) resistance forms: statoblast (b1), gemula (b2), cocoon (b3), cells against dehydration (b4), and diapause or dormancy (b5); 3) **voltinism:** semivoltine (c1), univoltine (c2), and multivoltine (c3). **B. Reproductive:** ovovivipara (d1), isolated free eggs (d2), isolated eggs, segmented (d3), segmented nested eggs (d4), free nested eggs (d5), vegetation nested eggs (d6), terrestrial nested eggs (d7), endophytic eggs (d8), and asexual reproduction (d9). **C. Behavioural and physiological:** 1) breathing: cutaneous (e1), gills (e2), plastron (e3), aerial (e4), and respiratory pigments (e5); 2) locomotion: flyer (f1), surface swimmer (f2), all swimmer (f3), walker (f4), epibenthic burrower (f5), endobenthic burrower (f6), and temporarily fixed to the substrate (f7); 3) feeding: collector (g1), filter (g2), fragmenter (g3), scraper (g4), piercer (g5), and predator (g6); 4) food: sediment particles (h1), fine debris (h2), coarse debris (h3), microphytes (h4), macrophytes (h5), microinvertebrates (h6), macroinvertebrates (h7), vertebrates (h8), and dead animals (h9); 5) habitat preference: sediment (i1), leaf litter (i2), macrophytes (i3), rocks (i4), branches (i5), and water surface (i6). **D. Morphological:** 1) body armour: sclerotized body (j1), strong case/shell (j2), and without adaptation (j3); 2) maximum size: <2.5 mm (k1), 2.5-5 mm (k2), 5-10 mm (k3), 11-20 mm (k4), 21-40 mm (k5), and 41-80 mm (k6); 3) body shape: streamlined (l1), flattened (l2), cylindrical (l3), and spherical (l4).

**Supplementary Files**

This is a list of supplementary files associated with this preprint. Click to download.

- Annex1.docx
- Functionaltraitmatrix.xlsx