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1 **Spatio-temporal beta diversity of plankton species and their interactions in**
2 **permanent and temporal waterholes in a semi-arid savannah**

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1 **Abstract**

2 Freshwater communities can vary greatly across space and time. Studying these variations,
3 that is spatial and temporal beta diversity, provides fundamental information on the processes
4 that maintain diversity and on the consequences of environmental changes on communities.
5 Recently, drying events have been shown to strongly affect the spatial and temporal beta
6 diversity of temperate freshwater ecosystems, but the effects of such events are mostly
7 unknown for freshwater communities in semi-arid climates that are frequently submitted to
8 drying up. In addition, studies have so far focused on variations in species composition that is
9 species beta diversity, while variations in species trophic interactions that is food-web beta
10 diversity can give additional insights on how community functioning vary in space and time.
11 Here, we combine species and food-web perspectives to explore the spatiotemporal beta
12 diversity of plankton species and their trophic interactions in waterholes undergoing different
13 water-level regimes: either an alternation between dry and water-full states, or a permanent
14 water-full state due to water pumping. Our results show that waterholes with artificial water
15 pumping do not differ from natural waterholes in their contribution to spatiotemporal beta
16 diversity. Instead, beta diversity is strongly driven by temporal variations of species
17 composition and food-web structure during the dry season, which is characterized by
18 degraded planktonic communities with a low richness, diversity and connectance. Species-
19 and interaction-based approaches give complementary information on the spatiotemporal beta
20 diversity, as they highlight different planktonic communities with contrasted functioning.

21
22 **Keywords**

23 Food-web beta diversity, food web connectance, trophic level, Hwange National Park, planktonic food
24 web, temporary ponds

1 Introduction

2 The study of the variations of species composition across space and time (i.e. beta diversity) is
3 of major importance to explain diversity patterns on earth and to provide fundamental
4 information on the processes that maintain this diversity (Whittaker 1972). Planktonic
5 communities and their dynamics have been widely studied in isolated freshwater ecosystems.
6 However these ecosystems are connected by biological processes such as individual active
7 and passive dispersal (Kappes et al. 2014; Incagnone et al. 2015; Juracka et al. 2016;
8 Slusarczyk et al. 2017), and as for other types of ecosystems, their diversity depends both on
9 stochastic processes related with colonization and extinction dynamics, and on deterministic
10 processes associated with differences in species niches to environmental conditions (Chase
11 2007). While the variations of communities across space (i.e. spatial beta diversity) have been
12 generally studied separately from the variations across time (i.e. temporal beta diversity),
13 recent studies have emphasized the importance of considering spatial and temporal
14 dimensions at the same time (Cook et al. 2018; Musters et al. 2019; Crabot et al. 2020;
15 Sarremejane et al. 2020). Indeed, the spatial and temporal beta diversity of freshwater
16 ecosystems are together affected by environmental perturbations such as drying events or
17 eutrophication. For instance, Sarremejane et al. (2020) showed that the temporal beta diversity
18 of aquatic invertebrates in streams in UK increased with longer drought events while the
19 spatial beta diversity decreased as flow permanence increased.

20 So far, the study of spatiotemporal variations in freshwater communities has been mainly
21 restricted to a few temperate stream ecosystems. Aquatic ecosystems in semi-arid areas
22 display a wide range of dynamics from temporary to permanent systems, which may vary
23 from year to year. The alternation between completely dry state and water-full state is a strong
24 selective pressure on aquatic species, which have consequences on aquatic systems
25 functioning (Thomas et al. 2000; Coops et al. 2003; Thomaz et al. 2006; Bazzanti et al. 2009;

1 Zohary and Ostrovsky 2011; Michaloudi et al. 2012; Teferi et al. 2014; Medeiros et al. 2015).
2 Such alternation between dry and water-full states is expected to strongly affect both spatial
3 and temporal beta diversity. Repeated drying events might decrease spatial beta diversity as a
4 result of increasing environmental filtering in harsh conditions (Chase 2007) but it could also
5 increase spatial beta diversity if it leads to greater habitat heterogeneity (Sarremejane et al.
6 2020). Meanwhile, strong seasonal changes in water level may lead to very dissimilar species
7 assemblages at different times of the year, and thus to high temporal beta diversity, as is
8 expected in highly seasonal and predictable environments (Tonkin et al. 2017) . Our
9 understanding of the diversity of planktonic communities in semi-arid aquatic ecosystems
10 should thus gain from a spatiotemporal perspective of beta diversity.

11 The study of beta diversity has been classically considered from a species-based taxonomical
12 point of view, but other aspects of biodiversity such as functional trait diversity or diversity of
13 species interactions in ecological networks can offer complementary perspectives on this issue
14 (Pellissier et al. 2018; Crabot et al. 2019; Ohlmann et al. 2019). As for species diversity,
15 species interaction diversity may be explored at the local level (which species interactions
16 occur in a given place at a given time) but also at the spatial regional level (which species
17 interactions are common between communities or specific to some communities) and at the
18 temporal level (which species interactions persist or vanish in time) (Poisot et al. 2012;
19 Pellissier et al. 2018). Because the changes in abundance and occurrence of species across
20 space and time can depend on species traits and/or trophic groups, the drivers of beta diversity
21 can differ depending on the diversity metrics considered (Pellissier et al. 2018; Crabot et al.
22 2019). By building on recent developments on the study of the beta diversity of ecological
23 networks, linking species-based and network-based approaches should allow to better
24 characterize how the functioning of planktonic food webs in freshwater ecosystems vary
25 across time and space. Likewise, species interaction beta diversity assessed in a set of aquatic

1 ecosystems may help to identify the interactions that have a pivotal role and to assess the
2 impacts of drying up on ecosystem functioning.

3 We study here the spatiotemporal beta diversity of plankton species and plankton interactions
4 in waterholes located in a semi-arid area in Hwange National Park and its periphery,
5 Zimbabwe. Thirty waterholes, located in the park and the neighboring forestry and communal
6 areas, were monitored during a period of 10 months covering the rainy and dry seasons. While
7 some of these waterholes were temporal as they dried up during the dry season, other
8 waterholes remained permanent thanks to their large water stock or to artificial water
9 pumping from the water table (Msiteli-Shumba et al. 2018). Artificially pumped waterholes
10 (hereafter artificial waterholes) were developed as a management measure to provide water
11 for wildlife during the dry season (Chamaillé-Jammes, Valeix, et al. 2007). This study system
12 offers an opportunity to investigate the potential consequences of the alternation between dry
13 and water-full states on spatial and temporal beta diversity of freshwater ecosystems in
14 tropical semi-arid areas. More specifically, we address the following questions: (1) do the
15 location and pumping of water affect species and interaction-based beta diversity of
16 waterholes? (2) How do temporal changes in community composition in the waterholes
17 contribute to overall beta diversity? (3) What is the degree of uniqueness of the waterholes in
18 space and time and how does it relate with the diversity and food web structure of the
19 waterhole communities? (4) What are the characteristics of plankton species and interactions
20 that distinguish waterholes? We hypothesize that artificial pumping decreases both spatial and
21 temporal beta diversity as it might homogenize environmental conditions among artificial
22 waterholes and decrease seasonal variations in environmental conditions in these waterholes.
23 Artificial waterholes are then expected to contribute less than natural and temporal waterholes
24 to overall beta diversity. We also expect that temporal beta diversity plays a significant part of
25 overall beta diversity in this highly seasonal system. Finally, we expect that interaction beta

1 diversity will give a complementary perspective to species beta diversity. While both are
2 expected to be related with species diversity because species poor communities often tend to
3 be more dissimilar (Chase and Myers 2011; da Silva Brito et al. 2020), food web complexity
4 is also expected to matter for interaction beta diversity.

6 **Methods**

7 *Study site*

8 Hwange National Park (HNP) covers an area of about 14 651 km² and is situated in
9 Matabeleland North Province, Western Zimbabwe. It is located in a semi-arid area where the
10 rainfall is highly variable with an average of 650 mm and a coefficient of variation of 25%
11 (Arraut et al. 2018). The vegetation in most of the park, especially in the area where this study
12 was carried out, is typical of a highly heterogeneous dystrophic wooded savanna, dominated by
13 mixed woodlands and bushlands on Kalahari sands, with open grasslands along drainage lines
14 (Chamaillé-Jammes, Fritz, et al. 2007). The rainy season lasts from December to April. The
15 cool dry winter months extend from May to July and the hot dry months from August to
16 November.

17 The waterholes investigated in this study are located in HNP and the adjacent Sikumi Forest
18 and communal areas situated in the periphery of the park (Figure 1). The HNP is devoted to
19 wildlife conservation and there are no inhabitants. Domestic and wildlife species coexist in the
20 forest reserve and in the communal area but the latter is inhabited. Numerous depressions are
21 fed by rainwater runoff during the rainy season and, according to their size and depth, these
22 natural waterholes may dry out completely during the course of the dry season. To supply
23 wildlife with water during the dry season, underground water is pumped to maintain water in

1 some permanent artificial waterholes. Natural and artificial waterholes are found in the park
2 and forestry areas, while only natural waterholes are found in the communal area. Rainfalls may
3 be restricted to some areas, especially in the beginning and end of the rainy season, leading to
4 heterogeneity in waterholes filling and drying up.

6 *Field sampling and laboratory analyses*

7 Thirty waterholes were sampled between February and December 2013 over 7 months,
8 covering the wet, cool dry and hot dry seasons. The waterholes were selected to represent a
9 set of artificial and natural waterholes, located inside and outside the park. These comprised 5
10 waterholes in the communal area, 5 waterholes in the Sikumi Forest, and 20 waterholes in the
11 Hwange Main Camp area in HNP. All waterholes could not be sampled at each sampling date
12 because of impossible access during the wet season or because the waterholes had dried up
13 during the dry season. Please note that some artificial waterholes were also sampled
14 occasionally as some of the pumps may have been out of order causing the artificial
15 waterholes to dry up. In short, 28 waterholes were sampled in February and March, 26 in
16 April, 21 in July, 14 in September, 12 in November and December.

17 Samples were collected with the use of a 1L polyethene bottle fastened to a 3 m pole. Water
18 samples were taken between 8:00 and 12:00 to minimize variability in the sampling time of
19 the day. About 10L of water was filtrated first through a 100 μm filter and then through a 30
20 μm filter. Samples were collected in 50 ml falcon tubes and preserved in 4% formalin.

21 Taxonomic identification was carried out under an Olympus CK40 inverted microscope with
22 the assistance of taxonomic keys (Msiteli-Shumba et al. 2017). All plankton species were
23 identified to the lowest taxonomic level possible.

1 *Species beta diversity*

2
3 2 We quantified species beta diversity following the method of Legendre and Caceres (2013).
4
5 3 Because the waterholes were not all sampled at all dates, we could not compare the total beta
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7 4 diversity among waterholes only, or among dates only. Thus the total beta diversity was
8
9 5 computed over all waterholes and sampling dates, and it was expressed as the variance of the
10
11 6 Hellinger transformed species-by-sampling unit matrix. Each sampling unit corresponds here
12
13 7 to a waterhole-month combination. We then calculated the contribution of each sampling unit
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15 8 to beta diversity (hereafter $LCBD_{Sp}$) following Legendre and Caceres (2013). The $LCBD_{Sp}$
16
17 9 values represent the uniqueness of the sampling units, i.e. the waterhole a given month, in
18
19 10 terms of species composition. $LCBD_{Sp}$ values were tested for significance against the null
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21 11 hypothesis of random species distributions among waterholes and months. We also computed
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23 12 the Species Contributions to Beta Diversity (hereafter $SCBD_{Sp}$) to identify the species that
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25 13 contribute the most to species beta diversity. For instance, species with high abundances in
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27 14 only a few sites have high $SCBD_{Sp}$ values. The $LCBD_{Sp}$ and $SCBD_{Sp}$ indices were computed
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29 15 using the `beta.div` function of the `adespatial` package in R (Dray et al. 2019).
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41 *Interaction beta diversity*

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44 18 Building the meta-food web

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48 19 The first step to analyze food-web beta diversity is to describe all the potential trophic
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50 20 interactions among all the observed species in the waterholes, which constitutes the meta-food
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52 21 web. To build the corresponding prey-predator interaction matrix, we looked into the
53
54 22 literature for data on the predation of the zooplankton species on phytoplankton and
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56 23 potentially other zooplankton species. Not all species could be found in the literature.
57
58 24 According to personal expertise, allometric relationships between planktonic prey and
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1 predators (Brooks and Dodson 1965; Burns 1968) and species taxonomy (Gauzens et al.
2 2013), we hypothesized that species of the same size and belonging to the same genus have
3 the same diet. With this information, we were able to construct the meta-food web matrix
4 where all species observed in the waterholes are in lines and columns. The predation of the
5 species in the line by the species in the column was coded by a “1”. The absence of predation
6 was represented by a “0”. In the matrix, except for copepod nauplii, species with ontogenetic
7 omnivory appear in the matrix only once in the column with the multiple prey that they eat
8 during their lifetime, even though the species may be prey as a juvenile and a predator as an
9 adult. Therefore, cannibalism is represented by a “1” at the intersection of the same species in
10 the column and line. Copepod nauplii was represented in the matrix as a tropho-species. We
11 added in the matrix the groups “bacteria”, “small phytoplankton” (phytoplankton <30 μm),
12 “protists” and “POM and DOM” (particulate and dissolved organic matter) as some species
13 fed on these groups. Small phytoplankton, protists and POM and DOM are considered to be
14 basal species. These groups are essential in the network construction. Otherwise small filter-
15 feeders such as small rotifers and nauplii would be at the same trophic level than primary
16 producers and the diet of generalist filter-feeders such as cladocerans would be narrowed.
17 Once the meta-food web was built, we extracted local food webs for each waterhole at each
18 sampling month resulting in 141 food webs.

19 20 Calculating interaction beta diversity

21 To follow the same approach as detailed above for beta diversity on community composition
22 but on food webs, we adapted the method of Legendre and Caceres (2013) to food web data.
23 First, we calculated food web based LCBD values (hereafter LCBD_{FW}) using the interaction-
24 by-sampling unit matrix instead of the species-by-sampling unit matrix as used previously

1 (Figure S1, Appendix 2). Because we do not have data on interaction strengths but only on
2 interaction presence or absence, the $LCBD_{FW}$ values were derived from the Jaccard
3 dissimilarities in interactions among all pairs of sampling units. More specifically, the food
4 web dissimilarity D_{bi} between sampling units b and i is defined by $D_{bi} = \frac{B+C}{A+B+C}$ where B
5 (resp. C) corresponds to the number of interactions only present in the food web of sampling
6 unit b (resp. i), while A corresponds to the number of interactions present in the food webs of
7 both sampling units b and i .

8 Second, $LCBD_{FW}$ values were tested for significance against the null hypothesis of random
9 species distributions among waterholes and months (i.e. same null hypothesis as for $LCBD_{Sp}$
10 values). To do so, we built 999 permutations of the species-by-sampling unit matrix
11 (Legendre and De Caceres 2013), on which we derived 999 random interaction-by-sampling
12 unit matrices. Waterhole-month combinations with significant $LCBD_{FW}$ values correspond to
13 sampling observations with trophic interactions that differ from food webs in other months
14 and waterholes.

15 Third, we also proposed a measure of Species contribution to beta diversity for food webs
16 ($SCBD_{FW}$) adapted from the approach of Legendre and Caceres (2013). We first suggest a
17 calculation of the contribution of each interaction of the meta-food web to overall beta
18 diversity following the same philosophy as Legendre and Caceres (2013) but using the
19 Jaccard dissimilarity instead of the variance of the composition matrix as previously defined.
20 Then we defined the $SCBD_{FWi}$ of species i as half of the sum of the contributions to beta
21 diversity of the interactions in which species i participates as prey or predator. By doing so,
22 the sum of the $SCBD_{FW}$ values is equal to 1 as required. The precise definition and calculation
23 of $SCBD_{FW}$ is detailed in Appendix 2. Please note that by construction species that are not
24 connected in the meta- food web (i.e. inedible basal phytoplankton species) do not contribute

1 to food web beta diversity because the beta diversity calculation is based on the interaction-
2 by-sampling unit matrix.

3

4 *Describing local communities and species positions in the meta-food web*

5 Species and trophic groups were first described by their frequency of occurrence in the
6 sampling units. The frequency of occurrence was defined by the number of sampling units in
7 which a given species occurs divided by the total number of sampling units. In addition,
8 species were characterized by their positions in the meta-food web. Species degree
9 corresponds to the number of interactions of a species in the meta-food web (i.e. total number
10 of potential prey and predators). Species trophic level is defined by the average trophic
11 position of its prey plus 1.

12 We also characterized the local diversity and food web structure of each waterhole at each
13 sampled month by the following measures: (i) total species richness; (ii) Shannon diversity as
14 a function of species abundances; (iii) connectance as the number of interactions in the food
15 web divided by the number of total possible interactions; (iv) average trophic level as the
16 average of the trophic levels of species present in the food web.

17

18 *Statistical analyses*

19 All statistical analyses were done with R. We checked for spatial autocorrelation in $LCBD_{Sp}$
20 and in $LCBD_{FW}$ at each sampling month. To do so, we assessed the significance of Moran's I
21 using the R package *ape*. Both $LCBD_{Sp}$ and $LCBD_{FW}$ showed no sign of spatial
22 autocorrelation in any of the months studied (Table S1). We tested the additive effects of
23 waterhole management (i.e. pump presence), sampling month and location (i.e. HNP, forest or

1 communal area) on $LCBD_{Sp}$ and $LCBD_{FW}$ using a mixed linear model with the waterhole as a
2 random effect using the lmer function of the lmerTest package (Kuznetsova et al. 2017). We
3 then selected the more parsimonious model using the Akaike information criteria. We also
4 tested the effects of species diversity, Shannon diversity, average trophic level and
5 connectance on $LCBD_{Sp}$ and $LCBD_{FW}$ using a mixed linear model with the waterhole and the
6 sampling month as random effects. Finally, we tested the effects of the species occurrence
7 frequency, the species degree and its trophic level in the meta-food web on $SCBD_{Sp}$ and
8 $SCBD_{FW}$ with a linear model.

10 **Results**

11 *Species beta diversity*

12 The calculation of the $LCBD_{Sp}$ reveals dissimilarities between waterholes (Fig. 2A). Within
13 the natural waterholes, among those that are significantly dissimilar from the others, only
14 two are in HNP: Ballaballa (April) and Ngwenya (February). The others are either in the
15 forestry area (Jwapi in February) or in the communal area (Mambanje in February and March,
16 Marist in April, July and November, Nengasha in February, March and April, and Silewu in
17 March and September). Among artificial waterholes, significantly dissimilar waterholes are
18 mostly in HNP (Caterpillar in November, Kennedy 1, Livingi and Tchabema in February,
19 Kennedy 2 in November, Mabuyamabema in February and March, Makwa in March,
20 Ngweshla artificial in March, November and December, and Nyamandlovu and Tshebetshebe
21 in April). Two waterholes from the forestry area are distinguishable: Ganda in November and
22 December and Safari Lodge in February. We note that some waterholes are consistently
23 similar (Jambile and Ngweshla natural, Sedina and Magoli for natural waterholes and
24 Caterpillar, Dom, Dopi, Foster, Guvalala and Jambile artificial for artificial ones). We tested

1 as additive factors the effects of the pump presence, the sampling month and the location of
2 the waterholes to explain the LCBD_{Sp}. The results of the model show that the pump presence
3 has no effect but the sampling month and, marginally, the location affect the LCBD_{Sp} (Table
4 1): the LCBD_{Sp} values are significantly higher in November ($p < 0.001$) and marginally higher
5 in February ($P = 0.09$) and they are significantly lower in the forestry ($p < 0.03$) and communal
6 ($p < 0.04$) areas than in HNP.

7 To analyse the SCBD_{Sp}, we first looked at the species SCBD_{Sp} rank (Figure S2), which
8 reveals several groups of species according to their contribution to beta diversity (Figure 3B,
9 black diamonds and inverted grey triangles). *Tetraedron regulare* and total nauplii explain 9%
10 of the total SCBD_{Sp}. With an additional set of 3 species, *T. asymmetricum*, *Euglena* sp. and
11 *Anabaena* sp, 20 % of the total SCBD_{Sp} is explained. With 15 more species, that is a total of
12 20 species, up to 60% of the total SCBD_{Sp} is explained. These species are by decreasing
13 contribution order: *Microcystis aeruginosa*, *T. limnetica*, *Phacus curvicauda*, *Aphanocapsa*
14 sp., *Oscillatoria* sp., *Spyrogira* sp., *Melosira* sp., *Diatoma* sp., *Polyarthra vulgaris*,
15 *Pediastrum simplex*, *Cymbella* sp., *Chroococcus* sp., *Brachionus calyciflorus*, *Cyclotella* sp.
16 and *Camphylodiscus* sp. We note that out of these 20 taxa, only three are herbivorous
17 consumers (nauplii, *P. vulgaris* and *B. calyciflorus*), the others are primary producers. Among
18 the phytoplankton taxa, we find mostly Bacillariophyta and Cyanobacteria.

19 *Food-web beta diversity*

20 The LCBD_{FW} shows slightly different results than the LCBD_{Sp}. Within natural waterholes,
21 Nengasha, located in the communal area differentiates itself from other waterholes in March,
22 July and November and Ngewshla natural, located in HNP, in March (Figure 2B). Within
23 artificial waterholes, most dissimilarities between waterholes are observed during the dry
24

1 season in July, September and November and apply to waterholes located in HNP (Dom,
2 Dopi, Jambile artificial, Kennedy 2 and Ngewshla artificial) or in the forestry area (Ganda).
3 Only the sampling month has a significant effect on the LCBD_{FW} (Table 1). The LCBD_{FW} are
4 higher in November ($p = 0.008$) and September ($p = 0.04$) and marginally higher in February (p
5 $= 0.05$).

6 The analysis of the SCBD_{FW} reveals that the two species that have the higher SCBD_{FW} are
7 two copepods, *Macrocyclops varicans* and *Eudiaptomus gracilis* (Figure 3B, grey triangles).
8 They contribute to 9% of the total SCBD_{FW}. The next three higher contributions explaining up
9 to 21% of the total SCBD_{FW} are *Daphnia pulex*, *B. calyciflorus* and the microphytoplankton
10 group. To draw a parallel with the SCBD_{Sp}, 60% of the SCBD_{FW} is explained by an additional
11 set of 16 species or group of species by order of decreasing contribution: bacteria, *T.*
12 *assymmetricum*, protists, *P. vulgaris*, *T. limnetica*, *T. regulare*, *Filinia pejleri*, nauplii,
13 *Cyclotella* sp., *Daphnia longispina*, *Euglena* sp., *Macrocyclops albidus*, particulate and
14 dissolved organic matter, *Diaphanosoma tropicum*, *Afrocyclus gibsoni* and *Brachionus*
15 *patulus* (Figure 3B, black diamonds and grey triangles). Unlike SCBD_{Sp}, this set of species
16 gather together consumer species and primary producers.

17 As species and food-web based LCBD and SCBD do not provide the same information about
18 waterhole community and functioning dissimilarities, we plotted LCBD_{FW} and SCBD_{FW} as a
19 function of species LCBD_{Sp} and SCBD_{Sp} respectively (Figure 3). Linear regressions show that
20 they are positively correlated (adjusted $R^2 = 0.11$ and $p < 0.0001$ for LCBD and adjusted
21 $R^2 = 0.77$ and $p < 0.0001$ for SCBD). The waterholes that have high contribution to both
22 LCBD_{Sp} and LCBD_{FW} are Jwapi and Mabuyamabema in February, Nengasha in March and
23 Kennedy 2, Ganda and Ngewshla artificial in November (Figure 3A, black diamonds). The
24 species that have the higher contributions to both SCBD_{FW} and SCBD_{Sp} are the phytoplankton

1 species *T. asymmetricum*, *T. limnetica*, *T. regulare*, *Euglena* sp., *Cyclotella* sp. and the small
2 herbivorous zooplankton *B. calyciflorus*, *P. vulgaris* and nauplii (Figure 3B, black diamonds).

3 4 *Effects of diversity and food-web indices on LCBD and SCBD values*

5 We explored the relationships between diversity, food-web indices, and species and food-web
6 beta diversity. The $LCBD_{Sp}$ is positively correlated with the average trophic level of the
7 waterhole food-webs and negatively correlated with Shannon diversity (Figure 4B and Table
8 2). The local contribution of a waterhole to beta diversity is thus higher when the average
9 trophic level of the planktonic food-web it hosts is high and the species abundances are
10 unbalanced. The $LCBD_{FW}$ decreases significantly with species richness and food-web
11 connectance (Figure 4A and Table 2). Put another way, the more dissimilar waterholes from
12 the interaction perspective are waterholes with few species and simple planktonic food-webs.
13 The $SCBD_{Sp}$ increases significantly with species occurrence frequency and decreases
14 significantly with species degree in the meta-food web (Figure 5). In other words, species that
15 have high $SCBD_{Sp}$ are also widespread species, even if they might be in small abundances in
16 numerous waterholes, and have a low number of connections in the meta-food web. As for the
17 $SCBD_{FW}$, it increases significantly with species occurrence frequency, and with species
18 degree and trophic level in the meta-food web (Figure 5). In contrast with the $SCBD_{Sp}$,
19 species that most contribute to the $SCBD_{FW}$ are highly connected with other species of the
20 meta- food web and have a high trophic level. These species may be either top-consumers,
21 such as carnivorous copepods, or intermediate consumers with numerous prey and predators,
22 such as filter-feeder rotifers, cladoceran and nauplii.

23

24 **Discussion**

1 Contrary to our first expectation, waterholes with artificial water pumping did not contribute
2 less to spatiotemporal beta diversity than natural waterholes. Instead, the contribution of
3 waterholes to species and interaction beta diversity was mostly related to monthly changes in
4 their community composition. Species- and interaction-based approaches also gave
5 complementary information on the spatiotemporal beta diversity of this freshwater ecosystem.
6 While inedible phytoplankton species contributed importantly to species beta diversity, highly
7 connected species in the food web contributed the most to interaction beta diversity. We
8 discuss these different results in detail below.

9
10 *No significant effects of the presence of pumps on the contribution of waterholes to beta*
11 *diversity*

12 Depending on the drought intensity and on the waterhole size and depth, most of the natural
13 waterholes dry up during the dry season while the artificial ones only undergo water level
14 fluctuations thanks to water pumping. While we expected that artificial pumping would
15 decrease both spatial and temporal beta diversity by homogenizing environmental conditions
16 across space and time, we show it has no significant impact on the contribution of the
17 waterholes to species and interaction spatiotemporal beta diversity ($LCDB_{Sp}$ and $LCBD_{FW}$
18 respectively). This result is in agreement with the previous analyses of species community
19 composition in this system. Indeed, Msiteli-Shumba et al (2017) showed that ground water
20 pumping had no effect on the phytoplankton and zooplankton community structure, except in
21 July for zooplankton (Msiteli-Shumba et al. 2017).

22 The absence of difference in the beta diversity contribution between artificial and natural
23 waterholes, and the relatively weak spatial beta diversity observed, might be explained by
24 several complementary mechanisms. First, it might be explained by the fact that

1 environmental conditions become harsher during the dry season in the artificial waterholes
2 too and not only in the natural waterholes. Such harsh conditions in both artificial and natural
3 waterholes might lead to similarly strong environmental filtering in both types of waterholes,
4 consequently decreasing spatial beta diversity (Chase 2007). Indeed, in waterholes that do not
5 dry, the water level strongly decreases and fluctuates from day to day. The surface area varies
6 from 21 903 m² to 531 m² in the park from the rainy to the dry season (Msiteli-Shumba et al.
7 2017). In addition, large herbivores such as elephants, zebras, kudus and giraffes tend to
8 aggregate around waterholes for drinking water (Chamaillé-Jammes, Valeix, et al. 2007;
9 Ferry et al. 2016). Attendance favors dung deposition around waterholes which may induce
10 water nutrient enrichment (Hulot et al. 2019). As a consequence, water conductivity,
11 hardness, turbidity and ammonium concentration strongly increase during the dry season,
12 while the macrophyte abundance decreases as well as water level (Msiteli-Shumba et al.
13 2018). Ammonium can reach concentrations that are toxic to plankton species, leading to
14 strong differences in community composition between the dry and wet seasons in artificial
15 waterholes, as found in natural waterholes. Our analysis is based on species that easily form
16 resting stages and allow them to withstand adverse environmental conditions (Incagnone et al.
17 2015; Ellegaard and Ribeiro 2018). Such resting stage strategy may be developed by these
18 species to avoid unfavorable habitats in permanent waterholes as much as in nature
19 waterholes, resetting plankton communities during the dry season. At the onset of the rainy
20 season, plankton communities could thus build up from the sediment egg bank in all
21 waterholes whatever their dynamics during the dry season.

22 Second, dispersal among waterholes might also contribute to reduced spatial beta diversity
23 and to the lack of difference among natural and artificial waterholes. Plankton species are
24 efficient passive dispersers (Incagnone et al. 2015) provided there is no barrier between
25 favorable habitats (Juracka et al. 2016). The savannah landscape studied here is quite

1 homogeneous and we did not find any sign of spatial autocorrelation in the contribution to
2 species and interaction beta diversity. The mean distance between two waterholes is 23.1 km
3 (SD: 12.9 km), the longest distance among waterholes being 59 km (*i.e.* distance between
4 Mambanje and Jambile Artificiel). These distances are easily covered by potential vectors of
5 dispersion such as wildlife and birds, which could contribute to connect waterholes and
6 decrease spatial beta diversity of plankton communities. In summary, the similarity of species
7 and interaction spatiotemporal beta diversity in natural and artificial ponds might rely on
8 plankton resting stages that allow to endure the dry season and on dispersion. However, we do
9 not know the weight of resting stages responding similarly to harsh conditions vs. migration
10 in driving the observed spatial beta diversity, and more generally the relative importance of
11 species sorting and mass effects on the spatial dynamics of these waterholes.

12
13 *The contribution of waterholes to beta diversity depends on seasonal community changes*

14 Our results show that temporal beta diversity can be an important component of the beta
15 diversity of aquatic ecosystems in semi-arid areas, which are characterized by harsh
16 environmental conditions during the dry season. Both the $LCDB_{Sp}$ and the $LCBD_{FW}$ of the
17 waterholes depend significantly on the sampling month, the waterholes sampled in November
18 during the dry season showing larger contributions to beta diversity. The importance of the
19 seasonal dynamics for understanding the structure of these aquatic communities is consistent
20 with previous findings (Msiteli-Shumba et al. 2017; Msiteli-Shumba et al. 2018; Hulot et al.
21 2020). Previous studies on this system indeed showed the planktonic community composition
22 as well as food web structure varied mostly between the wet and the dry seasons rather than in
23 relation with water pumping. Our results also highlight the importance of considering
24 temporal beta diversity along with spatial beta diversity. Different waterholes indeed
25 contribute significantly to beta diversity at different times. For instance, Nyamandlovu

1 contributes significantly more than expected at random to species beta diversity in April only,
2 whereas Ganda contributes significantly to species beta diversity in November and December.
3 Although we expect to find a similar importance of temporal beta diversity in driving the beta
4 diversity of waterholes in other years than the one considered here, we should acknowledge
5 that our study was restricted to seven months and that the interannual variability should be
6 addressed in future studies. In particular, the drought intensity changes from one year to the
7 other and affects water level changes in ponds and, as a consequence, may affect planktonic
8 community dynamics. Considering this study system over several years would allow to
9 investigate how spatiotemporal beta diversity is affected by severe events such as prolonged
10 droughts, and whether differences between natural and artificial waterholes occur in this
11 context.

12 *The degree of uniqueness of the waterholes a given month depends on both diversity and food*
13 *web structure*

14 The LCBD has been shown to distinguish ecosystems that are either very rich or degraded
15 (Legendre and De Caceres 2013): high LCBD values might indeed indicate strongly different
16 communities with either rare species combination or communities missing otherwise
17 abundant and common species. In our study, higher values of $LCBD_{Sp}$ and $LCBD_{FW}$ are
18 associated with plankton communities with lower species richness and diversity as well as
19 lower connectance. Common species contribute the most to both species and food-web beta
20 diversity, and highly connected species and top consumers are also the main contributors to
21 food-web beta diversity. These results are consistent with the fact that our analysis of beta
22 diversity highlights the waterholes sampled during the driest months. Several studies showed
23 that catastrophic events such as drought may initiate losses of species and interactions,
24 especially top predators inducing a food-web simplification (Ledger, Brown, Edwards,
25 Hudson, et al. 2013; Ledger, Brown, Edwards, Milner, et al. 2013; Jackson et al. 2020). In a

1 study analyzing the planktonic food-webs of roughly the same set of waterholes sampled in
2 November 2012, February and July 2013, Hulot et al (2020) also showed that the food-webs
3 during the dry season have lower connectance, less intermediate species and more basal
4 species, lower omnivory index and lower mean trophic level than during the rainy season. Our
5 present results of higher LCBD values in dry months are in line with these findings except for
6 the mean trophic level, which increases with the LCBD_{Sp}. This relationship may rely on the
7 rich planktonic communities found during the rainy season where the top-consumers are more
8 abundant. It might also relate with strong top-down effects of consumers on phytoplankton
9 community composition in food webs with high mean trophic level, as phytoplankton species
10 are the main contributors to species-level beta diversity in our system. Thus, the opposite
11 response of the LCBD_{Sp} to the average trophic level and the Shannon diversity is consistent
12 with the fact that the dissimilarity pointed out by the LCBD pertains to both rich and degraded
13 waterholes.

14 *Species and food-web beta diversity bring complementary understanding*

15 LCBD_{Sp} and LCBD_{FW} are only partly related to the same indices of community structure.
16 Indeed, LCBD_{Sp} increases with food-web average trophic level while LCBD_{FW} decreases with
17 connectance. This is also true for the SCBD values: while species contribution to food-web
18 beta diversity increases with species degree and trophic level, species contribution to species-
19 level beta diversity is lower for more connected species. These differences arise from the fact
20 that by definition species degree matters to the calculation of food-web beta diversity,
21 inedible basal species being necessarily excluded. In addition, our measure of species beta
22 diversity includes species abundance, which is not the case for our measure of food-web beta
23 diversity. Consequently, while the set of waterholes identified as unique by both indices are
24 characterized by simple planktonic food-webs, waterhole uniqueness can also be defined by
25 the opposite values of LCBD_{Sp} and LCBD_{FW} of some waterholes. Waterholes that do not

1 contribute more than expected to beta diversity for one value may have a high value for the
2 other ones. That is for instance the case for Nengasha and Jambile artificial in July, and Dopi
3 in September and November, which have both low $LCBD_{Sp}$ and high $LCBD_{FW}$. Although
4 their planktonic communities are composed of common, evenly distributed phytoplankton
5 species, they miss highly connected top consumer species that have pivotal role in the
6 network such as *E. gracilis* and *M. varicans*. Conversely, some waterholes, such as Livingi in
7 February, Ballaballa, Nyamandlovu and Tshebetshebe in April and Marist in November, have
8 high $LCBD_{Sp}$ and low $LCBD_{FW}$. These waterholes are characterized by the dominance of a
9 few phytoplankton species in high abundance but which are poorly connected to other species
10 in the food web. These species include cyanobacteria, which are excluded for the computation
11 of the $LCBD_{FW}$ and $SCBD_{FW}$ because they have not involved in trophic interactions, and
12 poorly edible phytoplankton species. In summary, the combination of the two indices allows
13 to identify different sets of waterholes, which are likely related to very different functioning.
14 Waterholes with high $LCBD_{Sp}$ and low $LCBD_{FW}$ can be characterized by either planktonic
15 food-webs that are dominated by inedible or poorly connected phytoplankton species or by
16 food-webs with relatively high species abundance at higher trophic levels (e.g. Makwa in
17 March). In the former case, the primary production is diverted to dead-end or does not support
18 efficiently a rich food-web whereas it is the contrary in the latter case. Meanwhile, waterholes
19 with high $LCBD_{FW}$ are generally characterized by the lack of common and highly generalist
20 top consumers, which might play an important functional role in these ecosystems.

21 In conclusion, our analysis reveals that the beta diversity of plankton communities in the
22 waterholes of a semi-arid savanna is mainly driven by strong temporal variations of species
23 composition and food-web structure during the dry season. Meanwhile, the spatial variation of
24 these communities does not appear related with water management (i.e. pumping) contrary to
25 our initial hypothesis. This study highlights the importance of considering the spatio-temporal

1 dynamics of communities, and of combining approaches based on species composition and
2 trophic interactions. To predict the effects of global change stressors on food-web structure
3 and dynamics, we need simplified and intuitive indices related to community health (Heleno
4 et al. 2020). The species and food-web indices are complementary as they help to understand
5 why waterholes are dissimilar in space and time, bridging further the taxonomical and
6 functional perspectives needed to the study of beta diversity.

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Table 1: Effects of sampling month, pump presence and location on LCBD values. The table reports the results for the complete models.

LCBD values	Explanatory variables	df	Chisq (for LCBD _{Sp}) or F (for LCBD _{FW})	P value
LCBD _{Sp}	Month	6	22.80	0.0008
	Pump presence	1	0.018	0.89
	Location	2	5.167	0.07
LCBD _{FW}	Month	6	2.955	0.0097
	Pump presence	1	0.03	0.8628
	Location	2	0.471	0.6256

Table 2: Effects of diversity and food web indices on LCBD and SCBD values. The table reports the results for the best models.

LCBD and SCBD values	Explanatory variables	df	Estimates	Chisq (for LCBD) or F (for SCBD)	P value
LCBD _{Sp}	Average trophic level	1	4.587e-03	34.113	<0.0001
	Shannon diversity	1	-2.290e-03	97.793	<0.0001
LCBD _{FW}	Species richness	1	-3.020e-05	15.152	<0.0001
	Connectance	1	-1.234e-03	7.2067	0.0072
SCBD _{Sp}	Species occurrence frequency	1	2.917e-02	115.99	<0.0001
	Species degree in metaweb	1	-9.339e-05	5.4712	0.0212
SCBD _{FW}	Species occurrence frequency	1	3.413e-02	188.822	<0.0001
	Species degree in metaweb	1	1.611e-04	55.633	<0.0001
	Trophic level in metaweb	1	4.590e-03	19.492	<0.0001

Figure legends

Figure 1. Map of the study site and food-web examples. (A) Map with Hwange National Park, the forestry and the communal areas and the waterhole locations. B and C identify the waterholes Nengasha and Ganda. (B) and (C) Representation of the food-webs at the different dates (February to December) in Nengasha and Ganda respectively.

Figure 2. Species (a) and food-web (b) based LCBD over all waterholes and dates.

The two color scales are proportional to the LCBD. The white stars denote significantly dissimilar waterholes. The dates are February (Feb), March (Mar), April (Apr), July (Jul), September (Sep), November (Nov) and December (Dec). The waterholes are separated in the natural (left) and artificial (right) waterholes. The abbreviations are by order of appearance Ballaballa (Bal), Jambile Natural (JamNat), Mabuyamabema (Mab), Jwapi, Magoli (Mag), Mahule (Mahu), Mambanje (Mamb), Marist (Mar), Mazibomvu (Maz), Nengasha (Nenga), Ngweshla Natural (NgweNat), Ngwenya, Sedina (Sed), Silewu (Sil), Caterpillar (Cat), Dom, Dopi (Dop), Foster (Fos), Ganda (Gan), Guvalala (Guv), Jambile Artificial (JamArt), Kennedy 1 (Ken1), Kennedy 2 (Ken2), Livingi (Liv), Makwa (Mak), Ngweshla Artificial (NgweArt), Nyamandlovu (Nyam), Safari lodge (Saf), Tchabema (Tchab) and Tshebetshebe (Tsheb).

Figure 3. Species and food-web (A) LCDB and (B) SCBD over all waterholes and dates.

In both panels, black diamonds, grey triangles and inverted grey triangles identify respectively waterholes or species – groups that have highest values for both indices, food-web based index and species based index. The plain line represents the correlation line. (A) Particular pans are identified by their abbreviation (see Figure 2) and first letter of the sampling month. (B) Species abbreviations are *Afrocylops gibsoni* (AG), *Anabaena* sp.

1 (Ansp), bacteria (Bact), *Brachionus calyciflorus* (BC), *Camphylodiscus* sp. (CAsp),
2 *Chroococcus* sp. (CHsp), *Cymbella* sp. (CyMsp), *Cyclotella* sp. (Cysp), *Daphnia longispina*
3 (DLO), *Daphnia pulex* (DP), *Diatoma* sp. (Dsp), *Diaphanosoma tropicum* (DT), *Eudiaptomus*
4 *gracilis* (EG), *Euglena* sp. (Esp), *Filinia pejeri* (FP), *Microcystis aeruginosa* (MA),
5 *Macrocyclus albidus* (MAL) *Melosira* sp. (MELsp) microphytoplankton (MicroPhyto),
6 *Megacyclus viridis* (MV), *Oscillatoria* sp. (Ossp), *Phacus curvicauda* (PHC), particulate and
7 dissolved organic matter (PomDom), protists (Prot), *Pediastrum simplex* (PS), *Pinnularia* sp.
8 (Psp), *Polyarthra vulgaris* (PV), *Spyrogira* sp (SPYsp), *Tetraedron asymmetricum* (TA),
9 nauplii (TN), *T. limnetica* (TL) and *T. regulare* (TR).
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25 **Figure 4. Food-web (grey square) and species (yellow triangle) based LCBD as a**
26 **function of (a.) Shannon diversity, (b.) food web average trophic, (c.) species richness**
27 **and (d.) connectance** with significant regression lines (see text).
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36 **Figure 5. Food-web (grey square) and species (yellow triangle) based SCBD as a**
37 **function of (a.) species frequency of occurrence, (b.) species degree in metaweb and (c.)**
38 **species trophic level in metaweb** with significant regression lines (see text).
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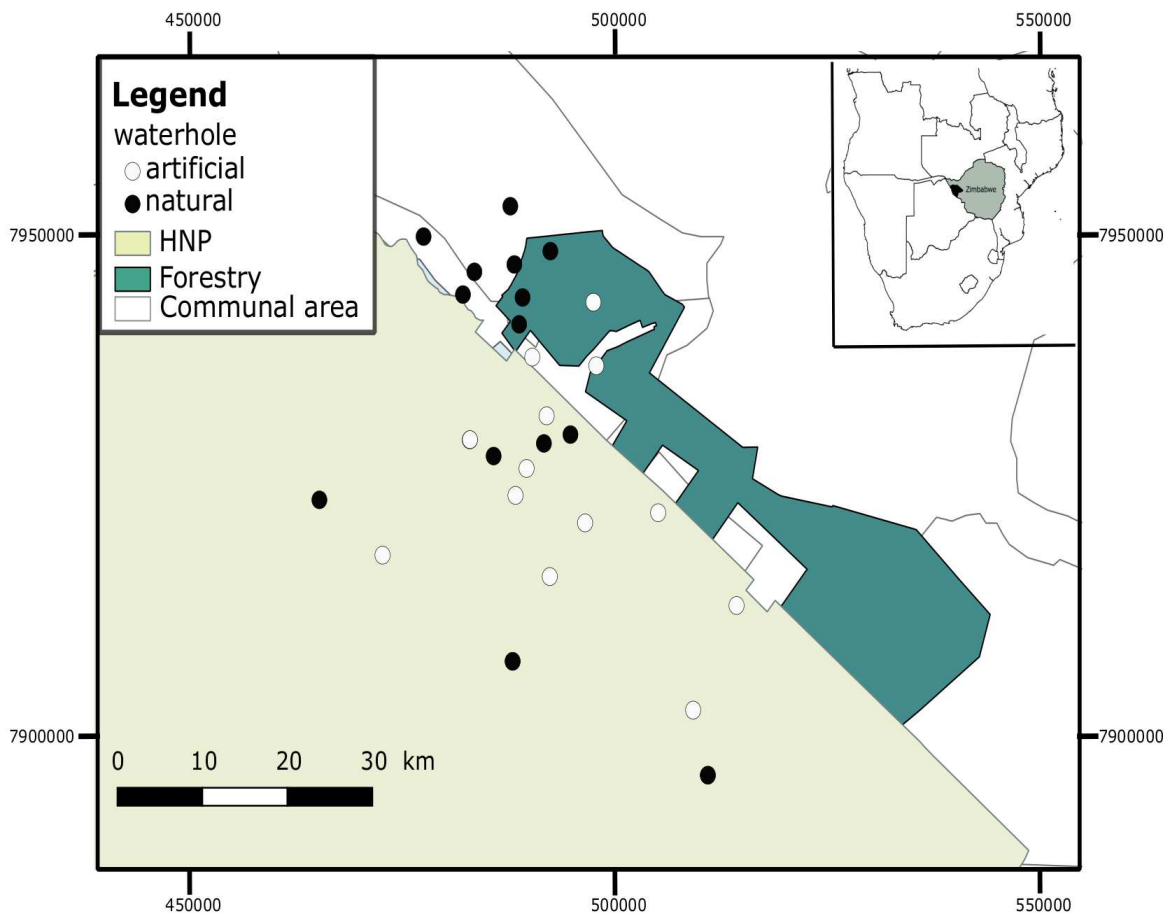
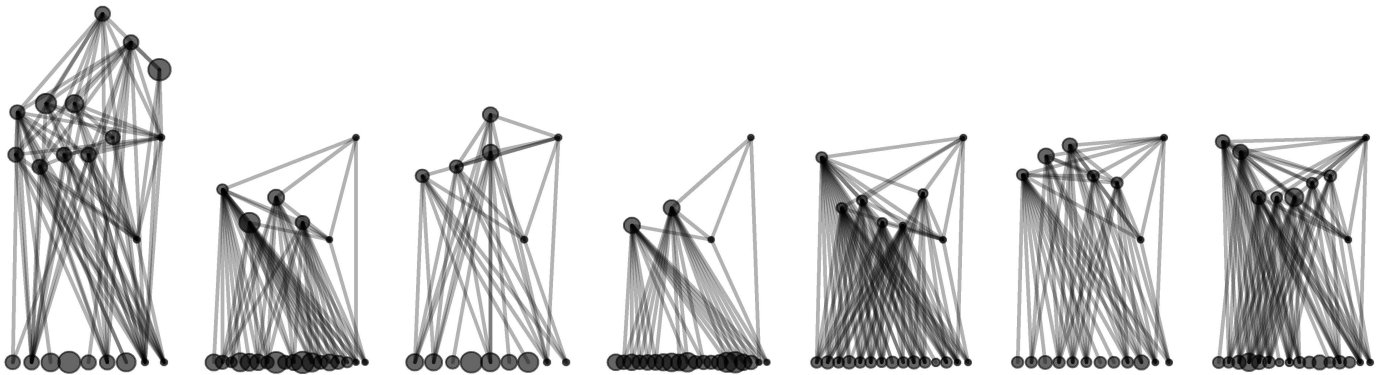
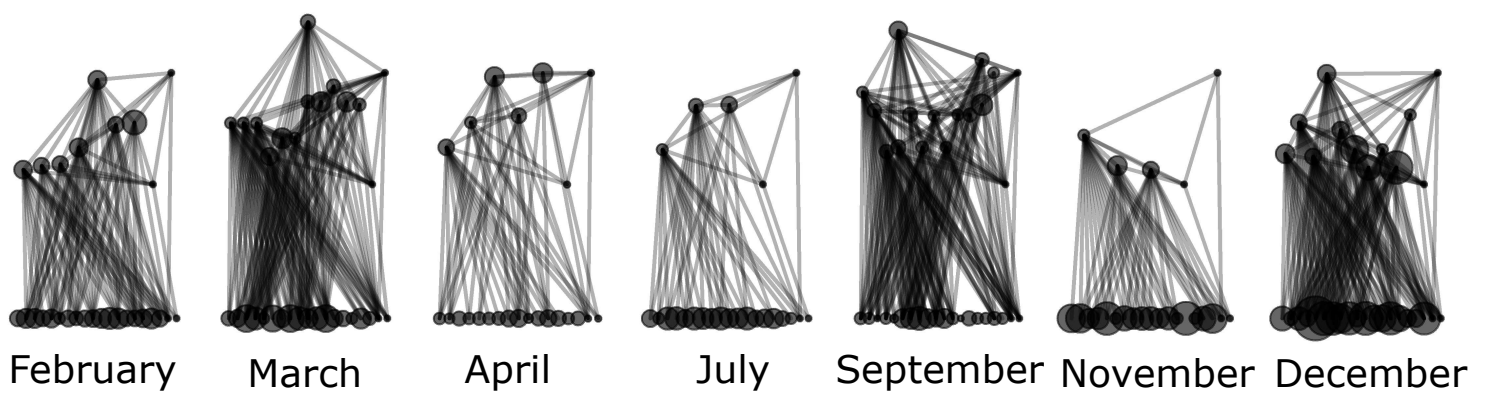
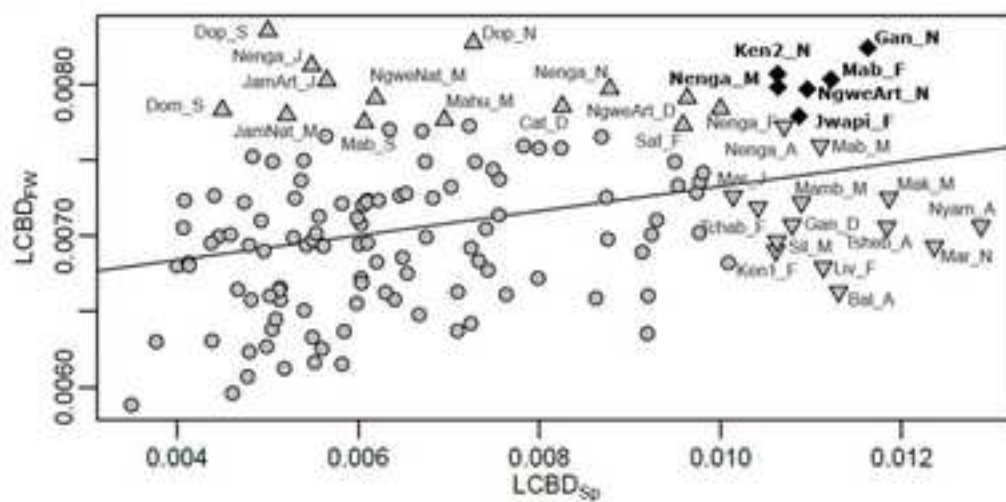
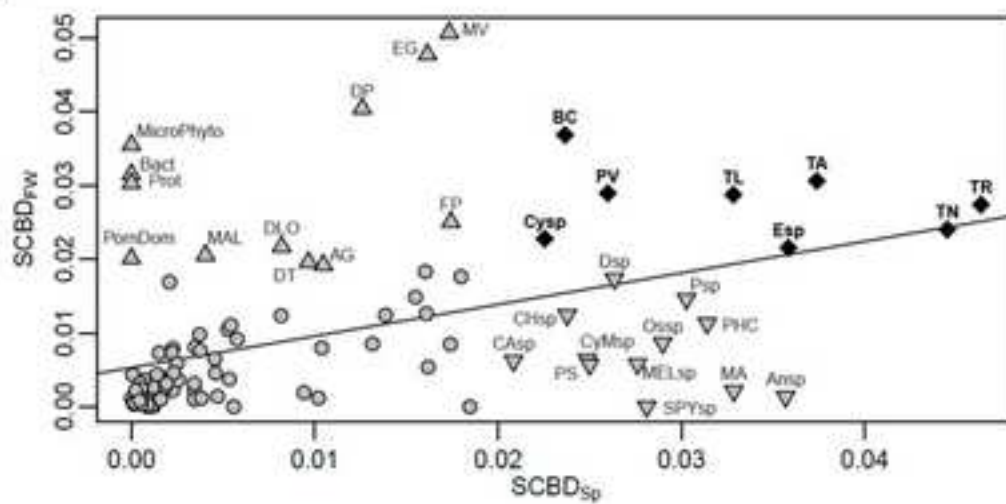
a.**b.****c.**

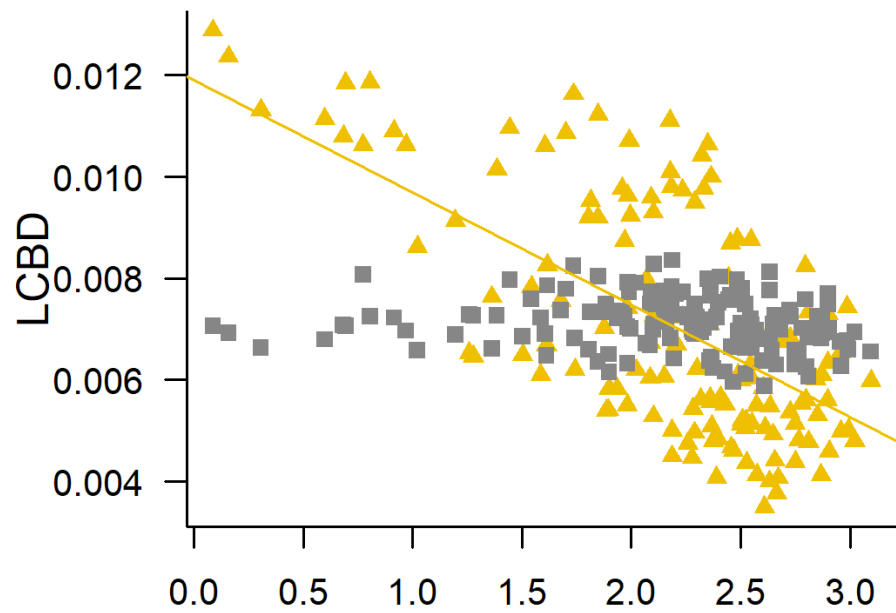
Figure 3

A

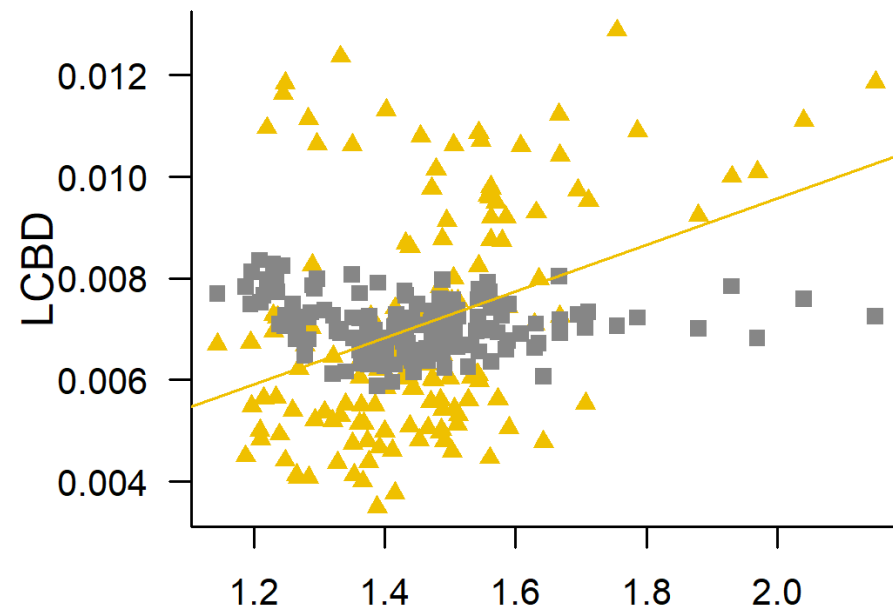


B

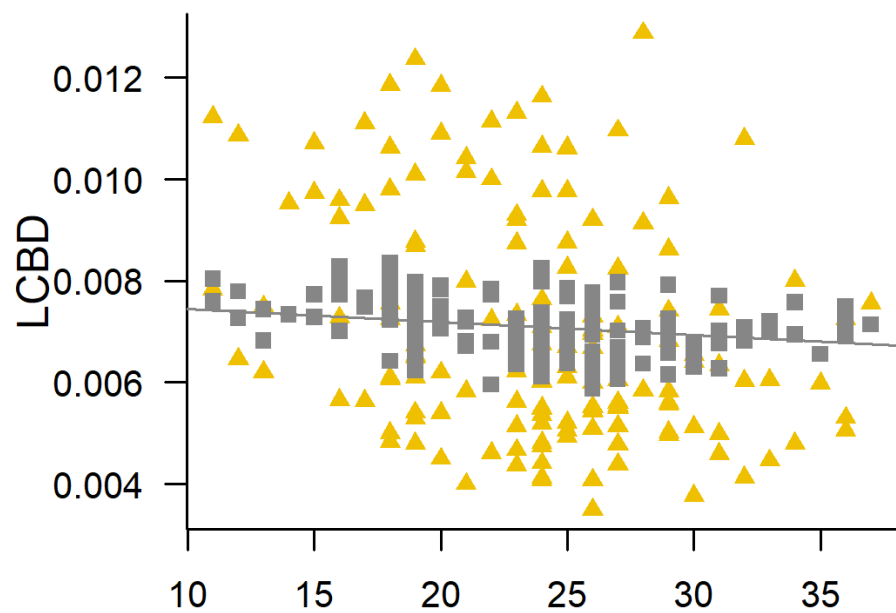


a.

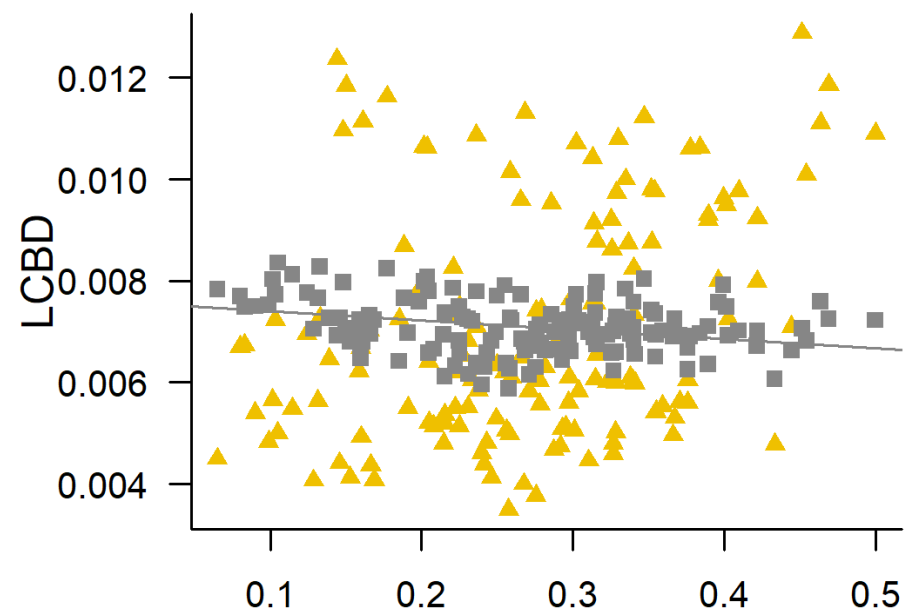
Shannon diversity

b.

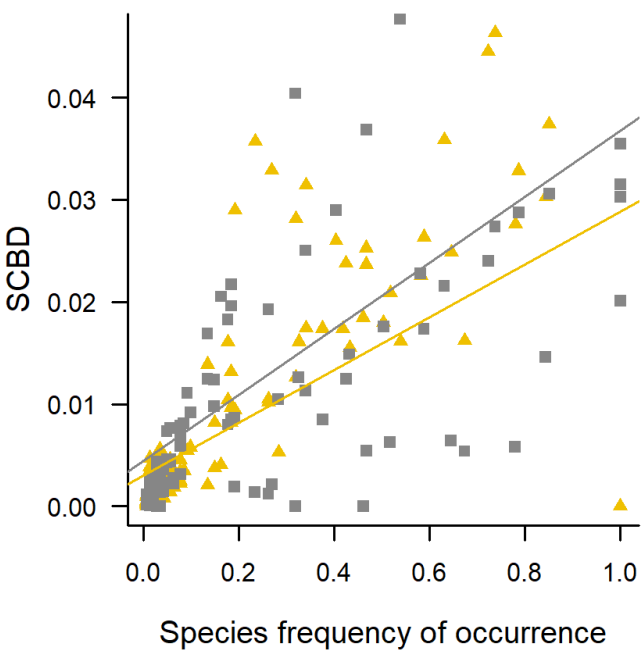
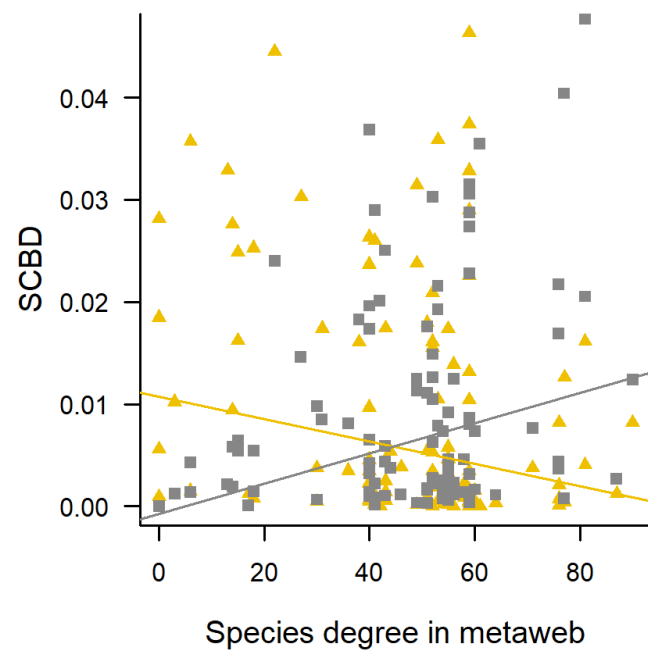
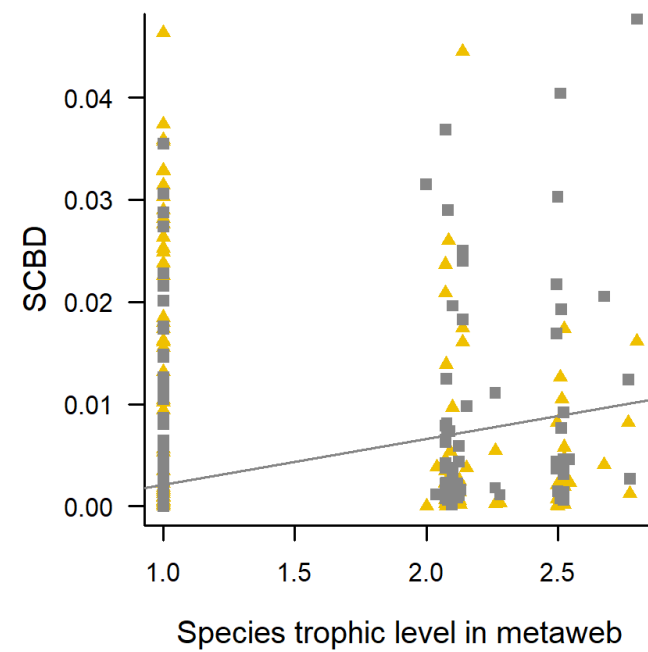
Food web average trophic level

c.

Species richness

d.

Connectance

a.**b.****c.**

Appendix 1

Table S1: Spatial autocorrelation of LCBD_{Sp} and LCBD_{FW} by sampling month, as measured by Moran's *I*.

Month	LCBD _{Sp}		LCBD _{FW}	
	Moran's <i>I</i>	<i>P</i> value	Moran's <i>I</i>	<i>P</i> value
February	-0.003	0.64	0.086	0.08
March	-0.004	0.65	-0.018	0.79
April	-0.03	0.89	-0.029	0.88
July	-0.11	0.51	0.069	0.20
September	0.082	0.25	-0.099	0.88
November	-0.094	0.97	-0.17	0.46
December	-0.18	0.55	0.06	0.35

Figure S1: Schematic diagram representing the procedure to build the interaction-by-sampling unit matrix from the meta food-web and the species composition of sampling units. The interaction-by-sampling unit matrix is then used to compute dissimilarities among sampling units and LCBD values, as done originally on the species-by-sampling unit matrix (Legendre and De Caceres 2013).

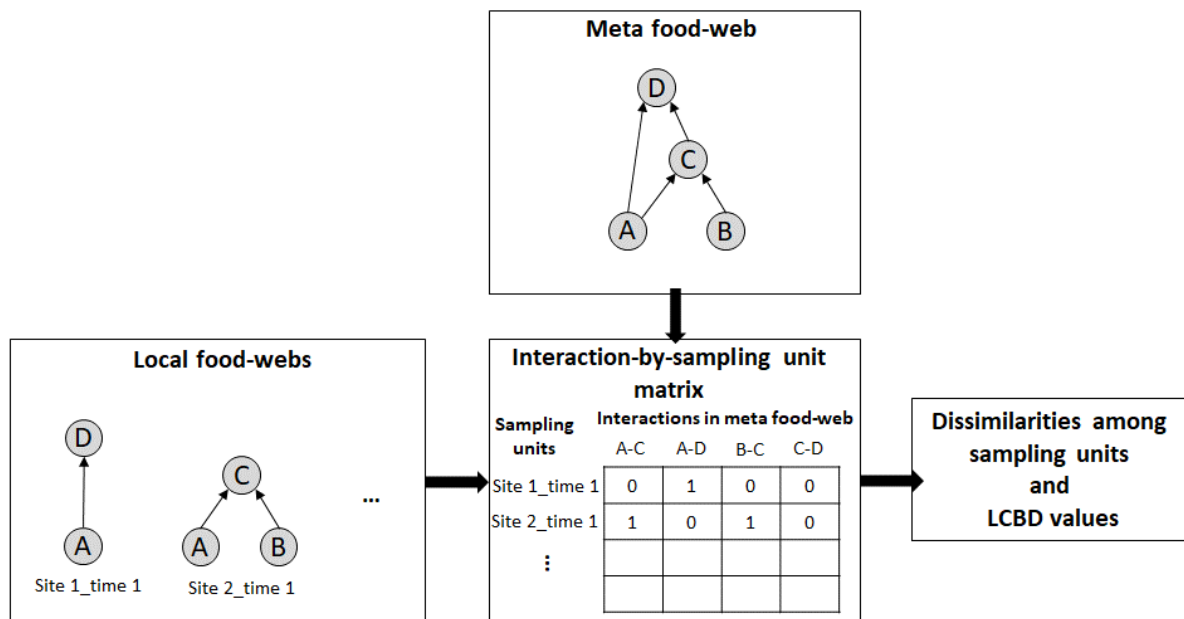
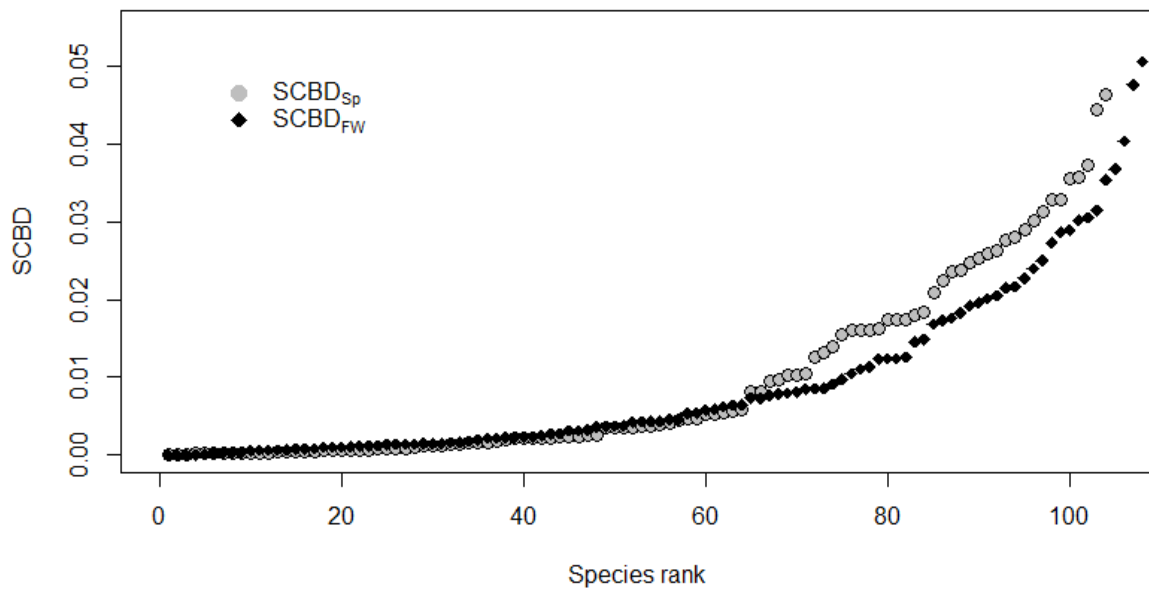
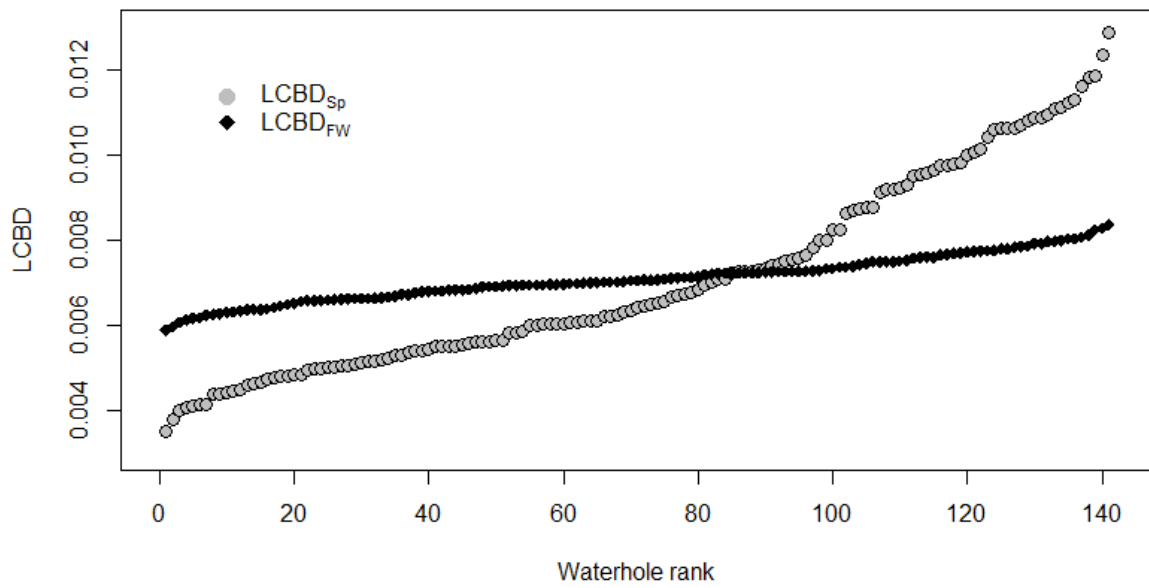


Figure S2. Species and food-web based SCBD and LCBF as a function of species (A) and waterhole (B) ranks.

A.



B.



MicroPhyto	0	1	0	0	0	0	0	0	0	1	1	1
1	1	1	1	1	1	1	1	1	1	0	1	1
1	1	1	1	1	0	0	0	0	0	0	0	1
0	0	0	1	1	1	1	1	0	1	1	1	1
0	0	1	0	1	0	1	1	0	0	0	0	1
1	1	1	1	1	1	1	1	1	1	1	0	0
1	0	0	0	1	0	1	1	1	1	1	0	0
0	1	0	1	1	0	0	0	0	1	0	0	0
0	0	0	0	0	1	1	1	1	1	1	1	1
0												
Anabaena sp.		0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	1	1	1	1	1	0	0	0
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0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0											
Ankistrodesmus spiralis				0	1	0	0	0	0	0	0	0
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0	1	0	1	1	1	1	1	0	0	0	0	0
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1	1	1	0	0	1	0	1	0	1	1	1	0
0	0	1	1	1	1	1	0	0	0	0	1	1
1	0	0	1	0	0	0	0	0	0	1	1	1
1	0	0	0	1	0	0	0	1	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1	0
0	1	1	0									
Ankistrodesmus spirilliformis					0	1	0	0	0	0	0	0
0	1	1	1	1	0	1	1	1	1	1	1	1
1	0	1	0	1	1	1	1	1	1	0	0	0
0	0	0	1	0	0	0	0	1	1	1	1	1
0	1	1	1	0	0	1	0	1	0	1	0	1
0	0	0	1	1	1	1	1	1	0	0	0	1
1	1	0	0	1	0	0	0	0	0	0	1	1
1	1	0	0	0	1	0	0	0	1	0	0	0
1	0	0	0	0	0	0	0	0	0	1	1	1
0	0	1	1	0								
Arthrodesmus sp.		0	1	0	0	0	0	0	0	0	1	1
1	1	1	1	1	1	1	1	1	1	1	0	1
0	1	1	1	1	1	0	0	0	0	0	0	0
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1	0	0	1	0	1	0	1	1	1	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	0
0	1	0	0	0	1	0	1	1	1	1	1	0
0	0	1	0	0	1	0	0	1	1	1	0	0
0	0	1	0	0	1	0	0	0	1	1	0	0
0	0	0	0	0	0	1	1	1	1	1	1	1
1	0											
Bacteria		0	0	0	0	0	0	0	0	1	1	1
1	1	1	1	1	1	1	1	1	1	0	1	1
1	1	1	1	1	0	0	0	0	0	0	0	0
0	0	0	1	1	1	1	1	1	0	1	1	1

	0	0	0	0	1	0	1	1	0	0	0	1
	1	1	1	1	1	1	1	1	1	1	0	0
	1	0	0	0	1	0	1	1	1	1	0	0
	0	1	0	1	1	0	0	0	1	0	0	0
	0	0	0	0	0	1	1	1	1	1	1	1
	0											
Bosmina brehmi	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	1	0	0	0	1	1	1	1	1	0	0	0
	0	0	0	1	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	1	1	1	0
	0	1	0	0	0	0	0	1	1	1	1	0
	0	0	0	0	0	1	0	0	0	0	0	0
	0	0	0	0	0	0	1	0	0	0	0	1
	1	0										
Brachionus unguularis	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	1	0	0	0	1	1	1	1	1	0	0
	0	0	0	0	1	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	1	1	1
	0	0	1	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	1	0	0	0	0	0
	0	0	0	0	0	0	0	1	0	0	0	0
	1	1	0									
Brachionus calyciflorus	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	1	1	1	1	1	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	1	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
Brachionus dolabratus	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	1	0	0	0	1	1	1	1	1	0	0
	0	0	0	0	1	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	1	1	1
	0	0	1	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	1	0	0	0	0	0
	0	0	0	0	0	0	0	1	0	0	0	0
	1	1	0									
Brachionus patulus	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
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	0	0	0	0	1	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	1	1	1
	0	0	1	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	1	0	0	0	0	0

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0	1	0	0	0	0	1	1	1	1	1	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	1	1
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0	0	0	0	0	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	0	0
1	1	0										
Brachionus quadridentatus				0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	1	1	1	1	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
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0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
Cephalodella gibba				0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
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0	0	0	0	0	0	0	0	0	0	0	0	0
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0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
Camphylodiscus sp.				0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	1	1	1	1	0	0	0	0	0	0
0	1	0	0	0	0	1	1	1	1	1	0	1
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0	0	0	0	0	0	0	0	0	0	0	0	0
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0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratium sp.				0	0	0	0	0	0	0	0	1
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0	0	0	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
Ceriodaphnia cornuta				0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
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0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	1

Pinnularia sp.	0	0	0	0	0	0	0	0	0	1	0
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0	0	0	0	0	0	0	0	1	0	1	0
0	0	0	0	0	0	0	0	0	0	0	0
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0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
Polyarthra vulgaris	0	0	0	0	0	0	0	0	0	0	0
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PomDom	0	0	0	0	0	0	0	1	1	1	1
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Protists	0	1	0	0	0	0	0	0	1	1	1
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0	0	0	0	1	1	1	1	1	1	0	0
1	0	0	0	1	0	1	1	1	1	0	0
0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	1	1	1	1
0	0	0	0	0	0	0	0	0	0	0	0
Scapholebris kingi	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0	0	0	0
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0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
Scenedesmus quadricauda	0	0	0	0	1	0	0	0	0	0	0
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0	1	0	1	1	1	1	1	0	0	0	0
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0	1	0	0	0	0	1	1	1	1	1	0	1
1	1	0	0	1	0	1	0	1	0	1	0	0
0	1	1	1	1	1	1	1	1	1	1	1	1
0	0	1	0	0	0	1	0	1	1	1	1	1
0	0	0	1	0	0	1	0	0	0	0	1	0
0	0	0	0	0	0	0	1	1	1	1	1	1
1	1	0										
Thermocyclops oblongata				0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0										
Trichotria elongata				0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	1	1	1	1	1	1	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0										
Trichocerca pusilla				0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	1	1	1	1	1	1	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	1	1
0	0	1	0	0	0	0	0	1	1	1	1	1
0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0
1	1	0										
Trichocerca similis				0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	1	1	1	1	1	1	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	1	1
0	0	1	0	0	0	0	0	1	1	1	1	1
0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0	0	0
1	1	0										
Trichotria tetractis				0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	1	1	1	1	1	1	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	1	1

