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**Temporal changes in food web structure in semi-arid waterholes**

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1 **Abstract**

2 Semi-arid climate aquatic ecosystems may be highly seasonal due to large-amplitude water-  
3 level fluctuations. These resulting habitat changes impact aquatic communities and food web  
4 structures as a result of species replacement or loss. To study the impact of water-level  
5 fluctuations on planktonic food web structure, we compared food web descriptors in  
6 contrasting seasons. We examined the planktonic food webs associated with semi-arid natural  
7 and artificial waterholes sampled in Hwange National Park, Zimbabwe, during the hot dry  
8 (HDS), wet (WS), and cold dry seasons (CDS). Natural waterholes are filled by rainwater,  
9 while water is pumped into artificial waterholes to provide drinking water to wildlife during  
10 the dry season. We computed the descriptors of 66 food webs. WS food webs tend to be more  
11 complex than those of HDS and CDS; the percentage of basal species was lower, whereas the  
12 food web connectance, percentage of intermediate species, omnivory index, mean trophic  
13 level, and maximum trophic height of species were higher. Pumping water to maintain pans in  
14 the dry season had no effect on food web properties. The drying up of waterholes in semi-arid  
15 environments simplifies planktonic food webs. The dominance of small rotifers may explain  
16 the observed low omnivory index and food web connectance in HDS compared to those  
17 observed in other studies.

18

19 **Keywords**

20 Food web complexity, food web connectance, omnivory, Hwange National Park, planktonic  
21 food web, temporary ponds, water-level fluctuations

22

## 1 **Introduction**

2 Studies on food webs have attracted much attention since the early work of C. S. Elton  
3 (1927). Studying the structure of a network of species and their predation links at a given site  
4 provides insights into the functioning of the underlying ecosystem (Loreau 2010). However,  
5 food webs provide snapshots of communities that vary in space and time (Paine 1988). In  
6 addition, local food webs are drawn from a metaweb (Dunne 2006), that is, a regional pool of  
7 species and their potential interactions. Local networks are thus realizations of metawebs,  
8 which may change in space and time (Poisot et al. 2012). Research questions in food web  
9 studies have recently moved from understanding ‘how networks vary’ to ‘why networks vary’  
10 (Pellissier et al. 2018). Thus, comprehending how networks – including food webs,  
11 mutualistic and host-parasitoid networks – change along environmental gradients and over  
12 time, and identifying the biotic and abiotic drivers of their realization is crucial in order to  
13 understand and predict their responses to environmental changes (Tylianakis and Morris  
14 2017).

15  
16 Network variation results from the turnover of species and their mutualistic and antagonistic  
17 interactions (Poisot et al. 2012; Pellissier et al. 2018). Multiple approaches have been  
18 developed to describe and quantify the variation of network structures (Pellissier et al. 2018).  
19 In particular, several descriptors such as species richness, connectance, and nestedness are  
20 regularly used. The analysis of network structure gives insights into the response of  
21 ecosystems to perturbations. For instance, Lu et al. (2016), who studied the response of  
22 stream food webs to droughts, found that hydrological perturbation resulted in the loss of  
23 extinction-prone species and a rewiring of interactions between the remaining species. These  
24 compensatory dynamics ensure the conservation of a substructure and the stability of  
25 impacted food webs (Lu et al. 2016). However, studies comparing ecological networks across

1 environmental gradients and/or through time are rare due to the lack of well-documented data  
2 (Tylianakis and Morris 2017; Pellissier et al. 2018).

3

4 In semi-arid climates, ecosystems may undergo strong seasonal variations with wet and dry  
5 periods. For aquatic ecosystems, the impact of this alternation ranges from water-level  
6 fluctuations to a complete drying up followed by the refilling of water. These abiotic changes  
7 to habitats strongly impact aquatic communities (Thomas et al. 2000; Coops et al. 2003;  
8 Thomaz et al. 2006; Bazzanti et al. 2009; Michaloudi et al. 2012; Teferi et al. 2014; Medeiros  
9 et al. 2015). Such impacts may be direct through drying up or indirect via changes in the  
10 chemical properties and nutrient concentrations of the water with alternating dilution and  
11 concentration due to water-level fluctuations (Coops et al. 2003; Nihwatiwa et al. 2011;  
12 Jeppesen et al. 2015; Coppens et al. 2016). Therefore, seasonal variations in semi-arid aquatic  
13 ecosystems may affect food web structures.

14

15 In Hwange National Park (HNP) in Zimbabwe, some waterholes are artificially fed by  
16 groundwater during the dry season to provide drinking water to wildlife, while natural  
17 waterholes usually dry up. As natural waterholes are depressions fed during the rainy season  
18 by rainwater runoff, we refer to them as pans (Fynn et al. 2015). Artificial pans are also  
19 subject to water-level fluctuations but are maintained throughout the year. This change in the  
20 natural physical dynamics may have a strong impact on ecological dynamics. Msiteli-Shumba  
21 et al. (2017, 2018) monitored 30 natural and artificial pans for 7 months in 2013 and showed  
22 decreases in the richness and diversity of phytoplankton and zooplankton species during the  
23 dry season. The analysis of environmental variables showed water eutrophication and  
24 seasonal variations in certain parameters such as increased conductivity and hardness with  
25 decreasing water levels (Msiteli-Shumba et al. 2018). In addition, providing water during the

1 dry season attracts animals around pans, which fouls the water with feces and urine,  
2 potentially leading to water eutrophication (Hulot et al. 2019).

3

4 In this study, to deepen our understanding of plankton communities affected by water-level  
5 fluctuations and the drying up of pans, we analyzed the effects of seasonal changes on  
6 planktonic food webs in semi-arid pans situated in HNP and its adjacent communal and  
7 forestry areas. We compared data on the wet season (WS) as well as the cold (CDS) and hot  
8 dry seasons (HDS). For each waterhole and in each season, we constructed a prey-predator  
9 matrix by identifying the predation links between planktonic species, which allowed us to  
10 generate planktonic food webs and identify their properties such as connectance and number  
11 of omnivorous and cannibalistic species. We particularly studied food web complexity (i.e.,  
12 more species, higher connectance, and higher mean species trophic level) in the different  
13 seasons, which determine the water level. We tested the following hypotheses: (1) planktonic  
14 food webs are more complex in WS than in CDS and HDS; (2) the properties of planktonic  
15 food webs in CDS are of intermediate level between WS and HDS; and (3) planktonic food  
16 webs in artificial pans show less variation than in natural pans. We assumed that our  
17 hypotheses should not be rejected if we found that the number of trophic interactions is higher  
18 in WS, due to an expected higher primary production. Also, HDS has a harsher climate and  
19 lower water levels than CDS due to evaporation. Lastly, the supply of water in artificial pans  
20 will mitigate the loss of species and trophic links due to drying up.

21

22

23

## 1 **Methods**

### 2 *Study site*

3 Hwange National Park (HNP) is situated in Western Zimbabwe at the border with Botswana.  
4 The climate is semi-arid with a rainy season from late November to March and a dry season  
5 from April to early November. The annual rainfall is highly variable with a mean of 600 mm  
6 and a coefficient of variation of 25% (Arraut et al. 2018). The vegetation is typical of a highly  
7 heterogeneous dystrophic wooded savanna dominated by woodlands or a mixed bushland  
8 community with open grasslands along drainage lines (Chamaillé-Jammes et al. 2007).  
9 Numerous temporary water pans are formed during the rainy season, and according to their  
10 size and depth, these natural pans may dry out completely in the course of the dry season. To  
11 supply wildlife with water during the dry season, underground water is pumped to some  
12 permanent artificial waterholes. The pans investigated in this study are located in HNP and  
13 the adjacent Sikumi Forest and communal areas situated in the periphery of the park. Natural  
14 and artificial pans are found in the park and forestry areas, while only natural pans are found  
15 in the communal area.

16

### 17 *Field sampling and laboratory analyses*

18 This study focuses on the monitoring of a total of 30 pans: 13 natural and 17 artificial pans,  
19 with 20 located in HNP, 5 in the forestry area, and 5 in the communal area. These pans were  
20 sampled in November 2012, February 2013, and July 2013. These dates are respectively  
21 characteristic of three different periods of the year: HDS, WS, and CDS. Not all 30 pans were  
22 sampled at every date because of their drying up or technical problems. Therefore, the total  
23 number of pans analyzed in this study is 16 for November 2012 (2 natural), 28 for February  
24 2013 (11 natural), and 22 for July 2013 (8 natural).

1 We collected 10 L for plankton analyses. Water was first filtrated through a 100  $\mu\text{m}$  filter and  
2 then a 30  $\mu\text{m}$  filter. Samples were collected in 50 ml falcon tubes and preserved in 4%  
3 formalin. Taxonomic identification was carried out under an Olympus CK40 inverted  
4 microscope with the assistance of taxonomic keys (Msiteli-Shumba et al. 2017). All plankton  
5 species were identified to the lowest taxonomic level possible.

6

### 7 *Food web construction and analyses with the N\_W program*

8 To analyze plankton networks in the pans during the different seasons, we constructed the  
9 prey-predator interaction matrix for each pan at each date, leading to 66 matrices. We then  
10 analyzed these matrices using the N\_W program (Legendre et al. 2013) to calculate the  
11 network properties. First, we searched the literature on the species identified in the pans with  
12 the aim to document the diet of zooplankton species and their predation on phytoplankton and  
13 potentially other zooplankton species. With this information, we were able to construct the  
14 matrices where all species are in lines and columns. A “1” in the matrix denotes the predation  
15 of the species in the line by the species in the column; the absence of predation is represented  
16 by “0”. Trophic links were not weighted; in other words, we constructed and analyzed binary  
17 webs. The different life stages of a species are represented only once in the matrix. Therefore,  
18 species with ontogenetic omnivory appear in the matrix only once in the column with the  
19 multiple prey that they eat during their lifetime, even though the species may be a prey as a  
20 juvenile and a predator as an adult. Cannibalism is represented by a “1” at the intersection of  
21 the same species in the column and line along the diagonal of the matrix. Not all species could  
22 be found in the literature. We therefore made approximations based on personal expertise, the  
23 species’ taxonomy (Gauzens et al. 2013), and the well-known allometric relationship between  
24 prey and predators (Brooks and Dodson 1965; Burns 1968). Phylogeny and trophic structure  
25 have a close relationship (Bersier and Kehrli 2008). In particular, species of the same size and

1 belonging to the same genus were hypothesized to have the same diet, and these  
2 approximations concerned 16 out of 44 zooplankton species. Some species fed on species or  
3 groups that were not identified in the sampled plankton. Therefore, we added the groups  
4 “bacteria,” “small phytoplankton” with a size below 30  $\mu\text{m}$ , “protists,” and “POM and DOM”  
5 (particulate and dissolved organic matter). In the following, these basal groups are considered  
6 to be basal species.

7 Using the N\_W program, the networks associated with the matrices were constructed, and  
8 their topological descriptors were computed. For our analyses, we selected the following  
9 descriptors: species richness (number  $S$  of species), network connectance (number  $L$  of links  
10 between species divided by  $S^2$ , the total number of possible links), number of basal species  
11 (species without prey), number of intermediate species (species with both prey and predators),  
12 number of top species (species without predators), number of isolated basal species (basal  
13 species without links to other species), and cannibalism (number of species that eat  
14 themselves). We also considered the mean trophic level and the maximum trophic height.

15 Basal species have a trophic level of 1, and the trophic level of a non-basal species is defined  
16 as 1 plus the average of the trophic levels of its prey. The trophic level of the whole food web  
17 (mean trophic level) is the average of the trophic levels of its constituent species. The trophic  
18 height of a species is a different descriptor. In this case, a base species has a trophic height of  
19 0, and the trophic height of a non-basal species is the average of the lengths of all directed  
20 paths leading to it from the basal species. The maximum height of the network is the maximal  
21 path length from basal to non-basal species. The omnivory index of a species is the standard  
22 deviation of the trophic heights of the prey species of this species. The food web omnivory  
23 index – here, omnivory index – is the mean value of the omnivory indexes of all constituent  
24 species. Food web complexity and robustness are characterized by entropy  $H$ , which  
25 quantifies the diversity of the pathways of energy flow between species in the network. In our

1 analyses, we use scaled entropy  $H/\ln(S)$ , which is entropy standardized by species richness  
2 (Gauzens et al. 2016).

3

#### 4 *Statistical analyses*

5 We tested the effects of season (HDS, WS, and CDS) and pumping status (i.e., natural versus  
6 artificial pans) using the analysis of variance (ANOVA) of food web properties (species  
7 richness, connectance, percentage of basal species, percentage of intermediate species, top  
8 species, isolated basal and cannibalistic species, omnivory index, mean trophic level,  
9 maximum trophic height, and scaled entropy). The Akaike information criterion (AIC) was  
10 used to select the best model from the following: a full model in which season interacts with  
11 pumping status; a model with the additive effects of season and pumping status; and a model  
12 with either season or pumping status. We made multiple comparisons with Tukey tests when a  
13 significant effect was revealed by ANOVA. The significance threshold was set at 5%.

14 To explore the relationship between food web descriptors and their description of pans in the  
15 different seasons, we first performed principal component analysis (PCA) using the  
16 FactoMiner package (Husson et al. 2015). To carry out PCA, collinearity should be avoided  
17 between the response data and explanatory variables. For this reason, our analysis took into  
18 account the following descriptors: the number of basal, intermediate, isolated, and  
19 cannibalistic species; connectance; omnivory index; maximum trophic height; and scaled  
20 entropy.

21

## 1 **Results**

2 We found a significant effect of season on several food web descriptors: species richness,  
3 connectance, percentage of basal and intermediate species, number of omnivorous species,  
4 mean trophic level, maximum trophic height, and scaled entropy (Table 1, Fig. 1, 2). Species  
5 richness and scaled entropy were significantly lower in HDS, higher in CDS, and intermediate  
6 in WS (Fig. 2a, k). Connectance, number of omnivorous species, and maximum trophic height  
7 were significantly higher in WS, lower in HDS, and intermediate in CDS (Fig. 2b, h, j). The  
8 percentage of basal species was significantly higher in HDS and CDS than in WS (Fig. 2c).  
9 The opposite was found for the percentage of intermediate species, which was higher in WS  
10 than in HDS and CDS (Fig. 2d). There was a significant effect of season and pumping status  
11 on the mean trophic level (Table 1, Fig. 2i), which was higher in natural than in artificial pans.  
12 The mean species trophic level was higher in WS than in HDS and CDS. No significant effect  
13 of season or pumping status was observed on the percentage of top, isolated, or cannibalistic  
14 species (Table 1, Fig. 2e, f, g).

15 Food web descriptors explained a large part of the differences between pans as shown by PCA  
16 (Fig. 3). The first two dimensions explain 89%, 76%, and 88% of the variability during HDS,  
17 WS, and CDS, respectively. The first and second dimensions explain between 50% and 72%  
18 and between 13% and 24% of pan variability, respectively. The pattern is very similar for the  
19 three analyses: scaled entropy, maximum trophic height, connectance, and the number of  
20 intermediate, omnivorous, and cannibalistic species are significantly positively correlated  
21 with the first dimension, while the number of isolated basal species is significantly negatively  
22 correlated with this dimension. The number of basal species is significantly positively  
23 correlated with the second dimension for the three seasons; the number of isolated basal  
24 species is significantly positively correlated with the second dimension for HDS and WS. In  
25 addition, during WS, the number of intermediate and omnivorous species is significantly

1 positively correlated with the second dimension, whereas connectance is significantly  
2 negatively correlated (Fig. 3). To summarize, in all cases, between 50% and 72% of pan  
3 variability is explained by food web complexity characterized by a high number of  
4 intermediate, omnivorous, and cannibalistic species, high-scaled entropy, maximum trophic  
5 height, and connectance, while a low number of basal isolated species. Between 13% and  
6 24% of additional variability is explained by the high number of basal species, potentially  
7 associated with a high number of isolated basal species.

8

## 1 **Discussion**

2 We analyzed the food web descriptors of 30 pans in contrasting seasons (66 food webs in  
3 total) and made three hypotheses. We discuss now our hypotheses. The pattern of food web  
4 structure in the pans across the seasons shows a gradient, ranging from food webs  
5 characterized by diverse diets, high connectance, and long pathways of energy flow toward  
6 the top species, to food webs with shorter pathways and less complex structures including a  
7 larger number of unconsumed species. Shorter pathways mean that small herbivorous species  
8 such as rotifers (*Brachionus* sp.) and nauplii are less consumed by predators such as cyclopids  
9 and instead become top consumers in the planktonic food webs. This pattern might be  
10 generated by organisms not studied in our survey such as macroinvertebrates, tadpoles during  
11 WS, and fish. The predation exerted by these potential consumers of zooplankton may have a  
12 strong influence on the food web structure (Brooks and Dodson 1965). We hypothesize that  
13 this pattern might be due to either predation or harsh environmental conditions during the dry  
14 season with desiccation and an increase in salinity, conductivity, and ammonium  
15 concentration, which can reach toxic concentrations in some pans (Robles-Vargas and Snell  
16 2010; Msiteli-Shumba et al. 2018).

17 Most of the descriptors studied here showed differences between HDS and WS, whereas the  
18 descriptors of CDS were close to those of either WS or HDS. November 2012 (HDS) was a  
19 particularly dry month, and out of the 16 sampled pans, only two were natural, because all the  
20 others dried up. In WS and CDS, the distribution of natural and artificial pans was more  
21 balanced. Therefore, the seasonal effect shown here is a real temporal effect and not a  
22 confounding effect of pan management. Overall, compared to HDS and CDS, the WS food  
23 webs appear more complex, with more nodes and links and with higher trophic levels: this is  
24 illustrated in two pans (Fig. 1). Higher connectance and complexity have been shown to  
25 render food webs more robust to species loss (Dunne et al. 2002; Dunne 2006; Dunne and

1 Williams 2009; Gilbert 2009; Gross et al. 2009). Planktonic food webs become less robust to  
2 perturbations during the dry season, especially during HDS. However, species and  
3 interactions loss during the dry season did not cause the food webs to collapse, as a rewiring  
4 of the interactions between the remaining species could occur (Staniczenko et al. 2010; Lu et  
5 al. 2016).

6 Since only one of the 11 studied descriptors responds to the pumping status of the pans -- the  
7 mean trophic level is lower in artificial pans than in natural ones -- we suggest that food web  
8 structure is similar in both natural and artificial pans. Pumping water during the dry season  
9 and maintaining pans throughout the year may increase water salinity and conductivity on  
10 account of saltwater intrusion (Borrok and Engle 2014; Msiteli-Shumba et al. 2018). In  
11 addition, in HNP and its periphery, artificial and natural pans that retain water all year round  
12 attract animals during the dry season, which fouls the water with urine and feces and may  
13 cause water eutrophication (Msiteli-Shumba et al. 2018). However, these side effects of  
14 pumping do not seem to affect the structure of the planktonic food webs in artificial pans, as  
15 they are similar to those in natural pans apart from the mean trophic level.

16 We compared the food web properties of our study to those already published for lakes and  
17 ponds (Warren 1989; Martinez 1991; Havens 1992; Dunne et al. 2004; Mendonça and  
18 Vinagre 2018). Our results for species richness, connectance, and percentage of top species  
19 are similar to those published in the literature. However, the percentage of intermediate and  
20 cannibalistic species was lower in our study, whereas the percentage of basal species was  
21 higher. This latter result might be explained by the high degree of determination of this  
22 compartment: all phytoplankton species larger than 30 $\mu$ m were identified (Msiteli-Shumba et  
23 al. 2017). Mendonça and Vinagre (2018) studied food webs in small intermittent estuaries and  
24 found higher cannibalism, shorter food chain lengths, and higher connectance compared to  
25 large open estuaries. They partly explain these results by opportunistic feeding by marine fish

1 and crustaceans that enter these systems and have a higher encounter rate with their juveniles.  
2 In our study, we could expect higher omnivory and cannibalism during the dry season,  
3 because the water volume shrinks and concentrates individuals in a smaller space. However,  
4 our results show no change in the percentage of cannibalistic species across seasons and even  
5 a decrease in the omnivory index in the HDS. Plankton monitoring in 2013 (Msiteli-Shumba  
6 et al. 2017) showed that the dominant zooplankton species in the pans are small rotifers that  
7 do not feed on conspecifics. In addition, the abundance of copepods, which are prone to  
8 cannibalism and omnivory, tends to decrease during the dry season. This might explain the  
9 absence of seasonal effects on cannibalism and the low omnivory index in the HDS.

10

11 In conclusion, we showed the seasonal changes of food web properties in semi-arid pans.  
12 These changes reveal that the planktonic trophic networks of the pans are more complex in  
13 WS and simplify as the pans dry up and concentrate ions and potential pollutants such as  
14 ammonium. The persistence of simplified food webs in the dry season points to the rewiring  
15 of interactions between the remaining species when the pans dry up, which implies that the  
16 population adapts to the environmental conditions as they become harmful. The results show  
17 no impact of pan management (i.e., pumping water during the dry season to maintain pans) on  
18 food web properties.

19

20

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3

## 1 **References**

- 2 Bazzanti M, Della Bella V, Grezzi F. 2009. Functional characteristics of macroinvertebrate  
3 communities in Mediterranean ponds (Central Italy): Influence of water permanence and  
4 mesohabitat type. *Ann Limnol-Int J Limnol.* 45(1):29-39. 10.1051/limn/09005
- 5 Bersier L-F, Kehrli P. 2008. The signature of phylogenetic constraints on food-web structure.  
6 *Ecological Complexity.* 5(2):132-139. 10.1016/j.ecocom.2007.06.013
- 7 Borrok DM, Engle MA. 2014. The role of climate in increasing salt loads in dryland rivers. *J*  
8 *Arid Environ.* 111:7-13. 10.1016/j.jaridenv.2014.07.001
- 9 Brooks JL, Dodson SI. 1965. Predation, body size, and composition of plankton. *Science.*  
10 150(3692):28-35.
- 11 Burns CW. 1968. The relationship between body size of filter-feeding Cladocera and the  
12 maximum size of particle ingested. *Limnol Oceanogr.* 13:675-678.
- 13 Chamaillé-Jammes S, Fritz H, Murindagomo F. 2007. Climate-driven fluctuations in surface-  
14 water availability and the buffering role of artificial pumping in an African savanna:  
15 Potential implication for herbivore dynamics. *Austral Ecology.* 32:740-748. 10.1111/j.1442-  
16 9993.2007.01761.x
- 17 Coops H, Beklioglu M, Crisman TL. 2003. The role of water-level fluctuations in shallow  
18 lake ecosystems - workshop conclusions. *Hydrobiologia.* 506(1-3):23-27.  
19 10.1023/b:hydr.0000008595.14393.77
- 20 Coppens J, Ozen A, Tavsanoglu UN, Erdogan S, Levi EE, Yozgatligil C, Jeppesen E,  
21 Beklioglu M. 2016. Impact of alternating wet and dry periods on long-term seasonal  
22 phosphorus and nitrogen budgets of two shallow Mediterranean lakes. *Sci Total Environ.*  
23 563:456-467. 10.1016/j.scitotenv.2016.04.028

1 Dunne JA. 2006. The network structure of food webs. In: Pascual M, Dunne JA, editors.  
2 Ecological networks: Linking structure to dynamics in food webs. Oxford: Oxford  
3 University Press.

4 Dunne JA, Williams RJ. 2009. Cascading extinctions and community collapse in model food  
5 webs. *Philosophical Transactions of the Royal Society B-Biological Sciences*.  
6 364(1524):1711-1723. 10.1098/rstb.2008.0219

7 Dunne JA, Williams RJ, Martinez ND. 2002. Network structure and biodiversity loss in food  
8 webs: robustness increases with connectance. *Ecology Letters*. 5(4):558-567.  
9 10.1046/j.1461-0248.2002.00354.x

10 Dunne JA, Williams RJ, Martinez ND. 2004. Network structure and robustness of marine  
11 food webs. *Marine Ecology Progress Series*. 273:291-302. 10.3354/meps273291

12 Elton CS. 1927. *Animal ecology*. London: Sidgwick and Jackson.

13 Fynn RWS, Murray-Hudson M, Dhliwayo M, Scholte P. 2015. African wetlands and their  
14 seasonal use by wild and domestic herbivores. *Wetl Ecol Manag*. 23(4):559-581.  
15 10.1007/s11273-015-9430-6

16 Gauzens B, Legendre S, Lazzaro X, Lacroix G. 2013. Food-web aggregation, methodological  
17 and functional issues. *Oikos*. 122(11):1606-1615. 10.1111/j.1600-0706.2013.00266.x

18 Gauzens B, Legendre S, Lazzaro X, Lacroix G. 2016. Intermediate predation pressure leads to  
19 maximal complexity in food webs. *Oikos*. 125:595-603. 10.1111/oik.02627

20 Gilbert AJ. 2009. Connectance indicates the robustness of food webs when subjected to  
21 species loss. *Ecological Indicators*. 9(1):72-80. 10.1016/j.ecolind.2008.01.010

22 Gross T, Rudolf L, Levin SA, Dieckmann U. 2009. Generalized Models Reveal Stabilizing  
23 Factors in Food Webs. *Science*. 325(5941):747-750. 10.1126/science.1173536

24 Havens K. 1992. Scale and structure in natural food webs. *Science*. 257(5073):1107-1109.  
25 10.1126/science.257.5073.1107

1 Hulot FD, Prijac A, Lefebvre J-P, Msiteli-Shumba S, Kativu S. 2019. Mega-herbivores  
2 subsidies in artificial ponds in Hwange National Park, Zimbabwe. *Hydrobiologia*. 837:161-  
3 175. 10.1007/s10750-019-3968-x

4 Husson F, Josse J, Le S, Mazet J. 2015. FactoMineR: Multivariate Exploratory Data Analysis  
5 and Data Mining. R package version 1.29. .

6 Jeppesen E, Brucet S, Naselli-Flores L, Papastergiadou E, Stefanidis K, Noges T, Noges P,  
7 Attayde JL, Zohary T, Coppens J et al. 2015. Ecological impacts of global warming and  
8 water abstraction on lakes and reservoirs due to changes in water level and related changes  
9 in salinity. *Hydrobiologia*. 750(1):201-227. 10.1007/s10750-014-2169-x

10 Legendre S, Gauzens B, Lacroix G. 2013. The N\_W program: trophic network analysis.;  
11 [accessed 2018 November]. [http://www.biologie.ens.fr/~legendre/n\\_w/n\\_w.html](http://www.biologie.ens.fr/~legendre/n_w/n_w.html).

12 Loreau M. 2010. From Populations to Ecosystems: Theoretical Foundations for a New  
13 Ecological Synthesis. Princeton: Princeton University Press. (Monographs in Population  
14 Biology.

15 Lu X, Gray C, Brown LE, Ledger ME, Milner AM, Mondragon RJ, Woodward G, Ma A.  
16 2016. Drought rewires the cores of food webs. *Nature Climate Change*. 6(9):875-879.  
17 10.1038/nclimate3002

18 Martinez ND. 1991. Artifacts or attributes - effects of resolution on the Little-Rock Lake food  
19 web. *Ecological Monographs*. 61(4):367-392. 10.2307/2937047

20 Medeiros LdC, Mattos A, Lurling M, Becker V. 2015. Is the future blue-green or brown? The  
21 effects of extreme events on phytoplankton dynamics in a semi-arid man-made lake. *Aquat*  
22 *Ecol*. 49(3):293-307. 10.1007/s10452-015-9524-5

23 Mendonça V, Vinagre C. 2018. Short food chains, high connectance and a high rate of  
24 cannibalism in food web networks of small intermittent estuaries. *Marine Ecology Progress*  
25 *Series*. 587:17-30. 10.3354/meps12401

1 Michaloudi E, Moustaka-Gouni M, Pantelidakis K, Katsiapi M, Genitsaris S. 2012. Plankton  
2 Succession in the Temporary Lake Koronia after Intermittent Dry-Out. *Int Rev Hydrobiol.*  
3 97(5):405-419. 10.1002/iroh.201101498

4 Msiteli-Shumba SM, Kativu S, Hulot FD. 2017. Influence of environmental variables on  
5 plankton community composition in permanent and temporal pools in and around Hwange  
6 National Park, Zimbabwe. *Trans Roy Soc S Afr.* 72(3):266-279.  
7 10.1080/0035919X.2017.1293571

8 Msiteli-Shumba SM, Kativu S, Utete B, Makuwe E, Hulot FD. 2018. Driving factors of  
9 temporary and permanent shallow lakes in and around Hwange National Park, Zimbabwe.  
10 *Water SA.* 44(2):269-282. 10.4314/wsa.v44i2.12

11 Nhiwatiwa T, Brendonck L, Waterkeyn A, Vanschoenwinkel B. 2011. The importance of  
12 landscape and habitat properties in explaining instantaneous and long-term distributions of  
13 large branchiopods in subtropical temporary pans. *Freshw Biol.* 56(10):1992-2008.  
14 10.1111/j.1365-2427.2011.02630.x

15 Paine RT. 1988. Food webs - road maps of interactions or grist for theoretical development.  
16 *Ecology.* 69(6):1648-1654. 10.2307/1941141

17 Pellissier L, Albouy C, Bascompte J, Farwig N, Graham C, Loreau M, Maglianesi MA,  
18 Melian CJ, Pitteloud C, Roslin T et al. 2018. Comparing species interaction networks along  
19 environmental gradients. *Biological Reviews.* 93(2):785-800. 10.1111/brv.12366

20 Poisot T, Canard E, Mouillot D, Mouquet N, Gravel D. 2012. The dissimilarity of species  
21 interaction networks. *Ecology Letters.* 15(12):1353-1361. 10.1111/ele.12002

22 Robles-Vargas D, Snell TW. 2010. Effects of desiccation on the toxicant sensitivity of  
23 rotifers. *Hydrobiologia.* 652(1):185-193. 10.1007/s10750-010-0330-8

1 Staniczenko PPA, Lewis OT, Jones NS, Reed-Tsochas F. 2010. Structural dynamics and  
2 robustness of food webs. *Ecology Letters*. 13(7):891-899. 10.1111/j.1461-  
3 0248.2010.01485.x

4 Teferi M, Declerck SAJ, De Bie T, Lemmens P, Gebrekidan A, Asmelash T, Dejenie T,  
5 Gebrehiwot K, Bauer H, Deckers JA et al. 2014. Strong effects of occasional drying on  
6 subsequent water clarity and cyanobacterial blooms in cool tropical reservoirs. *Freshw Biol*.  
7 59(4):870-884. 10.1111/fwb.12312

8 Thomas S, Cecchi P, Corbin D, Lemoalle J. 2000. The different primary producers in a small  
9 African tropical reservoir during a drought: temporal changes and interactions. *Freshw Biol*.  
10 45(1):43-56. 10.1046/j.1365-2427.2000.00616.x

11 Thomaz SM, Pagioro TA, Bini LM, Murphy KJ. 2006. Effect of reservoir drawdown on  
12 biomass of three species of aquatic macrophytes in a large sub-tropical reservoir (Itaipu,  
13 Brazil). *Hydrobiologia*. 570:53-59. 10.1007/s10750-006-0161-9

14 Tylianakis JM, Morris RJ. 2017. Ecological Networks Across Environmental Gradients. *Annu*  
15 *Rev Ecol Evol Syst*. 48:25-48. 10.1146/annurev-ecolsys-110316-022821

16 Warren PH. 1989. Spatial and temporal variation in the structure of a fresh-water food web.  
17 *Oikos*. 55(3):299-311. 10.2307/3565588

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19

## 1 **Legends**

2

3 **Table 1. Results of ANOVA on the effects of season and pumping status (pump) on food**  
4 **web properties.** For each food web property, the table gives the best model, degrees of  
5 freedom (DF), F-value, and *p*-value.

6

7 **Figure 1. Food webs in two pans, Caterpillar (a-c) and Makwa (d-f), in different seasons.**

8 Left column: HDS; middle column: WS; Right column: CDS. Numbers refer to species or  
9 tropho-species, and links to prey-predator interactions. Plain and dashed-dotted lines are  
10 respectively upward and downward energy and matter flows. Species are shown according to  
11 trophic height. Species and tropho-species are: 1: *Afrocylops gibsoni*; 2: Phytoplankton  
12 <30µm; 3: *Anabaena* sp.; 4: *Ankistrodesmus spiralis*; 5: *A. spirilliformis*; 6: Bacteria; 7:  
13 *Brachionus calyciflorus*; 8: *B. caudatus*; 9: *B. dimidiatus*; 10: *B. falcatus*; 11: *B. patulus*; 12:  
14 *B. quadridentatus*; 13: *Camphylodiscus* sp.; 14: *Cephalodella gibba*; 15: *Ceriodaphnia*  
15 *laticaudata*; 16: *Chroococcus* sp.; 17: *Coelastrum* sp.; 18: *Cosmarium* sp.; 19: *Cracticula* sp.;  
16 20: *Crucigena tetrapedia*; 21: *Cyclotella* sp.; 22: *Cymbella* sp.; 23: *Daphnia gessneri*; 24: *D.*  
17 *pulex*; 25: *Diaphanosoma dentatum*; 26: *Di. tropicum*; 27: Diatoma ; 28: *Eudiaptomus*  
18 *gracilis*; 29: *Eudorina elegans*; 30: Euglena; 31: *Filinia longiseta*; 32: *F. pejleri*; 33:  
19 *Keratella tecta*; 34: *Lecane luna*; 35: *Megacyclops viridis*; 36: *Melosira* sp.; 37:  
20 *Merismopedia* sp.; 38: *Micractinium* sp.; 39: *Micrasterias* sp.; 40: *Microcystis aeruginosa*;  
21 41: nauplii; 42: *Palmellopsis* sp.; 43: *Pediastrum simplex*; 44: *Phacus curvicauda*; 45:  
22 *Pinnularia* sp.; 46: *Polyarthra vulgaris*; 47: POM and DOM; 48: Protists; 49: *Scenedesmus*  
23 *quadricauda*; 50: *Spirogyra* sp.; 51: *Staurastrum tetracerum*; 52: *Synedra* sp.; 53: *Tetraedron*  
24 *asymmetricum*; 54: *T. limneticum*; 55: *T. regulare*; 56: *Trichocerca pusilla*; 57: *Volvox* sp.

25

1 **Figure 2. Seasonal and pumping status effects on food web descriptors (mean  $\pm$  sd).** (a)  
2 Species richness; (b) connectance; (c) percentage of basal species; (d) percentage of  
3 intermediate species; (e) percentage of top species; (f) percentage of isolated basal species; (g)  
4 percentage of cannibalistic species; (h) omnivory index; (i) mean trophic level; (j) maximum  
5 trophic height; (k) scaled entropy. Pumping status is significant only for the mean trophic  
6 height. It is not shown for the other food web descriptors. Seasons are HDS, WS, and CDS.  
7 Pumping status relates to natural (N) or artificial (A) pans. The different letters above the bars  
8 show treatments that are significantly different.

9

10 **Figure 3. Results of the PCA on food web descriptors for (a) HDS, (b) WS, and (c) CDS.**

11 The represented descriptors relate to the number of basal (B), isolated basal (Bisol),  
12 intermediate (I), and cannibalistic (Cann) species, omnivory index (Omni), connectance  
13 (Conn), maximum trophic height (Hmax), and scaled entropy (ScalEnt). The pans are  
14 Ballaballa (Bal), Caterpillar (Cat), Dom, Dopi (Dop), Foster (Fos), Ganda (Gan), Guvalala  
15 (Guv), Jambile Artificial and Natural (JamArt and JamNat, respectively), Jwapi, Kennedy 1  
16 and 2 (Ken1 and Ken2, respectively), Livingi (Liv), Mabuyamabema (Mab), Magoli (Mag),  
17 Mahule (Mahu), Makwa (Mak), Mambanje (Mamb), Marist (Mar), Mazimbovbu (Maz),  
18 Nengasha (Nenga), Ngweshla artificial and natural (NgweArt and NgweNat, respectively),  
19 Ngwenya, Nyamandlovu (Nyam), Safari Lodge (Saf), Sedina (Sed), Silewu (Sil), Tchabema  
20 (Tchab), and Tshebetschebe (Tsheb). Not all pans were sampled at the three dates.

21

1 **Table 1.**

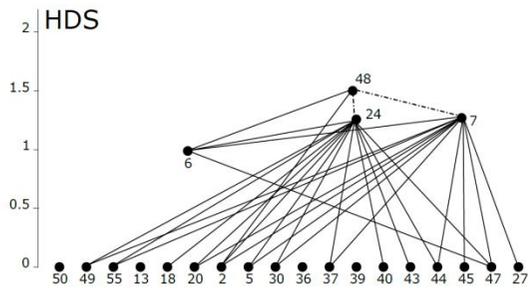
<b>Food web property</b>	<b>Model</b>	<b>DF</b>	<b>F-value</b>	<b><i>p</i>-value</b>
Richness	Season	2	3, 87	0.026
Connectance	Season	2	3, 89	0.025
Percentage of basal species	Season	2	6, 98	0.002
Percentage of intermediate species	Season	2	6, 30	0.003
Percentage of top species	Season * Pump	-	-	NS
Percentage of isolated basal species	Season * Pump	-	-	NS
Percentage of cannibalistic species	Season * Pump	-	-	NS
Omnivory index	Season	2	6, 21	0.003
Mean trophic level	Season * Pump	1	5, 89	0.018
Maximum trophic height	Season	2	4, 03	0.022
Scaled entropy	Season	2	4, 13	0.020

2

1 **Figure 1**

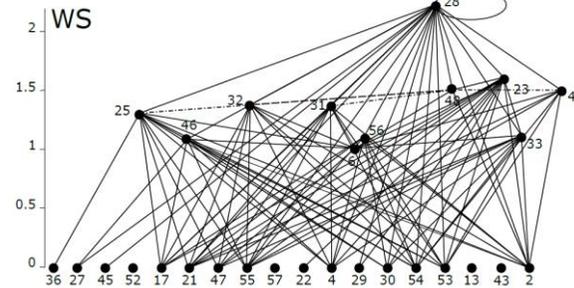
2

3 a.

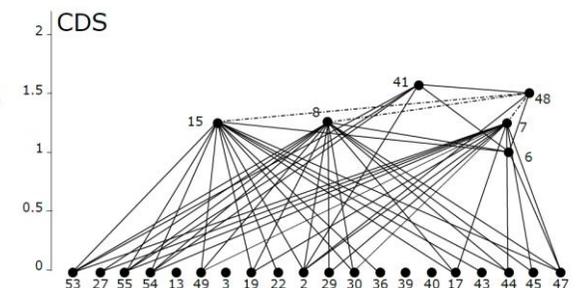


**Caterpillar**

b.

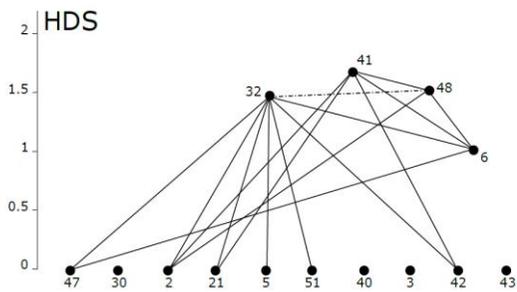


c.

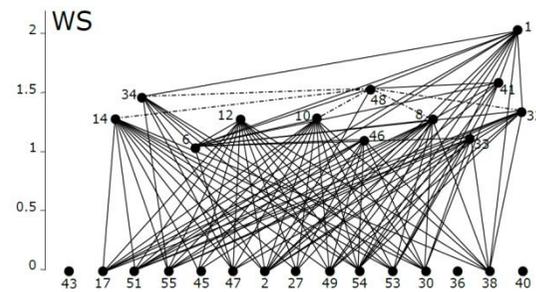


**Makwa**

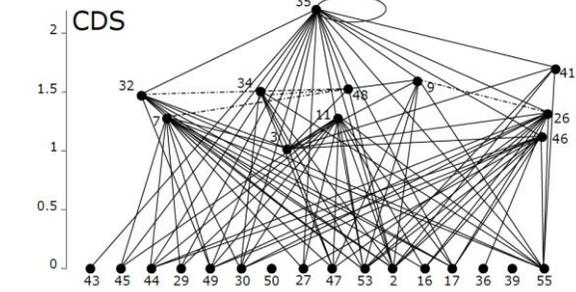
d.



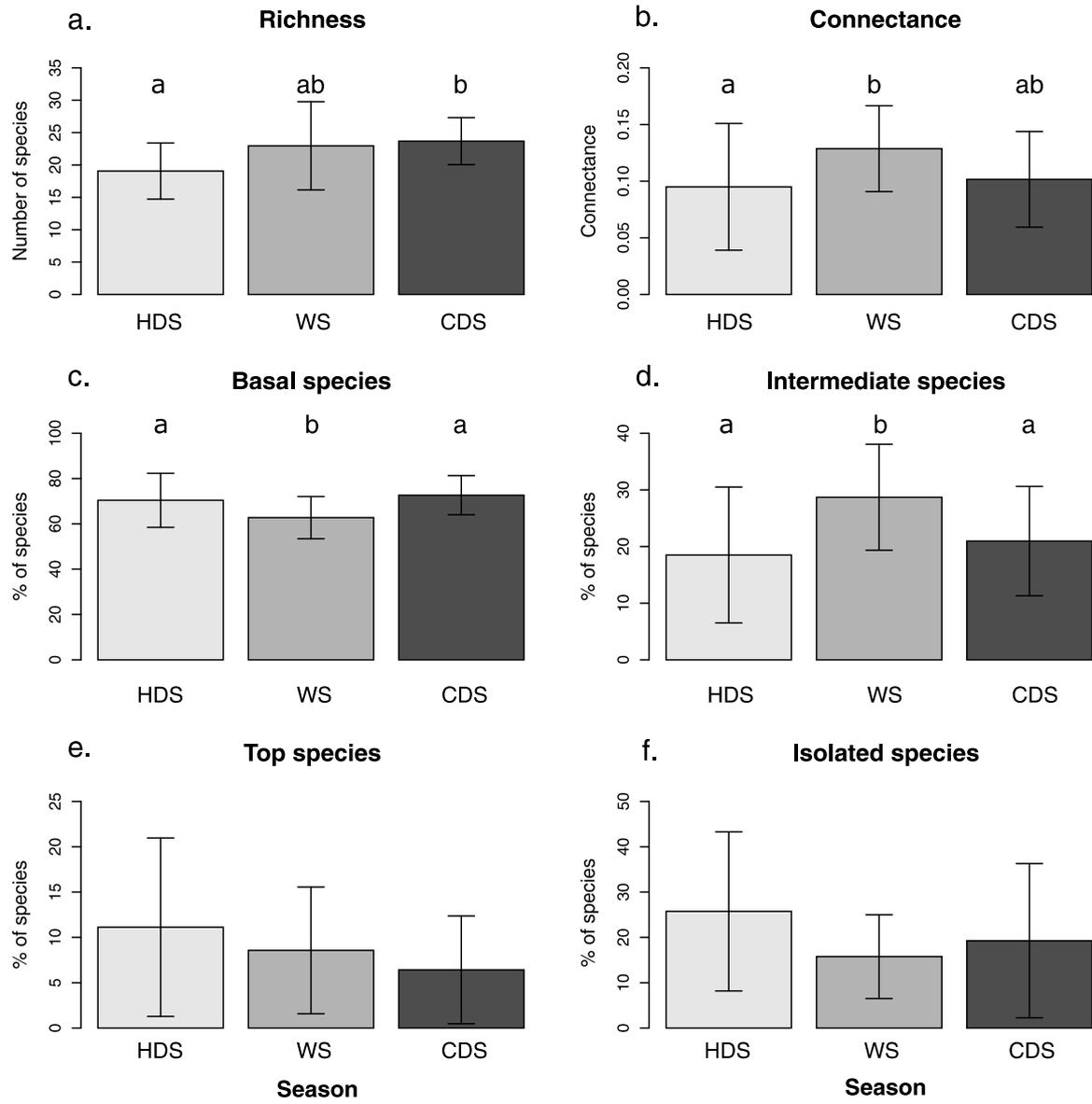
e.

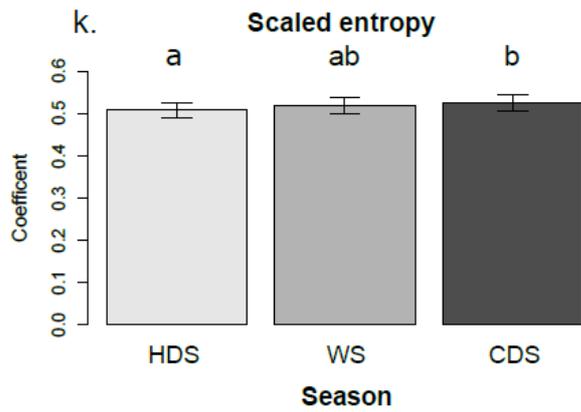
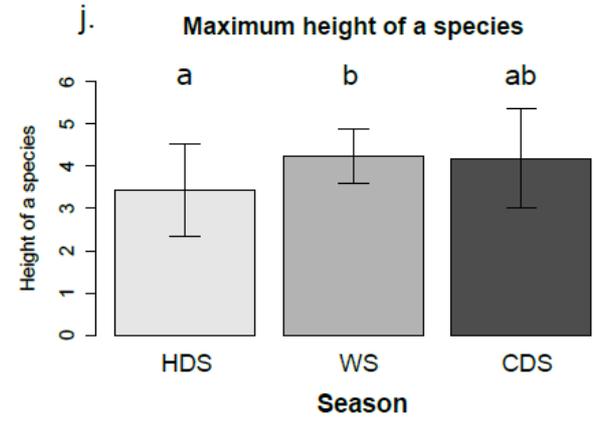
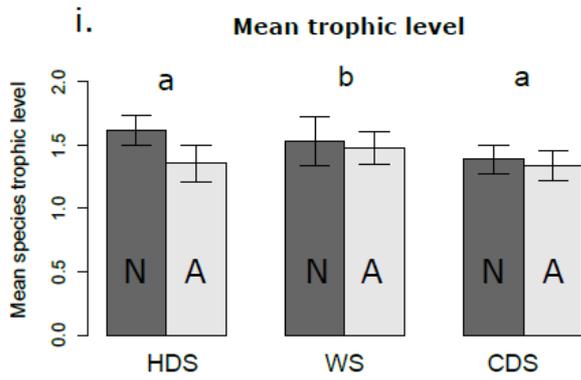
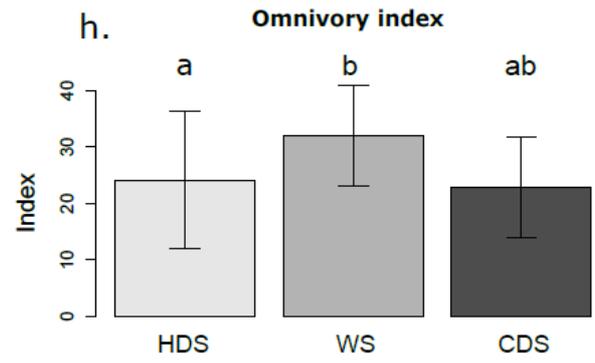
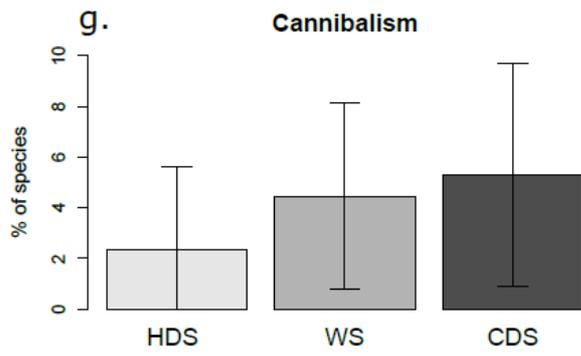


f.



**Figure 2**





**Figure 3**

