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Temporal changes in food web structure in semi-arid waterholes

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Abstract

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

Keywords

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

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

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

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

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

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

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

Methods

Study site

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

Field sampling and laboratory analyses

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

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

Food web construction and analyses with the N_W program

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

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

Statistical analyses

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

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

Results

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

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

Discussion

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

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

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

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

We compared the food web properties of our study to those already published for lakes and ponds (Warren 1989; Martinez 1991; Havens 1992; Dunne et al. 2004; Mendonça and Vinagre 2018). Our results for species richness, connectance, and percentage of top species are similar to those published in the literature. However, the percentage of intermediate and cannibalistic species was lower in our study, whereas the percentage of basal species was higher. This latter result might be explained by the high degree of determination of this compartment: all phytoplankton species larger than 30µm were identified (Msiteli-Shumba et al. 2017). Mendonça and Vinagre (2018) studied food webs in small intermittent estuaries and found higher cannibalism, shorter food chain lengths, and higher connectance compared to 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.

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3

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Legends

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

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

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

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

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

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

1 **Table 1.**

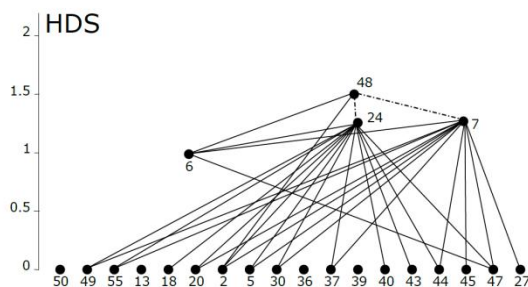
Food web property	Model	DF	F-value	<i>p</i>-value
Richness	Season	2	3, 87	0.026
Connectance	Season	2	3, 89	0.025
Percentage of basal species	Season	2	6, 98	0.002
Percentage of intermediate species	Season	2	6, 30	0.003
Percentage of top species	Season * Pump	-	-	NS
Percentage of isolated basal species	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

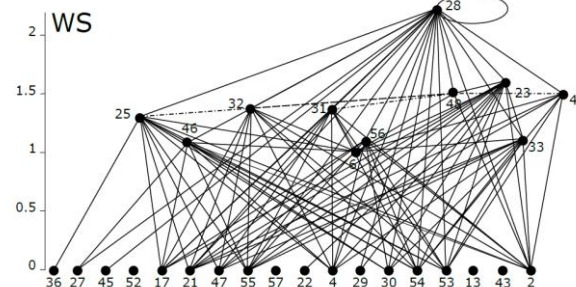
Figure 1

Caterpillar

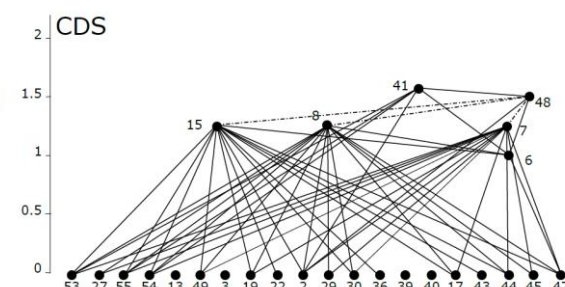
a.



b.

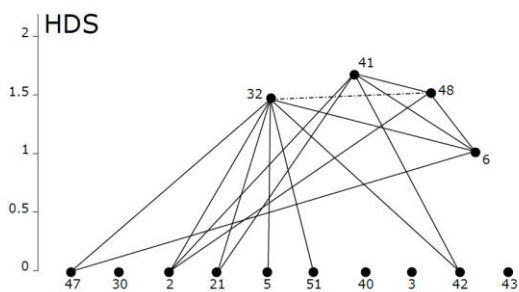


c.

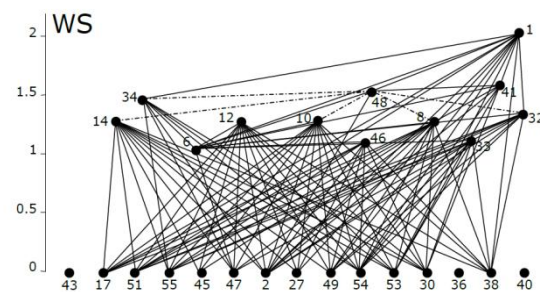


Makwa

d.



e.



f.

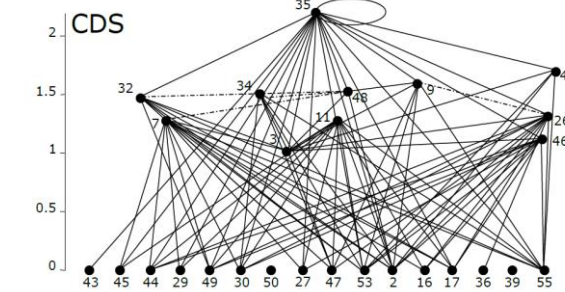
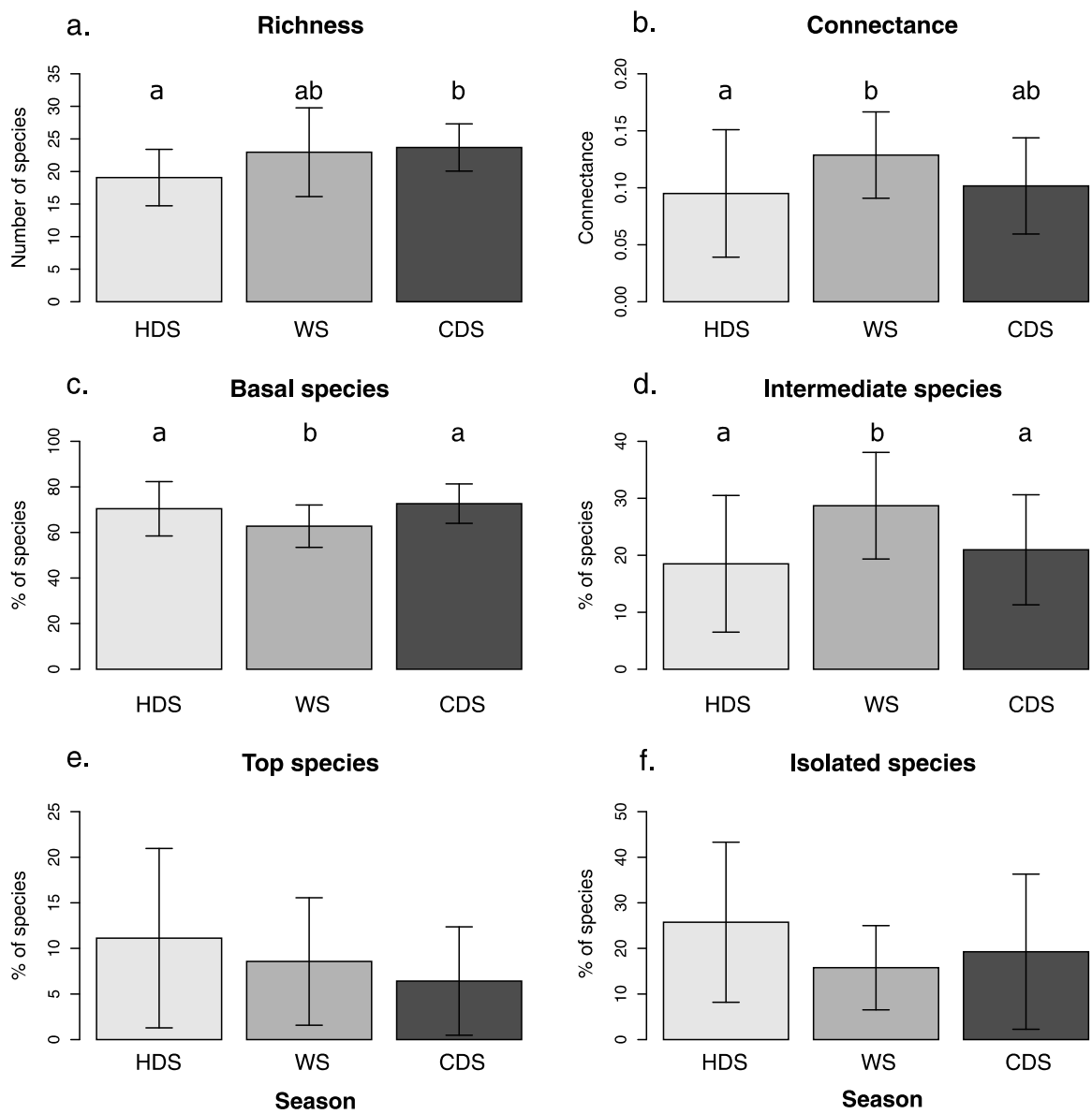


Figure 2



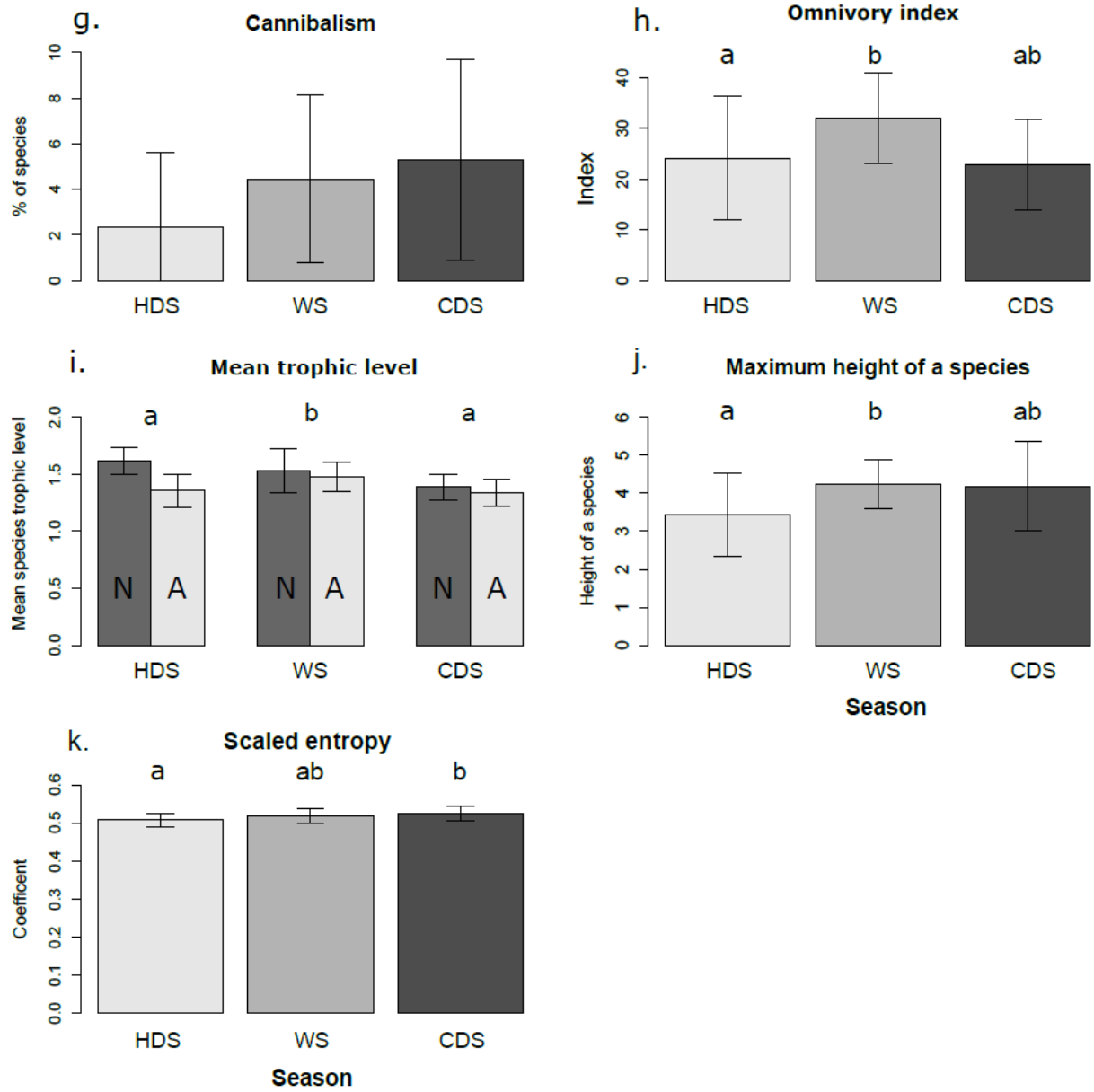


Figure 3

