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Rotifer Species Richness in Kenyan Waterbodies: Contributions of Environmental Characteristics

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Abstract: The aquatic microfauna of Africa is poorly characterized, especially in the case of planktonic rotifers inhabiting waterbodies other than large lakes. In addition, little is known about factors that structure these communities. Here, we assessed the roles of climatic region, habitat type, macrophyte abundance, and a suite of abiotic environmental factors in determining rotifer species' richness and composition in waterbodies located across a 2300 m altitudinal gradient in Kenya. Plankton samples were obtained from 33 sites in 23 waterbodies. From these, 93 rotifer taxa were identified from 18 families comprising 31 genera. About one fourth (25 taxa) were new records for Kenya, from which 4 species were new for Africa. Species richness was the highest in permanent as compared to temporary habitats. Richness was strongly positively correlated with all environmental factors and strongly influenced by macrophyte abundance. When spatial structure was added to the GLM model, species richness was no longer significantly correlated with macrophytes. Unconstrained detrended correspondence analysis conducted at the species level indicated four suites of species associated with either (1) longitude, (2) elevation, (3) latitude, temperature, and hydroperiod, or (4) macrophytes. This study contributes to our knowledge of the patterns of rotifer biogeography and species richness in Africa.

Keywords: conductivity; hydroperiod; macrophytes; Rift Valley lakes; Rotifera; species distribution; temperature; temporary habitats; zooplankton

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1. Introduction

Understanding species distributions and biogeographic patterns are important for interpreting ecological and evolutionary processes, as well as providing baseline data for potential impacts of climate change [1–4]. Of freshwater habitats, the Palearctic and Nearctic biogeographic realms have received the most attention. In contrast, important components of zooplankton such as rotifers are understudied in the Afrotropical zone. The most recent checklist of non-marine rotifers from African inland waters comprises 321 taxa, including 41 taxa found in Kenya, while the Afrotropical zone is characterized by 591 species in 85 genera [5]. Of all biogeographical realms, this is the lowest species richness recorded, despite the abundance and variety of habitats appropriate for rotifers. In comparison the Palearctic, the best-known and most-studied region, has a reported 1348 species representing 112 genera. Thus, as currently understood, the Afrotropical zone has less than half the rotifer diversity of the Palearctic zone. This disproportional situation is likely partially attributable to the "rotiferologist" effect [6], i.e., the distribution of rotifers seems to reflect more the distribution of rotifer scientists than that of rotifers themselves [7–9]. In addition, tropical Africa is notable for its relatively few endemic rotifer species [10]; however, Luo and Segers [11] recently described eight new species of Lepadellidae from the Congo basin. Not only are African freshwater habitats understudied, there also is little information on how abiotic and biotic factors influence community composition.

The known rotifer fauna of Kenya stems from surveys of large lakes of the Eastern Rift Valley conducted during the mid to late 1900s [5,12–20]. More recently, a few additional studies have taken place, but again these mainly focused on the plankton of large lakes including Lake Victoria, Lake Nakuru, and Lake Baringo [21–24]. In these studies, rotifer species richness varied from 13 to 42, with most large lakes being dominated by the genus *Brachionus*. The potential importance of including small waterbodies in studies of biogeography and in assessing species diversity in African aquatic ecosystems is illustrated in study of waterbodies in the Lake Victoria basin by Mutune et al. [21], where 63 rotifer taxa were identified. Of these taxa, 32 were found in samples from Lake Victoria, and 56 were found in smaller waterbodies.

Despite their ubiquity and ecological significance, shallow waterbodies are typically overlooked in limnological research. Recently, interest in small temporary waters including rock pools [25,26], freshwater puddles [27,28], and anthropogenic basins [29] has grown. Collectively they may support considerably more species than permanent waterbodies, because they often constitute biodiversity hotspots within a region and have endemic species inhabiting them (e.g., [30–34]). Except for a few specialist groups, many taxa inhabiting temporary waters appear to be habitat generalists that opportunistically exploit these waterbodies. Colonists from nearby large, permanent waterbodies often re-supply smaller basins that dry [35–37] through passive dispersal [38] or periodical hydrological connections. Small waterbodies are also often more sensitive to human impacts than larger ones, as they can easily be drained to provide space for agriculture or urban development [39]. Such waterbodies are widely distributed across the African continent and are commonly used for providing water supplies to rural communities, irrigation, as well as serving as watering stations for domestic animals [40].

There are some studies of the biota of temporary habitats in Africa, including investigations of ephemeral rock pools (Botswana: [33,41], South Africa: [41]), shallow waters (Ivory Coast: [42], Nigeria: [43–45]) and temporary ponds (e.g., Senegal: [46], Kenya: [47], South Africa: [48,49], Tunisia: [50]). However, these studies typically focused on crustaceans. Recently, Bird et al. [51] reviewed the faunistic composition of southern African shallow waters, including several studies that include some records of rotifers (e.g., [48,52]). While these studies and those on large lakes have increased our knowledge of the biogeography of rotifers, there are few investigations focused on rotifer community composition and none investigating the determinants of their community structure in African temporary waters.

Rotifers are found in a wide variety of freshwater habitats from large permanent lakes to damp mosses and are well adapted to life in temporary habitats [53]. They are known as opportunistic species that can persist under extreme conditions, mainly because of their high tolerance to changes in environmental conditions, high reproductive rates, and ability to produce diapausing stages [54,55]. Diapause, when combined with their ability to adapt to short-term environmental variability [56,57], allows rotifers to be successful in highly dynamic ephemeral ecosystems. Compared with other zooplankton rotifers have shorter generation times and faster population growth rates; however, they are regarded as relatively vulnerable to biotic interactions (i.e., predation [57,58], competition [59,60]). Thus, both abiotic and biotic conditions can be important determinants of rotifer community composition and structure (e.g., [58–62]).

The most common abiotic environmental factors correlated with rotifer richness and abundance in large waterbodies are temperature [63,64], dissolved oxygen [65,66], conductivity [67,68], and pH [69,70]. In temporary systems, species richness is often correlated with hydroperiod (reviewed by Walsh et al. [34]). Hydroperiod duration can be a critical factor for diversity in temporary waters as it determines the ability of organisms to complete their life cycles and/or the strength of biotic interactions [71]. However, Sahuquillo and Miracle [72] found that rotifers were more diverse and more abundant in a drier year with a short, interrupted hydroperiod than in a wetter year. Biotic factors strongly affect the physical structure of habitats [73–75] and species' occurrences [76]. These factors can be particularly important in waterbodies that are small and shallow [77]. For instance, habitats that contain littoral vegetation generally have higher rotifer richness (e.g., [78–80]). High diversity in macrophyte zones has been attributed to elevated spatial heterogeneity [81] and food availability [82] as well as providing a stable environment [83]. Aquatic vegetation may also provide a refuge from predation, which can be a major factor influencing rotifer diversity and abundance [84,85]. Nevertheless, no general consensus has emerged regarding when a factor or combination of factors is most important in determining rotifer community structure.

The objective of our study was to provide additional insights into rotifer community composition in a diverse variety of waterbodies in Kenya by investigating how selected geographic and habitat characteristics are correlated with rotifer species richness. We accomplished this by conducting an extensive survey of waterbodies, intentionally focused on less studied waters such as small ponds (including man-made reservoirs) and temporary pools. We predicted that the highest rotifer species richness would be found in large, permanent lakes where habitat heterogeneity is the greatest. We also hypothesized that rotifer assemblages are more affected by biotic factors (e.g., presence or absence of aquatic vegetation) than by biogeographic (e.g., climatic region, elevation) or abiotic conditions (e.g., temperature, salinity) in permanent habitats, while hydroperiod would dominate in temporary systems.

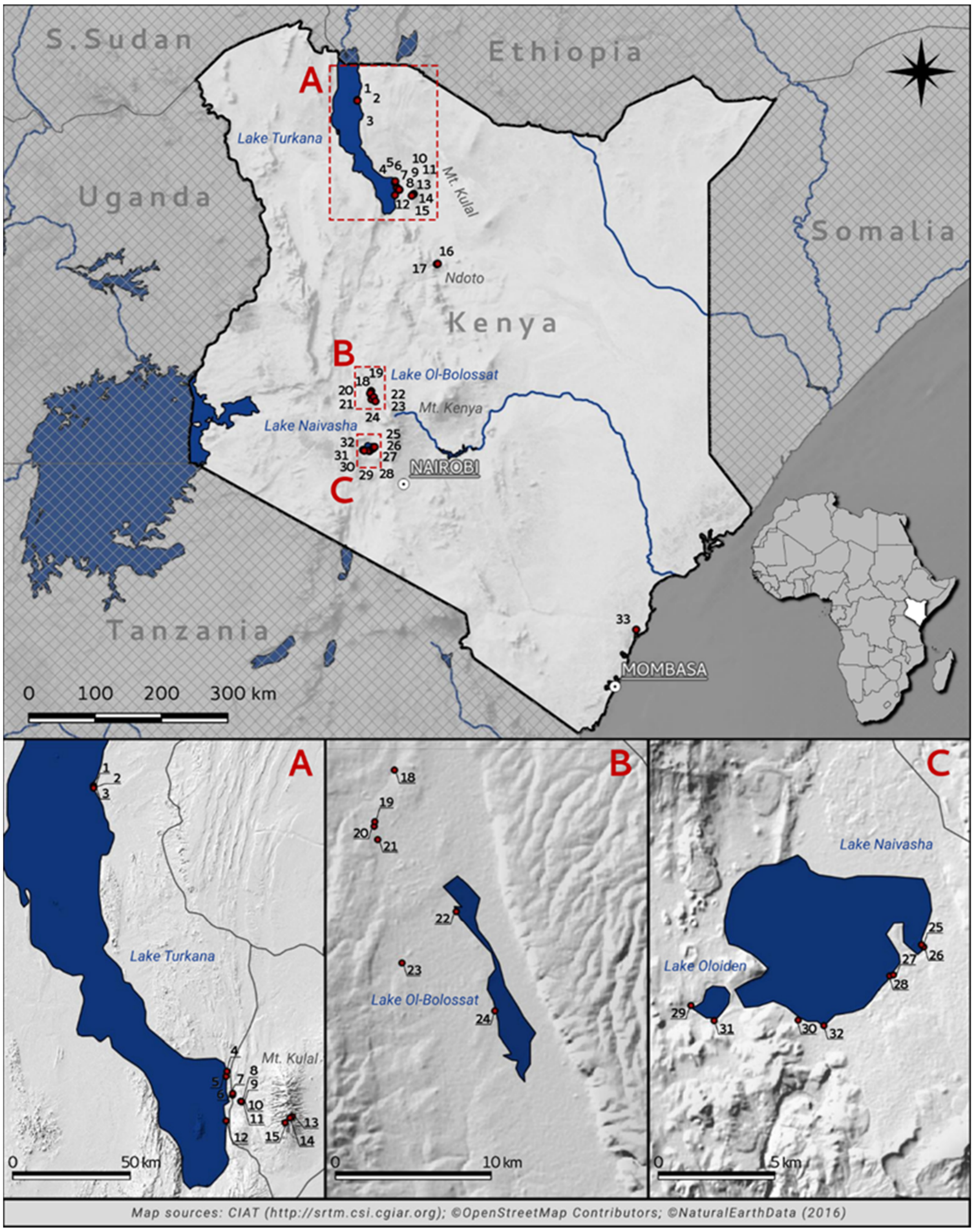
2. Materials and Methods

2.1. Study Area

We collected 112 samples from 33 sites in 23 waterbodies representing a wide spectrum of aquatic habitat types in over a 2300 m altitudinal range (from 45 m a.s.l. in the Arabuko Sokoke Forest to >2375 m a.s.l. at Kibindo reservoir located in the Nyahururu district) in north, central southwest, and southern coast of Kenya during January–February 2014 and February 2015. The sites (Figure 1) were located in diverse climate regions (based on the Köppen-Geiger climate classification [86]; see Table 1). In addition to five large waterbodies (Lake Turkana, Lake Ol'Bolossat, Lake Naivasha, Lake Oloiden, and Kibindo reservoir), we sampled mostly temporary ponds including shallow puddles, rock pools, streams, oases, and man-made systems.

Due to the large differences in the surface areas of the studied waterbodies, we classified them in two groups according to size. The five large lakes (Lake Turkana, Lake Ol'Bolossat, Lake Naivasha, Lake Oloiden, and Kibindo reservoir) were designated as large waterbodies. The surface area of the five large lakes ranged from ~6000 m^2 (Kibindo reservoir) to ~7560 km^2 (Lake Turkana) [88]. All others, mostly temporary ponds, were assigned to the category small waterbodies. Samples were taken from the 11 permanent sites including the five large lakes, a group of four interconnected basins at Loiyangalani oasis (pools H1-H4 [See Table 1], all connected during the rainy season), a permanent oasis at the Molo camp in Loiyangalani village, and Amina fishpond in the Nyahururu district. Permanent waterbodies had maximum depths between 0.4–30 m (mean ± standard error [SE]: 6.14 m ± 3.72) and surface area ranged from 3.15 m^2 (Molo camp oasis) to ~7560 km^2 (Lake Turkana). The second category included 12 temporary habitats. (1) A large clay-lined puddle located in Loiyangalani village near Lake Turkana. This site was situated in the warm desert climatic region. (2–4) Three additional temporary puddles (Nanta Mesi, Lelekan, and Lolkujita) were sampled on Mt. Kulal. These three sites have an elevational gradient from 1470 to 2149 m a.s.l., but all have a humid subtropical climate. (5–6) Three isolated rockpools in the upper part of Darawell stream that formed during the rainy season in the bed of the perennial stream in the Ndoto Mountains, ~100 km south of Mt. Kulal. (7) A small, isolated water basin connected to temporary stream (Bridge Hill). (8–9) A two temporary water channels designated as Ahiti farm and an artificial concrete cattle tank in the Nyahururu district. (10) An artificial concrete circular pond (diam. ~3 m; depth: 0.4 m) in the Arabuko Sokoke Forest; this site had the lowest elevation (45 m a.s.l.). (11) Lake Turkana Koobi Fora Pond (~50 m^2; depth: 0.45 m) and (12) a metal bucket near Lake Naivasha (0.12 m^2; depth: 0.6 m). Temporary ponds had maximum depths ranging from

0.1 to 1.2 m (0.38 ± 0.11 m) and surface areas from 0.12 m^2 (Lake Naivasha—metal bucket) to 60 m^2 (Loiyangalani village—clay puddle). Although Lake Turkana Koobi Fora Pond and the metal bucket near Lake Naivasha are temporary habitats due to their small water volume and high potential to dry, their rotifer species compositions are likely derived from the adjacent lake. Lake Turkana Koobi Fora Pond was separated from the main lake by a 5 m wide sandy mound created after water level of the lake decreased. Water in the metal bucket was taken from Lake Naivasha and left for an unknown period of time.



Map sources: CIAT (http://srtm.csi.cgiar.org); ©OpenStreetMap Contributors; ©NaturalEarthData (2016)

Figure 1. Location of the studied waterbodies in Kenya, with a close-up of four large lakes ((**A**) Lake Turkana, (**B**) Lake Ol'Bolossat, (**C**) Lake Naivasha and Lake Oloiden) (source data available in Jarvis et al. [87]). For a key to numbered sites, see Table 1.

Table 1. List of the 33 sampled sites from 23 Kenyan waterbodies and their main environmental features. Sites ordered as in map (Figure 1). Temp = temperature; Sal. = salinity; artif. = artificial; d. = downstream; t. Mediterranean = temperate Mediterranean.

#	Sampling Site	Latitude	Longitude	Altitude [m a.s.l.]	Climatic reg.	Temp. [°C]	pH	O_2 [%]	O_2 [mg L^{-1}]	Cond. [µS cm^{-1}]	Sal. [g kg^{-1}]	Habitat Type
1	Lake Turkana—Koobi Fora north	3°57′01.84″ N	36°11′09.96″ E	363	warm desert	25.5	9.32	54.2	4.29	3150	1.5	large lake
2	Lake Turkana—Koobi Fora pond	3°57′01.02″ N	36°11′09.65″ E	363	warm desert	24.5	9.46	60.04	4.91	6550	3.6	puddle
3	Lake Turkana—Koobi Fora south	3°56′31.85″ N	36°11′11.54″ E	363	warm desert	25.1	9.37	64.4	4.83	3350	1.5	large lake
4	Lake Turkana—Loiyangalani	2°50′50.88″ N	36°42′03.43″ E	363	warm desert	25.3	9.35	68.4	4.94	3660	1.7	large lake
5	Lake Turkana—Elmolo village	2°49′41.60″ N	36°41′51.56″ E	363	warm desert	24.6	9.32	30	2.38	3510	1.8	large lake
6	Loiyangalani—Molo camp	2°45′46.02″ N	36°43′22.65″ E	466	warm desert	30.0	8.82	80	6.83	849	0.2	oasis
7	Loiyangalani—Clay puddle	2°45′22.00″ N	36°43′20.14″ E	388	warm desert	31.2	9.34	69.8	5.04	3730	1.9	puddle
8	Loiyangalani—Oasis H1	2°43′56.01″ N	36°45′14.13″ E	453	warm desert	31.8	8.89	13.1	0.93	927	0.2	oasis
9	Loiyangalani—Oasis H2	2°43′48.07″ N	36°45′27.10″ E	466	warm desert	30.0	8.82	80	6.84	849	0.2	oasis
10	Loiyangalani—Oasis H3	2°43′51.96″ N	36°45′20.89″ E	464	warm desert	24.3	7.72	22.2	1.83	925	0.2	oasis
11	Loiyangalani—Oasis H4	2°43′55.70″ N	36°45′18.89″ E	458	warm desert	32.2	7.66	15.6	1.12	907	0.2	oasis
12	Lake Turkana—south	2°39′24.99″ N	36°41′25.40″ E	363	warm desert	25.1	9.37	64.4	4.83	3350	1.5	large lake
13	Mt. Kulal—Nanta Mesi	2°40′22.71″ N	36°57′08.09″ E	1881	humid subtropical	20.1	8.06	40.3	2.92	706	0	puddle
14	Mt. Kulal—Lelekan	2°40′06.94″ N	36°56′36.23″ E	2149	humid subtropical	16.6	7.27	0.9	0.08	448	0	puddle
15	Mt. Kulal—Lolkujita	2°38′59.17″ N	36°55′30.13″ E	1470	humid subtropical	21.1	7.43	10.3	0.88	532	0	puddle
16	Ndoto Mts.—Darawell upstream	1°43′08.83″ N	37°15′56.63″ E	1091	tropical savanna	25.3	6.68	8.5	0.63	178	0	rock pools
17	Ndoto Mts.—Darawell d.stream	1°43′21.54″ N	37°16′43.92″ E	881	tropical savanna	27.9	8.52	64.4	4.61	183	0	stream basin

Table 1. *Cont.*

#	Sampling Site	Latitude	Longitude	Altitude [m a.s.l.]	Climatic reg.	Temp. [°C]	pH	O_2 [%]	O_2 [mg L^{-1}]	Cond. [µS cm^{-1}]	Sal. [g kg^{-1}]	Habitat Type
18	Nyahururu—Ahiti farm	0°00′45.26″ S	36°22′24.79″ E	2352	tropical savanna	17.7	7.69	31.3	2.27	116	0	channel
19	Nyahururu—Bridge Hill stream	0°02′33.19″ S	36°21′43.83″ E	2366	tropical savanna	22.0	7.56	54.4	3.57	121	0	stream basin
20	Nyahururu—watering hole	0°02′42.62″ S	36°21′42.61″ E	2374	tropical savanna	20.4	7.08	0.9	0.06	136	0	art. waterhole
21	Nyahururu—Amina	0°03′10.55″ S	36°21′49.96″ E	2368	tropical savanna	17.5	7.79	28.1	2.02	324	0	fish pond
22	Lake Ol′Bolossat—north	0°03′11.99″ S	36°25′04.60″ E	2331	tropical savanna	24.8	7.98	28.5	2.12	1037	0.3	large lake
23	Nyahururu—Kibindo reservoir	0°07′29.08″ S	36°22′40.58″ E	2375	tropical savanna	19.2	8.17	62.6	4.34	88	0	fish pond
24	Lake Ol′Bolossat—south	0°03′11.99″ S	36°25′04.60″ E	2331	t. Mediterranean	24.8	7.98	29.5	2.15	1037	0.3	large lake
25	Lake Naivasha—Kijabe camp	0°46′27.64″ S	36°25′07.90″ E	1897	t. Mediterranean	18.0	8.53	46.3	3.49	673	0.1	large lake
26	Lake Naivasha—metal bucket	0°46′33.18″ S	36°25′13.43″ E	1904	t. Mediterranean	22.9	7.28	27.6	1.88	275	0	metal bucket
27	Lake Naivasha—Nini farm #1	0°47′41.22″ S	36°23′59.57″ E	1897	t. Mediterranean	23.6	7.72	56.9	3.83	288	0	large lake
28	Lake Naivasha—Nini farm #2	0°47′43.45″ S	36°23′50.71″ E	1890	t. Mediterranean	23.8	7.75	58.7	3.88	272	0	large lake
29	Lake Oloiden #1	0°48′55.60″ S	36°15′46.49″ E	1893	t. Mediterranean	22.9	9.37	36.1	2.49	2230	1	large lake
30	Lake Naivasha—Valley Breeze	0°49′31.25″ S	36°20′07.62″ E	1901	t. Mediterranean	24.7	6.72	33.7	2.26	278	0	large lake
31	Lake Oloiden #2	0°49′32.36″ S	36°16′42.96″ E	1893	t. Mediterranean	23.1	9.34	35.8	2.47	2282	1	large lake
32	Lake Naivasha—Cray Fish	0°49′44.61″ S	36°21′10.23″ E	1890	t. Mediterranean	24.6	7.39	28.4	2.02	284	0	large lake
33	Arabuko Sokoke Forest	3°15′46.76″ S	39°58′31.51″ E	45	tropical savanna	25.6	8.08	21.0	1.50	611	0	art. waterhole

2.2. Sampling

Qualitative, open water samples were collected using a plankton net (25 cm diameter; 25 µm mesh) attached to 0.5 m long handle from the shoreline. Samples and water chemistry measurements were taken from the surface (10–30 cm depth). From the temporary ponds and waterbodies with poorly developed or no littoral vegetation, samples were taken only from the water column near the shore. In the permanent large lakes, samples consisted of 10 plankton tows. Each tow consisted of a smooth pulling motion for 30 s. In the small temporary ponds where plankton tows could not be performed, the minimum volume of sampled water was 4 L. All samples were fixed immediately in 96% ethanol. Presence of rotifer taxa in these samples was recorded. Electrical conductivity, pH, temperature, dissolved oxygen, and salinity were measured in situ using a Multi 3401i WTW probe. We determined depth, surface area, macrophyte cover, GPS coordinates, elevation, climatic region, hydroperiod, and categorized sites by habitat type (Table 1). When measurements were not possible, depth and surface area were retrieved from published works (e.g., [17,89,90]). Due to the substantial differences in surface area among sites, for statistical evaluation they were placed into 5 categories (1: <5; 2: 5–20; 3: 21–100; 4: 101–1000; 5: >1001 m^2). Macrophyte percent cover was estimated by visual inspection at each sampling site. Macrophyte cover of Lake Naivasha differed among sampling sites from extensive (>50%), to very sparse (<5%), or littoral vegetation absent [17,90,91]. Preserved specimens were identified to the lowest possible taxonomic level using the Guides to the Identification of the Microinvertebrates of the Continental Waters of the World [89–93] and other appropriate keys [94,95]. As the samples were immediately preserved, this precluded identification to species level in several cases (e.g., bdelloids and other species whose identification rely on features seen only in live specimens). The taxonomic validity of each taxon follows the requirements established by the International Code of Zoological Nomenclature: i.e., the List of Available Names in Zoology, Candidate Part Phylum Rotifera (LAN) [96].

2.3. $Q_{B/T}$ and $Q_{B/L}$ Quotients

For a comparison of trophic status among the habitat types surveyed in our study, we calculated Sládeček's [97] trophic condition quotient, $Q_{B/T}$, where B is the number of *Brachionus* species and T is the number of *Trichocerca* species. *Brachionus* are generally associated with eutrophic waters, while members the genus *Trichocerca* are found primarily in oligotrophic habitats. Thus, the higher the index, the more eutrophic the system. Similarly, *Brachionus* is typically considered a planktonic or semi-planktonic species found in open waters in the pelagic and littoral zones of waterbodies, while members of the genus *Lecane* are closely associated with substrata such as submerged macrophytes or terrestrial plants [89]. As many of our systems were dominated by *Brachionus*, we also constructed a $Q_{B/L}$ quotient ($Q_{B/L}$ = #*Brachionus* spp./#*Lecane* spp.) to further categorize the sampled waterbodies. For this index, values of <1.0 represents lakes, ponds, or wetlands with a well-developed littoral zone with abundant macrophytes, values between 1.0 and 2.0 represent those with poorly developed littoral vegetation, and >2.0 represent waterbodies without a littoral zone (typically temporary puddles, rock pools, or man-made small waterbodies).

2.4. Statistical Analyses

For statistical analyses, sites were categorized by climatic region and habitat type. Four climatic regions were represented: tropical savanna (code = 1), warm desert (2), humid subtropical (3), and temperate Mediterranean (4; Table 1). Sites were also assigned a habitat type from: large lake (1), oasis (2), stream basin (3), puddle (4), rock pool (5), and anthropogenic habitats (6; e.g., metal bucket, waterhole).

To analyze species richness, we first did pairwise correlations to which environmental factors were correlated with species richness. We then used generalized linear model (GLM) forward and backward selection to determine which environmental parameters were associated with richness (*S*). Log (*S*) was used for all analysis and models were chosen based on AIC values. Further, because we are using geospatial data, we wanted to account for spatial autocorrelation in our statistical models. Thus, we used two methods: generalized least squares (GLS) with Gaussian spatial correlation to remove spatial effects and, as an alternate method to investigate the spatial effects, we used a Moran eigenvector spatial filtering approach. The second approach allows for spatial dependence present in the residuals to be included into the model. For climate and habitat types, we investigated whether there were significant differences among categories based on Tukey-adjusted *p* values. These analyses were conducted using R version 4.2.1 in the *nlMS* package.

To assess the similarities in the species composition among these waterbodies, we used a cluster analysis based on the Jaccard index and the unweighted pair group method with the arithmetic mean (UPGMA) algorithm. For hierarchical cluster analysis, we included 12 locations: six with the highest species richness from permanent sites (Lake Turkana, Lake Ol'Bolossat, Lake Naivasha, Lake Oloiden, Loiyangalani oasis, and Nyahururu Amina) and six temporary ponds (Loiyangalani clay puddle [Loiya CP]; Lelekan, Lolkujita, Nanta Mesi, Ndoto Mts.—Darawell rock pools [Darawell RP]; and Arabuko Sokoke Forest [Arabuko SF]). Some individual waterbodies included several sampling sites, so they were combined for this analysis to provide a comparison of waterbodies as opposed to sites. Further, sites with poor diversity (i.e., species richness of 1; sites: #6, 18, 19, 20) were not included. Box plots were computed to investigate patterns among species richness and hydroperiod classes (permanent versus temporary). We used an unconstrained detrended correspondence analysis (DCA) with supplementary variables to determine relationships of species occurrences with environmental factors using R version 4.1.2 [98]. This method was selected because response data were compositional, and the gradient is one dimensional. As many preserved specimens could not be identified to species, we conducted two analyses: one at the species level (subspecies were subsumed) and a second at the genus level. Unidentified bdelloids were not included in the species level analysis. We used *emmeans* to test for differences in richness among habitat types.

3. Results

3.1. $Q_{B/T}$ and $Q_{B/L}$ Quotients

Using trophic indices, we found that the $Q_{B/T}$ value was over 2.0 for both permanent and temporary habitat types, and thus the waterbodies we sampled were deemed as eutrophic. For permanent waterbodies, which mostly had abundant littoral vegetation, $Q_{B/L}$ was 0.92, while in temporary waterbodies, where littoral vegetation was generally reduced or lacking, it was 2.0.

3.2. Water Chemistry Parameters

During the survey, water temperature ranged from 16.6° C (Mt. Kulal—Lelekan, Table 1, #14) to 32.2° C (Loiyangalani—Oasis H4, #11), pH ranged from 6.68 (Darawell upstream site, #16) to 9.46 (Lake Turkana—Koobi Fora pond, #2), and electrical conductivity from 88 μ Scm^{-1} (Kibindo reservoir, #23) to 6550 μ Scm^{-1} (Lake Turkana—Koobi Fora pond, #2). Dissolved oxygen ranged from 0.06 mg L^{-1} (0.9%) (Nyahururu—watering hole, #20) to 6.84 mg L^{-1} (80%) (Loiyangalani—Oasis H2, #9).

3.3. Species Richness

In the 112 samples, we found 18 rotifer families (1 bdelloid, 17 monogonont) and four orders (Collothecaceae, Flosculariacea, Philodinida, and Ploima) comprising 31 genera and 93 taxa (74 were identified to species or subspecies, the remaining were identified to genus). Of these, 25 species were new reports for Kenya and four species (*Dipleuchlanis elegans*, *Cephalodella forficula*, *Cephalodella tenuiseta*, and *Lecane elsa*) were also new reports for Africa (Table 2). The most widespread taxa were unidentified bdelloids that were found in 16 of all 23 waterbodies and in all hydroperiod classes, followed by *Lecane bulla* (15 waterbodies) and *Brachionus calyciflorus* species complex (13 waterbodies). In addition, when compared to large habitats (large lakes) all other habitat types had significantly lower species richness, with the exception of the smallest habitats (anthropogenic watering holes).

Table 2. Rotifer taxa found in aquatic habitats surveyed in Kenya 2014–2015.

#	Taxon	Sites Found	Occurrence [%]
1	**Asplanchnidae** *Asplanchna brightwellii* Gosse, 1850	21, 22, 24, 28, 30, 32	18.2
2	**Bdelloidae** bdelloid (unidentified)	1, 2, 8, 10–12, 14–17, 21, 22, 26, 31, 33	45.5
3	**Brachionidae** *Brachionus angularis* Gosse, 1851	2, 10, 11, 16, 21, 28–30, 32, 33	30.3
4	*Brachionus bidentatus* Anderson, 1889	7, 21, 23, 33	12.1
5	*Brachionus budapestinensis* Daday, 1885 †	26	3.0
6	*Brachionus calyciflorus* Pallas, 1766	7–11, 13, 21, 23, 25, 27–32	45.5
7	*Brachionus caudatus* Barrois & Daday, 1894	22–24, 26, 27, 29–32	27.3
8	*Brachionus dimidiatus* Bryce, 1931	1–3, 7, 8, 12	18.2
9	*Brachionus dorcas* Gosse, 1851	7, 11	6.1
10	*Brachionus falcatus* Zacharias, 1898	22, 23, 26	9.1
11	*Brachionus leydigii rotundus* Rousselet, 1907 †	22, 29, 31	9.1
12	*Brachionus plicatilis* Müller, 1786	1, 2, 8, 9, 11, 12, 21, 24, 26, 33	30.3
13	*Brachionus plicatilis* "(SM9) Turkana" §	2	3.0
14	*Brachionus quadridentatus* Hermann, 1783	1–3, 9–13, 21, 26–28, 30, 32	42.4
15	*Brachionus rotundiformis* Tschugunoff, 1921	2	3.0
16	*Brachionus* sp.	2, 7, 11, 24-27, 30, 32	27.3
17	*Keratella cochlearis* (Gosse, 1851)	25, 26, 28, 30, 32	15.2
18	*Keratella tropica* (Apstein, 1907)	25, 26, 29–32	18.2
19	*Notholca* sp.	32	3.0
20	*Plationus patulus* (Müller, 1786)	28, 30, 33	9.1
21	*Platyias leloupi* Gillard, 1967 †	32	3.0
22	*Platyias quadricornis* (Ehrenberg, 1832)	26, 28, 30, 32	12.1
23	**Collothecidae** *Collotheca* sp.	23	3.0
24	**Dicranophoridae** *Dicranophorus grandis* (Ehrenberg, 1832) †	21, 23	6.1
25	*Encentrum* sp.†	21	3.0
26	*Kostea wockei* (Koste, 1961) †	21	3.0
27	**Euchlanidae** *Dipleuchlanis elegans* (Wierzejski, 1893) ‡	11	3.0
28	*Euchlanis deflexa* Gosse, 1851†	17, 27, 28, 32	12.1
29	*Euchlanis dilatata* Ehrenberg, 1832	8, 13, 16, 17	12.1
30	*Euchlanis* sp.	11	3.0
31	**Epiphanidae** *Epiphanes brachionus* (Ehrenberg, 1837)	11	3.0
32	*Epiphanes clavulata* (Ehrenberg, 1832)	33	3.0
33	**Filinidae** *Filinia limnetica* (Zacharias, 1893)	26, 27, 30, 32, 33	15.2
34	*Filinia novaezealandiae* Shiel & Sanoamuang, 1993 †	11, 21	6.1
35	*Filinia pejleri* Hutchinson, 1964 †	11, 23	6.1
36	*Filinia terminalis* (Plate, 1886)	8, 28, 29, 32	12.1
37	*Filinia* sp.	11, 21, 22, 29, 31–33	21.2
38	**Floscularidae** *Floscularia ringens* (Linnaeus, 1758) †	25, 30	6.1
39	*Limnias* sp. †	32	3.0
40	**Hexarthridae** *Hexarthra intermedia* (Wiszniewski, 1929) †	33	3.0
41	*Hexarthra mira* (Hudson, 1871)	25-27, 29	12.1
42	**Lecanidae** *Lecane bulla* (Gosse, 1851)	1, 2, 8, 10, 11, 14, 16, 17, 21–23, 27, 29–33	51.5
43	*Lecane candida* Harring & Myers, 1926 †	21	3.0
44	*Lecane closterocerca* (Schmarda, 1859)	14	3.0
45	*Lecane crepida* Harring, 1914 †	9	3.0

Table 2. *Cont.*

#	Taxon	Sites Found	Occurrence [%]
46	*Lecane curvicornis* (Murray, 1913)	23, 30, 32	9.1
47	*Lecane elsa* Hauer, 1931 ‡	10, 11, 21	9.1
48	*Lecane hamata* (Stokes, 1896)	2, 3, 8, 11, 23	15.2
49	*Lecane lateralis* Sharma, 1978	30, 32	6.1
50	*Lecane luna* (Müller, 1776)	2, 8, 10, 11, 21, 22	18.2
51	*Lecane lunaris* (Ehrenberg, 1832)	21, 29	6.1
52	*Lecane papuana* (Murray, 1913)	2, 8, 10, 11, 16, 17, 21	21.2
53	*Lecane quadridentata* (Ehrenberg, 1830) †	28, 32	6.1
54	*Lecane unguitata* (Fadeev, 1925)	30, 32	6.1
55	*Lecane ungulata* (Gosse, 1887)	23, 28, 30	9.1
56	*Lecane* sp.	1–3, 8, 12, 21, 22, 25	24.2
57	**Lepadellidae** *Colurella adriatica* Ehrenberg, 1831 †	8	3.0
58	*Colurella colurus* (Ehrenberg, 1830) †	26, 32	6.1
59	*Colurella obtusa* (Gosse, 1886)	1, 3, 27, 30, 32	15.2
60	*Colurella uncinata* (Müller, 1773)	16	3.0
61	*Lepadella latusinus* (Hilgendorf, 1899) †	27, 28	6.1
62	*Lepadella patella* (Müller, 1773)	30	3.0
63	*Lepadella triptera* (Ehrenberg, 1832)	30, 32	6.1
64	*Lepadella* sp.	1–3, 11, 12, 14	18.2
65	**Mytilinidae** *Mytilina ventralis* (Ehrenberg, 1830)	30, 32	6.1
66	*Mytilina* sp.	26	3.0
67	**Notommatidae** *Cephalodella forficula* (Ehrenberg, 1832) ‡	11	3.0
68	*Cephalodella gibba* (Ehrenberg, 1830)†	30	3.0
69	*Cephalodella tenuiseta* (Burn, 1890) ‡	25, 27, 30	9.1
70	*Cephalodella* sp.	13, 14, 30, 32	12.1
71	Notommata sp.	10, 11	6.1
72	*Pleurotrocha* sp.	11	3.0
73	**Philodinidae** *Rotaria neptunia* (Ehrenberg, 1830)	21	3.0
74	*Rotaria* sp.	26, 28, 33	9.1
75	**Proalidae** *Proales* sp.	7	3.0
76	**Synchaetidae** *Polyarthra remata* Idelson, 1925	25-27, 30, 32	15.2
77	*Polyarthra vulgaris* Carlin, 1943	26, 29, 30, 32	12.1
78	*Synchaeta* sp.	11,21,26,30,32	15.2
79	**Testudinellidae** *Testudinella parva semiparva* Hauer, 1938 †	30	3.0
80	*Testudinella patina dendradena* de Beauchamp, 1955	25, 27, 32	9.1
81	*Testudinella patina* (Hermann, 1783)	2, 28, 32	9.1
82	**Trichocercidae** *Trichocerca cylindrica* (Imhof, 1891) †	26, 27, 30	9.1
83	*Trichocerca similis* (Wierzejski, 1893) †	25, 30	6.1
84	*Trichocerca* sp.	22, 24, 27–30	18.2
85	**Trichotriidae** *Trichotria tetractis* (Ehrenberg, 1830)	18, 28, 30	9.1

† New species record for Kenya; ‡ new species record for Africa; § see [99]. Occurrence indicates the percentage of sites where the taxon was found.

Box plots of species richness (S) in permanent (S = 88; mean = 23.6, SE: ±6.0) versus temporary (S = 26; mean = 5.1, SE: ±1.5) waterbodies indicated that the highest richness occurred in permanent habitats (Figure 2). The most frequent taxon in permanent waterbodies was *L. bulla,* which occurred in all habitats; this was followed by unidentified bdelloids (75% of habitats). The most frequently found genus was *Brachionus.* From brachionids, *B. calyciflorus*, a thermophilic species and bioindicator of eutrophication, had the highest occurence (87.5%). *Brachionus angularis, Brachionus caudatus, Brachionus plicatilis*, *Brachionus quadridentatus*, and *Keratella tropica* were all found in 62.5% of the permanent habitats. The most frequently occurring taxa found in temporary habitats were unidentified bdelloids (57.1%), followed by *L. bulla* (42.9%) and *B. angularis, B. caudatus, Brachionus bidentatus,* and *Euchlanis dilatata* (28.6%).

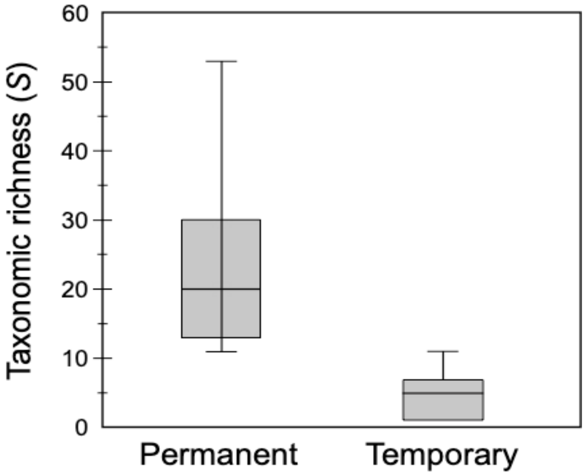


Figure 2. Box plots comparing rotifer taxonomic richness between permanent and temporary waterbodies surveyed in Kenya in 2014 and 2015. Horizontal lines are the median, boxes represent the interquartile range (25–75%), and whiskers represent minimum and maximum values.

Lecane bulla was found in all five sampled large lakes (Table 3). *Brachionus calyciflorus, Filinia* sp., *Trichocerca* sp., and unidentified bdelloids were found in 60% of large lakes. In small waterbodies, again unidentified bdelloids were most commonly encountered (69.2%). For monogononts, *L. bulla* was found in 61.5% while *B. calyciflorus* occurred in 53.9% of them. Two species, *B. caudatus* and *K. tropica*, were found only in four of the large lakes, while two species, *Lecane papuana* and *E. dilatata*, were found in six and four small waterbodies, respectively, but none of the large lakes.

Table 3. Rotifer taxa found in large lakes surveyed in Kenya 2014–2015. § see [99].

#	Taxon	LK	LOB	LN	LOD	KR
1	*Asplanchna brightwellii* Gosse, 1850		*	*		
2	bdelloid (unidentified)	*	*	*	*	
3	*Brachionus angularis* Gosse, 1851	*		*	*	
4	*Brachionus bidentatus* Anderson, 1889					*
5	*Brachionus budapestinensis* Daday, 1885			*		
6	*Brachionus calyciflorus* Pallas, 1766			*	*	*
7	*Brachionus caudatus* Barrois & Daday, 1894		*	*	*	*
8	*Brachionus dimidiatus* Bryce, 1931	*				
9	*Brachionus falcatus* Zacharias, 1898		*	*		*
10	*Brachionus leydigii rotundus* Rousselet, 1907		*		*	
11	*Brachionus plicatilis* Müller, 1786	*	*	*		
12	*Brachionus plicatilis* "(SM9) Turkana" §	*				
13	*Brachionus quadridentatus* Hermann, 1783	*		*		
14	*Brachionus* sp.	*	*	*		
15	*Cephalodella gibba* (Ehrenberg, 1830)			*		
16	*Cephalodella* sp.			*		
17	*Cephalodella tenuiseta* (Burn, 1890)			*		
18	*Collotheca* sp.					*
19	*Colurella colurus* (Ehrenberg, 1830)			*		

Table 3. *Cont.*

#	Taxon	LK	LOB	LN	LOD	KR
20	*Colurella obtusa* (Gosse, 1886)	*		*		
21	*Dicranophorus grandis* (Ehrenberg, 1832)					*
22	*Euchlanis deflexa* Gosse, 1851			*		
23	*Filinia limnetica* (Zacharias, 1893)			*		
24	*Filinia pejleri* Hutchinson, 1964					*
25	*Filinia* sp.		*	*	*	
26	*Filinia terminalis* (Plate, 1886)			*	*	
27	*Floscularia ringens* (Linnaeus, 1758)			*		
28	*Hexarthra mira* (Hudson, 1871)			*	*	
29	*Keratella cochlearis* (Gosse, 1851)			*		
30	*Keratella tropica* (Apstein, 1907)	*	*	*	*	
31	*Lecane bulla* (Gosse, 1851)	*	*	*	*	*
32	*Lecane curvicornis* (Murray, 1913)			*		*
33	*Lecane hamata* (Stokes, 1896)	*				*
34	*Lecane lateralis* Sharma, 1978			*		
35	*Lecane luna* (Müller, 1776)	*	*			
36	*Lecane lunaris* (Ehrenberg, 1832)				*	
37	*Lecane papuana* (Murray, 1913)	*				
38	*Lecane quadridentata* (Ehrenberg 1830)			*		
39	*Lecane* sp.	*	*	*		
40	*Lecane unguitata* (Fadeev, 1925)			*		
41	*Lecane ungulata* (Gosse, 1887)			*		*
42	*Lepadella latusinus* (Hilgendorf, 1899)			*		
43	*Lepadella patella* (Müller, 1773)			*		
44	*Lepadella* sp.	*				
45	*Lepadella triptera* (Ehrenberg, 1830)			*		
46	*Limnias* sp.			*		
47	*Mytilina* sp.			*		
48	*Mytilina ventralis* (Ehrenberg, 1830)			*		
49	*Notholca* sp.			*		
50	*Plationus patulus* (Müller, 1786)			*		
51	*Platyias leloupi* Gillard, 1967			*		
52	*Platyias quadricornis* (Ehrenberg, 1832)			*		
53	*Polyarthra remata* Skorikov, 1896			*		
54	*Polyarthra vulgaris* Carlin, 1943			*	*	
55	*Rotaria* sp.			*		
56	*Synchaeta* sp.			*		
57	*Testudinella parva* Hauer, 1938			*		
58	*Testudinella patina* (Hermann, 1783)	*		*		
59	*Trichocerca cylindrica* (Imhof, 1891)			*		
60	*Trichocerca similis* (Wierzejski, 1893)			*		
61	*Trichocerca* sp.		*	*	*	
62	*Trichotria tetractis* (Ehrenberg, 1830)			*		

Abbreviations: Lake Turkana (LK), Lake Ol'Bolossat (LOB), Lake Naivasha (LN), Lake Oloiden (LOD), and Kibindo reservoir (KR). * indicates the presence of the rotifer taxa in the lake.

The highest number of species found at a given locality was 53 in Lake Naivasha (including species found in the nearby metal bucket filled with lake water). Waterbodies of the Loiyangalani Oasis (H1–H4) had 30 species, the Nyahururu Amina fishpond had 25 species, and Lake Turkana (including the adjacent pond) had 20 species. The highest species richness (S = 11) in temporary ponds was found in an artificial concrete pond in Arabuko Sokoke Forest, which serves primarily as watering station for elephants. In the Darawell riverbed rock pools and in Loiyangalani Clay puddle, we found seven species. Several species were found only in permanent waterbodies (e.g., *Lecane luna* was found in five permanent ponds but no temporary waterbodies; *B. quadridentatus*, *B. caudatus*, *K. tropica*, and *Lecane hamata* were found in four permanent waterbodies and no temporary ones). Alternatively, some species were found in waterbodies with variable hydroperiods, but were more frequent in permanent waterbodies (e.g., *B. calyciflorus* [8 permanent; 2 temporary], *B. plicatilis* [6; 1]). The taxa found only in temporary waterbodies were *E. dilatata* (0; 3) and *Proales* sp. (0; 1).

Based on area, we classified the studied habitats into (1) large lakes (Lake Turkana, Lake Ol'Bolossat, Lake Naivasha, Lake Oloiden, and Kibindo reservoir) where rotifer community composition has been studied in the past, and (2) small waterbodies (mostly temporary waters) that have not been previously studied. According to classification, of the 25 newly identified taxa for Kenya, 64% (16 species) were found in small waterbodies. This despite the higher richness typically found in larger waterbodies. Of the four new records for Africa, three (75%) were found in small waterbodies.

Unconstrained detrended correspondence analysis demonstrated the importance of latitude in determining species composition at both the species and generic level (Figure 3). When the analysis was conducted using the taxonomic dataset at the species level (n = 72) with 8 environmental variables including 21 sites, elevation, macrophytes, oxygen concentration, large lake, and anthropogenic habitats were positively associated with Axis 1. In this analysis, >30 species, including littoral species *Trichocerca cylindrica*, *Testudinella parva semiparva*, *Cephalodella gibba*, and sessile *Floscularia ringens* and *Limnias* sp., were positively associated with the presence of macrophytes along Axis 1 (Figure 3, upper panel). The geographic features of elevation and climatic region 4 (temperate Mediterranean) were also associated with Axis 1. When the analysis was done on the taxonomic dataset collapsed to genus level (n = 31), hydroperiod, latitude, temperature, conductivity, salinity, pH, and depth were positively associated with Axis 1. Elevation and macrophytes were associated with Axis 2 (Figure 3, lower panel).

To analyze species richness, a stepwise process was conducted to select the GLM model with the lowest AIC value. Macrophytes had a very strong effect and other variables had to be forced into the model. The resulting model indicated that species richness was positively correlated to all environmental variables, with stream basin (habitat type 3), temperate Mediterranean and humid subtropical climates (climate types 5 and 4, respectively), and pH being highly significant variables (Table 4A). When correcting for spatial autocorrelation and using the same model, macrophytes and many other environmental factors were no longer a significant predictor of species richness while pH and several habit types remained significant contributors (Table 4B). We found no significant differences when making comparisons among habitat types or between climatic zones. Using spatial regression with eigenvector spatial filtering, only macrophyte abundance ($p < 0.009$) was a significant predictor of species composition among sites (Table 4).

Cluster analysis showed high similarities in species composition in closely situated waterbodies (Figure 4). However, the closely situated (within 12 km) and highly turbid Loiyangalani CP (clay puddle) and Nanta Mesi systems formed a cluster even though they are in adjacent climatic regions. Rotifer assemblage similarity between Lake Turkana and Loiyangalani Oasis (H1–H4) is likely a consequence of their hydrologic connection. The lake was fed by a stream flowing through the oasis. Lake Ol'Bolossat and Nayhururu Amina lie in close proximity to one another, are in the same climate region, and are both permanent and used for fish production. Lake Naivasha and Lake Oloiden are connected by a narrow channel.

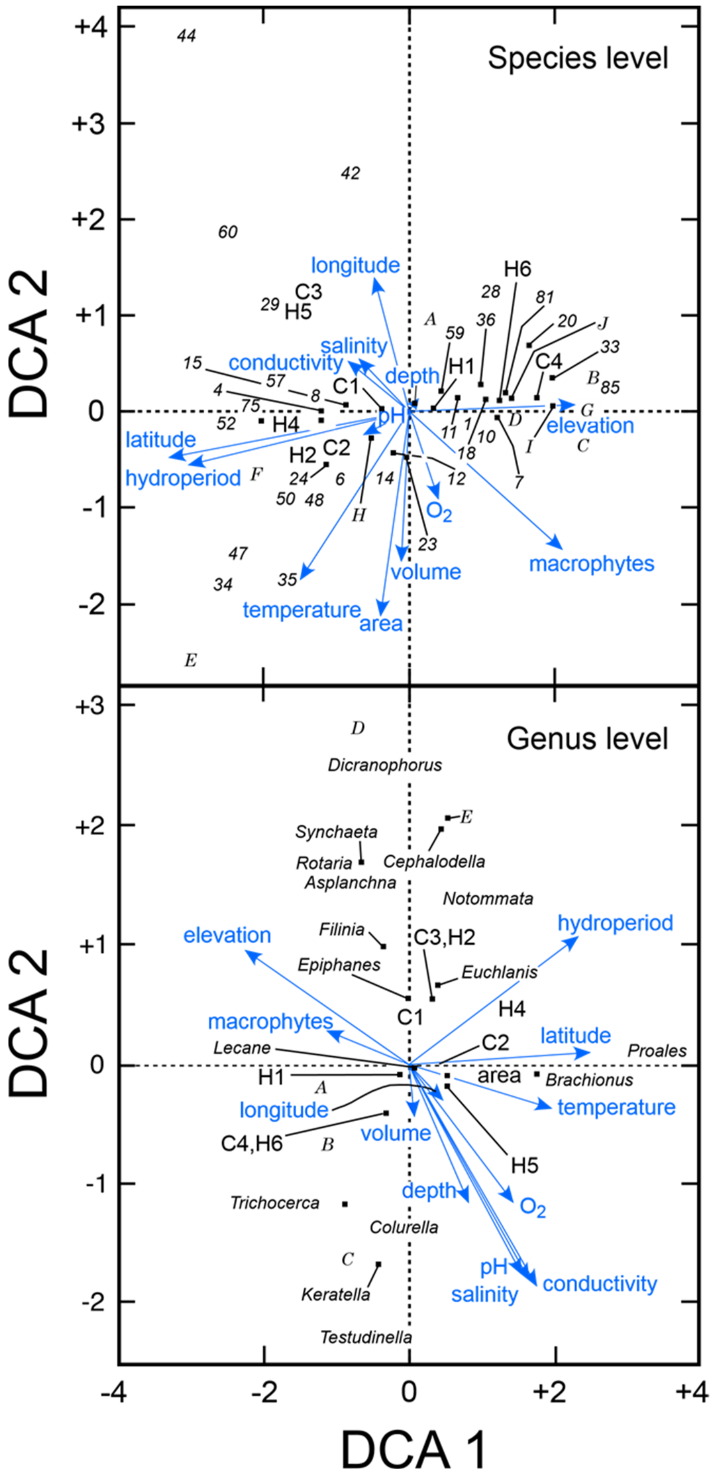


Figure 3. Unconstrained detrended correspondence analysis (DCA) of rotifers and key environmental factors for 21 Kenyan waterbodies. A. Analysis of taxa at species level. Numbers correspond to those given for species in Table 2. B. Analysis of taxa reduced to genus level. Numbers correspond to habitat types (H1–6) and climatic regions (C1–4) given in Table 1. Letters A–I include multiple species that overlapped. Upper panel: A = 32, 40; B = 19, 21, 38, 39, 49, 53, 54, 61–63, 65, 68, 69, 79, 83; C = 5, 66; D = 46, 55; E = 27, 30, 31, 45, 67, 72; F = 25, 26, 73, G = 17, 22, 58, 76, 82; H = 3, 13, 51; I = 11, 18; J = 46, 55. Lower panel: A = *Nolthoca*, *Floscularia*, *Limnias*, *Plationus*; B = *Platyias*, *Mytilina*; C = *Polyarthra*, *Hexarthra*; D = *Encentrum*, *Kostea*; E = *Pleurotrocha*, *Dipleuchlanis*.

Table 4. Importance of environmental features in determining species richness (S) in 21 Kenyan waterbodies. A. Generalized linear model (GLM): S = macrophytes + habitat type + climatic region + depth + temperature + pH + conductivity. B. Generalized least squares fit (GLS) with Gaussian spatial correlations using the same model but accounting for longitude, latitude, and elevation. AIC = 117.9. C. Moran's eigenvector with spatial filtering. Habitat types and climatic regions are defined in the text.

***A.* Coefficients**	**Value**	**Standard Error**	**t Value**	***p* Value**
Intercept	7.887	1.765	4.469	<0.001
macrophytes	−0.025	0.010	−2.549	0.010
Habitat type 2	−4.446	1.393	−3.192	0.001
Habitat type 3	−1.945	0.472	−4.118	<0.001
Habitat type 4	−3.541	1.115	−3.175	0.002
Habitat type 5	−2.716	0.608	−4.466	<0.001
Habitat type 6	−0.624	0.299	−2.089	0.037
Climatic reg 2	3.647	1.256	2.904	0.004
Climatic reg 3	2.558	1.223	2.091	<0.001
Climatic reg 4	1.773	0.436	4.070	<0.001
Depth	−0.076	0.027	−2.822	0.005
Temperature	0.087	0.032	2.741	0.006
pH	−0.819	0.230	−3.565	<0.001
Conductivity	−0.001	0.001	−2.044	0.041

***B.* Coefficients**	**Value**	**Standard Error**	**t Value**	***p*Value**
Intercept	80.447	25.948	3.100	0.017
Macrophytes	0.011	0.152	0.073	0.944
Habitat type 2	−36.671	16.169	−2.268	0.058
Habitat type 3	−14.441	4.670	−3.092	0.018
Habitat type 4	−27.741	12.337	−2.249	0.059
Habitat type 5	−28.314	8.597	−3.293	0.013
Habitat type 6	−5.719	4.827	−1.185	0.275
Climatic reg 2	29.097	15.237	1.910	0.098
Climatic reg 3	19.644	13.833	1.602	0.200
Climatic reg 4	18.129	6.228	3.348	0.023
Depth	−0.588	0.295	−1.992	0.087
Temperature	0.881	0.455	1.938	0.094
pH	−10.125	3.588	−2.821	0.026
Conductivity	−0.003	0.003	−1.144	0.290

***C.* Coefficients**	**Estimate**	**Standard Error**	**t Value**	***p* Value**
Intercept	3.0575	1.2785	2.3914	0.034
Macrophytes	−0.02263	0.0081	−2.808	0.016
Habitat type	−0.0591	0.06563	−0.9005	0.386
Depth	0.0135	0.0111	1.219	0.246
Temperature	0.0212	0.0209	1.0137	0.331
pH	−0.1454	0.1699	−0.8559	0.409
Conductivity	0.0007	0.0007	0.9350	0.368

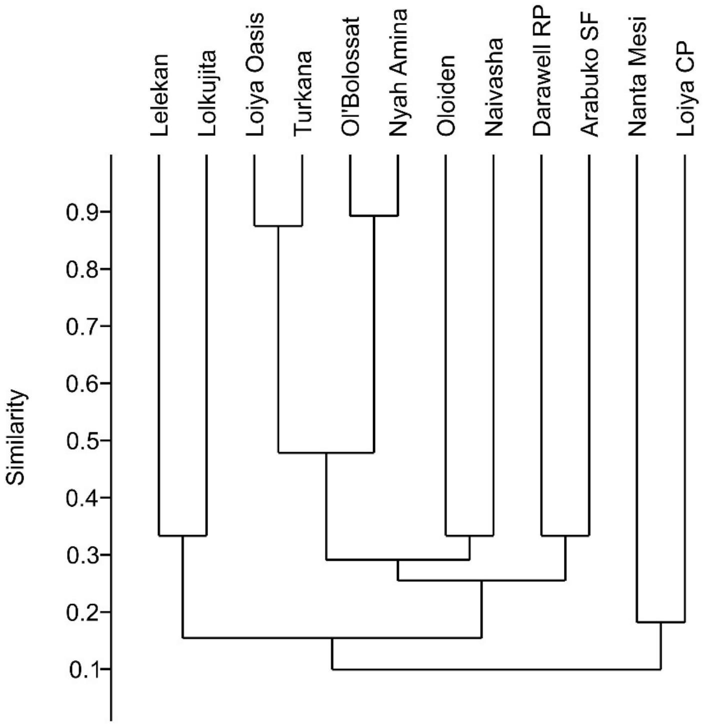


Figure 4. Hierarchical cluster analysis based on unpaired group (UPGMA) Jaccard similarity index. Abbreviations: Turkana (including species from: Lake Turkana—Koobi Fora north, Lake Turkana—Koobi Fora pond, Lake Turkana—Koobi Fora south, Lake Turkana—Loiyangalani, Lake Turkana—Elmolo village, and Lake Turkana—south); Ol'Bolossat (including species from: Lake Ol'Bolossat—north, and Lake Ol'Bolossat—south); Nyah Amina (Nyahururu—Amina); Naivasha (including species from: Lake Naivasha—Kijabe camp, Naivasha—NINI Farm #1, and #2, Naivasha—Valley Breeze camp, and Naivasha—Cray Fish camp); Oloiden (Lake Oloiden #1, and #2); Loiya CP (Loiyangalani—Clay puddle); Loiya Oasis (Loiyangalani—Oasis H1, H2, H3, and H4); Nanta Mesi (Mt. Kulal—Nanta Mesi); Lelekan (Mt. Kulal—Lelekan); Lolkujita (Mt. Kulal—Lolkujita); Darawell RP (Ndoto Mts.—Darawell upstream rock pools); Arabuko SF (Arabuko Sokoke Forest).

4. Discussion

Here we provide the first compiled species list for rotifers in Kenya. We expanded the known biogeography for 4 taxa in Africa and 25 in Kenya and improved the understanding of how abiotic and biotic conditions may influence species distributions. We found that both biogeographic (e.g., climatic region, elevation) and local habitat conditions (e.g., abundance of macrophytes, hydroperiod, and temperature) can influence species richness in temporary and permanent waterbodies. Species richness was highest in permanent habitats and lowest in those with shorter hydroperiods. However, many unique species were found only in temporary or artificial habitats.

Lake Turkana is a unique ecosystem, distinguished as the world's largest permanent desert lake and the largest alkaline water body with a surface area of about 7560 km^2 [88]. This lake is a sodium carbonate lake possessing a high pH and high dissolved salts, and with an ionic composition typical of East African saline lakes [100]. During our sampling period, conductivity ranged from 3150–3660 $\mu S\ cm^{-1}$ and salinity ranged 1.5–1.8 $g\ kg^{-1}$. Thus, it was not surprising that of the 20 species we found in Lake Turkana, half are brachionids, many of which are tolerant to high levels of salinity. Our finding confirmed those of De Ridder [5] with the exceptions of *Brachionus dorcas* and *B. calyciflorus*, which were not present in our samples. In addition, we recently reported that a new cryptic species of the *B. plicatilis* species was found in Lake Turkana, designated as *B. plicatilis* "(SM9)

Turkana" [99]. We found several additional specimens that likely represent new species. Additional studies of their genetics and ecology are needed to substantiate their status.

Lake Naivasha, an endorheic freshwater lake that lies in the Eastern Rift Valley, is the second largest freshwater lake in Kenya. It was formed as a result of tectonic faulting and volcanic activity associated with the formation of the Rift Valley [17]. In this study, Lake Naivasha had the highest rotifer species richness with 53 taxa (Table 3). This is greater than previously reported (Pejler, [14]: 12 taxa, in 1967–1968; Nogrady, [15]: 18 taxa, 1980; Mavuti, [19]: 16 taxa, 1978, 1980; Uku and Mavuti, [17]: 13 taxa, 1990, 1991). Brachionids predominated and were most abundant in our samples in terms of number of species but also anecdotally in terms of number of individuals. However, we were not able to determine absolute numbers of individuals due to the sampling method. We confirmed the dominance of three *Brachionus* species: *B. angularis*, *B. caudatus*, and *B. calyciflorus* as was observed by Nogrady [15] and Uku and Mavuti [17]. *Brachionus falcatus* and *Plationus patulus* were also abundant in the survey by Mavuti [19]. Nogrady [15] and Uku and Mavuti [17] found a few individuals of *B. falcatus* in their surveys. We did not find this species in the main lake, but it did occur in the nearby metal bucket. The relatively high abundance of macrophytes in some sampling locations within Lake Naivasha likely contributed to the high number of rotifer taxa found. Interestingly, the contribution of species (9 taxa) from the bucket resulted in this site having the highest species richness. The bucket had been left unattended in a shaded area and may have provided rotifers with a refugium from predators or provided another unknown factor that contributed to the success of the rotifer community.

Lake Oloiden, a saline-alkaline water body with a surface area ranging from 4 to 7.5 km^2 [101], is a remnant of Lake Naivasha that lies to the southwest of the main lake. Until 1955, Oloiden was a bay of Lake Naivasha during high water. A boat canal was built in the 1960s to connect it to the main lake, but the canal is now blocked by water hyacinth (*Eichhornia crassipes* (Mart.) Solms—Laub.) and papyrus (*Cyperus papyrus* L.). Currently, there is little water inflow from the main lake, and consequently the waters in Lake Oloiden are highly saline [17]. Uku and Mavuti [17] found 11 rotifer taxa, while Pejler [14] reported 7, and Nogrady [15] found 19 in their surveys of this lake. Our observations increased the total number of taxa to 22, with the additions of *Epiphanes clavulata*, *Hexarthra intermedia*, and *Rotaria* sp. Overall, Lake Oloiden had relatively low species richness consisting of taxa that are tolerant to high salinity levels. *Brachionus calyciforus*, *B. falcatus*, *K. tropica*, *Filinia* sp., *Hexarthra* sp., *Polyarthra* sp., *Trichocerca* sp., *Euchlanis* sp., and *Asplanchna* sp. were found in Lake Oloiden and Lake Naivasha. The most common genus found in Lake Oloiden was *Brachionus*. This is similar to the findings of Pejler [14] and Uku and Mavuti [17]. *Plationus patulus*, *B. calyciflorus*, *Filinia opoliensis*, and *Collotheca* sp. were dominant, followed by *B. quadridentatus* and *B. caudatus* in Pejler's [14] study. While in the survey of Uku and Mavuti [17] the dominant rotifer species was *B. angularis*, followed by *B. caudatus* and *B. calyciflorus*. Nogrady [15] noted high numbers of *Anuraeopsis coelata*, which he stated reflected eutrophic conditions at the time of sampling.

The rotifer community of Lake Ol'Bolossat has not been previously characterized to our knowledge. This shallow freshwater body that covers an area of 43 km^2 [101] is situated in the valley between the northwestern slopes of the Aberdares Mountains and the Dundori Ridge. This drainage basin, Ewaso Ngiro North Basin covering 210.2 km^2, is Kenya's largest. The altitude ranges from 2340 to 2400 m a.s.l. The area has an average precipitation of 975 to 1100 mm/year. The 13 rotifer taxa we identified from the lake are widespread and typical of those found in other lakes in our survey.

Kibindo reservoir is a natural lake that has been partially modified to raise water levels and to support fish production. The reservoir had an area of ~6000 m^2, low turbidity, and the lowest conductivity (88 $\mu\text{S cm}^{-1}$) of the 33 sites sampled. Due to its high elevation (2372 m a.s.l.), water temperature is generally <20 °C. This reservoir has not been previously surveyed for zooplankton. We identified 11 rotifer taxa: four brachionids, four lecanids, an unidentified *Collotheca*, *Dicranophorus grandis*, and *Filinia pejleri*.

In contrast to large lakes, little is known regarding smaller and more temporary systems. Riato et al. [48] provides a description of the zooplankton communities of 19 permanent and temporary freshwater pans in the Mpumalanga Highveld region of South Africa. Freshwater temporary pans included one rotifer species (*Platyias quadricornis*), while two rotifer species (*Brachionus dimidiatus*, and *B. plicatilis*) were found in permanent pans. Similarly, *B. plicatilis* was frequently encountered in ephemeral salt pans of the Makgadikgadi Basin in the northeast Botswana [102]. In Zimbabwe, Anusa et al. [52] found nutrient status and community diversity in rock pools are determined by pool area and depth, a proxy for habitat duration. They reported eight rotifer species (belonging to the genera *Asplanchna*, *Brachionus*, *Conochilus*, *Epiphanes*, *Lepadella*, *Rotaria*, and *Synchaeta*) as common inhabitants across a range of hydroperiods in temporary rock pools. Overall, the number of species present increased as pool area increased.

To our knowledge, there is only one published study that includes small waterbodies in Kenya. Masai et al. [21] investigated rotifer diversity of Lake Victoria (Kenya) and adjacent small waterbodies. They found that the small systems had the highest rotifer species richness. This may have been due to varied biological and chemical characteristics found in the large number of sampled sites. These are generally shallow waterbodies with heavy macrophyte growth. With 17 and 9 species respectively, Lecanidae and Brachionidae were the genera with the highest richness. The low species diversity in Lake Victoria may be attributed to the relatively harsh conditions and a relative lack of macrophytes. In our study, the species richness of permanent lakes was more than three times that of temporary waters (permanent lakes: 88; temporary waterbodies: 26), similar to the findings of other authors (e.g., [103–105]).

Geographic distance between aquatic habitats can play an important role in determining zooplankton distribution [106,107]. The size of the diapausing stage is a factor related to dispersal capacity [108], with larger, more dense stages less likely to be transported over long distances by hydrochory or anemochory. Consequently, the community composition of closely situated waterbodies often consists of nested subsets of taxa (e.g., [109,110]). Our cluster analysis indicated similarities in species composition in closely situated ponds (Figure 4), indicating an influence of geographic proximity and the climatic region on community composition. Sites that are in close geographical proximity were clustered based on species composition. For example, Lake Turkana (Table 1 sites #1–5, 12) and Loiyangalani—Oasis (H1–H4) (# 8–11) form a cluster, as do Lake Ol'Bolossat (#22, 24) and Nayhururu—Amina (#21). Lake Naivasha (#25, 27–28, 30, 32) shows species similarity to geographically close Lake Oloiden (#29, 31), similarly as Lelekan (#14) to Lolkujita (#15) (Figure 4). As noted above, one group comprised two sites: Loiyangalani—clay puddle (#7) and Nanta Mesi (#13), which are in close geographic proximity (12 km); these belong to two different climatic regions and differ in altitude. In addition, both sites are shallow, temporary puddles with high turbidity. The reason for the close association of taxa from the geographically separated Darawell stream sites (#16, 17) and Arabuko Sokoke Forest site (#33) is unknown.

Rotifer species composition can be used as an indicator of trophic conditions [111,112]. For comparison among the habitat types surveyed in our study, we calculated Sládeček's [97] trophic condition quotient and found that the $Q_{B/T}$ value was over 2.0 for both habitat types and thus the waterbodies were eutrophic during our survey. This is not surprising given that past studies of several of these lakes found eutrophic conditions (e.g., [15,19,113]) and many of the temporary habitats we sampled are highly impacted by human activities (livestock use, etc.). Interestingly, while water quality variables (e.g., temperature, pH, conductivity) were significant in determining species richness using a general linear model, those effects were removed after accounting for spatial autocorrelation in our study. Rather, our results indicated that climatic region, which can be considered as a combination of temperature, elevation, and relative distance between ponds, and macrophyte presence as important drivers of community composition.

One suite of species was associated with high elevation, while another large group correlated with permanent habitats, latitude, area, and temperature. In addition, several species were associated with a high abundance of macrophytes. Not surprisingly, sessile (e.g., *Floscularia*, *Collotheca*) and littoral (e.g., *Cephalodella gibba*, *Lecane lunaris*) species were highly associated with macrophytes. In addition, conductivity was associated with the occurrence of some species (e.g., *Brachionus plicatilis, Hexarthra mira*). While species of the genus *Lecane* are typically considered as freshwater (conductivity < 1000 µS cm^{-1}) or subsaline (1000–6000 µS cm^{-1} [68]; we confirmed their tolerance to high conductivity (272–6550 µS cm^{-1}), similar to that reported for saline waters (200 to over 7000 µS cm^{-1}) in the Chihuahuan Desert of México by Walsh et al. [67].

Macrophytes are known to modify habitat conditions [57,114] and strongly affect zooplankton occurrence [115,116]. The surface area of the waterbodies and presence or absence of specific macrophyte species [117] can affect the ability of rotifers to sustain significant populations [118]. In the permanent waterbodies in our survey, which are mostly large and have abundant littoral vegetation, $Q_{B/L}$ was 0.92, while in temporary waterbodies, where littoral vegetation was generally reduced or lacking, it was 2.0. For instance, Lake Naivasha had the highest species richness (S = 53) of our sampling sites and had a $Q_{B/L}$ = 1.14. This reflected that although most of the lake lacks submerged vegetation, a few of the sampled substations had macrophyte coverages of 70–90%. These findings support the results of our multivariate analyses and give additional evidence that macrophytes are important in structuring these rotifer communities.

Hydroperiod length is often the most influential hydrological parameter in temporary waters and is a major driver of community structure (e.g., [34,119,120]). The influence of hydroperiod has been evaluated for various faunal groups, with variable results depending on the taxa considered and the study area. Most of these studies show that invertebrate species richness increases with the length of hydroperiod [119–123]. In this study, hydroperiod played an important role in determining species richness. The most temporary habitats typically had few species. Although the species richness of individual habitats was low, they made a substantial contribution to overall rotifer diversity in the regions we sampled. In this study we did not find a strong relationship between hydroperiod and species richness. This may be a consequence of the relatively few samples in some of the hydroperiod classes.

While we identified 93 taxa in our survey, we acknowledge that this study underrepresents the true diversity of the Rotifera in these waterbodies. Undoubtedly, sampling additional sites and over longer temporal scales would yield additional taxa. However, our results yielded rotifer diversity similar to other survey-based studies such as those from the Upper Parana River floodplain (from 2 sites where samples were collected with a motorized pump daily for 14 days, S = 143 [124]; from 28 locations, S = 100 [125]; and from 36 environments, S = 104 [126]), aquatic systems in Costa Rica (40 habitats, S = 105 [127]), and the Salado River in Argentina (15 locations, S = 63 [128]). In the Salado River system, associated shallow lakes and tributaries were an important source of species, similar to our results showing that smaller, temporary habitats make important contributions to γ diversity. A final example is a survey of 19 sites in the Upper Tietê basin of Brazil (S = 109) with Lecanidae, Brachionidae, Trichocercidae, Notommatidae, and Lepadellidae as the predominant families [129]. Likewise in our study, we found *Lecane* (with 14 species) and *Brachionus* (12 sp.) to be the most common genera, as is typical for tropical and sub-tropical waters.

We worked with preserved material due to logistical constraints and many species of rotifers can only be identified while alive. This is particularly true for bdelloids [130]. Another limitation of this study is that samples were collected only in January and February following the rainy season. In larger habitats it is well known that there is seasonal succession of species [76,131]. Further, many temporary habitats had dried before the sampling effort. For some monogonont taxa we had only one or a few specimens and could not observe critical features of the body and trophi; these remain unidentified. DNA barcoding may be helpful in identifying some species [132] and this study is currently underway. It is also well documented that many traditional rotifer species are in fact complexes of morphologically cryptic species (e.g., [133–136]). We found a new species within the *B. plicatilis* species complex in Lake Turkana [99] (see also Tables 2 and 3); this species co-occurred with individuals representing other lineages within the complex. Other species we isolated may also represent new cryptic lineages, in particular *B. calyciflorus*, *E. dilatata*, and *Testudinella patina*.

5. Conclusions

Traditionally, estimates of aquatic biodiversity have focused on lakes, rivers, and other permanent water sources. It is becoming increasingly clear that temporary waters can make significant contributions to rotifer species richness. The results of this study indicted the highest species richness in permanent habitats compared to temporary habitats, but small, temporary systems made important contributions to regional diversity. Rotifer diversity was affected by macrophyte abundance, but also by some habitat types and climatic regions, and the geographic proximity of ponds. From an ecological perspective, permanent lakes with dense macrophyte beds were the habitats with the highest rotifer richness. Temporary waterbodies are typical mostly widespread or cosmopolitan rotifer species. However, the highest potential to discover new records or species is in small, unexplored isolated waterbodies. The diversity of climatic conditions and aquatic biotopes makes Kenya an interesting location for further investigations, including surveying additional waterbodies, repeated sampling over longer time periods, determining the ecological relevance of rotifer diversity in these systems, and genetic analyses of isolated populations to better understand evolutionary processes in rotifers. Our study enhanced research efforts in Eastern Africa by contributing 34 previously undocumented taxa for this region. The number of rotifer species identified in this study is the highest reported from Kenya. This study also supports the contention that small freshwater habitats such as ponds and pools are important for the conservation of aquatic biodiversity [137,138] by contributing to metapopulation and metacommunity dynamics and regional species diversity [139].

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