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Improving Aquatic Biodiversity Estimates in Africa: Rotifers of Angola and Ghana

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Abstract: Afrotropical inland waters are highly diverse ecosystems; however, they remain poorly studied, especially for rotifers. Here, we contributed to the knowledge of the rotifer species richness in the largely understudied African countries of Angola and Ghana. We assessed the roles of habitat type and a suite of abiotic environmental factors in determining rotifer species richness of Ghana. A total of 37 sites (Ghana 32, Angola 5) in 19 water bodies from a variety of aquatic habitat types were sampled. In Ghana, we identified 118 taxa (105 species or subspecies level, 13 identified to genus). We identified 15 taxa (13 species) in the Angola samples. For Ghana, 100 of 118 (~85%) taxa were new records for the country, of which 13 species (~11%) were also new records for Africa. Nearly all the species (~93%) were new records for Angola. Species richness was positively correlated with conductivity and reservoir habitat type and negatively with pH. Redundancy analysis (RDA), conducted at the species level for the Ghana dataset, indicated suites of species associated with latitude, longitude, temperature, TDS, or pH. We also evaluated the effect of climate on species distribution in 27 African countries by conducting a review of all reports from Africa to determine factors associated with species richness. A Spearman's correlation confirmed a significant positive correlation between the number of rotifer species and the number of climatic regions ($R = 0.53$, $p < 0.001$) for certain countries, based on species distributions in relation to Köppen–Geiger climate regions. This fact validates the environmental heterogeneity hypothesis for African rotifers. Lastly, we predicted that rotifer species richness in Ghana, as a country with a tropical climate, could approach ~190 taxa, while in climatically heterogeneous Angola we predict ~200 taxa. This study contributes to our knowledge of rotifer biogeography and species richness patterns in Africa.

Keywords: climate regions; environmental characteristics; Rotifera; species distribution; species richness

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1. Introduction

Based on Seger's 2008 [1] comparison of the diversity of rotifers in all biogeographical realms, the Afrotropical region (AFR) had the lowest species richness recorded. This is despite the variety and abundance of habitats appropriate for rotifers. Afrotropical inland waters are highly diverse ecosystems [2] but at the same time, they also remain poorly studied [3] in comparison to Palearctic (PAL) and Nearctic (NEA) biogeographic realms. This disproportional situation is likely attributable in part to the 'rotiferologist' effect; [4] i.e., the distribution of rotifers may reflect the distribution of rotifer scientists more than that of the rotifers themselves [5–7]. According to the World Rotifer Catalog [8], the PAL region contains 1688 valid taxa (1292 monogononts, 394 bdelloids, and 2 species of *Seison*) [8]. The most recent checklist (based on data published before 2023) of rotifers from the African continent and nearby islands is comprised of 957 valid taxa (789 monogononts, 167 bdelloids, and 1 seisonid) [9]. Thus, the diversity of the known African rotifers is ~56% of the PAL region. The African countries with the highest number of reported records and taxa are Nigeria, Algeria, South Africa, the Democratic Republic of Congo, and Egypt. No records are currently available for 12 African countries [9]. It is noteworthy that the ten most studied countries also have the highest reported species richness, thus the 'rotiferologist' effect is very evident for Africa. Consequently, there is much we do not know about African rotifers, particularly those found in unstudied regions/countries [10].

Although Ghana has abundant running and stagnant waters, little attention has been paid to its rotifers. To date, only general limnological or biological studies of Volta Lake have been published, and these mention only a few taxa of rotifers. Obeng [11] recorded three genera, *Filinia*, *Keratella*, and *Trichocerca*, while Obeng-Asamoa [12] reported two, *Brachionus* and *Keratella*. Preliminary observations of the fauna and flora of Barakese Lake by Frempong and Nyjhar [13] included seven rotifer genera. For Lake Bosumtwi, the largest and only natural lake in Ghana, seasonal and interannual variability [14], secondary production and biomass [15,16], and vertical distribution [17,18] of major pelagic zooplankton taxa have been studied. However, the only study that focused specifically on rotifers was carried out in two reservoirs (Pokoase and Tamale), which were investigated more than 80 years ago and the results of which were published in the middle of the 20th century by Russell [19]. Even less is known about rotifers of Angola. Only one extensive aquacultural study has been published by Kalous et al. [20]. They used local zooplankton as food resources for farmed fish, including two rotifer species (*Asplanchna priodonta* Gosse, 1850 and *Brachionus falcatus* Zacharias, 1898). These are the only records from Angola based on our survey of the available literature.

Rotifera are especially suited for the analysis of habitat relations, trophic conditions, and water quality because this group contains a high number of species inhabiting diverse environments, with short generation times and rapid population renewal rates [7,21–30]. Many rotifer species are euryecious, while relatively few are strongly restricted in their habitat distribution. The littoral vegetation of lakes and ponds typically houses a higher number of rotifer species than all other environments [22]. This has been attributed to the spatiotemporal variability of physicochemical variables, habitat heterogeneity, high number of microhabitats, availability of food, and refugia from predators [31–34]. In the littoral zone, it is also common to observe the presence of epiphytic rotifers, which depend on the presence of a suitable substrate for their growth [35]. In these habitats, rotifers represent a major part of the non-algal periphyton biomass [36,37]. Changes in the physical and chemical features of the water body can also determine the occurrence of certain rotifer species. The most common abiotic environmental factors correlated with rotifer richness and abundance are salinity [38–41], temperature [38,39,42–44], dissolved oxygen [44–46], conductivity [47–50], and pH [50–52]. In Africa, two studies have investigated relationships among species distributions and environmental factors. In Kenya, Smolak and Walsh [53] found that the presence of macrophytes was highly correlated with species richness. Similarly, a meta-analysis across the continent that included the few records from Ghana and Angola showed that permanent habitats with well-developed littoral zones had the highest species richness [10]. In addition, many authors have suggested that the abundance, density, or composition of Rotifera species can be used as indicators of trophic state [23,28,29,54–66]. For instance, Sládeček's $Q_{B/T}$ quotient (ratio of *Brachionus* to *Trichocerca* species) has been used to evaluate trophic level [25] and the $Q_{B/L}$ quotient (ratio of *Brachionus* to *Lecane* species) has been used to define the presence of the specific aquatic zones (littoral vs. pelagic) in water bodies [53]. Thus, indices based on rotifer species composition may be valuable in determining trophic status and habitat type in the absence of availability of physicochemical data for a given site.

Understanding patterns of species richness at broad geographic extents remains challenging. Knowledge of how and why species are currently distributed in their geographical range is fundamental in ecology, evolutionary biology, and biogeography [67–69]. While many rotifers are considered cosmopolitan, their distribution can be limited by environmental conditions or biogeographic barriers [7,70]. Many hypotheses have been proposed to account for the spatial variation in species richness; among them, environmental determinants have played a central role. Starting with Von Humboldt's original idea that climate affects species richness, the number of explanations that have been hypothesized to account for spatial patterns of biodiversity has increased greatly [71]. One of these is that total resource availability sets an "ecological limit" on the number of species that can be supported in a system. Derived from this, the Ecological Limits Hypothesis (ELH) argues that the limit to the number of species that can coexist is highest in the tropics. A related hypothesis, Environmental Heterogeneity Hypothesis (EHH), states that species richness increases with the number of ecological niches; that is, species coexistence is facilitated in a more heterogeneous environment because different taxa can capitalize on different environmental conditions [72,73]. Thus, an increase in environmental gradients, habitat types, resources, and structural complexity should allow more species to coexist [74,75]. These hypotheses have been tested using many taxonomic groups across a variety of spatial grains and extents ranging from meters to thousands of kilometers [76,77]. The ELH has been tested and supported in mammals [78], birds [79,80], amphibians [81], and fishes [82,83]. The EHH has mainly been applied to plant communities (e.g., [73,84–86]) and to a lesser extent to selected invertebrates and vertebrates [87–90]. These hypotheses have not yet been tested for zooplankton communities including rotifers.

In this study, we (1) provide estimates of the diversity of the rotifer communities for two poorly studied countries (Ghana and Angola); (2) analyze the influence of the habitat type, aquatic zone (littoral vs. pelagic), and the selected environmental parameters on the rotifer species richness for samples collected from Ghana; (3) use the rotifer assemblage as a bioindicator to assess water quality and habitat type (defined by aquatic zone) through $Q_{B/T}$ and $Q_{B/L}$ quotients; (4) test the hypothesis that rotifer species richness at broad geographic units of Africa is a function of the climate region heterogeneity; and (5) evaluate the applicability of two general ecological hypotheses (ecological limits hypothesis and environmental heterogeneity hypothesis) to rotifer diversity in Africa.

2. Materials and Methods

2.1. Study Area

We collected 37 samples (Ghana 32, Angola 5) from 19 water bodies (Ghana 14, Angola 5) representing different aquatic habitat types. The map of sampling sites was made in QGIS 3.30 [91] (Figure 1).

In Ghana, five habitat types were represented (one natural lake, one reservoir, three standing water channels, four fishponds, and five wetlands). The sites are located in five districts within three administrative regions of the central part of Ghana: (1) Ashanti (Kumasi) region (Ejisu-Juabeng and Bosomtwe-Kwanwoma districts), (2) Bono (Sunyani) region (Sunyani and Tain districts), and (3) Bole district from Savannah (Damango) region. All sampled sites were at a similar altitude, within the range of ~200 m (min. 98–max. 287 m.s.l.) and lie in the tropical savanna climate (Aw).

Lake Bosumtwi, the only natural lake in Ghana, is a deep tropical lake located in an ancient meteorite impact crater. The Lake lies at 99 m.s.l. and is estimated to be 1.07 million years old. The lake surface area is 48.6 km^2 and centered within the 103.1 km^2 catchment area of semi-deciduous forest and agriculture. Maximum water depth is 78 m [92,93]. The crater (10.5 km in diameter) displays a pronounced rim and is almost filled by the ~8.5 km diameter lake in its central part. The lake developed in a hydrologically closed basin [94], with a regional annual rainfall average of 1380 mm, with a monthly maximum in June and a secondary peak in October [95]. The annual mean conductivity, temperature, dissolved oxygen, salinity, and pH within the top 30 m of the water column were 1150 µS/cm, 28.1 °C, 52.4% saturation, 0.32 psu, and 8.9, respectively. The water column is stable with persistent stratification throughout the year and permanently anoxic deep water underlying a mixed layer of variable depth and oxygen content [93]. In this lake, the phytoplankton community is dominated by cyanobacteria [96] and desmids [97], while the zooplankton community consists of an endemic copepod *Mesocyclops bosumtwii* Mirabdullayev, Sanful, Frempong, 2007 [98], a dense larval *Chaoborus* assemblage, a small-sized cladoceran, *Moina micrura* Kurz, 1875, and six rotifer species with *Brachionus calyciflorus* Pallas 1766 and *Hexarthra intermedia* (Wiszniewski, 1929) being most abundant. Four other rotifer species were reported as uncommon by Sanful [14] and Sanful et al. [15–18]. The fish community is composed by 11 native species, one of them endemic (*Tilapia busumana*) [99]. However, there are currently four principal species in this fish community due to overfishing: *T. discolor*, *T. busumana*, *Sarotherodon galilaeus*, and *Hemichromos fasciatus* [100]; three of them are zooplanktivores (*T. discolor*, *T. busumana*, *H. fasciatus*) [96].

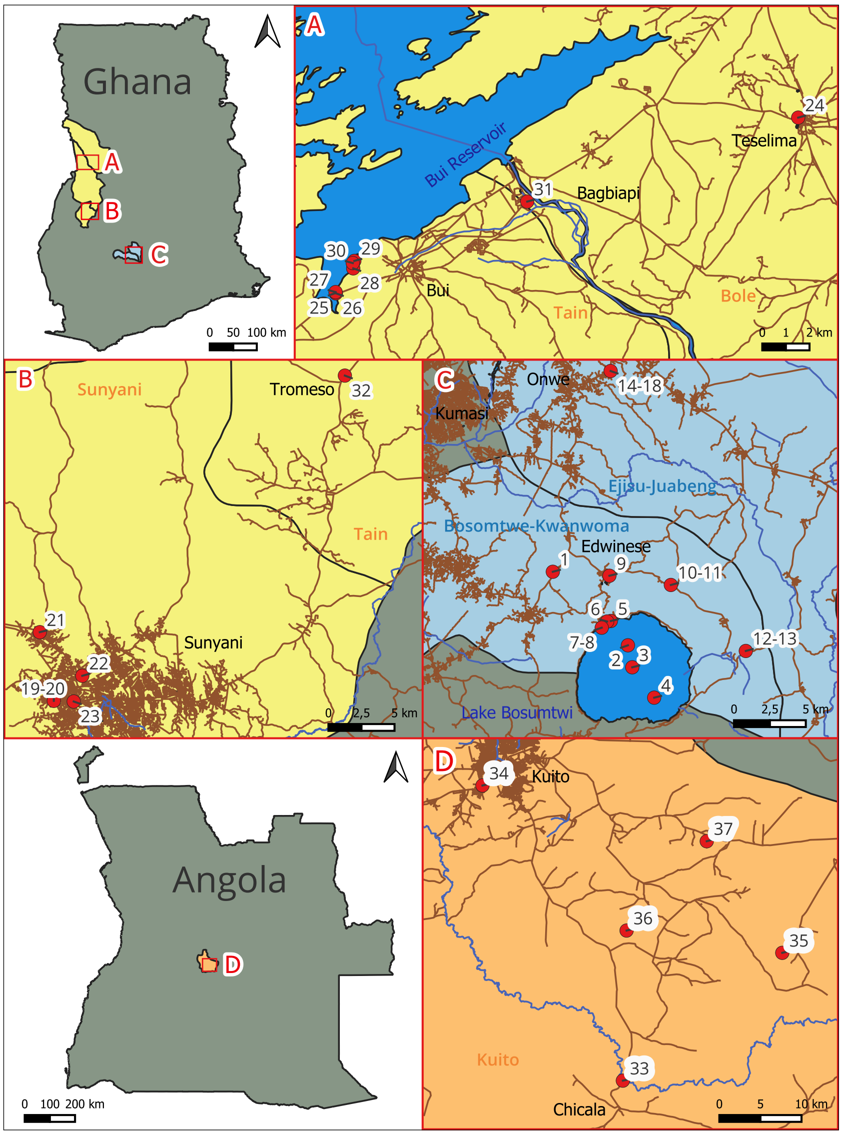

Figure 1. Location of the water bodies studied in Ghana (panels [**A**–**C**]) and Angola (panel [**D**]). For a key to the numbered sites, see Table 1.

Table 1. List of the 37 sampled aquatic sites (Ghana #1–32, Angola #33–37) and their environmental features. Sites ordered as in map (see Figure 1). T—temperature; Sal.—salinity; Cond.—conductivity; TDS—total dissolved solids; Alt.—altitude; SWCh—standing water channel; LZ—littoral zone; PZ—pelagic zone; N/A—no data available.

#	Ghana/Site Name	Date	Time	T (°C)	pH	Sal. (ppm)	Cond. (µS/cm)	TDS (mg/L)	Latitude	Longitude	Alt. (m a.s.l.)	Habitat Type	Aquatic Zone
1	Edwinese Deduako	13–Dec–18	9:30	26.5	7.76	159.0	298.0	212.0	6°33′58.8″ N	1°27′41.0″ W	238	SWCh	LZ
2	Lake Bosumtwi (surface #1)	13–Dec–18	12:40	31.6	10.13	640.0	1289.8	838.0	6°31′12.2″ N	1°24′50.7″ W	98	lake	PZ
3	Lake Bosumtwi (surface #2)	13–Dec–18	14:00	32.3	10.10	640.0	1293.0	840.0	6°30′22.4″ N	1°24′40.9″ W	98	lake	PZ
4	Lake Bosumtwi (surface #3)	13–Dec–18	15:00	32.2	10.07	630.0	1290.3	839.0	6°29′13.6″ N	1°23′51.2″ W	98	lake	PZ
5	Lake Bosumtwi Abono village #1	14–Dec–18	9:00	33.4	9.65	747.0	1358.0	959.0	6°32′07.3″ N	1°25′29.5″ W	98	lake	LZ
6	Lake Bosumtwi Abono village #2	14–Dec–18	10:00	33.4	9.65	747.0	1358.0	959.0	6°32′06.1″ N	1°25′37.8″ W	98	lake	LZ
7	Lake Bosumtwi Paradise Resort #1	14–Dec–18	13:00	34.6	9.19	662.0	1202.0	855.0	6°31′52.1″ N	1°25′50.1″ W	98	lake	LZ
8	Lake Bosumtwi Paradise Resort #2	14–Dec–18	13:20	34.6	9.19	662.0	1202.0	855.0	6°31′52.1″ N	1°25′50.1″ W	98	lake	LZ
9	Edwinese Deatie	15–Dec–18	10:30	27.6	8.04	95.0	171.9	122.0	6°33′49.8″ N	1°25′32.7″ W	270	wetland	LZ
10	Asisiwa Asonie #1	15–Dec–18	11:20	26.5	7.88	65.3	115.3	81.7	6°33′28.9″ N	1°23′13.4″ W	239	wetland	LZ
11	Asisiwa Asonie #2	15–Dec–18	11:30	26.5	7.88	65.3	115.3	81.7	6°33′28.9″ N	1°23′13.4″ W	239	wetland	LZ
12	Beposos wetland #1	15–Dec–18	13:00	29.5	8.05	180.0	334.0	236.0	6°30′59.4″ N	1°20′23.5″ W	209	wetland	LZ
13	Beposos wetland #2	15–Dec–18	13:10	29.5	8.05	180.0	334.0	236.0	6°30′59.4″ N	1°20′23.5″ W	209	wetland	LZ
14	Kumasi-Onwe Afenasu #1	15–Dec–18	15:00	25.6	7.89	97.7	179.3	128.0	6°41′33.6″ N	1°25′30.0″ W	230	wetland	LZ
15	Kumasi-Onwe Afenasu #2	18–Mar–23	7:00	25.6	6.58	90.0	192.0	96.0	6°41′33.6″ N	1°25′30.0″ W	230	wetland	LZ
16	Kumasi-Onwe Afenasu #3	18–Mar–23	7:10	25.6	6.58	90.0	192.0	96.0	6°41′33.6″ N	1°25′30.0″ W	230	wetland	LZ
17	Kumasi-Onwe Afenasu #4	18–Mar–23	7:20	25.6	6.58	90.0	192.0	96.0	6°41′33.6″ N	1°25′30.0″ W	230	wetland	LZ
18	Kumasi-Onwe Afenasu #5	18–Mar–23	7:20	25.6	6.58	90.0	192.0	96.0	6°41′33.6″ N	1°25′30.0″ W	230	wetland	LZ
19	Sunyani Berlin top #1	16–Dec–18	13:30	29.0	7.44	148.0	277.0	195.0	7°20′33.6″ N	2°21′33.5″ W	287	fishpond	PZ
20	Sunyani Berlin top #2	16–Dec–18	13:30	29.0	7.44	148.0	277.0	195.0	7°20′33.6″ N	2°21′33.5″ W	287	fishpond	PZ
21	Sunyani Dumasua	16–Dec–18	14:15	28.1	7.84	75.8	135.3	96.3	7°23′22.9″ N	2°22′08.2″ W	277	fishpond	PZ
22	Sunyani Atta Addae Zinco	16–Dec–18	14:35	28.0	9.10	101.0	185.1	132.0	7°21′35.4″ N	2°20′23.3″ W	276	SWCh	PZ
23	Sunyani SDA	16–Dec–18	15:15	33.1	10.30	81.4	83.3	59.0	7°20′32.0″ N	2°20′44.5″ W	281	fishpond	PZ
24	Teselima fishpond	17–Dec–18	10:40	21.9	9.61	64.4	112.2	79.8	8°17′46.1″ N	2°07′32.1″ W	180	fishpond	PZ
25	Bui reservoir (main lake #1)	17–Dec–18	12:20	31.3	9.14	46.6	74.6	53.0	8°13′43.7″ N	2°18′11.9″ W	172	reservoir	PZ
26	Bui reservoir (pool)	17–Dec–18	12:45	34.1	8.75	44.4	69.0	48.9	8°13′43.2″ N	2°18′11.7″ W	172	reservoir	PZ
27	Bui reservoir (main lake #2)	17–Dec–18	13:00	30.9	8.40	57.2	102.8	66.0	8°13′44.9″ N	2°18′12.1″ W	172	reservoir	PZ
28	Bui reservoir (main lake #3)	17–Dec–18	14:03	32.7	8.10	57.2	82.0	58.9	8°14′17.7″ N	2°17′47.7″ W	172	reservoir	LZ
29	Bui reservoir (main lake #4)	17–Dec–18	14:20	30.7	8.30	55.3	86.6	64.5	8°14′28.0″ N	2°17′46.2″ W	172	reservoir	LZ
30	Bui reservoir (main lake #5)	17–Dec–18	14:40	32.5	8.10	58.9	77.1	54.3	8°14′25.0″ N	2°17′48.3″ W	172	reservoir	LZ
31	Black Volta River (stagnant channel)	17–Dec–18	15:20	28.2	8.10	47.8	80.3	56.5	8°15′50.0″ N	2°13′47.0″ W	106	SWCh	LZ
32	Tromeso	18–Dec–18	10:05	22.3	8.60	84.5	157.4	111.0	7°33′55.4″ N	2°09′35.5″ W	223	wetland	LZ
33	Rio Kuquema	14–May–09	N/A	N/A	N/A	N/A	N/A	N/A	12°46′23.6″ S	17°03′48.7″ E	1462	river	PZ
34	Kalupanda	1–Nov–09	N/A	N/A	N/A	N/A	N/A	N/A	12°26′33.0″ S	16°54′21.9″ E	1687	fishpond	PZ
35	Chitundo	12–May–09	N/A	N/A	N/A	N/A	N/A	N/A	12°37′48.0″ S	17°14′32.3″ E	1381	fishpond	PZ
36	Nequilo	4–May–08	N/A	N/A	N/A	N/A	N/A	N/A	12°36′18.1″ S	17°04′03.7″ E	1591	fishpond	PZ
37	Chicava	30–Oct–06	N/A	N/A	N/A	N/A	N/A	N/A	12°30′17.8″ S	17°09′27.3″ E	1524	fishpond	PZ

The second larger water body we sampled was Bui reservoir. It is controversially located on the Black Volta River, where it flooded 21% of Bui National Park when it was constructed. The reservoir area at full capacity is 444 km^2 with an elevation of 183 m [101], and extends approximately 40 km upstream of the dam [102]. The climate in the study area is characterized by a single rainy season, with an annual average rainfall of ~1140 mm (estimated between 1983 and 2000) [103]. Monthly temperatures range from ~26 °C in August to ~30 °C in March. The littoral habitat along the reservoir shoreline includes aquatic and semi-aquatic vegetation (*Panicum* sp., *Polygonum* sp., *Ludwigia* sp., *Brachiara* sp., *Mimosa pigra*, and *Nymphaea* sp.) [104]. Alhassan [105] identified 35 species of phytoplankton in the reservoir. For zooplankton, no rotifers, only crustaceans, have been studied. *Leptodora* sp. dominated the cladocerans, whereas *Cyclops* sp. was the dominant copepod [106,107]. Detailed information about the other sampled water bodies (wetlands, fishponds, and standing water channels) has not been previously published; all measured parameters in situ are given in Table 1.

All samples from Angola were taken in the Kuito district within the Bié Province located on a plateau in central Angola, where several major rivers in sub-Saharan Africa originate. In Angola, the main river basins of the province are the Cuanza and Okavango Rivers. On the borders of the eastern part of the province, there are tributaries of the Congo, such as the Cuango and the Kassai, and tributaries of the Zambezi, such as the Lungue Bungo (Lungwebungu River). The Cunene and Cuvo-Keve rivers originate close to the Bié provincial boundary in the neighboring Huambo Province to the west. The rivers in this source area are oligotrophic, and many flows are interrupted by waterfalls and cascades. In Angola, overall, four fishponds (with an area of ~200 m^2 and a maximum depth of 1.5 m) and one river were sampled. All samples were collected within an altitude range of 1381–1687 m.s.l. In the sampled fishponds *Coptodon rendalli* (Boulenger, 1897) has been extensively grown. The lentic habitat of the Kuquema River was characterized by low turbidity and submerged vegetation. All sampled sites in Angola lie in Subtropical highland climate with dry winters (Cwb), according to the Köppen–Geiger climate classification.

2.2. Sampling, Water Chemistry, and Species Richness

Rotifer samples in Ghana were collected in December 2018 and March 2023 from the shoreline using a plankton net (25 cm diameter; 21 μm mesh) attached to a 0.5 m long handle. Samples and water chemistry measurements were obtained from the surface (10–30 cm depth). Each sample consisted of a minimum of 10 plankton tows with a smooth pulling motion for 30 s. All samples were preserved immediately in 96% ethanol. The temperature, pH, salinity, and electrical conductivity were measured at the time of sampling using a Multi 340i WTW probe (WTW Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). In total, 20 sites in the littoral zone and 12 sites in the pelagic zone were sampled. Pelagic samples from Lake Bosumtwi (#2–4) were collected on board a motorboat in the middle of the lake, while littoral samples (#5–8) were taken from the lake side from a wooden plank (padua) traditionally used by local fishermen.

Samples from Angola were collected in October 2006, May 2008 and 2009, and November 2009 using a plankton net (21 μm mesh) from the shore with no developed littoral vegetation, according to the methods of Hrbáček et al. [108]. Qualitative samples were obtained via 5 horizontal plankton net tows across each pond. Concentrated plankton were fixed in situ in 70% ethanol. Details for each sampling site are given in Table 1.

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 [109–113] and other appropriate keys [114,115]. As the samples were immediately preserved, this precluded identification to the species level in several cases (e.g., bdelloids and other species whose identification relies on features seen only in live specimens). The taxonomic validity of each taxon was verified using the List of Available Names in Zoology, Candidate Part Phylum Rotifera (LAN) [116].

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

For a comparison of trophic status among the habitat types surveyed, we calculated Sládeček's [25] trophic condition quotient, $Q_{B/T}$, where B is the number of *Brachionus* species and T is the number of *Trichocerca* species. Species of the genus *Brachionus* generally reach high population densities in highly eutrophic lakes [117], while members of the genus *Trichocerca* are found primarily in oligotrophic habitats. Values of $Q_{B/T}$ less than 1.0 indicate oligotrophy, values between 1.0 and 2.0 indicate mesotrophy, and values over 2.0 indicate eutrophy [25].

Similarly, *Brachionus* is typically considered as a planktonic or semi-planktonic species found in open waters in the pelagic and littoral zones of water bodies, whereas members of the genus *Lecane* are closely associated with substrata such as submerged macrophytes or terrestrial plants [109]. As many of the study systems we studied were dominated by *Brachionus*, we also calculated a $Q_{B/L}$ quotient ($Q_{B/L}$, #*Brachionus* spp./#*Lecane* spp.) [53] to further categorize the sites. For this index, values of <1.0 represent water bodies with a well-developed littoral zone with abundant macrophytes, while values between 1.0 and 2.0 represent those with poorly developed littoral vegetation, and those >2.0 represent water bodies without a littoral zone (typical for fishponds and temporary habitats) [53].

2.4. Effect of Climate Conditions on Species Distribution

The Köppen–Geiger climate classification scheme divides climates into five main climate groups: A (tropical), B (dry), C (temperate), D (continental), and E (polar) [118]. In Africa, climatic regions of all the five main groups occur. To evaluate species distribution, we used rotifer species richness of certain continental African countries (plus Madagascar), which we grouped into three larger climatic groups. The source data for climatic regions were gathered from Köppen–Geiger maps following Beck at el. [118]. The online maps are available at https://koppen.earth (accessed on 11 September 2023). As the source data for rotifer distribution, we used a freely available dataset from the Open Science Framework (OSF) and the Global Biodiversity Information Facility (GBIF). This dataset comprises ~27,500 records of rotifer occurrence in Africa, where 957 taxa from 706 published papers were collated [9].

A recent review by Fresno Lopez et al. [9] compiled records of rotifer distribution in 41 African countries and seven nearby islands; however, no records are yet available for another dozen countries. We included 27 of the best studied African countries (26 inland countries and Madagascar, where at least five publications with rotifers were recorded) for species distribution analyses. Based on this, we divided the countries into three groups. Groups 1 and 2 are climatically homogeneous, with domination of one characteristic climate region (complemented by 1–5 (Ø 4 per country) marginal climate regions) for the particular country. The 3rd group has spatially diverse and heterogeneous climatic conditions, where the climate is fragmented into 10–18 (Ø 14) regions, and only one prevailing characteristic climate type cannot be determined. The 1st climatically homogenous group consisted of ten countries (Algeria, Botswana, Chad, Egypt, Mali, Morocco, Namibia, Senegal, Tunisia, Sudan), where dry (arid (desert) or semi-arid (steppe)) climate dominate. The 2nd group was represented by 12 climatically homogenous countries where tropical or subtropical (temperate) climates dominate (Benin, Burundi, Cameroon, DR Congo, Ghana, Ivory Coast, Malawi, Nigeria, Rwanda, Uganda, Zambia, and Zimbabwe). Finally, the 3rd group consisted of five countries with climatically heterogeneous conditions (Ethiopia, Kenya, South Africa, Tanzania, and Madagascar). For each of the three climatic groups, we calculated the average number of rotifer species per country allowing us to predict an average species richness for still unexplored African countries. For testing applicability of the EHH, the numerical variables, consisting of the number of the climatic regions in the country, were correlated with the number of species in the analyzed countries. We also calculated the average number of rotifer species per country in climatically homogenous countries (the 1st and the 2nd group together) to compare it with the group of climatically heterogeneous countries (the 3rd group). For the evaluation of the ELH, differences between two ordinal variables, the species richness of the tropical climate countries and all other ("non-tropical") countries, were tested. Seven countries (Benin, Cameroon, Ivory Coast, DR Congo, Ghana, Nigeria, and Uganda) were identified as countries with a tropical climate (tropical climate makes up 90–100% of their area). The remaining 20 countries had different climatic structure.

2.5. Statistical Analyses

To analyze species richness, we created several generalized linear models with different error distributions for the response variable, including Poisson, Gaussian, and negative binomial models using the *Mass* package in R. Covariates were chosen for each model utilizing forward and backward selection in a stepwise approach with the R function "Step." The covariates we selected from included temperature, pH, conductivity, total dissolved solids (TDS), habitat type, altitude, and aquatic zonation with species richness as the response variable. The best model was then chosen based on AIC. We tested for spatial autocorrelation in our data using Moran's test (*spdep* package). To analyze what environmental parameters were associated with a particular species, we applied an ordination analysis. Linear versus unimodal models were selected based on the values of the first axis of the Unconstrained Detrended Correspondence Analysis (DCA) conducted on the species matrix. Based on this, ordination analysis was performed in the program PC-ORD [119] using a RDA. Unidentified bdelloid species were not included in ordination analysis. Variables with high variance inflation factors were removed from the RDA until no substantial variance inflation remained. When two variables were collinear with one another, the variable chosen for removal was based on the inflation factor and the subsequent model performance based on the r-squared adjusted value.

To assess the similarities in species composition, we used cluster analysis based on Simpson's similarity index and the unweighted pair group method with the arithmetic mean algorithm (UPGMA). We choose Simpson's similarity index because this index is robust to datasets in which some samples are much richer than others, where conventional similarity indices (such as Jaccard's and Sørensen's) are not [120]. To test the EHH, we determined the Spearman's correlation between the number of species, the number of early published papers, and the number of Köppen–Geiger climate regions. To test the ELH, we used the non-parametrical Mann–Whitney U test expressing differences in the species richness between tropical climate and "non-tropical" countries. The EHH and ELH were tested using the statistical program PAST [121].

For these analyses, sites were assigned a habitat type: (1) natural lake, (2) reservoir, (3) stagnant water channel, (4) fishpond, and (5) wetlands. Species lists from collections were combined by site and average scores computed for corresponding abiotic environmental parameters. Pelagic and littoral zone collections, however, were kept separate. Collections from Kumasi-Onwe Afenasu (2018 and 2023) were kept separate because of the five-year time gap between sampling events. For the general linear model (GLM) and Redundancy Analysis (RDA), we merged collections from aquatic zones located within one water body and those nearby into 14 meta-communities. In all, 10 meta-communities had less than 20 species (five of them were species-poor, <10 species), one had 21 species, and three were occupied by >30 species. For hierarchical cluster analysis, we separated pelagic from littoral samples for Lake Bosumtwi, and for Bui reservoir we analyzed three separate samples, nearby pool, pelagic, and littoral samples. All other sites were analyzed as a single collection based on their small sizes.

3. Results

3.1. Water Physicochemical Parameters

During the survey, water temperatures ranged from 22.3 °C (Tromeso—wetland, #32) to 34.6 °C (Paradise Resort—Lake Bosumtwi, #7–8), pH ranged from 7.44 (Sunyani Berlin top—fishpond, #18–19) to 10.30 (Sunyani SDA—fishpond, #23), electrical conductivity and salinity ranged from 69 μScm^{-1} and 44.4 ppm (Bui Reservoir (pool), #26) to 1358 μScm^{-1} and 747 ppm (Lake Bosumtwi—Abono village, #5–6), respectively. A summary of environmental parameters for all sampled sites are presented in Table 1.

3.2. Species Richness

Of the 32 samples from Ghana, we identified 22 rotifer families (1 in class Bdelloidea, 21 in class Monogononta) and four orders (Collothecaceae, Flosculariaceae, Ploimida, and Bdelloidea) comprising 38 genera and 118 taxa (105 were identified to species or subspecies; the remaining 13 were identified to genus). In Angola samples, we recorded 15 taxa (13 species) belonging to 8 genera, 8 families (1 class Monogononta), and 2 orders (Flosculariacea and Ploima).

In Ghana, the most widespread and diverse taxon we identified was the genus *Lecane*, found in 29 of the 32 samples (~90% occurrence) and 18 species. *Lecane bulla* (Gosse, 1851) occurred in 25 (~78%) samples and was the most common rotifer species in Ghana. The second most frequent occurring were species of the genus *Brachionus* which were found in 23 (~72%) samples, represented by 10 species including *Brachionus calyciflorus* (found in 38% of samples). Other commonly occurring species were *Plationus patulus* (Müller, 1786), *Lepadella patella* (Müller, 1773), *Lecane curvicornis* (Murray, 1913), *Mytilina ventralis* (Ehrenberg, 1830), and *Testudinella patina* (Hermann, 1783). A large proportion (~64%) of the species were recorded only once or twice across all sites. Unidentified bdelloids were found in 75% of samples.

In Angola, the most frequently found species was *Keratella tropica* (Apstein, 1907) which occurred in four of the five samples (80%). We found *Asplanchna brightwellii* Gosse 1850 in three samples (60%), and all other species were identified once or twice.

Our study extended by 13 species (~11% of all identified taxa—all found in Ghana; in Table 2 marked with a symbol Ā) the most recent review [9] reporting all known records of rotifer taxa in Africa. We also recorded 100 of 118 (~85%) as taxa new to Ghana (in Table 2 marked with Ḡ) and 14 of 15 (~93%) new to Angola (in Table 3 marked with L̄). We also identified 17 species and 2 subspecies (~8% of all Ghana taxa) that were rarely reported in Africa, which means they were recorded before only in one or two of 13 African countries. The list of the rare species records for Africa is available in Table 2, marked with a symbol R̄. Bui reservoir, with 43 taxa, was the water body with the highest species richness. The adjacent pool (#26) contributed to the reservoir meta-community with the addition of 12 taxa, while the stagnant outflow channel (#31) added another 5 taxa. We also found 43 taxa in the Kumasi-Onwe Afenasu wetland. The high numbers found here may be attributed to several factors including (1) presence of a dense vegetation of littoral zone and (2) increased sampling effect. This site was sampled in 2018 and 2023 and had the highest total number of samples examined. Two other sites with high richness are Edwinese Deduako (35 taxa) and Lake Bosumtwi (21).

Table 2. Rotifer taxa found in aquatic habitats surveyed in Ghana (2018 and 2023).

#	Taxon	New Record	Sites Found	Occurrence [%]
	Asplanchnidae			
1	*Asplanchna brightwellii* Gosse, 1850	Ḡ	19–21, 29, 30	15.6
	Bdelloidea			
2	bdelloid (unidentified)	Ḡ	1–3, 5, 6, 8, 10–19, 21, 25, 26, 28–32	75.0
	Brachionidae			
3	*Anuraeopsis fissa* (Gosse, 1851)	Ḡ	27	3.1
4	*Brachionus angularis* Gosse, 1851	Ḡ	19, 21	6.3
5	*Brachionus bidentatus* Anderson, 1889	Ḡ	16	3.1
6	*Brachionus calyciflorus* s.l. Pallas, 1766	Ḡ	2–6, 9, 13, 19, 20, 22–24	37.5
7	*Brachionus caudatus* Barrois & Daday, 1894	Ḡ	25, 27	6.3
8	*Brachionus dimidiatus* Bryce, 1931	Ḡ	20, 21	6.3
9	*Brachionus dorcas* Gosse, 1851	Ḡ	2, 15, 25	9.4
10	*Brachionus falcatus* Zacharias, 1898	Ḡ	9, 24–27, 29	18.8
11	*Brachionus mirabilis* Daday, 1897		1, 12, 13	9.4
12	*Brachionus quadridentatus* Hermann, 1783	Ḡ	7, 12, 16, 18, 21, 26	18.8
13	*Brachionus urceolaris* Müller, 1773		5	3.1
14	*Keratella lenzi* Hauer, 1953	Ḡ	30	3.1
15	*Keratella tropica* (Apstein, 1907)	Ḡ	26–29, 31	15.6
16	*Plationus patulus* (Müller, 1786)		1, 7, 14–18, 26, 27, 32	31.3
17	*Platyias quadricornis* (Ehrenberg, 1832)	Ḡ	1, 15, 16, 18, 24, 32	18.8
	Collothecidae			
18	*Collotheca* sp.	Ḡ	7	3.1
19	*Stephanoceros fimbriatus* (Goldfuss, 1820)	Ḡ R̄	1	3.1
20	*Stephanoceros* sp.	Ḡ	1, 9	6.3
	Dicranophoridae			
21	*Dicranophoroides caudatus* (Ehrenberg, 1834)	Ḡ	1	3.1
22	*Dicranophorus epicharis* Harring & Myers, 1928	Ḡ	8	3.1

#	Taxon	New Record	Sites Found	Occurrence [%]
	Euchlanidae			
30	*Euchlanis dilatata* Ehrenberg, 1830	Ḡ	[illegible]	18.8
32	*Euchlanis* [illegible]	Ḡ	27	3.1
	Filiniidae			
34	*Filinia* [illegible]	[illegible]	[illegible]	12.5
35	*Filinia* [illegible]	Ḡ	[illegible]	6.3
36	*Filinia* [illegible]	[illegible]	[illegible]	3.1
	Flosculariidae			
36	*Floscularia* [illegible]	[illegible]	[illegible]	3.1
37	*Limnias* [illegible]	[illegible]	[illegible]	3.1
38	*Ptygura* [illegible]	[illegible]	[illegible]	3.1
39	*Sinantherina* [illegible]	Ḡ, Ṛ	[illegible]	12.5
40	*Sinantherina* [illegible]	[illegible]	[illegible]	9.4
41	*Sinantherina* [illegible]	[illegible]	[illegible]	3.1
	Hexarthridae			
42	*Hexarthra* [illegible]	Ā Ḡ	[illegible]	9.4
43	*Hexarthra intermedia* (Wiszniewski, 1929)	Ḡ	[illegible]	3.1
	Ituridae			
44	*Ituria* [illegible]	Ḡ, Ṛ	[illegible]	6.3
	Lecanidae			
45	*Lecane* [illegible]	Ḡ	[illegible]	3.1
46	*Lecane* [illegible]	[illegible]	[illegible]	3.1
47	*Lecane* [illegible]	Ḡ, Ṛ	[illegible]	3.1
48	*Lecane bulla* (Gosse, 1851)	Ḡ	[illegible]	78.1
49	*Lecane clara* (Bryce, 1892)	Ḡ	[illegible]	3.1
50	*Lecane curvicornis* (Murray, 1913)	Ḡ	[illegible]	34.4
51	*Lecane* [illegible]	Ḡ, Ṛ	[illegible]	3.1
52	*Lecane* [illegible] Harring & Myers, 1926	Ḡ, Ṛ	[illegible]	3.1
53	*Lecane* [illegible] Hauer, 1931	Ḡ	[illegible]	9.4
54	*Lecane* [illegible] Harring, 1914	Ḡ, Ṛ	[illegible]	3.1
55	*Lecane hornemanni* (Ehrenberg, 1834)	Ḡ	[illegible]	3.1
56	*Lecane lateralis* Sharma, 1978	Ḡ	1, 6–8, 30	15.6
57	*Lecane leontina* (Turner, 1892)		25, 26, 28, 30, 32	15.6
58	*Lecane luna* (Müller, 1776)		8, 15	6.3
59	*Lecane papuana* (Murray, 1913)	Ḡ	1, 2, 7, 8, 10, 12–14, 17, 24–27, 31, 32	46.9
60	*Lecane quadridentata* (Ehrenberg, 1830)	Ḡ	1, 9, 12, 14, 21	15.6
61	*Lecane unguitata* (Fadeev, 1925)	Ḡ	1, 18, 25–27	15.6
62	*Lecane ungulata* (Gosse, 1887)	Ḡ	1, 13, 22, 25, 26, 32	18.8
	Lepadellidae			
63	*Colurella adriatica* Ehrenberg, 1831	Ḡ	26	3.1
64	*Colurella hindenburgi* Steinecke, 1916	Ḡ	1, 8	6.3
65	*Colurella obtusa* (Gosse, 1886)	Ḡ	1	3.1
66	*Colurella* sp. 1	Ḡ	16, 32	6.3
67	*Colurella* sp. 2	Ḡ	16	3.1
68	*Colurella* sp. 3	Ḡ	16	3.1
69	*Lepadella ovalis* (Müller, 1786)	Ḡ	1, 7–9, 22	15.6
70	*Lepadella patella* (Müller, 1773)		1, 2, 8–11, 13–15, 32	31.3
71	*Lepadella rhomboides* (Gosse, 1886)	Ḡ	31	3.1

Table 2. Rotifer taxa found in aquatic habitats surveyed in Ghana (2018 and 2023).

#	Taxon	New Record	Sites Found	Occurrence [%]
	Asplanchnidae			
1	*Asplanchna brightwellii* Gosse, 1850	Ḡ	19–21, 29, 30	15.6
	Bdelloidae			
2	Bdelloid (unidentified)	Ḡ	1–3, 5, 6, 8, 10–19, 21, 25, 26, 28–32	75.0
	Brachionidae			
3	*Anuraeopsis fissa* (Gosse, 1851)	Ḡ	27	3.1
4	*Brachionus angularis* Gosse, 1851		19, 27	6.3
5	*Brachionus bidentatus* Anderson, 1889	Ḡ	16	3.1
6	*Brachionus calyciflorus* s.l. Pallas, 1766		2–6, 9, 13, 19, 20, 22–24	37.5
7	*Brachionus caudatus* Barrois & Daday, 1894	Ḡ	25, 27	6.3
8	*Brachionus dimidiatus* Bryce, 1931		20, 21	6.3
9	*Brachionus dorcas* Gosse, 1851	Ḡ	2, 15, 25	9.4
10	*Brachionus falcatus* Zacharias, 1898		9, 24–27, 29	18.8
11	*Brachionus mirabilis* Daday, 1897	Ḡ	1, 12, 13	9.4
12	*Brachionus quadridentatus* Hermann, 1783	Ḡ	7, 12, 16, 18, 21, 26	18.8
13	*Brachionus urceolaris* Müller, 1773		5	3.1
14	*Keratella lenzi* Hauer, 1953	Ḡ, Ṛ	30	3.1
15	*Keratella tropica* (Apstein, 1907)		26–29, 31	15.6
16	*Plationus patulus* (Müller, 1786)		1, 7, 14–18, 26, 27, 32	31.3
17	*Platyias quadricornis* (Ehrenberg, 1832)		1, 15, 16, 18, 24, 32	18.8
	Collothecidae			
18	*Collotheca* sp.	Ḡ	7	3.1
19	*Stephanoceros* cf. *fimbriatus* (Goldfuß, 1820)	Ḡ, Ṛ	1	3.1
20	*Stephanoceros* sp.	Ḡ	1, 9	6.3

Ḡ—new species record for Ghana, Ā—new species record for Africa, Ṛ—rare species record for Africa. Occurrence indicates the percentage of sites where the taxon was found.

...tats surveyed in Angola (2006, 2008, and 2009).

Sites Found	Occurrence [%]
35–37	60
37	20
34	20
36, 37	40
34	20
33–36	80
37	20
37	20
37	20
37	20
34	20
36	20
37	20
36–37	40
34–35	40

...ndicates the percentage of sites where the taxon was found.

...ds for Africa is available in Table 2, marked with a ... was the water body with the highest species richness. ... the reservoir meta-community with the addition ... channel (#31) added another 5 taxa. We also found ... wetland. The high numbers found here may be ... (1) presence of a dense vegetation of littoral zone ... This site was sampled in 2018 and 2023 and had the ... mined. Two other sites with high richness are Edwinese Deduako (35 taxa) and Lake Bosumtwi (21).

... We found that richness was significantly positively influenced by the habitat type and ... the strength of the effect was low) and negatively influenced by pH (Table 4). In the RDA (Figure 2), axis 1 was most positively influenced by TDS, and negatively influenced by latitude and longitude, pH, and temperature. Axis 2 was similarly structured, except for pH and temperature which positively influenced this component. Several rotifers were strongly associated with these axes; positive relationships for axis ... *pallida*, *L. curvicornis*, *M. ventralis*, negative associations included *T. similis*, ... *B. falcatus*, and *T. truncata*; for axis 2, positive relationships included *B. calyciflorus*, ... "bosumtwi" sp. nov., *B. angularis*, and *B. dimidiatus*, while *L. curvicornis*, ... *T. similis* and *L. papuana* were negatively associated.

Cluster analysis showed similarities in species composition in spatially closely situated water bodies (Figure 3). The first and the largest cluster of species similarity represented by ... sites #1–18 shown in Figure 1C) extends around Lake Bosumtwi. The highest similarity was observed among the samples (#10–18) collected from the littoral zone of three wetlands (Abisinya Asonie, Be...os, and Kumasi-Onwe Afenasu). A high similarity was also recorded ... sites of Lake Bosumtwi (LZ–littoral zone #2–4 vs. PZ–pelagic zone #5–8). In the ... Lake Bosumtwi are the recorded water bodies with the overall highest species richness: ... Kumasi-Onwe Afenasu (#14–18) with 43 rotifer taxa, and Edwinese Deduako (#1) with 35 taxa.

Table 4. Coefficients for the negative binomial GLM for species richness. SWCh—standing water channel. * $p < 0.05$; *** $p < 0.001$.

	Estimate	Std. Error	z Value	Pr (>|z|)
(intercept)	6.585	1.84	3.578	0.000346 ***
temperature	−0.072	0.05	−1.551	0.120821
pH	−0.344	0.14	−2.423	0.015375 *
conductivity	0.003	0.001	2.33	0.019817 *
lake	−2.711	1.72	−1.574	0.115418
reservoir	1.665	0.42	3.976	7.02×10^{-5} ***
SWCh	0.291	0.30	0.968	0.333106
wetland	0.143	0.28	0.518	0.604596

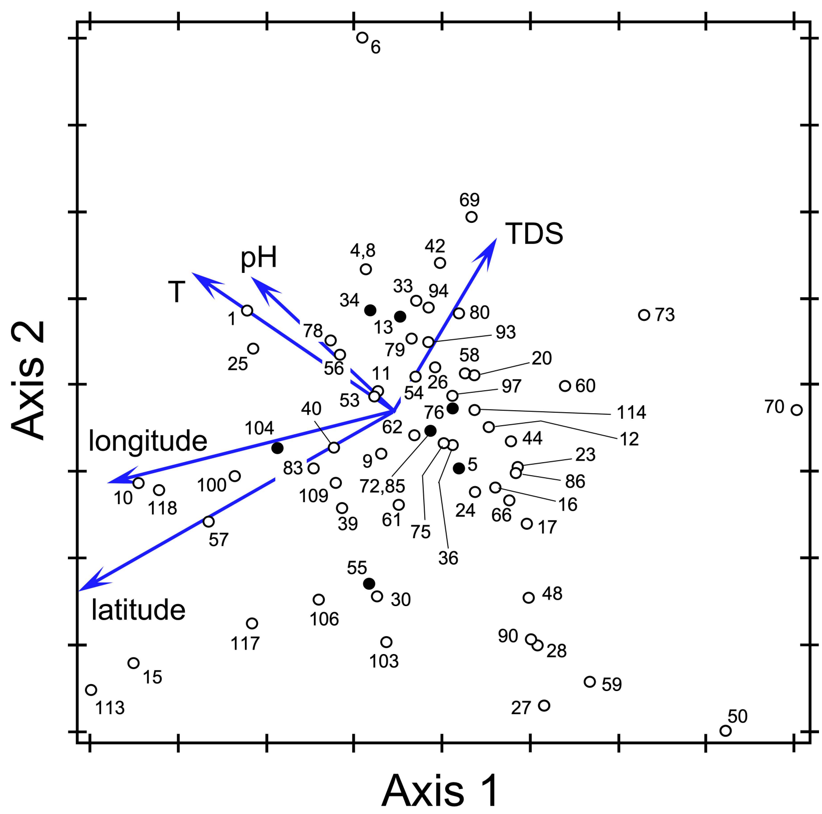

Figure 2. Redundancy Analysis (RDA) of rotifers and key environmental factors for 14 water bodies from Ghana. Open circles = numbers correspond to species list given in Table 1. Filled circles include more than one species. The first species is listed, the others are given after =; 5 = 31, 46, 47, 49, 51, 52, 67, 68, 87, 115; 13 = 18, 22, 38, 74; 34 = 43, 89, 95, 96, 101, 102; 55 = 71, 99; 76 = 19, 21, 32, 35, 45, 65, 81; 104 = 3, 7, 14, 29, 41, 63, 82, 84, 88, 91, 98, 105, 107, 108, 110, 111, 112, 116; open circles, numbers correspond to species list given Table 1.

The second cluster (Figure 1B) is represented by three intensively farmed fishponds (Sunyani Berlin top 1, #19, Sunyani Berlin top 2, #20, and Sunyani Dumasua, #21) within the city of Sunyani. Sampled sites within this group were similar habitats of man-made water bodies without the presence of a developed littoral zone and geographically close (within the range of 5 km). The third cluster (Figure 1A) of the sampled water bodies was found in the northernmost part of Ghana and encompasses the Bui reservoir area (#24–31). The samples from the Bui reservoir (#25–30) were collected within the range of 22–24 km air distance from the border with the Ivory Coast. The highest similarity in this cluster was recorded among the samples from the pelagic zone of Bui reservoir (#25, #27) and the adjacent Bui reservoir pool (#26) (1.5 m from the main reservoir, 2 m in diameter, 30 cm in depth). Species composition of the pelagic and littoral zone of the Bui reservoir was also similar.

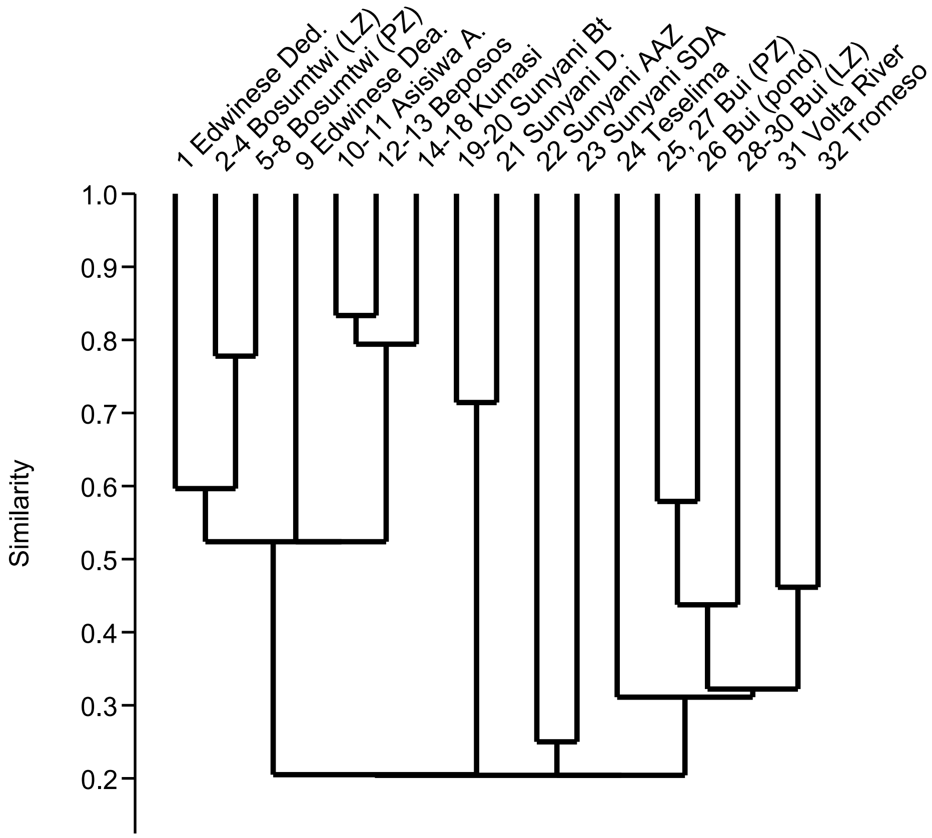

Figure 3. Hierarchical cluster analysis based on unpaired group (UPGMA) Simpson's similarity index. Sampling sites are shown in Figure 1 and characterized in Table 1.

Comparing the species richness of the littoral zone (LZ) with the pelagic zone (PZ) in the two large water bodies in Ghana, the littoral zone was on average inhabited by twice the number of species (~20 taxa in LZ vs. ~10 taxa in PZ). The most comprehensive sample collection for the comparison of these two zones within one lake (3 samples from PZ, 4 from LZ) was taken from Lake Bosumtwi where LZ was well developed. Here, we found 19 taxa in the LZ and 9 taxa in the PZ.

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

Using trophic indices, we found that the $Q_{B/T}$ value was over 2.0 for fishponds, wetlands, and standing water channels (SWCh), and thus the water bodies we sampled were deemed eutrophic. For Lake Bosumtwi, wetlands, and SWCh (water bodies with developed littoral vegetation), the $Q_{B/L}$ was 0.92. In the sites where the samples were collected from a littoral zone, species of the genus *Lecane* were very common, with an average $Q_{B/L}$ 0.39.

3.4. *Effect of Climate Conditions on Species Distribution*

Based on the characteristic climatic features of the countries, individual climatic regions had the following species richness: The first group of ten countries with domination of arid or semi-arid climate is represented by an average of 124 (median: 132) rotifer taxa by country. The second group, of twelve countries where tropical or subtropical climate dominate, is represented by an average of 159 (147) taxa/country. In the third group of climatically heterogeneous conditions, represented by five countries, 203 (204) rotifer taxa per country were identified. Based on the three species richness groups formed by the characteristic climate conditions, we can predict that in Africa, the average rotifer species richness in arid/semi-arid climates is ~120 taxa/country, tropical/subtropical climate ~160 taxa/country, and the highest diversity in climatically diversified countries on average, is ~200 taxa/country. The rotifer species distribution related to the Köppen–Geiger climate regions shows increasing diversity among the stated groups by ~40 taxa/country. Ghana belongs to the second climatic group where we predict ~160 rotifer taxa but also to a narrow group of five countries with about 100% of the territory with a tropical climate, where a species richness is predicted to ~190 taxa.

The result of the Spearman's correlation used for testing EHH confirmed a significant positive correlation between the number of rotifer species and the number of climate regions (R = 0.53, $p < 0.001$) for certain countries. In the group of countries characterized by heterogeneous climatic conditions, an average of 203 (median: 204) rotifer taxa per country were identified, whereas in climatically homogenous African countries with a dry climate or (sub) tropical climate, an average of 144 (147) taxa were recorded. In the comparison, the species richness of rotifers in the climatically heterogeneous conditions was one third (~30%) higher than in climatically homogenous countries. There was also a strong relationship between the number of species and the number of published papers (R = 0.78; $p < 0.001$), thus confirming the 'rotiferologist' effect.

However, the results of the non-parametrical Mann–Whitney U test assessing differences in the species richness did not confirm significantly higher species richness in the tropical climate countries (U = 55, z = 0.802, $p = 0.422$) which was expected in ELH. We found higher species richness in countries with a tropical climate (average 194 taxa, and a median of 170, per country), and lower in the other countries with a different climate (141 average taxa and 152 median taxa/country).

4. Discussion

Recent efforts have been made to consolidate all known reports of rotifers in African waters to gain an understanding of their biogeography by Fresno et al. [9] and Smolak et al. [10]. These studies highlight the paucity of data for many countries and ecoregions. This investigation was an effort to uncover the diversity of rotifers of unknown, unexplored areas for two countries, Ghana and Angola, which represent geographically and climatically distinct regions. To the diversity of African rotifers, we contributed an additional 13 species, all of which were found in Ghana. Previously, the underlying patterns of species distribution in these countries were unexplored. Not surprisingly, we found that species richness was associated with conductivity, pH, and habitat type of reservoir. We also found that certain species assemblages were associated with geography, temperature, pH, and TDS. In our review, we found that rotifer species richness was positively correlated with the number of climate regions. Further, our analysis showed that species diversity in countries with homogenous, tropical, or subtropical climates was higher than in countries with dominant arid and semi-arid climates and that the highest diversity occurred in countries with heterogeneous climates. These results support the environmental heterogeneity hypothesis, while the ecological limits hypothesis was not confirmed.

Except for Russel's (1956) [19] research, no work has focused specifically on rotifer species distribution in Ghana and Angola. Previously, 49 rotifer taxa divided among 20 genera were reported for Ghana. Our findings confirmed the occurrence of 24 taxa (~20%) including 16 species and 8 genera. In the early study by Russel [19] on zooplankton in reservoirs associated with Pokoase and Tamale dams, 34 rotifer species were reported. In our work, we did not sample these reservoirs, but confirmed country records for 14 previously reported species. A prior study of Lake Bosumtwi published by Sanful et al. [14–16] yielded six species; we increased the number of taxa to 21. A few other studies reported rotifers at only the generic level. *Brachionus*, *Filinia*, *Keratella*, and *Trichocerca* were found in Volta Lake [11,12], and seven genera (i.e., *Anuraeopsis*, *Brachionus*, *Conochilus*, *Hexarthra*, *Philodina*, *Polyarthra*, *Trichocerca*) are reported from Barakese Lake [13]. These genera were also present in our survey. From the two rotifer species previously recorded in Angola

(*A. priodonta*, *B. falcatus*) by Kalous et al. [20], we confirmed the presence of *B. falcatus*; however, we found *A. brightwellii* and not *A. priodonta*.

We found several environmental parameters tied to species richness and community composition. Our GLM analysis showed that habitat type, temperature, and pH are all important in influencing richness at a site. Our analysis showed a positive association of richness and the habitat type of reservoir. It should be noted that Bui reservoir has adjacent intermittent pools that may have contributed to this relationship since it is well known that nearby temporary sites to larger water bodies may act as refugia, adding a significant contribution in richness to the surrounding lake [69,122–125]. These adjacent ponds are periodically disconnected and inundated from the major water bodies that supply them with biodiversity. Recolonization after inundation generally increases taxon richness [126] until the number of species in the pond resembles the regional species pool, or until the strength of local biotic interactions results in decreased establishment success for immigrants [122,127]. In our study, we can consider the adjacent pools or nearby small ponds as highly concentrated samples of the main water body in terms of rotifer species composition. The evidence of the positive effect of temperature on rotifer species richness in general has been recorded repeatedly (e.g., [48,128–131]). Richness and density can be also inversely correlated with water temperature and pH [132] as the result of the habitat type and environmental conditions which reflects in the certain community composition. Sharma's [132] results were for a wetland of the tropical, north-eastern part of India where environmental conditions and the rotifer fauna was characterized by notable richness of Lecanidae, Lepadellidae, Trichocercidae, Brachionidae, and had general 'tropical character' similar to the prevailing environmental conditions and results found in Ghana. Taxonomic specificity in response to temperature was also shown by the findings of Ejsmont-Karabin et al. [133], when *B. angularis*, *T. pusilla*, *P. sulcata*, and *K. cochlearis* show a clear negative correlation with summer temperature. *Filinia terminalis*, *B. calyciflorus*, *T. porcellus*, and two species of the genus *Polyarthra* do not react or react positively to temperature rise. Denys and De Smet [134] identified 22% of the observed taxa as useful pH indicators, most of them in non-alkaline waters. For instance, Denys and De Smet [134] reported that pH/alkalinity and trophic conditions explained most of the variation in rotifer assemblage composition. Although less important morpho-structural features of water bodies, their general setting and spatial context do not appear to be insignificant.

Our redundancy analysis (RDA) showed a separation along the axis of the rotifers known to inhabit the pelagic and littoral zones. The RDA clustered sites similarly to the rotifers (not shown), with mostly wetland and channel sites, which are expected to have well developed littoral zones, grouping together and the remaining lakes separating by TDS. The grouping of sites in the RDA is very similar to that found in our cluster analysis. Most *Trichocerca* associated with oligotrophic conditions occurred in the bottom left quadrant of the first two axes of the RDA, whereas most brachionids, typically associated with eutrophic conditions, were in the upper middle region of the graph. However, *K. tropica*, a common pelagic rotifer, was clustered near the *Trichocerca* which violates this pattern of oligotrophic/eutrophic separation. Based on Simpson's similarity cluster analysis of the species composition in Ghana, rotifer distribution appears to be influenced by geographical proximity to large lakes (Lake Bosumtwi (#1–18) and Bui reservoir (#25–30)) and by similar habitat type (three wetlands in close proximity (#10–18), and three intensively farmed fishponds (#19–21) in the city of Sunyani within the range of 5 km) which creates meta-communities. Species distribution cluster based on the spatial and trophic characteristics were also identified in lakes in North Island, New Zealand, by Duggan et al. [57,58].

Our results for the species richness comparison between littoral and pelagic zone showed that the littoral zone was in average inhabited by twice the number of species. In Lake Bosumtwi, we found 19 taxa in the LZ and 9 taxa in the PZ. Our results are in accordance with many investigations in that greatest diversity of rotifers occurs in the littoral region [28,29,124,125,135]. Similarly, Tasevska et al. [28,29] showed differences in species richness among the littoral and pelagic zones of Lake Ohrid and Lake Dojran, as well as among the lakes. Rarefaction curves for Lake Ohrid showed high species richness for the littoral compared to the pelagic zone. This is presumably due to the low productivity level and habitat homogeneity found in the pelagic zone and the habitat complexity of the littoral zone. These findings are supported by many studies reporting complex and diverse assemblages of rotifers in structurally more complex macrophyte beds in littoral zones as compared to the pelagic zone (e.g., [31,32,35,136–138]).

The rotifer community structure which varies from lake to lake can be used to indicate the real-time environmental health status. Several indices have been developed for this purpose based on the occurrence of particular taxa (e.g., *Brachionus* as an indicator of eutrophic conditions [139,140]) or the relative number of particular taxa (e.g., $Q_{B/T}$, *Brachionus*/*Trichocerca*; $Q_{B/L}$, *Brachionus*/*Lecane*). Others have posited that rotifer abundance [65,141] or density [142] is a more reliable indicator of trophic status. For instance, Pandit and Yousuf [138] stated that the rotifer community increases qualitatively as well as quantitatively from oligotrophy to mesotrophy then finally to eutrophy. This has been well documented for Loch Lomond, Great Britain, where rotifer abundance reflected the trophic gradient along the length of the loch [143]. Many other studies support this relationship between increasing rotifer density and biomass with increasing trophic state [28,29,135,144–147]. Generally, this is attributed to the high biomass of decomposed phytoplankton in eutrophic waters which results in elevated concentrations of detritus and bacteria that form important food sources for rotifers [148]. Using the trophic $Q_{B/T}$ index for productive water bodies in Ghana, we found that fishponds, wetlands, and standing water channels (SWCh) were deemed eutrophic. The $Q_{B/L}$ index value showed a high proportion of the genus *Lecane* species in the littoral zone with dense macrophytes coverage. Habitat was found to have a marked effect on the distribution of both the pelagic (highest in the open water areas) and littoral community. Furthermore, both fractions of the pelagic community, with respect to trophic state of water (eutrophic and mesotrophic communities), varied between the types of habitats.

Ghana is climatically homogenous where tropical climates dominate. Based on our sampling effort, we predicted that after more thorough sampling the species richness could approach ~190 rotifer taxa. Of its neighboring countries, only the Ivory Coast can be considered as well studied. In this climatically similar country, a similar number of taxa (170) has been reported in >20 studies. The rotifer community of its northern neighbor, Burkina Faso, with climatically mixed conditions (from the tropical savannah to the south, to the hot, arid desert to the north), is poorly studied (i.e., three surveys, total of 31 taxa). Its eastern neighbor, Togo, has yet to be surveyed for rotifers. In our previous study, per site alpha richness for the regions of Ghana sampled was between 8–9 species, similar to our average site richness of 10 species. The Ivory Coast was predicted to have a per site alpha richness of 12–15 species [10].

In Angola, there are nine climatic regions (from the tropical savannah to the hot, arid desert), with the highest proportions consisting of the tropical and subtropical regions. Since none of the climatic regions are dominant, we characterized this climate region as heterogeneous. Angola is bordered by two countries of the second group, "tropical" DR Congo and "subtropical" Zambia. In Zambia, a total of 126 rotifer taxa have been found in the 11 investigations published to date. For conservation issues and priority settings, nations with the highest species diversity on Earth (i.e., discovered and still undiscovered) have been selected and grouped together into 18 biologically megadiverse countries [149,150]. Two of these appear in Africa, Madagascar, and DR Congo [151]. Studies (n = 29) of rotifer diversity of DR Congo found 244 rotifer taxa (the fourth highest after Nigeria, Algeria, and South Africa) [9]. Angola shares its longest border (770 km) with DR Congo and has similar ecological conditions from the border to the south, which indicates high biodiversity; this is supported further by the diversified climatic regions in the country. Thus, our prediction for the climatically heterogeneous countries suggests ~200 rotifer taxa for Angola and high species richness of the neighboring DR Congo could indicate even higher diversity for this country. Smolak et al. [10] predicted rotifer richness in central Angola to be ~5–6 species per site, similar to of the 4.4 species per site found in this study. It should be noted that alpha richness is lower because it does not account for species turnover.

A large number of studies, covering a wide variety of ecosystems and organisms, suggest that species richness tends to vary strongly with ecosystem production and habitat heterogeneity [152]. Based on our findings and the comparison between ELH and EHH, we can confirm the environmental heterogeneity hypothesis, while the ecological limits hypothesis for rotifers was not confirmed. Thus, for the 27 African countries included, with land area of 13.8 mil. km^2, the highest rotifer species richness is in climatically heterogeneous areas followed by tropical regions. More rotifer taxa were found in regions with climatically heterogeneous conditions than those in a homogenous climate. Stein et al. [90] did not detect significant differences among taxa (invertebrates, vertebrates, and plants), suggesting that EHH is a universal driver of species richness across taxonomic groups. The similarity in correlates of plant and animal species richness has been pointed out before [153]. We found more rotifer taxa in the tropical part of Africa than in other climate regions, although this difference was not significant. The present results support the hypothesis of Segers et al. [154] indicating (sub)tropical floodplains to be the world's richest habitats for rotifers. The 'rotiferologist' effect must be considered in the presented findings, since a strong relationship between the number of species and the number of published papers has been confirmed statistically.

We identified several potential new species of rotifers including members of *Hexarthra* and *Macrochaetus*. In addition, many species of rotifers consist of cryptic species complexes, including several found in this study (e.g., *B. calyciflorus*, *E. dilatata*, and *P. patulus*). Additional genetic work on these species would allow better resolution of the rotifer diversity of Ghana and Angola. We also had many specimens that could not be identified to the species level due to poor preservation and inability to observe features seen only in live animals. Our study provides a first glimpse of the diversity of rotifers in these understudied countries, but additional sampling and especially in Angola is needed.

5. Conclusions

Africa continues to provide a fertile ground for understanding rotifer biogeography but remains incompletely surveyed. Our work on Ghana and Angola begins to fill the gaps in coverage of the continent. We recorded 118 rotifer taxa of which 100 (~85%) as new to this country and 14 of 15 (~93%) identified taxa new to Angola. To the diversity of African rotifers, we bring another 13 species (all found in Ghana). Rotifer species richness positively correlated with climate diversity (the number of climate regions); thus, future efforts should focus on understudied countries with heterogeneous climatic regions. Sampling efforts in countries with tropical climates such as Benin, Cameroon, Ivory Coast, DR Congo, Ghana, Nigeria, and Uganda should be prioritized to enable a better estimate of African rotifer species diversity and confirm biogeographic trends reported here. However, we can provisionally conclude that for a large portion of Africa, the highest rotifer species richness is in climatically heterogeneous areas followed by tropical regions. We can confirm the validity of the environmental heterogeneity hypothesis, while the ecological limits hypothesis for rotifers was not confirmed significantly. These hypotheses should be revisited after a more thorough survey of the rotifer diversity in Africa has been completed.

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Data Availability Statement: Source data for creating the map of location of the studied water bodies in (Figure 1) are available in Geofabrik (OpenStreetMap, ODbL 1.0) [155]. All other data are reported in the manuscript or in Fresno Lopez et al. [9] and in Beck et al. [118].

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