

Article

Rotifer Diversity in Botswana with an Analysis of Functional–Morphological Traits Along a Latitudinal Gradient in Africa and Europe

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Abstract

Afrotropical inland waters remain poorly studied for rotifer diversity. Here, we provide new distribution data from Botswana and connect these local patterns to continental-scale biogeography using an Africa–Europe occurrence dataset. In Botswana, we analyzed rotifer species richness, functional traits, and environmental drivers using 37 samples from 15 water bodies spanning natural and anthropogenic habitats. We recorded 107 rotifer taxa: 92 identified to species or subspecies level, 14 to genus, and one group of unidentified bdelloids. Seventy taxa (~65%) are new records for Botswana, and one species, *Donneria sudzukii*, is reported for the first time in Africa. Physicochemical gradients explained community structure, with the first two constrained RDA axes accounting for 40.7% and 23.7% of variation. Axis 1 captured a mineralization gradient linked to total dissolved solids and temperature, whereas Axis 2 reflected oxygen concentration and pH. Traits tracked these gradients: warmer, more mineralized waters were associated with specific trophi types, compact body shapes, and intermediate body sizes, whereas less mineralized, better oxygenated sites were related to smaller taxa and alternative feeding morphologies. To place these trait–environment relationships in a broader geographic context, we then analyzed an Africa–Europe dataset (67,170 records) to quantify latitudinal patterns in thermal classes and morphological traits (geometric body shape and trophi type). Diversity showed clear latitudinal structuring: warm-water genera clustered at low latitudes, only *Kellicottia* and *Didymodactylos* had mean distributions above 50° N, and bdelloid families were associated with higher latitudes. Morphological traits also varied with latitude, with trilateral truncated pyramid body shapes and malleoramate trophi occurring closest to the equator. Overall, by combining new species-level data from Botswana with continent-scale occurrence patterns, we link local community assembly to macroecological structure in rotifer functional and biogeographical organization.

Keywords: biodiversity; body shape; environmental parameters; geographic distribution; Rotifera; species richness; trophi type



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1. Introduction

1.1. Known Biogeography of Rotifers in Europe, Africa and Botswana

Rotifers are a diverse and ecologically important component of freshwater zooplankton, playing key roles in energy transfer, nutrient cycling, and trophic dynamics across a wide range of aquatic ecosystems [1–3]. Despite their global distribution and high adaptive capacity, large-scale patterns of rotifer diversity and biogeography remain unevenly documented, with substantial biases in sampling effort and taxonomic knowledge [2,4,5]. One notable bias is the “rotiferologist” effect [4], i.e., reported distributions may reflect where rotifer scientists work more than where rotifers occur [6–8]. Because early research on rotifer distribution concentrated on Europe, the Palearctic (PAL) region is comparatively well documented. The World Rotifer Catalog lists 1688 valid taxa for the region [7]. The most recent checklist (based on an unpublished dataset updated in November 2025) for Africa and nearby islands comprised 905 valid taxa: 902 identified to species or subspecies level, and three taxa (*Balatro*, *Drilophaga*, *Wigrella*) identified to genus level. Thus, African rotifer diversity is ~53.7% of that in the PAL region. The African countries with the highest numbers of reported taxa and records are Nigeria, Algeria, South Africa, the Democratic Republic of Congo, and Egypt [9]. Despite the presence of numerous inland waters, the rotifer fauna of Botswana remains poorly documented. Existing information is largely restricted to general limnological or zooplankton studies from northern and northeastern Botswana, especially the Okavango Delta [10–14]. Additional data come from studies of zooplankton assemblages in the Makgadikgadi salt pans and temporary pools near the lower Nata River [11]. Collectively, these studies report 59 rotifer species in 27 genera, which is substantially lower than expected given Botswana’s wide range of aquatic habitats and environmental conditions. Thus, there is a need to improve our understanding of geographic patterns across scales, from local to regional and ultimately global.

1.2. Environmental Gradients and Functional–Morphological Traits in Botswana

The ability of rotifers to respond rapidly to environmental change has led to their use as indicators of ecological status and water quality in continental waters [1,2,15–17]. Trait-based approaches complement taxonomic analyses by providing mechanistic explanations for community turnover along environmental gradients [18–22]. Key rotifer traits include trophi type (jaws), body size, and body shape, which jointly constrain resource acquisition, physiological tolerance, and trophic interactions [23–25]. Environmental gradients in semi-arid flood-pulsed systems, such as those characterizing inland waters of Botswana, are often dominated by variation in conductivity, oxygen availability, and pH driven by evaporation-concentration processes and flood dilution [26–28]. These gradients are known to strongly structure zooplankton assemblages, including rotifers [2,15,29].

1.3. Biogeographical Thermal Classes Along a Latitudinal Gradient in Africa and Europe

Latitude is a first-order geographic proxy integrating long-term thermal regime, photoperiod, and seasonality, and is often used to interpret distribution patterns and community turnover in freshwater biota [30–32]. Latitudinal gradients are commonly interpreted through climatic filtering and thermal niche breadth [33]. For instance, Janzen’s hypothesis predicts narrower thermal tolerances in the tropics due to weak seasonality, whereas stronger seasonality at higher latitudes should select for broader tolerances (eurythermy) and facilitate wider geographic ranges [34,35]. Comparative analyses indicate that cold limits are often constrained by physiological tolerance, while warm limits can reflect both physiology and biotic interactions [36]. For rotifers, temperature is recognized as a major determinant of population growth, phenology, and seasonal succession, yet it is typically treated as a species-specific thermal optimum rather than as a strict binary of stenothermy

versus eurythermy. Many rotifer species are eurythermal because they persist in shallow, small water bodies with rapid, large daily temperature fluctuations [37,38]. Nevertheless, clear interspecific differences exist: some taxa tolerate wide temperature ranges but peak in warm periods while others peak under cold conditions and decline during summer warming [17,18].

Building on these foundations, it is useful to subdivide eurythermal taxa by warm-versus cold-water preference. Warm-water-preferring eurytherms tolerate low temperatures but achieve high fitness at elevated temperatures, often producing summer maxima and persisting via dormant stages [17,18,39–41]. Cold-water-preferring eurytherms tolerate moderate warming yet retain low thermal optima (often ~4–12 °C), show early-spring or cold-season dominance, and can collapse when temperatures exceed ~20 °C [18,42]. For example, *Brachionus calyciflorus* Pallas, 1766 peaks under warm conditions, with field maxima at ~20–28 °C [43] and culture optima around 30 °C [44], whereas the cold-associated *Notholca squamula* (Müller, 1786) is rarely recorded above ~10 °C [42]. Other warm-water-preferring eurytherms include *Keratella tropica* (Apstein, 1907) and *Asplanchna priodonta* Gosse, 1850, whereas cold-water-preferring eurytherms include *Synchaeta pectinata* Ehrenberg, 1832 and *Filinia terminalis* (Plate, 1886) [17,18,42,45,46].

Here, we extend an occurrence-based latitudinal framework for Africa–Europe rotifers by refining the previous three-class scheme—warm water (WW), eurythermic (ERT), and cold water (CW)—into two additional eurythermic preference classes: warm-water-preferring eurytherms (WWP ERT) and cold-water-preferring eurytherms (CWP ERT). We quantify the distribution of rotifer genera and families using mean latitude, and classify taxa using thresholds based on the astronomical definition of the tropics (23.5°) and the widely used temperate–boreal transition around ~50° [47–50]. By explicitly distinguishing warm- versus cold-water-preferring eurytherms, we aim to improve ecological characterization of latitudinal trends and to provide a thermal labelling scheme that can be extended to species-level analyses and trait-based hypotheses [51,52].

1.4. Functional–Morphological Traits Along a Latitudinal Gradient in Africa and Europe

Two trait complexes are especially informative at large scales: (i) geometric body shape (including lorica and defensive structures) and (ii) trophi (jaw) morphology. Trophi type reflects feeding mode (microphagy vs. raptory vs. scraping), trophic position, and prey size spectrum, and is among the most diagnostic functional traits in rotifers [17,39,40,53,54]. Because both trait groups mediate how taxa exploit habitat structure and food resources, they are expected to show non-random geographic patterns, including latitudinal tendencies that reflect the combined effects of temperature, seasonality, resource regimes, and predator assemblages [18,30,51,55–57]. Macroecological and limnological studies show that rotifer richness and phenology are structured by broad-scale climate, temperature, and seasonality [4,58–61]. Functional approaches further indicate that habitat and trophic structure select for trait syndromes—sets of correlated traits related to feeding and defense—rather than independent traits [62–68]. For example, a pelagic microphagous syndrome often combines streamlined/compact body shape with malleate trophi and small-to-medium body size [67,69,70], whereas a benthic/periphytic syndrome combines flattened/elongate forms with substrate-associated feeding (scraping/browsing), including bdelloids with ramate trophi typical of biofilm/periphyton habitats [67,71,72]. However, explicit tests linking latitude to rotifer morphological categories across continental scales remain relatively scarce, partly due to inconsistent trait definitions and the difficulty of trait assignment in big-data contexts. Recent efforts to standardize trait matrices and terminology (including trophi and defensive traits) have improved the feasibility of trait-based macroecology in rotifers [68,73].

Geometric body shape influences locomotion, stability, and habitat use. Streamlined and elongated shapes are frequently associated with pelagic taxa that persist in open water where drag reduction and stability can be advantageous [2,53,55,74–77]. Flattened or asymmetrical forms are more typical of benthic and periphytic taxa that move among sediments, detritus, and macrophyte surfaces [16,53,54]. Lorica development, spines, and other defensive morphologies can reduce vulnerability to invertebrate predators by increasing handling time or preventing ingestion; these defenses can be fixed or inducible [2,45,69,70,78–80]. Predator-induced morphological defenses are well documented in several *Keratella* and *Brachionus* taxa and illustrate how morphology is coupled to trophic context and predation regime [69,78–80].

Trophi morphology is strongly linked to diet in rotifers. Malleate trophi typify microphagous planktonic filter feeders, while virgate and forcipate/uncinate forms are associated with raptorial or omnivorous feeding modes [39,40,53,54]. Malleoramate types often represent trophic generalists, and ramate trophi in bdelloids are adapted for scraping and grinding biofilms and detrital surfaces [17,53,54]. Thus, trophi types can be interpreted as a functional axis spanning pelagic microphagy to raptory to benthic scraping, and are expected to covary with resource regimes and habitat structure that also vary with latitude and climatic zone [18,51,55–57,79,81].

Despite a growing number of trait-based studies, a key gap remains—linking local-scale trait–environmental filtering that informs community structure to continental-scale biogeographical patterns. Here, we bridge this gap by (1) quantifying rotifer species richness and community composition in inland water bodies of southern Botswana, an unstudied region for rotifers within the Afrotropical region, thereby contributing new baseline data on local diversity; (2) evaluating how environmental gradients and functional–morphological traits structure rotifer assemblages at the local scale in Botswana; (3) assessing the latitudinal distribution of biogeographical thermal classes of rotifer families and genera along a combined Africa–Europe gradient, placing regional African patterns into a broader continental context; and (4) testing whether functional–morphological trait categories exhibit statistically detectable latitudinal differentiation across Africa and Europe.

2. Materials and Methods

2.1. Study Area in Botswana

The sampled sites are in two administrative districts: the South-east District with the capital city Gaborone and the Kgatleng District (Figure 1). Both are in the south of the country, bordering South Africa. All sampled sites lie in an arid, cold steppe climate and occur at similar elevations, spanning 863–1017 m a.s.l. (range: 154 m).

We collected 37 samples from 15 water bodies in southeastern Botswana in 2022 (see Table 1 for site details and in situ parameters). A broad gradient of aquatic habitats (artificial pool, fishpond, pond, quarry pond, reservoir, river, rock pool, wetlands) differing in origin, size, hydrological regime, and degree of anthropogenic influence were included. Locality #1 is a small semi-permanent wetland pool (~5 × 5 m) with shallow standing water and dense emergent vegetation (*Typha*). Locality #2 is a large, permanent, eutrophied artificial pond (~60 m Ø). Locality #3 is a shallow lowland river section with slow flow and muddy substratum. Locality #4 is a shallow reservoir littoral zone with standing water and well-developed emergent vegetation. Localities #5 and #6 are small, shallow artificial pools (5 × 5 m and ~4 m Ø) with standing water and dense vegetation; #5 was almost completely covered by filamentous algae (*Vaucheria*), whereas #6 was dominated by *Chara*. Locality #7 is a large reservoir; samples were collected in deep standing water with floating macrophytes. Locality #8 is an extensive shallow wetland (~100 × 50 m) with emergent macrophytes and surrounding urban influence. Locality #9 is a very small

temporary rock pool ($\sim 2 \times 1$ m; ~ 10 cm depth) with partial *Lemna* cover ($\sim 10\%$). Locality #10 is a large shallow wetland–pond complex ($\sim 100 \times 50$ m) with $\sim 90\%$ surface covered by aquatic vegetation (eutrophic conditions). Locality #11 is a natural wetland (~ 400 m $\varnothing$) with standing water and abundant floating/emergent macrophytes, whereas Locality #12 is a permanent, artificial pond ($\sim 60 \times 100$ m) with a narrow *Typha* belt; samples from #11 and #12 were taken from the shore at sites lacking developed littoral vegetation. Locality #13 is an artificial pond ($\sim 300 \times 50$ m) with a continuous *Typha* margin and moderate eutrophication. Locality #14 is a managed, permanent fishpond ($\sim 60 \times 40$ m) with muddy substrate, high turbidity, and sparse macrophytes. Locality #15 is an artificial quarry pond with clear standing water, steep margins, and poorly developed littoral vegetation.

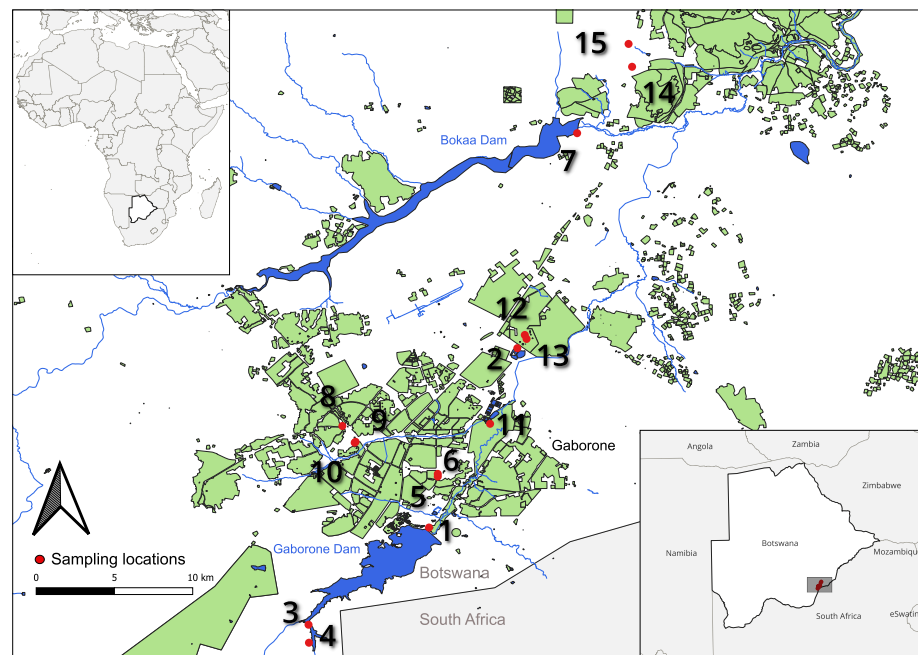


Figure 1. Locations of water bodies surveyed for Rotifera in Botswana. Numbers shown on the main map correspond to locality numbers (L#) in Table 1. The inset provides the country-scale orientation of the sampling area within Botswana. The map was produced in QGIS 3.30 [82].

2.2. Field Sampling in Botswana and Laboratory Identification

Water samples were collected in March 2022 from the shoreline with a plankton net (25 cm $\varnothing$, 25 μ m mesh) on a 0.5 m handle. Samples and water chemistry were taken from the surface (10–30 cm depth). At each water body, we collected one composite shoreline sample using ≥ 10 plankton tows (30 s) and preserved it immediately in 96% ethanol. When the net clogged (e.g., high turbidity/filamentous algae) or the concentrate volume was large, material from the same collection was split into multiple bottles (see Table 1, multiple S# per locality). Geometric body shape and trophi-type categories were assigned at the species, genus, or family level depending on data availability in the literature (see Supplementary Files S2 and S3, respectively). Body size was categorized into three classes following previously used size-class schemes, e.g., [83]. All environmental parameters listed in Table 1 were measured in situ using a WTW Multi 340i probe (WTW Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). 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 [22,84–87] and other keys [54,88]; immediate preservation precluded species-level identification in some cases (e.g., bdelloids and taxa requiring live characters). Taxonomic validity was verified using the List of Available Names in Zoology, Candidate Part Phylum Rotifera (LAN) [89].

Table 1. List of sampled water bodies and environmental variables. Localities ordered as in Figure 1. Multiple S# per locality denote subsamples from a single ≥ 10 -tow collection. All samples were collected in March 2022, in the afternoon (12:40–17:20). Abbreviations: S# = sample number; L# = locality number; T = temperature; Cond. = conductivity; Sal. = salinity; m a.s.l., meters above sea level. Habitat type codes: AP = artificial pool; FP = fishpond; QP = quarry pond; P = pond; Re = reservoir; Ri = river; RP = rock pool; W = wetland.

S#	L#	Locality Name	Date	Habitat	T (°C)	O ₂ (mg L ⁻¹)	O ₂ (%)	pH	Cond. (μS cm ⁻¹)	TDS (mg L ⁻¹)	Sal. (ppm)	Altitude (m a.s.l.)	Latitude	Longitude
1	1	Gaborone Dam pond	3–March	W	27.8	3.83	45.7	7.45	344	172	111	980	24°41′44″ S	25°55′28″ E
2, 3	2	Phakalane lagoons	3–March	P	29.8	3.87	46.3	8.41	938	679	377	863	24°34′56″ S	25°58′49″ E
4	3	Ngotwane (Taung river)	4–March	Ri	27.9	5.36	72.4	8.71	266	183	130	1011	24°45′25″ S	25°50′54″ E
5	4	Ngotwane (Crocodile pools)	4–March	Re	27.5	4.33	46.8	8.09	285	207	127	1001	24°46′06″ S	25°50′55″ E
7, 8	5	University of Botswana #1	7–March	AP	29.3	9.84	142.8	9.23	377	271	173	991	24°39′48″ S	25°55′48″ E
6, 9, 10	6	University of Botswana #2	9–March	AP	22.5	1.63	18.8	7.74	363	255	174	985	24°39′42″ S	25°55′48″ E
11–14	7	Bokaa Dam	10–March	Re	28.8	11.43	157.4	9.05	224	156	101	955	24°26′47″ S	26°01′05″ E
15–16	8	Mogoditshane wetland	11–March	W	27.4	8.53	107.5	7.95	335	232	149	1017	24°37′53″ S	25°52′11″ E
17, 18, 22	9	Grand Palm Hotel #1	11–March	RP	31.2	3.36	42.1	7.85	41	29	18	1011	24°38′29″ S	25°52′41″ E
19–21	10	Grand Palm Hotel #2	11–March	W	27.7	1.77	24.7	6.77	282	196	131	1011	24°38′31″ S	25°52′39″ E
23–25	11	Gaborone Game Reserve	12–March	W	30.4	4.54	71.5	7.91	307	205	134	981	24°37′48″ S	25°57′47″ E
26–28	12	Phakalane Golf Course #1	16–March	P	25.0	5.33	72.3	9.01	842	590	408	986	24°34′26″ S	25°59′06″ E
29–31	13	Phakalane Golf Course #2	16–March	P	24.1	3.93	25.3	8.32	935	655	453	987	24°34′35″ S	25°59′10″ E
32–33	14	Kgatleng District #1	18–March	FP	23.6	2.68	29.5	7.98	918	646	37	975	24°24′16″ S	26°03′10″ E
34–37	15	Kgatleng District #2	18–March	QP	23.5	4.82	42.3	8.48	1121	784	548	974	24°23′24″ S	26°03′02″ E

2.3. Linking Environmental Gradients with Rotifer Functional Traits: In Botswana (RDA)

Redundancy analysis (RDA) was conducted on Hellinger-transformed presence–absence data for 107 rotifer taxa sampled from 15 inland water bodies. RDA and permutation tests ($n = 4999$) were conducted in R v4.5.2 [90] using vegan package version 2.7-2 [91]. For the RDA, the environmental predictors retained after collinearity screening were water temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}), pH, total dissolved solids (TDS, mg L^{-1}), and altitude (m a.s.l.); all were standardized (z-scores) before analysis. Conductivity and salinity were excluded due to collinearity with TDS, and oxygen saturation (%) due to collinearity with dissolved oxygen (mg L^{-1}).

Functional traits (geometric body shape, body size class, trophi type) were not used as constraining variables but were projected passively as centroids to facilitate ecological interpretation of the ordination space, with environmental vectors and trait centroids interpreted using biplot scores. Trait centroids represent the mean ordination position of taxa sharing a trait category and are shown for interpretation only. Geometric body shape categories and trophi types are defined in Supplementary Files S2 and S3, respectively, while body size was treated as a categorical functional trait with three classes (small $< 200\ \mu\text{m}$, medium $200\text{--}400\ \mu\text{m}$, large $> 400\ \mu\text{m}$), following established size-based classifications in rotifer ecology that capture broad ecological differences rather than strict morphometric thresholds [1,68,81,83,92,93]. For taxa with polymorphic defensive morphologies (e.g., spine length variation), we coded traits according to the standard adult morphology used in taxonomic treatments and trait matrices; inducible variants were not separated unless explicitly recorded as distinct morphs in the occurrence/source data. Trophi type was coded for each species; taxa with uncertain or variable assignments were coded as ‘unknown’ and excluded from trait-level tests.

2.4. Construction and Optimization of Source Datasets for Africa and Europe

Data on rotifer occurrences in Europe were obtained from GBIF [94]. The raw, publicly available European dataset contained 153,507 records. The dataset of African rotifer distribution records was compiled from a continuously updated proprietary database, which on 2 December 2025 contained 29,520 records derived from 878 scientific publications. These two datasets were merged into a single dataset for the assessment of the latitudinal distribution of rotifers. The combined dataset underwent rigorous quality control and validation. First, all GPS coordinates were converted to a numeric format; records in which GPS coordinates remained in a date format were removed, as were records with missing coordinate values. Records with erroneous GPS coordinates (predominantly outside the defined study area) were removed. Records with non-specific values in the scientificName field (e.g., BOLD: AAA2193, BOLD: AEL4926) were excluded. Duplicate records were removed, retaining only the first occurrence. Finally, taxonomic validation was performed using custom Python scripts (version 3.12) [95] to validate all scientific names in the dataset. Taxonomic information was retrieved from the Rotifer World Catalog (RWC) [7], which operates on the WoRMS/Aphia infrastructure [96]. Queries were performed via the official Aphia REST web service [96]. Validation of all 1588 unique taxonomic names yielded the following results: Accepted species: 1064; Unaccepted names (synonyms): 80; Species/taxa inquirenda: 29; other status categories: 86; No Aphia/RWC match: 402. All unaccepted names (synonyms) were converted to their corresponding accepted names. All names not falling under the category of accepted taxa were removed from the dataset.

As a result of this stringent validation process, 115,857 erroneous or problematic records were excluded. Consequently, the original total of 183,027 records was reduced to 67,170 validated records. Because the analyses were based on a large dataset, which initially comprised ~1.3 million individual cells requiring sorting, validation, and consis-

tency checks, data processing and spatial analyses of rotifer distribution were performed using Python [95], with the pandas library (version 2.3.3) [97] for data manipulation and Matplotlib (version 3.10.1) [98] for data visualization. For analyses of the latitudinal distribution of biogeographical thermal classes of rotifer families, only families represented by ≥ 100 records were included. For analyses at the genus level, only genera represented by ≥ 50 records were considered. This thresholding was applied to exclude poorly represented families or genera. Definitions and taxon-level assignments of biogeographical thermal classes are provided in Tables S1–S3 (Supplementary File S1).

2.5. Biogeographical Thermal Classes Along a Latitudinal Gradient in Africa and Europe

For each taxon (family or genus), mean ($\bar{x}$) latitude was calculated as the arithmetic mean of decimal latitude across all validated records. Variability was expressed as the standard deviation (SD), and uncertainty in the mean was quantified using a parametric 95% confidence interval (CI):

$$CI\ 95\% = \bar{x} \pm 1.96 \times \frac{SD}{\sqrt{n}}$$

where n is the number of records. Because thermal affinity is conceptualized here as association with broad climatic zones rather than hemisphere-specific direction, the absolute value of mean latitude ($|\text{mean}|$) was used for thermal-class assignment. We use genus- and family-level mean latitudinal centroids as an operational summary of realized distributions in the occurrence dataset. Although ecological variability exists within higher taxa, centroids (with 95% CI) provide a transparent, reproducible descriptor of the dominant latitudinal tendency; taxa with broad or bimodal distributions are reflected by wider SD/CI rather than by a forced narrow assignment.

To provide reproducible definitions, taxa were assigned to five operational thermal classes based on $|\text{mean latitude}|$. The first and last classes represent warm-water and cold-water centroids, respectively, while the intermediate classes partition eurytherms into warm-water-preferring, neutral, and cold-water-preferring groups: (1) WW (warm water), $|\text{mean}| \leq 23.5^\circ$ (astronomical tropics); (2) WWP ERT (warm-water-preferring eurytherms), $23.5^\circ < |\text{mean}| \leq 30^\circ$; (3) ERT (eurytherms), $30^\circ < |\text{mean}| \leq 45^\circ$; (4) CWP ERT (cold-water-preferring eurytherms), $45^\circ < |\text{mean}| \leq 50^\circ$; and (5) CW (cold water), $|\text{mean}| > 50^\circ$. The 23.5° boundary reflects the tropical-to-extratropical transition in insolation and seasonality [34]. The 50° boundary approximates the temperate–boreal transition in Eurasia [47–50]. The intermediate breaks (30° and 45°) are introduced to identify eurythermal taxa with clear preference toward warm versus cold regimes, consistent with classic rotifer temperature-occurrence syntheses [17,18] and with theory on plasticity constrained by evolutionary preference [99,100]. To assess robustness, we performed a sensitivity analysis by shifting each threshold by $\pm 2^\circ$ and reassigning taxa based on $|\text{mean latitude}|$. Class membership was largely stable; any changes were limited to taxa whose mean latitude lay close to a boundary and did not alter the qualitative latitudinal patterns reported.

2.6. Functional–Morphological Traits Along a Latitudinal Gradient in Africa and Europe

Geometric body shapes and trophi types were assigned using standardized trait categories derived from published works [17,39,40,53,54]. Trait codes were treated as categorical predictors; mapping between codes and descriptive labels was taken from the dataset legend sheet. Latitudinal statistics were calculated at the level of individual occurrence records (taxon $\times$ site), rather than at the taxon level. Each record represents a documented occurrence of a given taxon at a specific geographic location with an associated latitude and assigned trait category. Consequently, mean and median latitudes for

each morphological or trophi category reflect the realized geographic distribution of all occurrences belonging to that category, rather than averages of species-level centroids. This occurrence-based approach preserves information on the full spatial extent and frequency of records, avoids biases arising from unequal sampling effort and range size differences among taxa, and is widely used in analyses of diversity and trait–environment relationships [49,101,102]. The list of body shape codes and categories, including their assignments to specific taxonomic ranks, is provided in Supplementary File S2, and the classification of trophi types is summarized in Supplementary File S3.

To test for differences in latitude among categorical trait classes, we used the Kruskal–Wallis test because latitude distributions were non-normal and sample sizes varied among categories. Effect size was quantified using epsilon-squared (ϵ^2), which estimates the proportion of rank variance attributable to group differences. Pairwise differences were assessed using Dunn’s *post hoc* tests with the Holm correction for multiple comparisons. Given the very large occurrence dataset, extremely small *p*-values are reported as *p* < 0.001 to avoid spurious precision.

3. Results

3.1. Species Richness in Botswana

From 37 Botswana samples, we identified 22 rotifer families (2 Bdelloidea, 20 Monogononta) and five orders (Collothecaceae, Flosculariacea, Philodinida, Philodinavida, and Ploima), comprising 36 genera and 107 taxa (92 identified to species/subspecies, 14 to genus, and one group of unidentified bdelloids).

The most widespread and diverse genus was *Lecane*, occurring in 31 of the 37 samples and in 13 of the 15 water bodies (~87%), represented by 16 species. *Lecane bulla* (Gosse, 1851) was the most frequent species (25 samples; ~68%), and the genus *Brachionus* was recorded in the same number of samples (25; ~68%). *Brachionus* comprised 10 species and occurred in 12 of 15 water bodies (80%); *B. quadridentatus* (Hermann, 1783) occurred in 11 samples (~30%). Other frequent species were *Platyonus patulus* (14 samples), *Euchlanis dilatata* (13), *L. luna* (13), and *Keratella tropica* (12). In total, 29 species (~32% of species richness) occurred in only one or two samples, indicating a strongly right-skewed occurrence distribution. Unidentified bdelloids occurred in ~76% of samples. Species richness was highest in two wetlands (L#10, 39 taxa; L#8, 38 taxa), whereas the lowest richness was recorded in two small concrete pools (L#5, 7 taxa; L#6, 6 taxa), where lecanids and lepadellids dominated (L# denotes locality number in Table 1). Comparison with the continental African rotifer dataset identified nine rare species (≤ 3 African records prior to this study). Four species (*Cephalodella hollowdayi* Koste, 1986; *C. sterea* (Gosse, 1887); *Proalinopsis caudata* (Collins, 1872); and *Wulfertia kivuensis* De Smet, 1992) were previously known from a single African record, and five (*C. boettgeri* Koste, 1988; *Dicranophoroides claviger* (Hauer, 1965); *L. abanica* Segers, 1994; *Lophocharis gracilis* Dvořáková, 1960; and *Notommata cerberus* (Gosse, 1886)) from three records. These represent new country-level records. Overall, 69 of 107 taxa (~65%) are new to Botswana (Table 2). *Donneria sudzukii* (Donner, 1968) represents the first record for Africa; it was collected in the Bokaa Dam reservoir and extends the most recent African rotifer checklist [8].

Table 2. Rotifer taxa found in aquatic habitats surveyed in Botswana (2022). T# = taxon number, see Figure 2A. Species record codes: A = new record for Africa; B = new record for Botswana.

T#	Taxon	New Record	Sites Found	Occurrence [%]
	Asplanchnidae			
1	<i>Asplanchna brightwellii</i> Gosse, 1850		2, 12, 13, 15	26.7
2	<i>Asplanchna sieboldii</i> (Leydig, 1854)		2	6.7
	Bdelloidea			
3	bdelloid (unidentified)		1–10, 12, 13, 15	86.7
	Brachionidae			
4	<i>Anuraeopsis</i> sp.	B	13	6.7
5	<i>Brachionus angularis</i> Gosse, 1851		2, 11–13	26.7
6	<i>Brachionus bidentatus</i> Anderson, 1889	B	11, 12	13.3
7	<i>Brachionus budapestinensis</i> Daday, 1885		2, 12, 13	20
8	<i>Brachionus calyciflorus</i> Pallas, 1766		2, 8, 12–14	33.3
9	<i>Brachionus caudatus</i> Barrois & Daday, 1894		3, 4, 13	20
10	<i>Brachionus dimidiatus</i> Bryce, 1931	B	13	6.7
11	<i>Brachionus diversicornis</i> (Daday, 1883)	B	10	6.7
12	<i>Brachionus falcatus</i> Zacharias, 1898		3, 4, 7, 15	26.7
13	<i>Brachionus quadridentatus</i> Hermann, 1783		7–11, 14	40
14	<i>Brachionus urceolaris</i> Müller, 1773	B	2, 3, 4, 11, 12	33.3
15	<i>Keratella cochlearis</i> (Gosse, 1851)	B	3, 4, 7, 15	26.7
16	<i>Keratella tecta</i> (Gosse, 1851)		3, 4, 7	20
17	<i>Keratella tropica</i> (Apstein, 1907)		3, 4, 6, 7, 9, 14, 15	46.7
18	<i>Plationus patulus</i> (Müller, 1786)		1, 2, 8–10, 12, 14, 15	53.3
	Dicranophoridae			
19	<i>Dicranophoroides caudatus</i> (Ehrenberg, 1834)	B	1, 10	13.3
20	<i>Dicranophoroides claviger</i> (Hauer, 1965)	B	8, 10	13.3
21	<i>Dicranophorus epicharis</i> Harring & Myers, 1928	B	3, 4, 7, 14	26.7
22	<i>Dicranophorus forcipatus</i> (Müller, 1786)	B	3	6.7
23	<i>Encentrum</i> sp.	B	9	6.7
	Epiphanidae			
24	<i>Epiphanes brachionus</i> (Ehrenberg, 1837)	B	8–11	26.7
25	<i>Epiphanes clavulata</i> (Ehrenberg, 1831)	B	2, 8, 10, 13, 15	33.3
26	<i>Epiphanes macroura</i> (Barrois & Daday, 1894)		2, 13	13.3
27	<i>Epiphanes senta</i> (Müller, 1773)		9, 10, 13	20
	Euchlanidae			
28	<i>Dipleuchlanis propatula</i> (Gosse, 1886)	B	8, 10, 11, 14, 15	33.3
29	<i>Euchlanis dilatata</i> Ehrenberg, 1830		4, 7, 8, 14, 15	33.3
30	<i>Euchlanis</i> sp.		7, 15	13.3
31	<i>Tripleuchlanis plicata</i> (Levander, 1894)	B	15	6.7
	Filinidae			
32	<i>Filinia longiseta</i> (Ehrenberg, 1834)		7, 8, 13	20
33	<i>Filinia novaezealandiae</i> Shiel & Sanoamuang, 1993	B	8, 10	13.3
34	<i>Filinia opoliensis</i> (Zacharias, 1898)		3, 4, 7	20
35	<i>Filinia passa</i> (Müller, 1786)	B	10	6.7
36	<i>Filinia terminalis</i> (Plate, 1886)	B	2, 10	13.3
37	<i>Filinia</i> sp.		12	6.7
	Floscularidae			
38	<i>Limnias</i> sp. Schrank, 1803 (tube)	B	3	6.7
39	<i>Sinantherina aripipes</i> Edmondson, 1939	B	4, 15	13.3
40	<i>Sinantherina semibullata</i> (Thorpe, 1889)	B	8	6.7
41	<i>Sinantherina</i> sp. (colony)		5, 13	13.3
	Hexarthridae			
42	<i>Hexarthra fennica</i> (Levander, 1892)	B	9	6.7
43	<i>Hexarthra intermedia</i> (Wiszniewski, 1929)	B	12, 13	13.3
44	<i>Hexarthra jenkiniae</i> (de Beauchamp, 1932)	B	12	6.7
45	<i>Hexarthra</i> sp.		9, 15	13.3

Table 2. Cont.

T#	Taxon	New Record	Sites Found	Occurrence [%]
Lecanidae				
46	<i>Lecane abanica</i> Segers, 1994	B	8, 9	13.3
47	<i>Lecane agilis</i> (Bryce, 1892)	B	7	6.7
48	<i>Lecane bulla</i> (Gosse, 1851)		1–10, 14, 15	80
49	<i>Lecane clostercerca</i> (Schmarda, 1859)	B	8	6.7
50	<i>Lecane curvicornis</i> (Murray, 1913)		5, 7–10, 14, 15	46.7
51	<i>Lecane elsa</i> Hauer, 1931	B	8, 10	13.3
52	<i>Lecane furcata</i> (Murray, 1913)		8	6.7
53	<i>Lecane hamata</i> (Stokes, 1896)	B	6–10, 13, 15	46.7
54	<i>Lecane leontina</i> (Turner, 1892)		15	6.7
55	<i>Lecane luna</i> (Müller, 1776)		6, 7, 10, 14, 15	33.3
56	<i>Lecane lunaris</i> (Ehrenberg, 1832)		14	6.7
57	<i>Lecane nana</i> (Murray, 1913)	B	7	6.7
58	<i>Lecane papuana</i> (Murray, 1913)		3, 7–11, 14	46.7
59	<i>Lecane punctata</i> (Murray, 1913)	B	14	6.7
60	<i>Lecane pusilla</i> Haring, 1914	B	8	6.7
61	<i>Lecane unguata</i> (Gosse, 1887)	B	7, 10	13.3
62	<i>Lecane</i> sp.		7, 8	13.3
Lepadellidae				
63	<i>Colurella adriatica</i> Ehrenberg, 1831	B	1, 8, 14, 15	26.7
64	<i>Colurella colurus</i> (Ehrenberg, 1830)	B	5, 8, 10	20
65	<i>Colurella obtusa</i> (Gosse, 1886)	B	8, 10	13.3
66	<i>Colurella uncinata bicuspidata</i> (Ehrenberg, 1832)	B	8	6.7
67	<i>Lepadella latusinus</i> (Hilgendorf, 1899)	B	15	6.7
68	<i>Lepadella ovalis</i> (Müller, 1786)	B	6, 15	13.3
69	<i>Lepadella patella</i> (Müller, 1773)	B	5, 7, 8, 10, 12, 14	40
70	<i>Lepadella rhomboides</i> (Gosse, 1886)		10	6.7
71	<i>Lophocharis gracilis</i> Dvořáková, 1960	B	7	6.7
Mytilinidae				
72	<i>Mytilina acanthophora</i> Hauer, 1938	B	10	6.7
73	<i>Mytilina ventralis</i> (Ehrenberg, 1830)	B	3, 7, 8, 11, 14, 15	40
Notommatidae				
74	<i>Cephalodella boettgeri</i> Koste, 1988	B	5	6.7
75	<i>Cephalodella catellina</i> (Müller, 1786)	B	8	6.7
76	<i>Cephalodella forficula</i> (Ehrenberg, 1838)	B	1, 7	13.3
77	<i>Cephalodella gibba</i> (Ehrenberg, 1830)	B	10	6.7
78	<i>Cephalodella hollowdayi</i> Koste, 1986	B	1, 10	13.3
79	<i>Cephalodella sterea</i> (Gosse, 1887)	B	8	6.7
80	<i>Cephalodella</i> sp. Bory de St. Vincent, 1826	B	8, 10	13.3
81	<i>Donneria sudzukii</i> (Donner, 1968)	A, B	7	6.7
82	<i>Eosphora anthadis</i> Haring & Myers, 1922	B	1	6.7
83	<i>Notommata cerberus</i> (Gosse, 1886)	B	15	6.7
84	<i>Notommata</i> sp.		15	6.7
Philodinavidae				
85	<i>Philodinavus paradoxus</i> (Murray, 1905)	B	10	6.7
Philodinidae				
86	<i>Philodina citrina</i> Ehrenberg, 1830	B	10	6.7
87	<i>Philodina</i> sp.	B	9	6.7
88	<i>Rotaria neptunia</i> (Ehrenberg, 1830)		1, 3, 7–9	33.3
89	<i>Rotaria rotatoria</i> (Pallas, 1766)	B	10, 12	13.3
90	<i>Rotaria tardigrada</i> (Ehrenberg, 1830)	B	8, 9	13.3
91	<i>Rotaria</i> sp.		3, 8, 10	20
Proalidae				
92	<i>Proalinopsis caudata</i> (Collins, 1872)	B	9	6.7

Table 2. Cont.

T#	Taxon	New Record	Sites Found	Occurrence [%]
	Scaridiidae			
93	<i>Scaridium longicaudum</i> (Müller, 1786)	B	7, 10, 15	20
	Synchaetidae			
94	<i>Polyarthra dolichoptera</i> Idelson, 1925	B	1, 8, 10, 14, 15	33.3
95	<i>Polyarthra indica</i> Segers & Babu, 1999	B	10, 13	13.3
96	<i>Polyarthra remata</i> Skorikov, 1896		8, 10	13.3
97	<i>Polyarthra vulgaris</i> Carlin, 1943		13	6.7
98	<i>Polyarthra</i> sp.		10	6.7
	Testudinellidae			
99	<i>Testudinella patina</i> (Hermann, 1783)		4, 7, 10, 14	26.7
	Trichocercidae			
100	<i>Trichocerca braziliensis</i> (Murray, 1913)	B	1, 7, 10, 14, 15	33.3
101	<i>Trichocerca cylindrica</i> (Imhof, 1891)	B	13, 15	13.3
102	<i>Trichocerca similis grandis</i> Hauer, 1965	B	14	6.7
103	<i>Trichocerca</i> sp. Lamarck, 1801		13	6.7
	Trichotriidae			
104	<i>Wulfertia kivuensis</i> De Smet, 1992	B	7	6.7
	Conochilidae			
105	<i>Conochilus hippocrepis</i> (Schrank, 1803)	B	8	6.7
106	<i>Conochilus natans</i> (Seligo, 1900)	B	7	6.7
	Trochosphaeridae			
107	<i>Trochosphaera aequatorialis</i> Semper, 1872	B	13	6.7

3.2. Linking Environmental Gradients with Rotifer Functional Traits in Botswana (RDA)

During the survey, water temperatures ranged from 22.5 °C (L#6) to 31.2 °C (L#9). The pH ranged from 6.77 (L#10) to 9.23 (L#5). Electrical conductivity and salinity ranged from 41.3 $\mu\text{S cm}^{-1}$ and 17.9 ppm, respectively (L#9), to 1121 $\mu\text{S cm}^{-1}$ and 548 ppm, respectively (L#15). Locality numbers (L#) and environmental parameters are provided in Table 1.

The RDA indicated that physicochemical gradients explained a substantial fraction of variation in rotifer assemblage composition (Figure 2; Table 3). The first two constrained axes accounted for 40.7% and 23.7% of the constrained variation. Permutation tests indicated that the overall RDA model was not significant (pseudo-F = 1.22, $p = 0.120$). Axis-level tests showed a marginal first constrained axis (RDA1: pseudo-F = 2.48, $p = 0.057$) and a non-significant second axis (RDA2: pseudo-F = 1.44, $p = 0.171$). RDA1 primarily reflected a mineralization gradient most strongly aligned with TDS, whereas RDA2 was aligned with pH and, to a lesser extent, dissolved oxygen. In permutation tests, TDS and pH were significant, whereas temperature and dissolved oxygen were not. More mineralized conditions (higher TDS) were associated with taxa such as *Brachionus* sp., *Plationus patulus*, and *Hexarthra* sp. Trait projections further indicated that the high-TDS area of RDA1 was associated with compact/truncated-pyramidal body shapes, malleoramate or virgate trophi, and predominantly intermediate body sizes, consistent with pelagic microphagous/generalist feeders in warm, mineral-rich waters. Conversely, less mineralized, better-oxygenated sites were linked to *Lecane* sp., *Trichocerca* sp., and *Cephalodella* sp., and were associated with elongated/flattened body shapes, ramate trophi, and smaller body sizes typical of benthic/periphytic microhabitats.

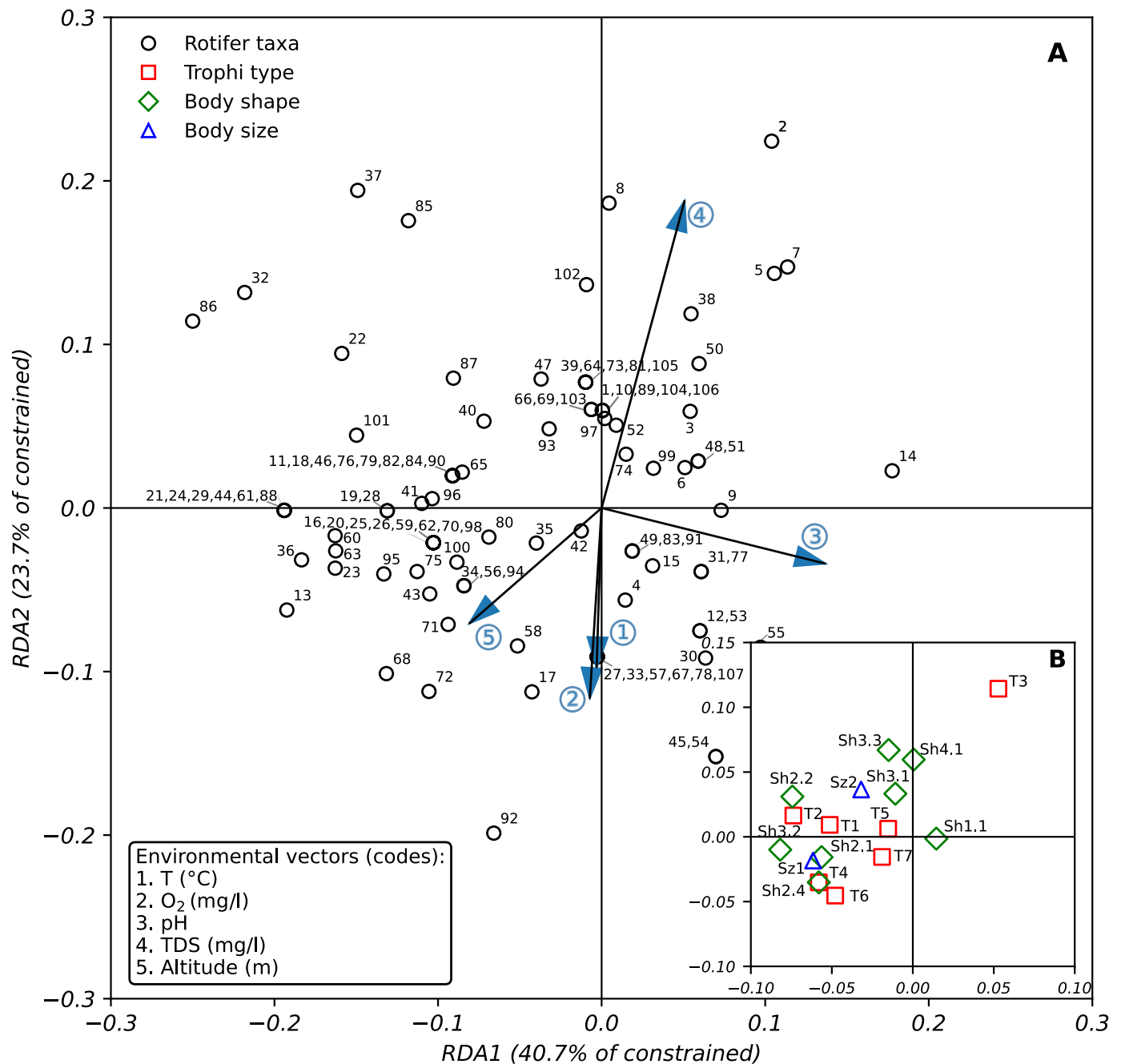


Figure 2. Redundancy analysis (RDA) of rotifer assemblages from 15 inland water bodies in Botswana based on presence–absence data of 107 taxa. (A) Ordination of rotifer taxa (open circles, with numbers corresponding to taxon numbers (T#) in Table 2) constrained by environmental variables. Blue arrows indicate fitted environmental vectors; pH and TDS were significant ($p < 0.05$), whereas altitude was marginal ($p = 0.053$) and temperature and dissolved oxygen were not significant (Table 3). (B) Inset showing projections of functional trait categories plotted as passive centroids: trophi type (red squares), body shape (green diamonds), and body size (blue triangles). Trait distributions indicate systematic shifts along the main environmental gradients, with distinct associations between mineralization (TDS), oxygen availability, and rotifer feeding morphology, body form, and size. Definitions of body shape and trophi type code categories are provided in Table 5 and Supplementary File S2, and in Table 6 and Supplementary File S3, respectively. Body size codes: Sz1 = small (<200 μm), Sz2 = medium (200–400 μm), and Sz3 = large (>400 μm); only categories present in the Botswana RDA dataset are shown in panel (B).

Table 3. Environmental variables fitted to the RDA ordination of rotifer assemblages in inland waters of Botswana. Values for RDA1 and RDA2 are correlations (loadings) with the first two constrained axes. Vector r^2 indicates the strength of the marginal (univariate) fit of each variable to the ordination configuration; significance was assessed using permutation tests ($n = 4999$). Sequential (Type I; order-dependent) permutation tests of predictors within the full RDA model are provided in Supplementary File S1 (Table S4).

Environmental Variables	RDA1	RDA2	r^2	p (Perm)
Temperature (°C)	−0.144	0.104	0.032	0.820
O ₂ (mg L ^{−1})	−0.172	0.348	0.151	0.376
pH	0.415	0.568	0.495	0.017
TDS (mg L ^{−1})	0.688	−0.302	0.565	0.009
Altitude (m a.s.l.)	−0.563	0.139	0.337	0.053

3.3. Biogeographical Thermal Classes Along a Latitudinal Gradient in Africa and Europe

After filtering and validation, the dataset contained 24 families (each with ≥ 100 records) and 59 genera (each with ≥ 50 records). Applying the five-class thermal framework yielded the distributions shown in Table 4. Most taxa clustered in the eurythermal class (ERT), with smaller subsets assigned to warm-water (WW/WWP ERT) and cold-water-related classes (CWP ERT/CW).

Table 4. Number of taxa per thermal class (families and genera). Thermal classes are defined by $|\text{mean latitude}|$ as follows: WW (warm water), $|\text{mean}| \leq 23.5^\circ$; WWP ERT (warm-water-preferring eurytherms), $23.5^\circ < |\text{mean}| \leq 30^\circ$; ERT (eurytherms), $30^\circ < |\text{mean}| \leq 45^\circ$; CWP ERT (cold-water-preferring eurytherms), $45^\circ < |\text{mean}| \leq 50^\circ$; CW (cold water), $|\text{mean}| > 50^\circ$. Values in the “Families (n)” and “Genera (n)” columns indicate the number assigned to each class after filtering and validation.

Thermal Class	Families (n)	Genera (n)
WW	2	8
WWP ERT	4	10
ERT	16	29
CWP ERT	2	10
CW	0	2

3.3.1. Family-Level Latitudinal Positioning and Thermal Classes

Family mean latitudes spanned from equatorial to mid-high latitudes (Figure 3). The most equatorward families (WW) were Hexarthridae (mean = 18.85° , 95% CI 17.42–20.27; $n = 1033$) and Epiphanidae (mean = 21.79° , 95% CI 19.91–23.67; $n = 492$). Four families (Trochosphaeridae, Scaridiidae, Flosculariidae and Lecanidae) were classified as WWP ERT (23.5 – 30°). Most families were ERT (30 – 45°), consistent with broad temperate occupancy. Representative families with mean latitudes near the center of the ERT class (30 – 45°) included Proalidae, Dicranophoridae, Gastropodidae, Conochilidae and Notommatidae. Two families fell into CWP ERT (45 – 50°): Habrotrichidae (mean = 45.56° , 95% CI 44.58–46.53; $n = 965$) and Adinetidae (mean = 47.01° , 95% CI 45.83–48.19; $n = 626$). No family exhibited a mean occurrence at latitudes $\geq 50^\circ$, and therefore no family can be considered typical of cold-water conditions (CW). Table S1 lists family-level mean latitude ($^\circ$) and 95% CI by thermal class, and Table S3 provides an explanation of variables, metrics, and detailed thermal classes (Supplementary File S1).

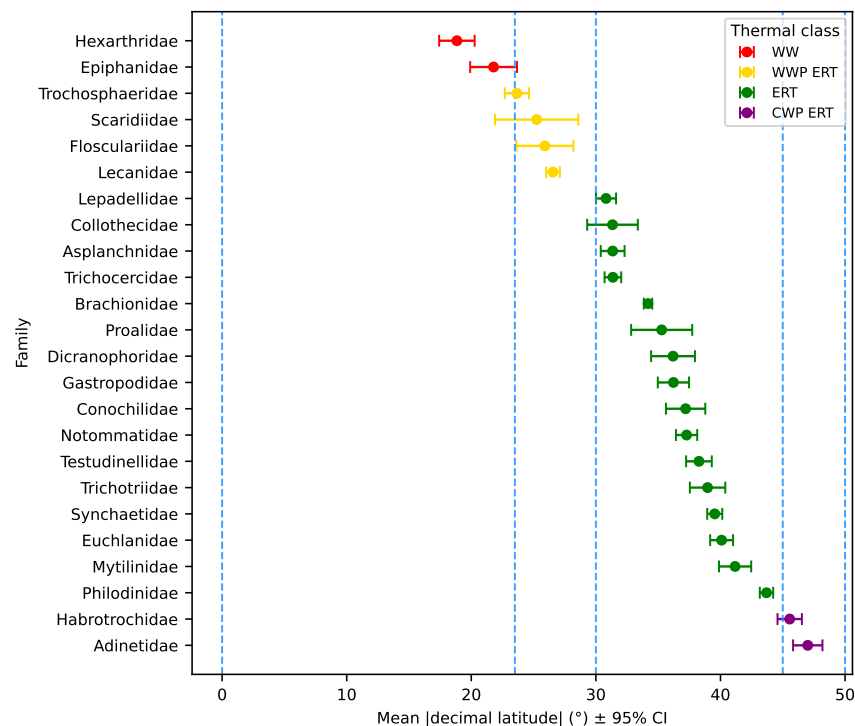


Figure 3. Mean latitudinal position ($\pm 95\%$ CI) of rotifer families in the Africa–Europe dataset, color-coded by thermal class (abbreviations as defined in Table 4). Vertical dashed blue lines indicate 0° , 23.5° , 30° , 45° , and 50° . Ecologically, most families cluster within the eurythermal classes (ERT, WWP ERT and CWP ERT), suggesting broadly conserved thermal tolerance at higher taxonomic levels, whereas only two families (Hexarthridae and Epiphanidae) were predominantly warm water (WW), consistent with comparatively stronger thermal specialization.

3.3.2. Genus-Level Latitudinal Positioning and Thermal Classes

Genus-level means showed a wider spread than families and therefore provided finer resolution of latitudinal structure (Figure 4). Eight genera were classified as WW ($\leq 23.5^\circ$), including *Macrochaetus* (mean = 10.31° , 95% CI 6.72–13.90; $n = 145$) and *Platinius* (mean = 13.65° , 95% CI 11.81–15.50; $n = 447$). Ten genera were WWP ERT (23.5 – 30°), 29 genera were ERT (30 – 45°), and 10 genera were CWP ERT (45 – 50°). Genera with mean latitudes near the class centers included the following: ERT—*Testudinella*, *Monommata*, *Itura*, *Rotaria*, and *Mytilina*; WWP ERT—*Scardium*, *Brachionus*, *Ptygura*, and *Beauchampiella*; CWP ERT—*Pleuretra*, *Lophocharis*, *Pleosoma*, and *Adineta*. Two genera were classified as CW ($>50^\circ$): *Didymodactylos* (mean = 50.16° , 95% CI 48.57–51.75; $n = 71$) and *Kellicottia* (mean = 54.34° , 95% CI 53.75–54.93; $n = 1583$). Table S2 lists genus-level mean latitude ($^\circ$) and 95% CI by thermal classes and Table S3 provides an explanation of variables, metrics, and detailed thermal classes (Supplementary File S1).

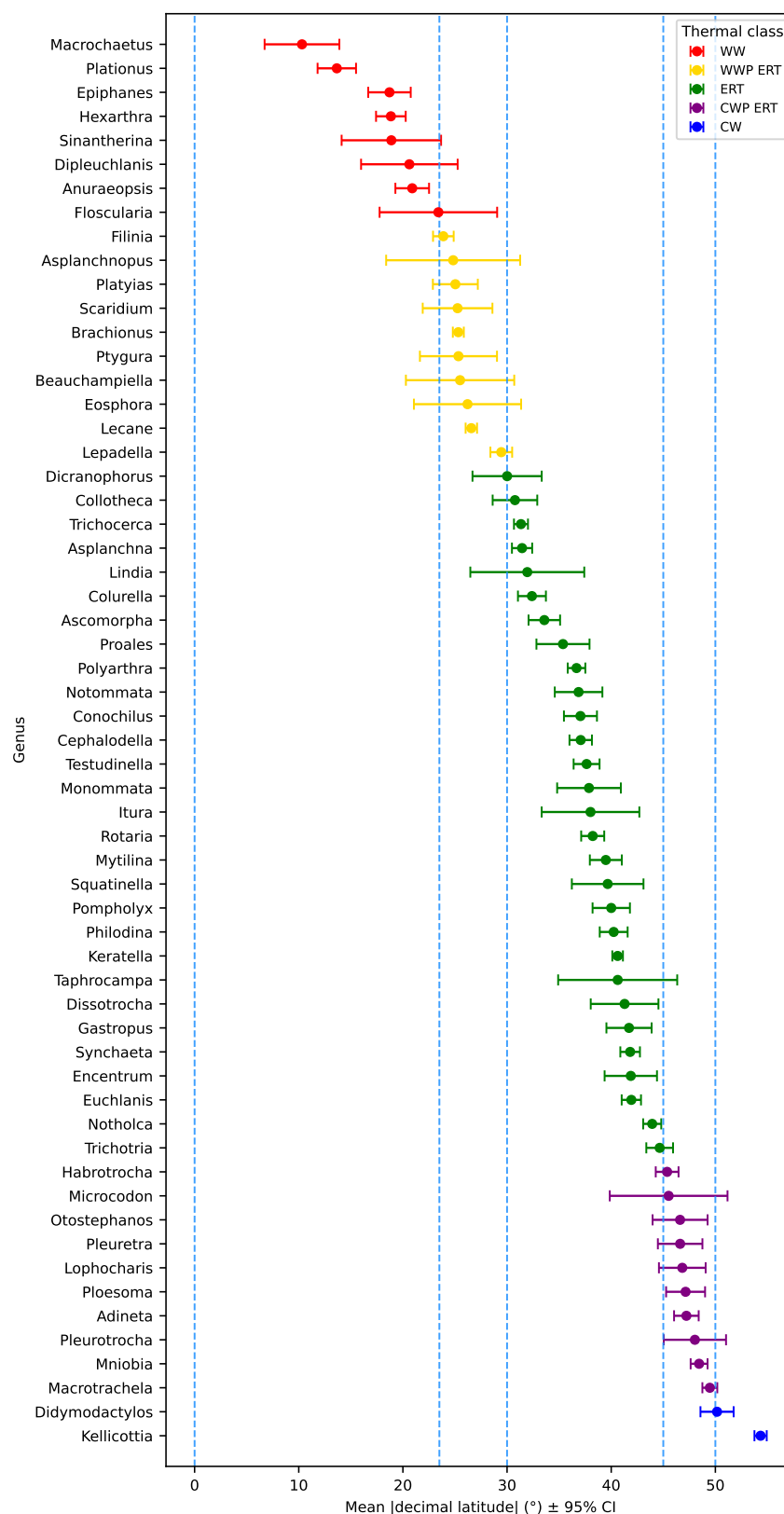


Figure 4. Mean latitudinal position ($\pm 95\%$ CI) of rotifer genera in the Africa–Europe dataset, color-coded by thermal class (abbreviations as defined in Table 4). Vertical dashed blue lines indicate 0° , 23.5° , 30° , 45° , and 50° . Ecologically, genus-level centroids span the full thermal gradient, indicating latitudinal structuring and niche partitioning at this taxonomic level; only a small subset of genera was predominantly warm water (WW) or cold water (CW), whereas most remain within the eurythermal classes (ERT, WWP ERT and CWP ERT).

3.4. Functional–Morphological Traits Along a Latitudinal Gradient in Africa and Europe

3.4.1. Geometric Body Shapes

Latitude differed strongly among geometric body shape categories (Table 5, Figure 5). The overall Kruskal–Wallis test was highly significant ($H = 4730.31$, $p < 0.001$) with a moderate effect size ($\epsilon^2 = 0.071$), indicating that body shape categories explain ~7% of the rank-variance in latitude. Dunn post hoc tests (Holm) identified 46 significant pairwise contrasts out of 55 possible pairs, confirming that most shape categories occupy distinct latitudinal distributions rather than reflecting minor stochastic deviations.

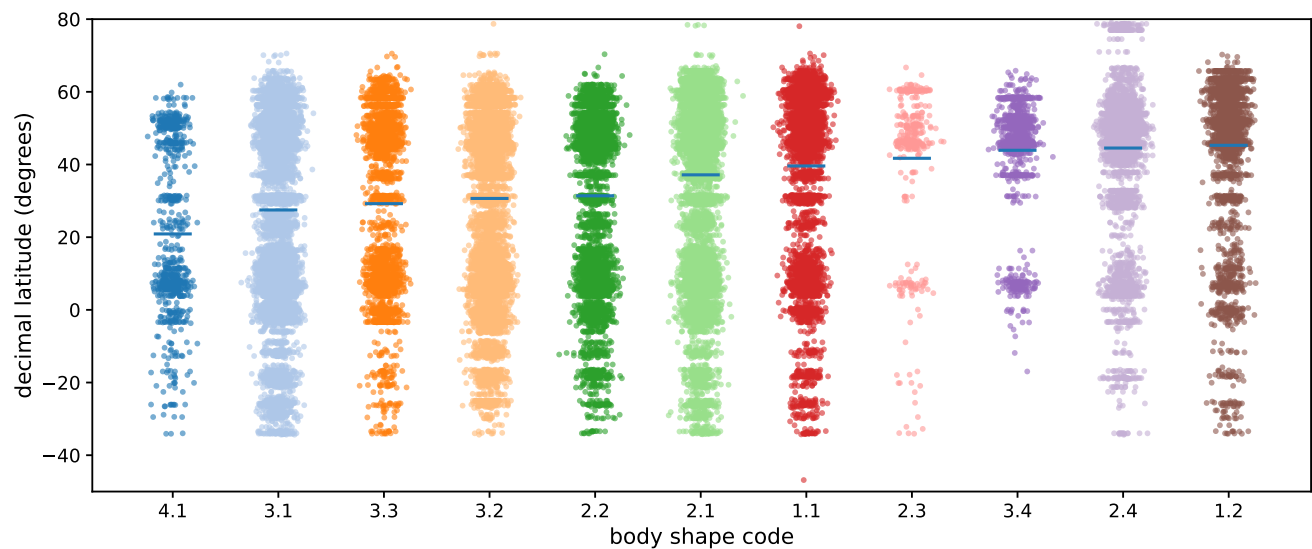


Figure 5. Latitudinal distribution of body shapes (jittered points; median bars). Each jittered point represents a single occurrence record (taxon × site) assigned to a body shape category; points are randomly subsampled for visualization. Median bars indicate the category median. Definitions of body shape categories are provided in Table 5 and in Supplementary File S2. Ecologically, differences in median latitude among categories indicate consistent latitudinal structuring of body shape composition across the Africa–Europe dataset.

Table 5. Latitudinal summaries by geometric body shape category. Shape code = body shape category code; n = number of records; mean lat = mean latitude (°); median lat = median latitude (°); SD = standard deviation. Latitudes are given in decimal degrees; categories are ordered by median latitude.

Shape Code	Body Shape Category	N	Mean Lat	Median Lat	SD
4.1	trilateral truncated pyramid	766	20.89	11.37	22.82
3.1	general ellipsoid	14,041	26.85	30.46	24.64
3.3	ellipsoid of revolution	3039	29.34	37.02	23.93
3.2	half ellipsoid	12,570	30.65	40.84	24.08
2.2	conical cylinder	6065	31.37	44.30	23.16
2.1	general cylinder	12,970	37.18	46.26	23.76
3.4	segment of ellipsoid	1216	43.94	46.60	15.45
2.3	elliptic cylinder	380	41.71	46.67	21.59
1.1	cone	6183	39.54	48.70	23.89
2.4	elliptic cylinder (tapered ends)	5872	44.54	49.28	17.08
1.2	half cone	3274	45.29	51.56	20.60

3.4.2. Trophi Types

Trophi types also differed significantly in latitude (Table 6, Figure 6), but with a smaller effect size than body shape. The Kruskal–Wallis test was highly significant ($H = 1409.28$, $p < 0.001$) with $\epsilon^2 = 0.021$. Dunn post hoc tests (Holm) identified 19 significant pairwise contrasts out of 28 possible pairs, suggesting that feeding-mode differentiation is latitudinally structured but more overlapping than body shape categories, consistent with generalist feeding and trophic plasticity in many rotifers [39,54,68].

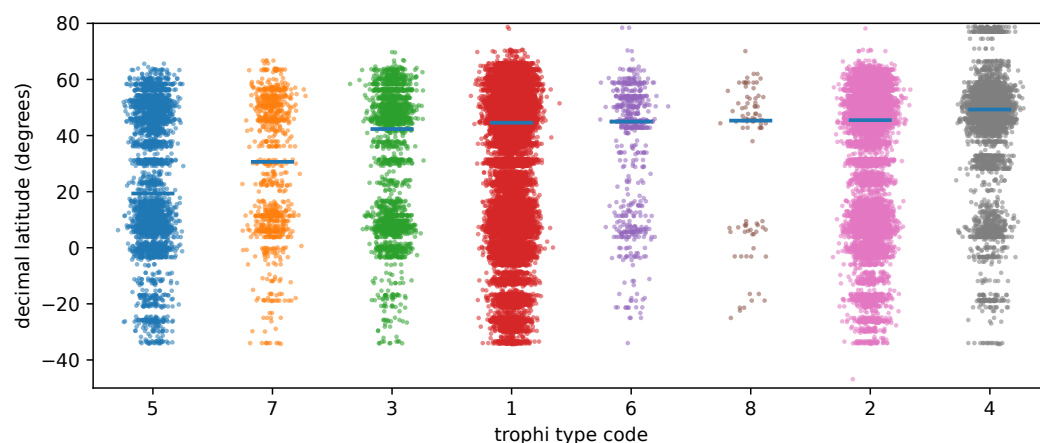


Figure 6. Latitudinal distribution of trophi types (jittered points; median bars). Each jittered point represents a single occurrence record (taxon $\times$ site) assigned to a trophi-type category; points are randomly subsampled for visualization. Median bars indicate the category median. Definitions of trophi type categories are provided in Table 6 and in Supplementary File S3. Ecologically, differences in median latitude among categories indicate consistent latitudinal structuring of trophi type composition across the Africa–Europe dataset.

Table 6. Latitudinal summaries by trophi-type category. Trophi code = trophi-type category code; n = number of records; mean lat = mean latitude ($^{\circ}$); median lat = median latitude ($^{\circ}$); SD = standard deviation. Latitudes are given in decimal degrees; categories are ordered by median latitude.

Trophi Code	Trophi Type	N	Mean Lat	Median Lat	SD
5	Malleoramate	3879	24.50	19.16	24.55
7	Uncinate	897	28.19	30.06	23.80
3	Incudate	2333	31.07	42.32	23.52
1	Malleate	36,758	32.99	44.57	24.73
6	Forcipate	622	36.08	44.98	22.74
8	Cardate	90	31.94	45.32	26.48
2	Virgate	15,854	35.79	45.50	22.99
4	Ramate	5943	44.60	49.28	17.01

4. Discussion

This study addresses key knowledge gaps in rotifer ecology by integrating taxonomic, functional, and biogeographical perspectives across spatial scales. It (i) increases knowledge of rotifer diversity in Botswana and improves continent-scale understanding through new national records and range extensions; (ii) quantifies trait–environment relationships in Botswana using RDA and functional traits (body shape, trophi type, body size); and (iii) embeds these local patterns in an Africa–Europe latitudinal framework of thermal classes and morphological traits (body shape and trophi type). Together, the results show how functional traits mediate rotifer community assembly from local to continental scales and highlight the utility of trait-based approaches for macroecological inference.

4.1. Species Richness in Botswana

The Botswana survey documented several rotifer species previously recorded only rarely in Africa, enabling comparison between historical ranges and their newly confirmed occurrence in southern Africa. Examples previously known from single localities include *Cephalodella hollowdayi* (Ghana) [103], *C. sterea* (Western Sahara–Morocco) [104], and *Proalinopsis caudata* (Kilimanjaro, Tanzania) [105]. *Wulfertia kivuensis*, originally described from Lake Kivu (DR Congo) [106], was previously restricted to that lake and is here recorded from Bokaa Dam [107]. Several taxa with only three African records prior to this study (*C. boettgeri*, *Dicranophoroides claviger*, *Lecane abanica*, *Lophocharis gracilis*, *Notommata cerberus*) were previously known mainly from northern and western Africa, with scattered records elsewhere. Our findings represent the southernmost records for several of these taxa and support the “rotiferologist effect” [4]. Two exceptions had prior southern occurrences: *N. cerberus* was also reported from South Africa [108,109], and *L. abanica* was recorded from isolated sub-Saharan localities and Madagascar [110], including brackish water, indicating salinity tolerance. *Donneria* (*Paradicranophorus*) *sudzukii*, originally described by Donner [111] as a benthic, mud-dwelling species, was first reported from fine bottom sediments of Neusiedler See (Austria) and later from the psammon of the Colorado River, Colorado, USA and the Tigris River in Turkey [112]. Our specimens were also associated with sediments.

4.2. Linking Environmental Gradients with Rotifer Functional Traits in Botswana

The redundancy analysis demonstrated that rotifer assemblages in inland waters of Botswana are structured primarily by physicochemical gradients related to mineralization, temperature, oxygen availability, and pH. The first RDA axis (RDA1), dominated by total dissolved solids (TDS) and temperature, represents a mineralization-thermal gradient that is widely recognized as a major driver of rotifer community composition in arid and semi-arid regions [113–115]. Elevated mineralization imposes strong physiological constraints on freshwater microinvertebrates, favoring taxa with broad osmotic tolerance, efficient ion regulation, and life-history strategies adapted to environmental instability [1,84]. Taxa associated with the high-TDS, warm end of RDA1—most notably *Brachionus* sp., *Platyonus patulus*, and *Hexarthra* sp.—are characteristically medium- to large-bodied rotifers with robust loricae and compact or truncated-pyramidal body shapes, traits commonly linked to tolerance of mineral-rich and eutrophic conditions [45,84,113]. These taxa are also typically characterized by malleoramate or virgate trophi, enabling efficient exploitation of abundant phytoplankton and bacterial resources under high nutrient and mineral loads [1,67]. Their consistent association with warm, mineralized habitats across continents suggests a conserved functional strategy combining osmotic tolerance, flexible feeding, and rapid population growth. In this context, the Botswana assemblages broadly fit the thermal/biogeographical framework derived from the Africa–Europe dataset. Trait centroids associated with high mineralization in Botswana (compact/truncated-pyramidal body shapes; malleoramate/virgate trophi) match the low-latitude tendency of these categories in the continental analysis (Figures 5 and 6), with local deviations likely reflecting strong site-level physicochemical filtering (TDS and oxygen/pH). In contrast, taxa clustering toward the low-mineralization, better-oxygenated region (e.g., *Lecane*, *Trichocerca*, *Cephalodella*) are mainly small-bodied rotifers with elongated, conical, or dorsoventrally flattened body shapes, often associated with benthic, periphytic, or structurally complex habitats [15,53,54]. These taxa frequently possess ramate or modified trophi types, which facilitate selective feeding on detritus, bacteria, or small algae within heterogeneous microhabitats [3].

RDA2 (oxygen, partly pH) highlights metabolic constraints: small-bodied taxa typically have higher mass-specific metabolic rates and lower hypoxia tolerance [115,116],

consistent with the association of *Cephalodella* and *Trichocerca* with higher oxygen concentrations [3,53]. Compact body shapes and intermediate to large body size classes predominated along the mineralization gradient, likely reflecting reduced surface-area-to-volume ratios that mitigate osmotic stress and favor persistence in high TDS environments [67,117]. In contrast, small body size classes, combined with elongated or flattened body shapes, were associated with low-mineralization, well-oxygenated habitats, consistent with ecological strategies emphasizing microhabitat exploitation and reduced exposure to turbulence. Body size thus emerges as a key integrative functional trait linking morphology, feeding strategy, and environmental tolerance. We acknowledge that the observed size–environment relationships may be partly phylogenetically structured, because several rotifer genera have characteristic adult size ranges (e.g., larger-bodied *Brachionus* versus smaller-bodied *Lecane*), which is consistent with trait-based environmental filtering. However, the association between higher TDS and larger/intermediate body-size classes is not driven by a single genus: the high-TDS end includes multiple genera with similar size-associated strategies (e.g., *Brachionus*, *Platyonus*, *Hexarthra*), while the low-mineralization end is likewise represented by several mainly small-bodied genera (e.g., *Lecane*, *Trichocerca*, *Cephalodella*). In rotifers, size strongly mediates vulnerability to predation, feeding efficiency, and habitat use [1]. We did not quantify predator assemblages in the Botswana water bodies; however, likely rotifer predators include invertebrate predators (e.g., cyclopoid copepods and insect larvae) and, in fishponds/reservoirs, larval/juvenile fishes. In addition, our samples included taxa commonly classified as raptorial rotifers; the most frequently recorded examples were *Asplanchna brightwellii*, *Dicranophorus epicharis*, *Scaridium longicaudum*, and *Dicranophoroides caudatus* (Table 2), suggesting that intraguild predation may occur. Similar size-based trait filtering along environmental gradients has been documented in rotifer assemblages across trophic and physicochemical gradients [67] and reflects broader plankton-ecological principles in which body size acts as a “master trait” integrating metabolic constraints, trophic interactions, and niche occupancy [118,119]. Our findings reinforce the value of trait-based approaches for interpreting rotifer community assembly and demonstrate that functional traits—particularly body shape and body size—provide mechanistic insight beyond taxonomic patterns alone in semi-arid inland waters. Botswana results primarily reflect warm-season (late wet season) community structure because field sampling was conducted during a single campaign in March 2022; seasonal dynamics therefore could not be assessed.

The RDA results indicate that rotifer assemblages in Botswana are not randomly structured but reflect predictable, trait-mediated responses to interacting environmental gradients. TDS and temperature act as dominant filters shaping body size distributions and body geometry, while oxygen availability—and to a lesser extent pH—further refine community composition through metabolic and feeding constraints. These findings reinforce the value of trait-based approaches for interpreting rotifer community assembly and demonstrate that functional traits—particularly body shape and body size—provide mechanistic insight beyond taxonomic patterns alone in semi-arid inland waters.

4.3. Biogeographical Thermal Classes Along a Latitudinal Gradient in Africa and Europe

Partitioning eurytherms into warm-water-preferring (WWP ERT) and cold-water-preferring (CWP ERT) reveals systematic structure consistent with temperature-driven phenology and seasonal succession [24,120,121]. This framework is useful for rotifers, which experience rapid thermal variation, especially in shallow and temporary systems. Rotifers respond quickly due to short generation times and temperature-sensitive development [122,123]. Warm-water-preferring eurytherms typically exhibit high intrinsic rates of increase at warm temperatures and thus dominate summer assemblages, partic-

ularly in productive waters. In temperate regions, resting eggs can decouple seasonal persistence from continuous growth and inflate apparent thermal breadth in occurrence data [40,124–126]. Cold-water-preferring eurytherms exploit early-season production pulses under low temperatures and may dominate under-ice or immediately post-ice conditions in northern lakes. May's Loch Leven analysis shows that temperature can drive distinct seasonal windows for many taxa [121]. Cold-season dominance is also shaped by food availability, phytoplankton composition, and altered predator-prey regimes across seasons [24,127–129]. These patterns are consistent with plasticity constrained by evolutionary thermal preference, where performance asymmetries persist even under substantial phenotypic plasticity [130–132]. At broad scales, the $\pm 23.5^\circ$ tropical boundary captures a major shift in seasonality and insolation [30,34], relevant to the duration of favorable growth periods and the selective value of dormancy [34,124–126,133]. The $\sim 50^\circ$ boundary approximates the temperate-boreal transition in Eurasia [47–49,134].

Our results are consistent with earlier reports of latitudinal structuring in rotifer communities [4,135]. However, large-scale inference depends on data quality and sampling effort [4,136]. In Africa, where systematic sampling remains uneven, literature-based synthesis is essential to balance repository coverage and to recover biogeographic signals [9]. Limitations include (i) the use of latitude as a proxy for temperature, which can be decoupled by elevation and habitat type [30,31,137–139], and (ii) sampling bias across regions [61,94,140–143]. Future work should integrate gridded climate metrics and trait-based approaches to link thermal classes to functional strategies [69,70,78,144]. In summary, introducing WWP ERT and CWP ERT provides an operationalization of a common ecological reality in rotifers: broad tolerance does not preclude strong preference. The Africa–Europe synthesis indicates that the $45\text{--}50^\circ$ and $\sim 50^\circ$ N thresholds represent meaningful transition zones where ecological dominance can shift from warm-leaning to cold-leaning generalists, and in some genera to cold-water centroids.

4.4. Functional–Morphological Traits Along a Latitudinal Gradient in Africa and Europe

Across Africa and Europe, rotifer morphological traits show consistent, non-random latitudinal structuring; however, effect sizes indicate that latitude explains a modest fraction of variation ($\epsilon^2 \approx 0.07$ for body shape; $\epsilon^2 \approx 0.02$ for trophi type). Geometric body shape showed a larger effect size than trophi type, suggesting that latitudinal differences in lake physical habitat (e.g., morphometry, macrophyte development, and mixing/turbulence regime) contribute more strongly to trait turnover than feeding mode [39,54,68,81]. Trophi type also differed significantly, but with a smaller effect size. Body shape patterns likely reflect shifts in pelagic–littoral habitat balance and physical forcing. Streamlined/compact body shapes are often associated with pelagic taxa, where drag reduction and stability under physical forcing are advantageous, whereas flattened/elongate forms are more typical of benthic/periphytic taxa exploiting structurally complex littoral microhabitats (e.g., macrophytes, detrital surfaces, boundary-layer refugia) [53,54,68]. At broader (latitudinal) scales, higher-latitude lakes commonly show stronger seasonal mixing and wind-driven turbulence, favoring pelagic morphotypes, whereas warmer shallow systems tend to sustain more persistent macrophyte development and littoral habitat complexity that favor periphytic/flattened forms [10,23,55]. Because shape integrates substrate use and exposure to turbulence, it can respond more directly to these habitat differences than trophi type, which can remain functionally redundant across multiple diets in mixed-resource environments [62–68].

Latitudinal variation in predator communities may also contribute to the patterns observed. For instance, selective pressure from invertebrate predators (e.g., *Asplanchna*, copepods, *Chaoborus*) can induce defenses (spines, lorica thickening) that alter morphology, with defense

expression depending on predator identity and community composition [69,70,78–80]. Trait-based frameworks that explicitly incorporate defense traits, lorica development, and habitat affinity have proven useful for interpreting community assembly and functional diversity patterns in lakes [65–68,73]. Our results extend this perspective to a continental latitudinal gradient. Several caveats apply: latitude is a proxy integrating multiple drivers (temperature, seasonality, elevation, habitat configuration), so mechanistic inference would benefit from explicit climate and habitat predictors [30–32,36,49]; occurrence data are subject to spatial and expertise biases [4,61,140,141]; and trait coding can be uncertain for poorly studied taxa, underscoring the need for standardized trait matrices [68,73]. Despite these limitations, rotifer morphological traits—especially body geometry—show pronounced latitudinal structuring at large scales. This association is not necessarily causal, as latitude integrates multiple environmental drivers, but it supports incorporating body shape and trophi traits into biogeographic syntheses and trait–environment analyses (thermal regimes, habitat gradients, climate-change projections) [62–64,74,77,79,81,145].

Our findings are consistent with core macroecological theory, which predicts that large-scale gradients in climate and habitat availability structure not only species richness but also the functional and morphological composition of assemblages [49,101]. From this perspective, the pronounced latitudinal structuring of rotifer body shape and trophi type reflects differential occupation of ecological space across continents, driven by systematic changes in energy input, habitat complexity, and biotic interactions. Rather than representing gradual shifts in species identities alone, the observed patterns indicate coordinated turnover of functional strategies along latitude. Overall, the latitudinal trait turnover likely reflects both species replacement and intraspecific variability, but our presence–absence, species-level trait approach primarily captures replacement among taxa with different trait syndromes. Disentangling these mechanisms would require population-level trait measurements across latitude—ideally with genetic resolution and/or common-garden experiments. Importantly, the strong signal detected here is unlikely to be an artefact of species-level averaging, because we analysed individual occurrence records that capture both within-species range breadth and among-species turnover. Accordingly, shifts in dominant body shapes and feeding structures likely reflect changes in the relative contribution of functional guilds to regional assemblages rather than simple latitudinal displacement of taxa.

Overall, this study demonstrates that combining regional biodiversity inventories, trait-based analyses, and large-scale biogeographical datasets provides a robust and reproducible framework for quantifying rotifer diversity and community assembly. Trait-based approaches offer mechanistic insight into how environmental and climatic gradients structure rotifer assemblages and are essential for interpreting biodiversity patterns in environmentally heterogeneous and under-sampled regions such as southern Africa.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d18030173/s1>, File S1: Table S1: Family-level mean latitude (°) and 95% confidence intervals by biogeographical thermal class; Table S2: Genus-level mean latitude (°) and 95% confidence intervals by biogeographical thermal class; Table S3: Explanation of variables, metrics, and thermal class definitions used in Tables S1 and S2; Table S4: Sequential effects of environmental predictors in the RDA model. File S2: Taxon-level assignments of geometric body shape categories; File S3: Taxon-level assignments of trophi type categories. All references cited in Supplementary Files S1–S3 are included in the main reference list (i.e., [1–3,7,15,22,39,53,54,74,79,94,96,110,146,147]).

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