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Trait-Based Research on Rotifera: The Holy Grail or Just Messy?

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Abstract: In recent years, trait-based research on plankton has gained interest because of its potential to uncover general roles in ecology. While trait categories for phytoplankton and crustaceans have been posited, rotifer trait assessment has lagged behind. Here, we reviewed the literature to assess traits key to their life histories and provided a data matrix for the 138 valid genera of phylum Rotifera. We considered seven traits: habitat type, trophi type, presence of lorica and foot, predation defense attributes, corona type, and feeding traits. While most traits were morphological attributes and supposedly easy to assess, we were faced with several challenges regarding trait assignment. Feeding traits were especially difficult to assess for many genera because relevant information was missing. Our assembled trait matrix provides a foundation that will initiate additional research on rotifer functional diversity, diminish the misclassification of rotifer genera into trait categories, and facilitate studies across trophic levels.

Keywords: aquatic ecology; functional ecology; corona; community dynamics; food; guild ratio; functional groups; rotifer trophi



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1. Introduction

In recent years, trait-based research has gained interest because of its promise to provide generality and predictability of ecological patterns [1]. This generality in trait-based ecology is reached by using traits that allow for an ecological viewpoint beyond species-specific statements [2]. Traits may be defined at the level of species and can include morphological, physiological, and/or phenological characteristics, which impact individual fitness [3,4]. The use of traits fosters a better understanding of the forces that drive the diversity of communities across several scales [2,5–9]. More importantly, such studies can identify both the loss and recovery of ecosystem resilience [10]. Additionally, tracking the extent of changes in traits may provide insight into how communities rebound either by hysteretic or non-hysteretic pathways [10,11] and also may provide information about the subtle changes indicating a regime shift that ultimately leads to alternative stable states [12–16].

For plankton, trait-based research is commonly used for phytoplankton with widely used definitions and trait classifications [9], but for zooplankton, the situation is less ideal. Trait coverage and its usage differ for crustaceans and rotifers, with the most complete information available for the former [2,17]. Over a decade ago, Barnett et al. [18] published their seminal article on crustacean traits. This work, which contained an extensive trait matrix, has been cited almost 300 times. Litchman et al. [19] further recommended the use of functional traits in zooplankton studies, but they focused only on crustaceans. Nevertheless, rotifer functional diversity has gained interest in recent years because of its promise to find general roles [20–22]. While standardized traits for organisms such as plants, phytoplankton, and crustaceans exist, studies on rotifer functional diversity have used different terminologies, trait definitions, and approaches.

In rotifer trait diversity studies, terminology such as bacterivorous, herbivorous, and partly carnivorous is often used without any reference to existing literature [23]. Missing information on how traits were attributed is regrettable because it is impossible to rebuild analyses under the principles of findable, accessible, interoperable, and reusable. Even though sources for trait assignment are often cited (e.g., Fintelman-Oliveira et al. [24]), the fact that trait assignment is not shown (either as a table in the study or Supplementary Material) impedes constructive discussion of trait categorization. Another extreme presents the classification of rotifers as purely small herbivores [25] without consideration of their diverse feeding strategies [26]. For example, despite recognizing the range of trophic diversity of rotifers, Kakouei et al. [23] did not differentiate rotifers into feeding groups in statistical analyses on the long-term, zooplankton functional diversity of Lake Müggelsee (Berlin, Germany).

In the era of big data [27], the lack of taxonomists [28] hampers trait assignment and restricts data analyses, thereby limiting the reliability of studies that attempt to evaluate rotifer community structure. While morphological traits might be easily assessed by rotifer guidebooks, assessment of feeding traits is more challenging. Recently Gilbert [26] observed, “basic information on rotifer diets is not readily available to aquatic ecologists and limnologists.” As a result, the availability of standardized traits is needed to avoid misclassifications of rotifer traits. With that assessment in mind, we posit that any open-source database on rotifer traits facilitates research. Furthermore, we believe that a standard categorization of rotifer traits will improve our ability to compare studies. Accordingly, the aim of this study is to summarize knowledge of rotifer trait diversity, clarify existing terminology thereby reducing erroneous rotifer species classification, and provide a trait matrix for valid genera of phylum Rotifera.

2. Material and Methods

The advanced research engines in Scopus and Web of Science databases (searching for titles, abstracts, or keywords) were used with “rotifer” AND “trait” AND “functional” as search criteria. Articles found were checked for their appropriateness. Only studies with rotifer trait diversity within the aim of the study were considered, articles only referring in the discussion section to rotifer traits were not considered. Body size is a master trait because related to rotifer food threshold concentrations [29]. Nevertheless, studies using only rotifer body size as a trait were also not considered because body length does not present any inherent problem in trait assignment because it is a measurable property. Additionally, Web of Science was used to assess bibliometric indices (i.e., the 5-year impact factor (IF) and the category quartile). In cases where the journal was part of more than one category (e.g., Aquatic Ecology), the highest quartile was reported.

Rotifers consist of the groups Bdelloidea, Monogononta, and Seisonacea [30]. We compiled a trait matrix for rotifer genera listed in Fontaneto & De Smet [31] ($n = 132$) plus a newly described genus (*Coronistomus*; [32]) and additional ones indicated as valid genera in the Rotifer World Catalogue of Rotifers (*Allodicanophorus*, *Pleurata*, *Pourriotia*, *Pseudoeuchlanis*, *Pulchritia*; [33]). The assembled trait matrix contains the following information: family, habitat type, trophi type, presence of lorica and foot, predation defense attributes (e.g., spines, escape swimming; gelatinous case), corona type, feeding mode after Smith et al. [34], feeding types according to Karabin [35], feeding type, feeding mechanism, and ingested particle size after Monakov [36], feeding types after Gilbert [26], and feeding types after Palazzo et al. [37]. Monakov [36] was originally written in Russian and is used by Russian researchers [38], but an English translation exists. Feeding traits were not modified, and we do not warrant their correctness or appropriateness. For feeding traits, we reported relevant literature in some cases where no missing information on traits was found (e.g., *Asplanchna*) to provide readers with additional information.

We performed hierarchical clustering of genera by morphological traits. For clustering of our trait matrix, we used the Gower distance provided by package *cluster* [39]. Validation of clusters (i.e., compact and distinct clusters; package *fpc*; [40]) was assessed by the

average distance among observations between clusters (should be small) and the silhouette coefficient (should be large). We chose between agglomerative and divisive clustering based on cluster performance. In plotting with package ggplot2 [41], we used colors that can be distinguished by color-blind people (package viridis [42]). All analyses were performed with R 4.2.2 [43].

3. Results

3.1. Analysis of Articles on Rotifer Functional Diversity

We found 66 articles focusing on rotifer functional traits (Supplementary Table S1). While the first article was published in 2005, after 2015 the number of articles using rotifer traits increased (Figure 1A). The two published studies early in 2023 (Supplementary Table S1) were indicative of the continuing interest in zooplankton and rotifer functional diversity. These 66 articles were published in 40 different journals with most having a reported IF; only four articles were not referenced in the Web of Science database. Most articles were published in *Hydrobiologia* ($n = 14$), followed by *Water* ($n = 5$), *Ecological Indicators* ($n = 3$), and *Journal of Plankton Research* ($n = 3$). Most studies were from Brazil ($n = 15$), followed by China ($n = 12$), Poland ($n = 6$), and Argentina, Croatia, and Italy ($n = 5$) (Figure 1A). Most articles had a 5-year IF between 2 and 5 ($n = 38$; Figure 1B) and were located in the first ($n = 11$) or second quartile ($n = 32$) of journal categories (Figure 1C). Among study sites, most were from lakes ($n = 32$), followed by reservoirs ($n = 10$), and rivers ($n = 10$).

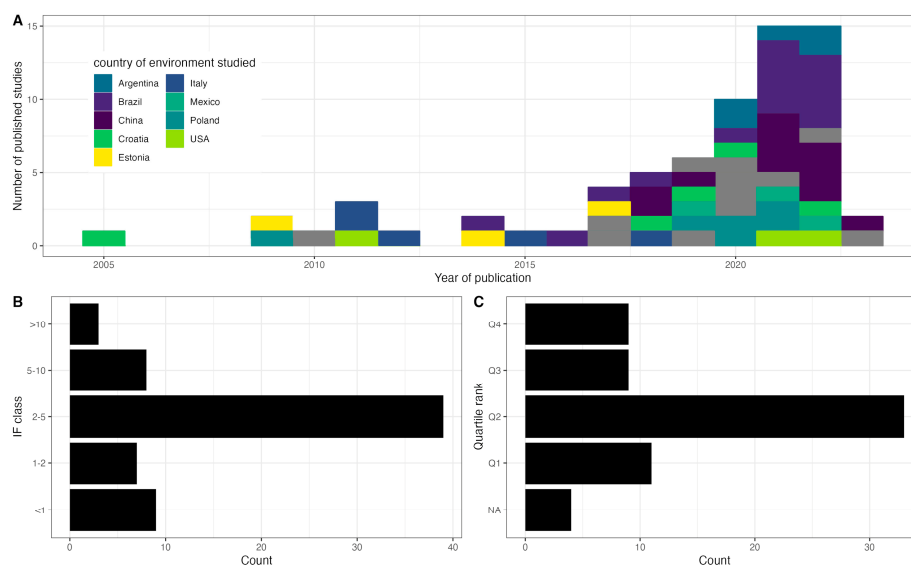


Figure 1. Articles on rotifer functional diversity: (A) Country of environment studied; the countries with at least three published studies are shown; grey color refers to countries with <3 published studies; (B) number of studies binned by IF classes; (C) number of studies binned by the quartile rank; NA refers to studies with no IF.

Statistical analyses on rotifer traits fell into four categories: (1) single traits were related to environmental conditions; (2) all traits were used in multivariate analyses and calculation of diversity indices; (3) rotifer traits were used in clustering methods to construct functional groups; these functional groups were used in following analyses such as functional diversity and regression analysis; and (4) rotifer traits were merged with crustacean traits when analyzing zooplankton functional diversity. Most studies used analyses of categories (1) and (2) to analyze environment–trait relationships, while seven articles adopted strategy (3), and 15 studies adopted strategy (4). Mostly community-weighted means, functional diversity indices, and/or raw traits were used in statistical analyses.

While most articles cited other studies to state how rotifer traits were assigned, eight studies did not cite any source for trait assignment. Among citations for trait assignment, Obertegger et al. [20] were most often cited ($n = 24$), followed by Obertegger and Manca [44]

($n = 10$), and Karabin [35] ($n = 6$). Older literature such as Pourriot [45,46] was cited only once.

Citations and explanations in the text of an article do not implicitly mean that a study can be repeated. Reconstruction of trait assignment was possible for most studies ($n = 36$; Supplementary Table S1) based on tables, figures, or text within the article, while for five studies the respective information was placed into Supplementary Material, and for 25 studies trait assignment was not possible to reconstruct. For two articles, errors in rotifer trait assignment were found. When the guild ratio or feeding guilds according to Obertegger et al. [20], Obertegger and Manca [44], and/or Smith et al. [34] were used ($n = 13$), we trustfully believed that traits were correctly assigned, but when size or biomass was further mixed with traits (e.g., [47,48]), trait assignment was unknown. We found that when trophi types were combined with size, an unambiguous reconstruction of traits was impossible. For example, Palazzo et al. [37] established a classification into small, medium, and large, which was related to absolute size, and Wang et al. [49] used relative size based on quartiles, but Tavsanoğlu and Akbulut [50] did not provide an explanation for how they assessed size categories. Interestingly, Jannsson et al. [51] assigned to zooplankton, including rotifers, a complexity trait, probably based on behavioral and morphological diversity. Furthermore, O'Brien et al. [52] used fuzzy coding for zooplankton, including rotifer traits. Fuzzy coding is based on a scoring system that describes the affinity of a specific taxon to a certain trait category [53]. No information on the coding is provided in O'Brien et al. [52], and therefore its appropriateness cannot be assessed. An interesting example of aquatic functional diversity is the study of Neury-Ormanni et al. [54] who assembled a detailed trait matrix based on diverse attributes such as chemical preferences, life cycle, morphology, life history, physiology, and diet and feeding behavior for the meiofauna, including eight rotifer species.

Judgements on the utility of rotifer traits were mixed, and in the case of merging rotifer traits with other zooplankton taxa, a judgement was impossible. Of the remaining studies ($n = 48$), few studies criticized the performance of rotifer traits in discerning environmental differences [55–57].

3.2. Rotifer Trait Matrix

Based on our literature review, we compiled a trait matrix for the 138 rotifer genera (Supplementary Table S2) reporting family, habitat type, trophi type, presence of lorica and foot, predation defense attributes, corona type, and feeding traits. We can provide Supplementary Table S2 only as Supplementary Material because of its huge size but concomitantly this allows for easy access to filtering within traits and integration of data into analyses. Considering the array of different habitat types that rotifers occupy, we summarized the information into eight categories (Supplementary Table S2), a necessity for statistical analyses. We submit these categories as a proposal that may be evaluated by other researchers who may find a better way of classification based on the habitat information we provided and the composition of the genera they are studying. For example, some genera possess species that are free swimming in the juvenile state and sessile as adults (i.e., families Atrochidae, Collothecidae, and Flosculariidae). Several genera form intra- or inter-specific colonies or inhabit the colonies of other species, these include *Acyclus*, *Beauchampia*, *Collotheca*, *Cupelopagis*, *Floscularia*, *Lacinularia*, *Lacinularoides*, *Limnias*, *Octotrocha*, *Pentatrocha*, *Ptygura*, *Sinantharina*, and *Stephanoceros* [58]. Sessile taxa sometimes can be dislodged, either by currents or by the action of towing a net through a bed of hydrophytes. For the sake of simplicity, we merged these genera into the category of littoral periphytic, even though four genera (*Collotheca*, *Lacinularia*, *Ptygura*, and *Sinantharina*) also possess planktonic species. Similarly, psammic genera were merged into the category of littoral periphytic. Limnoterrestrial taxa live on mosses, lichens, leaf litter, and soil, but can also be found in the littoral and psammon. Moreover, in this case, these genera were merged into the category of littoral periphytic.

Researchers have categorized rotifer trophi into eight basic forms with several transitions and combinations (e.g., Koste [59]). We reported trophi types according to Koste [59] and in the case of transitional forms (e.g., *Microcodon*: virgate, but a transition to malleate; Koste [59]) reported the principal form seen in the genus (i.e., virgate for *Microcodon*). The rotifer cuticula can be stiffened to form a lorica or can be soft (illoricate). We acknowledge that some genera possess a lorica that can be partially stiffened (e.g., *Encentrum*: ‘cuticula mostly soft, only sometimes partially stiffened’; Koste [59]). To avoid the splitting of genera into many categories with few entries, we considered only two categories of lorica types (loricate, illoricate), and classified a genus as loricate only when the whole body is stiff and not only parts of it.

According to Koste [59], Monogonont rotifers show six different corona types (*Asplanchna*-, *Collotheca*-, *Conochilus*-, *Euchlanis-Brachionus*-, *Hexarthra*-, and *Notommata*-type) with a few genera not possessing any corona in the adult state (i.e., *Atrochus*, *Acyclus*, *Balatro*, and *Cupelopagis*). However, in the general description of Notommatidae, Koste [59] states that taxa possess a *Notommata*- or *Dicranophorus*-type corona, but states that only the genus *Wigrella* possesses the *Dicranophorus*-type corona. Koste and Shiel [60] also describe six different corona types for Monogononta and attribute to Notommatidae and Dicranophoridae only the *Notommata*-type corona. Finally, Fontaneto and De Smet [31] differentiate seven corona types (the six originally from Koste [59] plus the *Dicranophorus*-type) attributing to Notommatidae a *Notommata*-, *Dicranophorus*-type, or *Asplanchna*-type corona and to Dicranophoridae the *Dicranophorus*-type corona. For most Dicranophoridae, Koste [59] states only that the corona is vertically tilted. Thus, a corona type that might seem to be an easily defined trait turned out to be quite complicated for some taxa. We took a pragmatic approach and classified corona types of Monogononta according to Koste and Shiel [60] and cross-checked with Koste [59]. Thus, only in the case of *Eosphora*, family Notommatidae, we stated *Asplanchna*-type corona because Koste [59] describes it as reduced with few cilia. For Bdelloidea, three corona types have been differentiated [31]. Therefore, we differentiated 10 corona types (i.e., six for Monogononta, three for Bdelloidea, and one for Seisonidae); the newly described genus *Coronistomus* shows a similar corona as species in the family Philodinavidae [32].

Classification of rotifers into feeding guilds/trophic groups is based on several criteria. Rotifers are often divided into predators and filter feeders (cf. [26]). Rotifer predators or raptors are defined in several ways: species without any buccal tube and whose mouth opening leads directly to the mastax [36]; rotifers showing a grasping action and having access to larger food particles [46]; rotifers actively grasping food (also known as macrofilter feeders) and *Asplanchna* [35]; large-bodied rotifers that consume relatively large prey items individually [34]; and rotifers that feed on a large range of algae, protozoans, and metazoans [26]. The terminology carnivorous (e.g., *Eothinia*: [59]; *Abrochtha*: [61]) refers to zoophagous rotifers that feed on other animals such as rotifers or oligochaetes. Definitions regarding non-predatory rotifers are also diverse. In filter-feeding rotifers, mouth size determines the size of particles ingested [46]. Karabin [35] defines microfilter feeders (or sedimentators) based on trophi types and identifies several subgroups linked to the particle size ingested. Smith et al. [34] define microphagous rotifers as rotifers that consume multiple small prey nearly simultaneously. Gilbert [26], instead of focusing on how species gather food, proposes four, broad overlapping categories based on the types and sizes of food ingested, and rotifers feeding on algae are found in all four categories [26]. Palazzo et al. [37] discriminate suctors, predators, and filter feeders, but do not give a proper definition for this separation except for a trophi-based classification. In benthic and soil rotifers (e.g., *Adineta*), the terminology of scrapers is applied in contrast to filter feeding [62]. These taxa feed on biofilms [63] and may nevertheless be classified as microfilter feeders. Monakov [36] pursued a different strategy; he discriminated three types of feeding traits by (1) how food is captured, (2) by food type ingested, and (3) by particle size. For (1), Monakov [36] discriminates (i) rotifers whose corona creates strong currents that guide and concentrate food particles at the mouth opening and have malleate or ramate trophi;

(ii) rotifers that actively capture food and have virgate or forcipate trophi; (iii) sessile species whose infundibulum encloses food. For (2), Monakov [36] discriminates bacteriophages, tryptophages, phytophages, and/or zoophages, and for (3), he discriminates micro- or macrophages, with a separating threshold around 20 μm .

Several researchers grouped rotifer genera into specific feeding categories with different genus coverage. Neglecting subgroups, all rotifer genera can be assigned to a trophic group sensu Karabin [35], except those with a forcipate and cardate trophi for which Karabin [35] did not state a trophic group. Smith et al. [34] classified rotifers into microphagous and raptorial taxa based on trophi types alone, and because they were defined for all trophi types, except for ramate trophi, they can be applied to any rotifer genus or species except Bdelloidea. Similarly, Palazzo et al. [37] discriminate trophic groups of rotifers based on trophi types alone allowing for complete coverage. Karabin [35] classified 52 genera into trophic groups; Monakov [36] classified 49 genera into feeding mechanism types based on four out of nine trophi types; Monakov [36] classified 22 genera into feeding types; and Gilbert [26] classified 21 genera into feeding-niche categories (Supplementary Table S2). Therefore, all these classifications are not complete for all rotifer genera except in the case where trophi types were used (Palazzo et al. [37] excluding ramate trophi; Smith et al., 2009).

In comparing feeding traits classifications for Monogononta (Supplementary Table S2), we did not seek a complete comparison of all possible combinations of comparisons and focused on the rotifer classification sensu Smith et al. [35] and Monakov [36]. Microphagous rotifers sensu Smith et al. [34] are equivalent to microfilter feeders sensu Karabin [35], microphages sensu Monakov [36] and microphagous sensu Gilbert [26], and polyphagous rotifers sensu Gilbert [26] except for three genera (i.e., *Epiphanes*, *Notholca*, and *Rhinoglena*). Raptorial taxa sensu Smith et al. [34] are equivalent to macrophages sensu Monakov [36], macrofilter feeders/raptors sensu Karabin (1985), and macrophagous algivores sensu Gilbert [26] and macrophagous omnivores/predators sensu Gilbert [26]. Microphages sensu Monakov [36] are equivalent to microfilter feeders sensu Karabin [35], microphagous sensu Smith et al. [34], and microphagous sensu Gilbert [26], and polyphagous sensu Gilbert [26]. Macrophages sensu Monakov [36] are equivalent to macrofilter feeders/raptors sensu Karabin [35], raptors sensu Karabin [35] except for 6 out of 16 genera, raptorial sensu Smith et al. [34] except for 5 out of 22, and macrophagous algivores sensu Gilbert [26], macrophagous omnivores/predators sensu Gilbert [26], and polyphagous rotifers sensu Gilbert [26] (Supplementary Table S2). Therefore, feeding traits classifications sensu Smith et al. [34] showed vast accordance among classifications while that of Monakov [36] showed less accordance.

In providing feeding trait information for all rotifer genera, we stuck to classifications by trophi types [34–36] and by food types [26,36], which required a rigorous literature search to develop a trait matrix that was as complete as possible. For this aim, we additionally classified rotifers with malleoramate trophi as rotifers whose corona creates strong currents that guide and concentrate food particles at the mouth opening. In several cases, missing information could be inferred by examining other categories. For example, *Gastropus* spp. are macrophagous algivores sensu Gilbert [26] and consequently may be inferred to be phytophages sensu Monakov (2003). Collotheid rotifers were classified as raptors even though the terminology ambush predators might better describe their feeding behavior. This is because collotheid rotifers possess an expanded and elongated corona of lobes and cilia lobes that form a fyke-like structure by which mobile prey (both zoo- or phytoplankton) are guided into an enlarged, funnel-shaped infundibulum [64]. Parasitic species, whether endo- or epibionts, were not classified into feeding niche categories sensu Gilbert [26], feeding types sensu Monakov [36], and the category “particle size ingested” sensu Monakov [36].

3.3. Clustering of Morphological Rotifer Traits

Based on indices of cluster performance, we selected divisive clustering to create 10 clusters (Figure 2, Supplementary Material Table S3). Cluster 1 genera ($n = 21$) were almost all Bdelloidea (except for *Ceratotrocha*) and Seisonidae. Cluster 2 genera ($n = 4$) were all illoricate and possessed uncinuate trophi (except for *Ceratotrocha*). Cluster 3 was the largest cluster (46 genera from 11 families) and comprised mostly littoral or periphytic genera with a *Notommata*-type corona. Cluster 4 genera ($n = 7$) were all endobionts. Cluster 5 genera ($n = 11$) all possessed a *Hexarthra*-type corona. Cluster 6 genera ($n = 31$) all had malleate trophi and nearly all possessed a *Euchlanis-Brachionus*-type corona; the exception was *Bryceella*. Cluster 7 genera ($n = 6$) were all loricate lacking an obvious defense. Clusters 8 ($n = 2$) and 9 genera ($n = 4$) were quite similar (i.e., illoricate and planktonic or semi-planktonic genera); the difference in these two was genera with *Asplanchna*-type corona and no foot or those with a foot. Cluster 10 genera ($n = 6$) were all illoricate, planktonic, or semi-planktonic, and had malleoramate trophi.

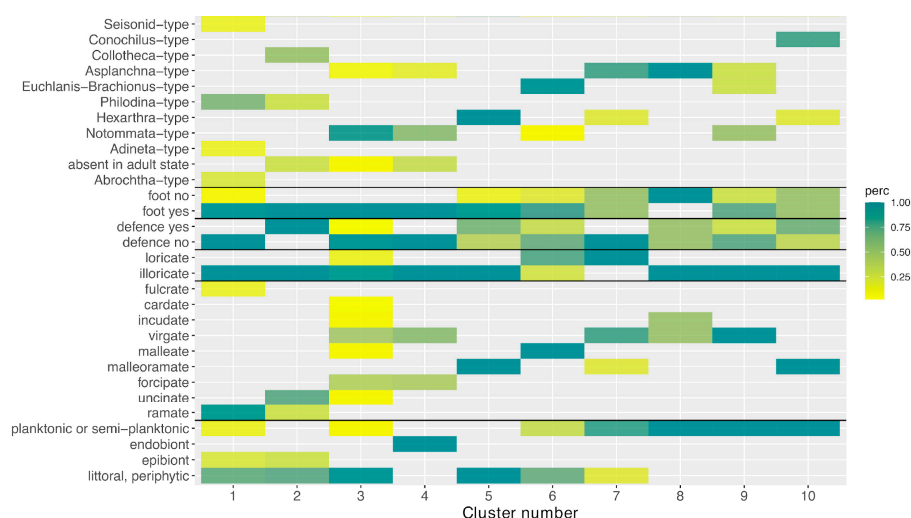


Figure 2. Heatmap of percent distribution of morphological traits within clusters 1 to 10 as assembled by hierarchical, divisive clustering. Black horizontal lines separate different traits; within traits, numbers sum up to 100%.

4. Discussion

The number of trait-based rotifer studies has increased in recent years, and these studies indicate the explanatory power of traits to indicate environmental change. An important issue in trait-based research is the question of which traits to consider [19,56]. For rotifers, morphological attributes and feeding traits are generally used, while physiological and phenological traits are almost never assessed because those features are temperature dependent and critical information is missing for most species. Morphological traits are often those that can be easily assessed [21,22], and, in that way, a trait approach is more indulgent when faced with a coarse taxonomic resolution because many functional attributes are shared among closely related species. The morphological traits used usually relate to rotifer life history strategies such as locomotion, predation, feeding, and habitat preferences. Except for habitat, the traits we summarized are generally functional traits that are part of an organism's phenotype in response to environmental factors [65].

The assembled morphological traits and habitat preferences summarize the potential rotifer niche at the genus level. Habitat preferences are linked to abiotic (e.g., temperature variability, mixing, and light exposure) and biotic (e.g., food resources, predation exposure, and competition) factors that collectively determine major elements of the rotifer niche. Therefore, habitat preferences may be considered an overarching trait, while morphological traits address specific aspects of rotifer life. Predation defense is achieved by a variety of methods including spines, different swimming behaviors that lead to escape, and gelati-

nous sheaths [66]. Specifically, loricate species might be better protected against predation with appendices enhancing protection [67], even though the presence of spines is subject to phenotypic variability based on predator abundance [68]. The corona is important for locomotion [59] and perception of prey items [69], and is linked to mastax and trophi structure [70], both of which influence food types ingested [35]. In our analysis, the seemingly easy trait of corona type turned out to be quite problematic with unclear descriptions in several sources; this problem urged us to consult Koste [59] the cornerstone work for aquatic biologists [71]. We acknowledge that the consultation of Koste [59] is challenging because it is written in German and even with Google Translate, a clear understanding is sometimes difficult to achieve. On the other hand, assigning taxa to trophi types was relatively easy because they do not change much within genera and are clearly described. Moreover, the action of how trophi process food is quite different among trophi types [72], and it can be speculated that the presence of different trophi types is linked to food resources. The presence or absence of a foot is also related to lifestyle characteristics; e.g., planktonic species often do not possess a foot, while sessile species do [31]. To simplify our trait matrix, we did not discriminate between a swimming, creeping, sessile, or jumping foot [31]. While we considered several traits, certain traits were not. Rotifer biomass or body size is an important trait because it is linked to rotifer food threshold levels [29]; however, it depends on study-specific measurements, and in case of missing information, literature data can be used with the geometric mean as an average estimate for species or genera. Other traits related to pH tolerance or saprobic valency might not be useful rotifer traits; the former because most rotifers show a wide tolerance [73] and the latter because of high intra-genera variation [74].

Our genus-level trait matrix, while providing information on the rotifer niche, may, in certain cases, be misleading by obscuring species-specific details. For example, within *Epiplanes*, both loricate and illoricate species are found, and within the genus *Floscularia*, subtle trophi differences are present [75]. Therefore, a species-specific assessment might be necessary to gain a better trait assessment in certain cases. We took a pragmatic approach and reported obvious characteristics that are valid for the majority of species within a genus. While intraspecific trait variation [76] might bias the assessment of a trait matrix, this aspect is mostly valid for numerical traits such as body mass and size, while other morphological traits are generally stable through time and space. Therefore, we are confident that our trait matrix is the best that can be obtained.

While morphological traits such as corona and trophi types can be interpreted as proxies for food resources, they cannot indicate any food types or sizes consumed. Therefore, traits summarizing feeding aspects have been gaining interest. With respect to the relative ease of assessing morphological traits, assessment of feeding traits requires expert knowledge and expert judgement. Different authors classified rotifer feeding traits [26,34–37,46], and different opinions exist on the classification of feeding traits. Wallace et al. [30] note that the distinction between predatory and herbivory rotifers is not always easy, and thus they advise considering the way how rotifers process food rather than what they eat. The feeding guilds sensu Smith et al. [34] and Palazzo et al. [37] followed this advice and took a pragmatic approach in classifying rotifers into gross feeding guilds based on trophi structure alone. In contrast, Gilbert [26] suggests that the rotifer food niche is best described by its food and rotifer feeding efficiency because there is much overlap in the diets of rotifers designated as microphagous or raptorial and species can shift between different food types. We attempted to provide feeding traits for all 138 rotifer genera, but quickly realized that detailed information on food sources sensu Gilbert [26] is missing for most genera (79 genera out of 136; Supplementary Table S2). However, applying less detailed feeding categories (e.g., sensu Monakov, [36]) was also not possible because that information was not available for many genera. While for environmental factors such as temperature or salinity, observational data can be used to determine sensible ranges, knowledge of food sources relies on laboratory experiments or observations of gut contents. This type of information is less common than environmental data, and when this

information is available, it is not without inherent problems. For example, Pourriot [46] states that the bdelloid *Habrotrocha thienemanni* is purely bacteriophage, while Ricci [77] maintained a culture of *H. elusa vegeta* with algal food; therefore, species might switch to a less preferred food and survive albeit while only maintaining a low population level or this is a species-specific difference, impossible to reflect in a genus-based trait matrix. Often in the case of missing data, statistical imputation methods are used but prove to be inappropriate in the case of rotifer feeding traits. Fuzzy coding of zooplankton traits [52] relies on a minimal understanding of rotifer feeding and cannot be applied when no information is available. Moreover, machine learning cannot be used because feeding guilds sensu Gilbert [26] or Monakov [36] cannot be inferred from morphological traits based on an underlying relationship. Only laboratory experiments can clarify whether a certain food source can sustain a viable population. Therefore, feeding guilds sensu Gilbert [26] or Monakov [36] can only be applied in statistical analyses when information for all taxa of the study community is available.

Classification of rotifer feeding guilds is difficult. In addition, for phytoplankton, the classification into functional groups poses problems leading to erroneous classifications [78]; therefore, Zhang et al. [79] proposed a method to derive habitat-specific phytoplankton templates. We suggest that rotifers prosper in environments where their feeding tools (i.e., corona and trophi types) best fit, and therefore, we posit that feeding guilds could be abandoned in favor of morphological traits. Traits are the basis for any statistical analysis of trait-based ecology. We suggest that using single traits as dependent variables is a simplistic approach neglecting the multi-dimensionality of the rotifer niche. Multivariate analyses that consider all traits are to be preferred. A step further in the consideration of the trait space is the construction of groups based on clustering [80]. The construction of groups also allows the combination of rotifers with other zooplankton groups. We grouped rotifer genera based on morphological traits and found a gross separation of planktonic from littoral genera (clusters 1 to 6 versus clusters 7 to 10). The clustering result further outlined the combination of traits that are not random, an important point when creating artificial communities to test for assembly processes [22]. *Bryceella* clustering with genera of *Brachionus*-*Euchlanis*-type corona forced us to check the trait assignment for this genus. We acknowledge that this genus has a special corona with cirri with which animals can move [59].

Recently, Litchman et al. [81] advised using traits across trophic levels to gain insights into general roles, but to do so with rigor requires a complete list of traits. Therefore, such approaches are rare, and few studies attempt to consider more than just one trophic level. For example, Colina et al. [82] found group-specific feeding preferences of zooplankton linked to phytoplankton traits. Lansac-Tôha et al. [83] found low levels of cross-taxon (from algae to zooplankton and fish) congruence of taxonomic and functional beta diversity. Even though not directly related to studies across trophic levels, small bacterivorous and detritophagous rotifers increase with trophic state [84] indicating a link between algae and rotifers.

Trait-based ecology advances our understanding of ecological dynamics in a rapidly changing, human-influenced world [85] and is mentioned among the five future challenges for plankton diversity [86]. Several topics may be studied by trait-based analysis such as (1) trophic mismatch [87], (2) natural [88] and artificial [89] stresses from acids, (3) changes in salinity [90,91], (4) experimental studies of effects of heavy metals [92] and organics [93,94], (5) effects of ingesting nanoparticle microplastic pollutants [95,96], (6) combinatorial effects [97–99], and (7) functional homogenization [95]. We hope that our assembled trait matrix paves the way for more research on rotifer functional diversity, diminishes the misclassification of rotifer genera into trait categories, and enables studies across trophic levels. We, furthermore, believe that the open-source matrix on rotifer traits that we provide here will promote research in the above-cited research areas. Researchers may refine the data in our matrix with additional information gleaned from the literature or improve them as new genera are described and/or new characters are recognized. We also

encourage researchers to disclose their trait assignment to allow for constructive discussion and advancement of rotifer science.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w15081459/s1>, Table S1: List of the 66 inspected studies with their publication year, studied habitat, country of provenance, journal name, impact factor, quartile rank, provision of traits, and application of the guild ratio [20–22,24,34,37,38,44,47–52,54–57,80,83,100–145]; Table S2: Trait assignment for the 138 genera of phylum Rotifera [31,32,59,60,64,77,146–192]; Table S3: Rotifer genera with their traits and their cluster number as assigned by hierarchical, divisive clustering.

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