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Review Paper

Niche differentiation in rotifer cryptic species complexes: a review of environmental effects

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Abstract Adaptation to different ecological niches is considered one of the main drivers of species diversification, also in cryptic species complexes, notwithstanding their morphological stasis. We here review all the published information on ecological differentiation within cryptic species complexes within the phylum Rotifera. We found 177 instances of cryptic species identified genetically, published in 101 papers. Only a subset of the papers contained available information on ecological differences and only for two of the 54 known complexes, namely *Brachionus calyciflorus* s.l. and *Brachionus plicatilis* s.l., sufficient data were available for analyses of ecological differences. For the *B. calyciflorus* complex, *B. fernandoi* consistently occurred at a significantly lower temperature than the other species in the complex; no differences were found for other environmental variables. For the *B. plicatilis* complex, *B. paranguensis* occurred in waters with higher pH than the other species; no differences were found for other environmental variables. These results, even if preliminary and based on scattered information, reveal that adaptation to different ecological niches exists also between closely related species. Our aim is to showcase this

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interesting field of research spurring further detailed studies to focus on the mechanisms of ecological speciation using rotifer cryptic species as a model system.

Keywords Sibling species · Niche segregation · Ecological species concept · Rotifera

Introduction

Complexes of cryptic species are groups of taxa classified under one nominal species name due to their similar morphology even if there is evidence, mostly from DNA-based analyses, of them representing distinct evolutionary lineages (Bickford et al., 2007; Fišer et al., 2018; Struck et al., 2018). Species inhabit multidimensional niche spaces, which include species tolerances and requirements regarding environmental conditions, biotic interactions, and resource availability (Begon et al., 2006). Therefore, speciation is always associated with niche differentiation.

Studies focusing on cases of ecological speciation involving niche differentiation in sympatry (Coyne & Orr, 2004) reported spectacular cases of adaptive radiations in aquatic animals, for example, in whitefish in Switzerland (Bernatchez et al., 1999, 2010), cichlid fishes in Africa (Seehausen et al., 1999; Chapman et al., 2000; Seehausen, 2006), and amphipods in lake Baikal (Macdonald et al., 2005), with fast ecological and morphological differentiation between species. However, in cryptic species complexes, species retain their morphology in stasis, even when living in sympatry (Fišer et al., 2018). Ecological diversification could indeed evolve along niche axes (e.g. salinity, pH, or temperature) that are not related to morphology (Wiens & Graham, 2005; Losos, 2008; Wiens, 2011; Fišer et al., 2018).

In practice, scholars have revealed various niche differentiations involving a wide range of aquatic organisms. Luo et al. (2017) found the different species within the bloom-forming dinoflagellate *Akashiwo sanguinea* species complex bloom in different seasons, segregating in relation to distinct thermal optima. In crustaceans, Cheng et al. (2008) revealed that the estuarine copepod *Acartia tonsa* cryptic species complex comprises two clades living in contrasting salinity regimes, even if coexistence was observed in intermediate salinity conditions. Eisenring et al. (2016) investigated the habitat preference of the freshwater amphipod *Gammarus fossarum* cryptic species complex and found that the occurrence of the two clades can be distinguished by different anthropogenic influences on river ecomorphology. In amphibians, Rissler & Apodaca (2007) discovered that the patterns of genetic divergence between species of the black salamander *Aneides flavipunctatus* cryptic species complex are strongly associated with divergence in the climatic niche. In fish, Shen et al. (2015) studied the three cryptic species within the flathead mullet *Mugil cephalus* complex and found spatio-temporal and behavioural segregation represented by spawning time and ground and philopatry differentiation.

Recent technological advances have allowed discerning boundaries of cryptic species using DNA taxonomy and also integrative approaches from various genetic markers and advanced morphological and ecological observations (Bickford et al., 2007; Padial et al., 2010; Fontaneto et al., 2015; Struck et al., 2018; Vyskočilová et al., 2018; de Sousa-Paula et al., 2021; Yeom et al., 2021). Amongst the groups of aquatic animals with the highest level of occurrence of cryptic species, there is the Phylum Rotifera (Fontaneto et al., 2009; Gabaldón et al., 2017; Korbachech et al., 2023). Rotifers are microscopic animals living in diverse habitats such as freshwater, brackish, marine environments, soil, mosses, lichens, and glaciers and represent excellent model organisms for studying ecological differentiation and species divergence (Serra & Fontaneto, 2017). Whilst historically considered to have a ubiquitous biogeographic distribution (Dumont, 1983; Fontaneto et al., 2012), DNA taxonomic analyses revealed the occurrence of cryptic species complexes that could mask geographically restricted taxa not distinguishable using morphology (Fontaneto, 2014; Papakostas et al., 2016; Gabaldón et al., 2017). Yet, rotifers are also known to

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be dispersed due to their long-surviving resting stages (Fontaneto, 2019); the existence of species within a complex with equal broad distribution of the complex itself (e.g. Fontaneto et al., 2008; Mills et al., 2017) implies that rotifer populations may not be geographically isolated. Thus, sympatric speciation may be a more likely scenario for rotifers rather than allopatric speciation (e.g. Papakostas et al., 2016; Michaloudi et al., 2018).

Co-occurrence of closely related species within cryptic species in rotifers revealed that species often coexist in the same location due to differentiated environmental factors (e.g. salinity, temperature) and/or biotic interactions (e.g. resource competition, predation) (Gabaldón et al., 2017), with fluctuations in both time and/or space. For instance, the occurrence of different species in the *Ascomorpha ovalis* complex is defined by altitude (García-Morales & Elías-Gutiérrez, 2013). Temperature limitations seem to be the factor defining species co-occurrence in the *Brachionus calyciflorus* species complex (Li et al., 2010; Xiang et al., 2010, 2011a, b; Wen et al., 2016; Zhang et al., 2018). These species typically succeed each other seasonally with overlap under intermediate temperatures. Within the *Brachionus calyciflorus* species complex, *Brachionus calyciflorus* s.s. Pallas, 1776 and *Brachionus dorcas* Gosse, 1851 occupy warmer niches (summer period) and *Brachionus fernandoi* Michaloudi, Papakostas, Stamou, Nedela, Tihlariková, Zhang & Declerck, 2018 is found in colder ones (Zhang et al., 2018). Other environmental parameters such as chlorophyll a concentration were also suggested to be differently exploited amongst the *B. calyciflorus* cryptic species (Li et al., 2010).

Overall, the best available information regarding the mechanisms that allow cryptic species coexistence comes from the *Brachionus plicatilis* complex (Gabaldón et al., 2017). The *B. plicatilis* complex comprises 15 species (Mills et al., 2017), of which six inhabit saline ponds in Spain (Gómez et al. 2002, 2007) and subsets of these six species commonly co-occur in the same habitat (Ortells et al., 2003; Gómez, 2005). According to information present for the species complex, when species differ in body size, niche differentiation is related to abiotic and biotic factors. Cryptic species characterized by different body sizes developed specialization to different microalgae species enhancing food partitioning and thus differential use of resources, promoting their coexistence (Ciros-Pérez et al., 2001). Predation was also found to be size dependent with smaller species being more vulnerable to predation (Lapesa et al., 2002, 2004; Ciros-Pérez et al., 2004). On the contrary, in case of species with almost identical body size, niche differentiation may be mediated by their different physiological responses to fluctuating environments, e.g. related to temperature, salinity, and oxygen concentration (Gabaldón et al., 2017; Serra & Fontaneto, 2017; Walczyńska & Serra, 2022), together with divergence in life-history traits related to diapause (Gabaldón et al., 2017).

In this study, we refer to the idea of niche differentiation sensu MacArthur (Walter, 1991), which refers to species dividing the available resources as a consequence of being limited by different biotic and abiotic factors. Our model organisms are the cryptic species complexes from Rotifera. We collected and reviewed all the available information on the environmental conditions behind the occurrence of sister species within cryptic species complexes in rotifers. Thus, our goal was to gain deeper insight into the ecological facets of cryptic diversity, focusing on the description of the patterns of ecological differences to allow future studies to get reliable data in order to eventually infer the processes involved in speciation, shaping biodiversity (Fišer et al. 2018; Marrone et al. 2023), analysing cryptic species complexes in rotifers as a rich and diverse test case.

Methods

A literature search was performed through academic databases, such as Web of Science, Scopus, Zoological Records, and Google Scholar, with keywords (rotifer* AND (cryptic OR DNA taxonomy OR sibling OR hidden)) and all the retrieved papers downloaded and analysed. We retained only papers dealing with Rotifera in the traditional meaning of the term, which includes Bdelloidea, Monogononta, and Seisonidea, but not the parasitic Acanthocephala (Sielaff et al., 2016). We set a temporal limit to the last 30 years, starting from the approximate period when the first cryptic species complexes were identified in rotifers (Fu et al., 1991a, b).

All retrieved papers were screened for the presence of data and/or analyses using genetic data to identify complexes of cryptic species in rotifers. Papers simply mentioning cryptic species complexes without using genetic analyses were not included in the dataset. For the complexes that have been resolved and are now considered complexes of pseudocryptic species (sensu Korshunova et al. (2017) and Struck et al. (2018)), distinguishable also from detailed morphological analyses, the identification of (pseudo) cryptic taxa within the complex was considered valid even in the absence of additional genetic data and analyses and the manuscripts considered for further screening. The only currently resolved cryptic species complexes in rotifers are *Brachionus calyciflorus* s.l., with four described species, *B. calyciflorus* s.s., *B. dorcas*, *Brachionus elevatus* Michaloudi, Papakostas, Stamou, Nedela, Tihlariková, Zhang & Declerck, 2018, and *B. fernandoi* according to Michaloudi et al. (2018), and *Brachionus plicatilis* s.l., with fifteen species, six of which are already described as *Brachionus asplanchnoidis* Charin, 1947, *Brachionus ibericus* Ciros-Pérez, Gómez & Serra, 2001, *Brachionus manjavacas* Fontaneto, Giordani, Melone & Serra, 2007, *Brachionus paranguensis* Guerrero-Jimenez, Vannucchi, Silva-Briano, Adabache-Ortiz, Rico-Martinez, Roberts, Neilson & Elias-Gutierrez, 2019, *Brachionus plicatilis* s.s. Müller, 1786, and *Brachionus rotundiformis* Tschugunoff, 1921, and other nine with only an informal name, according to Mills et al. (2017), Michaloudi et al. (2017) and Guerrero-Jiménez et al. (2019). The results of the literature screening were also compared with lists provided in the two most recent reviews on rotifer cryptic species (Gabaldón et al., 2017; Kordbacheh et al., 2023).

Searching through the papers that were kept by the first screening, reliably identifying cryptic species complexes, we marked whether ecological data and/or analyses were available regarding cryptic species and their differences within a complex. We considered as valid ecological metrics only those that contained measurements of abiotic limnological variables (e.g. water temperature, pH, dissolved oxygen, nutrients, salinity), identification of habitat, biotic pressures (e.g. competition, predation), and lab experiments on food quality and quantity.

Focusing only on the two most studied cryptic species complexes, *Brachionus calyciflorus* s.l. and *Brachionus plicatilis* s.l., we further screened the retained papers and any other paper we had from the overall literature search to obtain actual raw data on environmental measurements for each species within the complexes, intending to describe the ‘niche’ of each cryptic species in the complex and compare whether the ecological requirements of each species could be narrower than those of the whole complex and if significant differences could exist between species within each complex. The rationale for the search was to gather data to perform quantitative analyses of convex hulls or hypervolumes (Blonder, 2018; Mammola et al., 2021), as already performed on rotifers (Jaturapruek et al., 2021), but not yet used to disentangle niche differentiation within cryptic species complexes. Unfortunately, due to the scattered and heterogeneous data that became available from the literature survey, we could not perform analyses on hypervolumes, but only for each variable separately. We kept only the variables that had available data for most of the species within a complex. We performed a series of ANalyses Of VAriance (ANOVA) tests with Tukey Honestly Significant Difference (HSD) post hoc tests to identify potential ecological differences between species within a complex using R v4.0.3 (R Core Team, 2022). Tukey HSD tests were performed with the default settings of the TukeyHSD function of the stats package v4.0.3. Model fit was checked with the R package performance v0.6.1 (Lüdecke et al., 2021): all models passed the assumptions of normality of residuals, absence of outliers, homoscedasticity, homogeneity of variance, and influential observations (Lüdecke et al., 2021).

Results

We found 177 instances of cryptic species in rotifers (Bdelloidea and Monogononta) identified with genetic data, published in 101 papers (Table 1, Supplementary Table S1). No analyses on Seisonidea were found. Overall, 6 taxa were not identified to the rank of species complex but remained at genus or family rank, whereas the other 171 instances belonged to 54 proper cryptic species complexes; the most frequently studied complexes were *Brachionus plicatilis* s.l., with 40 papers, and *Brachionus calyciflorus* s.l., with 33 papers.

From the 171 instances of 54 cryptic species complexes, only in 53 instances potential ecological differences between cryptic taxa within the same complex were analysed (Table 1). Amongst the potential ecological differences between cryptic species,

Table 1 List of cryptic species complexes for which information on potential ecological differences between cryptic species exists

Cryptic species complex	References	Species identification	Variable
Brachionus calyciflorus	Papakostas et al. (2016)	*Brachionus calyciflorus* s.l	Food
	Schälicke et al. (2019)	*Brachionus calyciflorus* s.s. *and B. fernandoi*	Food
	Schälicke et al. (2020)	*Brachionus calyciflorus* s.s. *and B. fernandoi*	Food
	Li et al. (2009b)	*Brachionus calyciflorus* s.l.	Limnological
	Li et al. (2010)	*Brachionus calyciflorus* s.l.	Limnological
	Xiang et al. (2010a)	*Brachionus calyciflorus* s.l.	Limnological
	Li et al. (2014)	*Brachionus calyciflorus* s.l.	Limnological
	Wang et al. (2014)	*Brachionus calyciflorus* s.l.	Limnological
	Xiang et al. (2015)	*Brachionus calyciflorus* s.l.	Limnological
	Wen et al. (2016)	*Brachionus calyciflorus* s.l.	Limnological
	Xiang et al. (2017)	*Brachionus calyciflorus* s.l.	Limnological
	Paraskevopoulou et al. (2018)	*Brachionus calyciflorus* s.s. *and B. fernandoi*	Limnological
	Xu et al. (2018)	*Brachionus calyciflorus* s.l.	Limnological
	Zhang et al. (2018)	*Brachionus dorcas, B. calyciflorus* s.s.*, B. fernandoi*	Limnological
	Paraskevopoulou et al. (2020)	*Brachionus calyciflorus* s.s. *and B. fernandoi*	Limnological
	Zhang et al. (2015)	*Brachionus calyciflorus* s.l.	Pollution
	Xue et al. (2017)	*Brachionus calyciflorus* s.l	Predation, pollution
Brachionus plicatilis	Ciros-Pérez et al. (2001)	*Brachionus plicatilis* s.s.*, B. ibericus, B. rotundiformis*	Food
	Kostopoulou and Vadstein (2007)	*Brachionus plicatilis* s.s.*, B. koreanus, B. paranguensis*	Food
	Franch-Gras et al. (2017)	*Brachionus plicatilis* s.s.	Limnological
	Ortells et al. (2000)	*Brachionus plicatilis* s.l.	Habitat
	Malekzadeh-Viayeh et al. (2014)	*Brachionus plicatilis* s.s.*, B. 'Austria', B. 'Tiscar' and unidentified clones*	Habitat
	Moka et al. (2016)	*Brachionus koreanus*	Habitat
	Mills et al. (2017)	*Brachionus plicatilis* s.l.*, all the species in the complex*	Habitat
	Fu et al. (1991a, b)	*Brachionus plicatilis* s.l.	Limnological
	Gómez et al. (1995)	*Brachionus ibericus, B. plicatilis, B. rotundiformis*	Limnological
	Gómez & Snell (1996)	*Brachionus ibericus, B. plicatilis, B. rotundiformis*	Limnological
	Gómez et al. (1997)	*Brachionus ibericus, B. plicatilis, B. rotundiformis*	Limnological

Table 1 (continued)

Cryptic species complex	References	Species identification	Variable
	Derry et al. (2003a, b)	*Brachionus plicatilis* s.l.	Limnological
	Ortells et al. (2003)	*Brachionus plicatilis* s.s., *B. ibericus, B. rotundiformis, B. 'Tiscar', B. 'Almenara'*	Limnological
	Lowe et al. (2007)	*Brachionus plicatilis* s.s., *B. rotundiformis*	Limnological
	Montero-Pau et al. (2011)	*Brachionus plicatilis* s.s., *B. manjavacas*	Limnological
	Alcántara-Rodriguez et al. (2012)	*Brachionus plicatilis* s.s., *B. 'Mexico'*	Limnological
	Gabaldón et al. (2015a)	*Brachionus plicatilis* s.s., *B. manjavacas*	Limnological
	Gabaldón et al. (2015b)	*Brachionus plicatilis* s.s., *B. manjavacas*	Limnological
	Kim et al. (2017)	*Brachionus plicatilis* s.l.	Limnological
	Walczyńska and Serra (2022)	*Brachionus plicatilis* s.s., *B. manjavacas, B. ibericus, B. rotundiformis, SM?*	Limnological
	Aránguiz-Acuña et al. (2018)	*Brachionus paranguensis*	Pollution
	Lapesa et al. (2002)	*Brachionus plicatilis* s.s., *B. ibericus, B. rotundiformis*	Predation
	Ciros-Pérez et al. (2004)	*Brachionus plicatilis* s.s., *B. ibericus, B. rotundiformis*	Predation
Euchlanis dilatata	Kordbacheh et al. (2019)	*Euchlanis dilatata* s.l.	Limnological
Keratella cochlearis	Derry et al. (2003a, b)	*Keratella cochlearis* s.l.	Limnological
	Cieplinski et al. (2018)	*Keratella cochlearis* s.l.	Limnological
Lecane bulla	Walsh et al. (2009)	*Lecane bulla* s.l.	Limnological
Macrotrachela quadricornifera	Fontaneto et al. (2009)	*Macrotrachela quadricornifera* s.l.	Habitat
Polyarthra dolichoptera	Obertegger et al. (2014)	*Polyarthra dolichoptera* s.l.	Limnological
Polyarthra remata	Obertegger et al. (2014)	*Polyarthra remata* s.l.	Limnological
Polyarthra vulgaris	Obertegger et al. (2014)	*Polyarthra vulgaris* s.l.	Limnological
Rotaria rotatoria	Xiang et al. (2016)	*Rotaria rotatoria*	Limnological
Rotaria sordida	Fontaneto et al. (2009)	*Rotaria sordida* s.l.	Habitat
Synchaeta pectinata	Obertegger et al. (2012)	*Synchaeta pectinata* s.l.	Limnological
Synchaeta tremula	Obertegger et al. (2012)	*Synchaeta tremula* s.l.	Limnological
Testudinella clypeata	Leasi et al. (2013)	*Testudinella clypeata* s.l.	Limnological

Supplementary Table S1 reports the extended list with all cryptic species complexes that have been studied in rotifers, not clearly including ecological differences between cryptic species environmental metrics (including limnological variables, fluctuating environments, etc.) were the mostly used ones ($n=37$, mainly temperature and salinity), followed by habitat type ($n=6$) and food quality and quantity ($n=5$). Only occasionally differential responses to pollution ($n=3$) and predation ($n=3$) were included, with one study dealing with both.

The species with more data on ecological differences were *B. plicatilis* s.l. ($n=23$) and *B. calyciflorus* s.l. ($n=17$). All the previously mentioned ecological differences were studied, with special emphasis on salinity for *B. plicatilis* s.l. and temperature for *B. calyciflorus* s.l. The other cryptic species complexes, nine belonging to monogononta (*Euchlanis dilatata* s.l., *Keratella cochlearis* s.l., *Lecane bulla* s.l., *Polyarthra dolichoptera* s.l., *Polyarthra remata* s.l., *Polyarthra vulgaris* s.l., *Synchaeta pectinata* s.l., *Synchaeta tremula* s.l., and *Testudinella clypeata* s.l.) and three to bdelloids (*Macrotrachela quadricornifera* s.l., *Rotaria rotatoria* s.l., and *Rotaria sordida* s.l.), were included only in one or two studies each. No taxonomic identification is available for the cryptic species within the complexes. For these cryptic species complexes, no meta-analysis is possible at the moment, due to the lack of available data and taxonomic resolution. Amongst these cryptic species complexes, the only hint to a differential species-specific response to environmental features within a cryptic species complex seems to be related to phosphorus for the cryptic species of *Synchaeta pectinata* s.l. (Obertegger et al., 2014); none of the other studies was able to identify ecological differences between cryptic species within each complex.

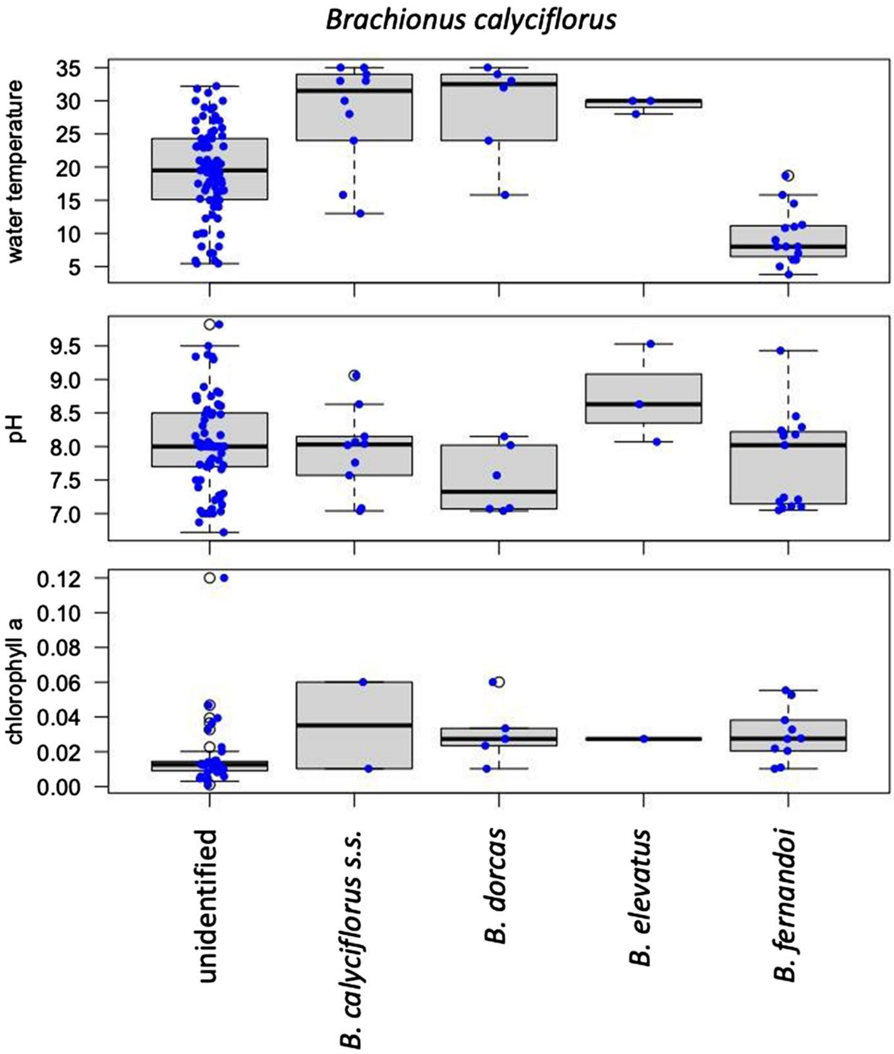
Regarding *B. calyciflorus* s.l., we gathered 128 records mentioning ecological data for the complex (Supplementary Table S2), but only 40 records framed the taxonomic backbone of the study according to the currently accepted knowledge of four species in the complex, namely *B. calyciflorus* s.s., *B. dorcas*, *B. elevatus*, and *B. fernandoi*. For these data, only water temperature, pH, and chlorophyll a had enough measurements to compare variability within and between species within the complex (Fig. 1). No significant differences between species were revealed for pH (ANOVA: $F_{3,30}=2.54$, $P=0.0751$) and for chlorophyll a ($F_{3,14}=1.36$, $P=0.2610$), but water temperature seemed to be different between species ($F_{3,30}=27.33$, $P<0.0001$), with *B. fernandoi* being different from the other three species (Tukey test: $P<0.0001$ for all pairwise comparison involving this species), always found at lower temperatures than the other species (Fig. 1).

Regarding *B. plicatilis* s.l., we found 82 records mentioning ecological data for cryptic species in the complex (Supplementary Table S2), with 69 of them that framed the taxonomic backbone according to the currently accepted knowledge of fifteen species in the complex, including data for eleven of them. For these data, only water temperature, pH, and salinity had enough measurements to compare variability within and between species within the complex (Fig. 2). No significant differences between species were revealed for water temperature (ANOVA: $F_{7,26}=0.17$, $P=0.9890$) and salinity ($F_{10,55}=1.34$, $P=0.2333$), but pH seems to be different between species ($F_{7,28}=3.85$, $P=0.0047$), with *B. paranguensis* being different from most of the other species (Tukey test: $P<0.05$ for pairwise comparisons with *B.* 'Tiscar', *B. ibericus*, *B. plicatilis* s.s., and *B. rotundiformis* but not with *B.* 'Almenara', *B. asplanchnoidis*, and *B.* 'Turkana'), even if only two measurement exist for this species (Fig. 2). All the information on environmental parameters that accompanied the sampling of rotifers belonging to so far known rotifer species complexes, which could not be used for analyses due to too limited information per complex, was collected in Supplementary Table S3. This table contains nearly 2,000 records covering all the information available to date in the literature.

Discussion

The first unambiguous evidence for the existence of cryptic species in rotifers was found in what was until then considered a species, *Brachionus plicatilis*, by Fu et al. (1991a, b). The following cryptic species complex was identified for *the Keratella cochlearis* complex by Derry et al. (2003a, b). In the following years, rotifers became one of the groups of animals with the highest occurrence of cryptic species complexes (Fontaneto et al., 2009). The most recent reviews listed 42 cryptic species complexes in rotifers (Gabaldón et al., 2017; Kordbacheh et al., 2023): the increased number we found in the current review, namely 54, is due to the inclusion of bdelloid rotifers in addition to a few more recent studies.

Fig. 1 Variability of environmental metrics (chlorophyll a, pH, and water temperature) in habitats where records of the *B. calyciflorus* species complex are available. Records are visualized for the four species in the complex and for the ones that used DNA taxonomy but did not manage to identify the four species, named 'unidentified'. The actual values of the observations are overimposed on the boxplots as blue dots to show sample size



Previous reviews on cryptic species in rotifers focused on reproductive barriers between species within a complex (Kordbacheh et al., 2023) and on levels of niche differentiation between sympatric cryptic species (Gabaldón et al., 2017). This is the first study that attempts quantitatively to assess whether ecological differentiation could have been one of the drivers of the speciation process within cryptic species complexes in rotifers. Our survey revealed that, despite the increasing number of instances of cryptic species in rotifers, scarce ecological information is currently available for these species. Except for the *Brachionus calyciflorus* and *Brachionus plicatilis* complexes, very few studies address potential ecological differences between cryptic species belonging to the same complex in the field and even when such attempts were performed, results were often negative. For example, Leasi et al. (2013) tried to disentangle the drivers of the differential occurrence of the cryptic species within the *Testudinella clypeata* species complex, a brackish water rotifer, but did not find any difference in salinity tolerance between species. Obertegger et al. (2012, 2014) analysed cryptic species in complexes of the genera *Polyarthra* and *Synchaeta* and identified only a minor effect of phosphorus levels and only for one species complex.

Previous studies on the *Brachionus calyciflorus* and *Brachionus plicatilis* species complexes were the only ones suggesting potential ecological differences between species. Our detailed meta-analysis performed on these two species, gathering all

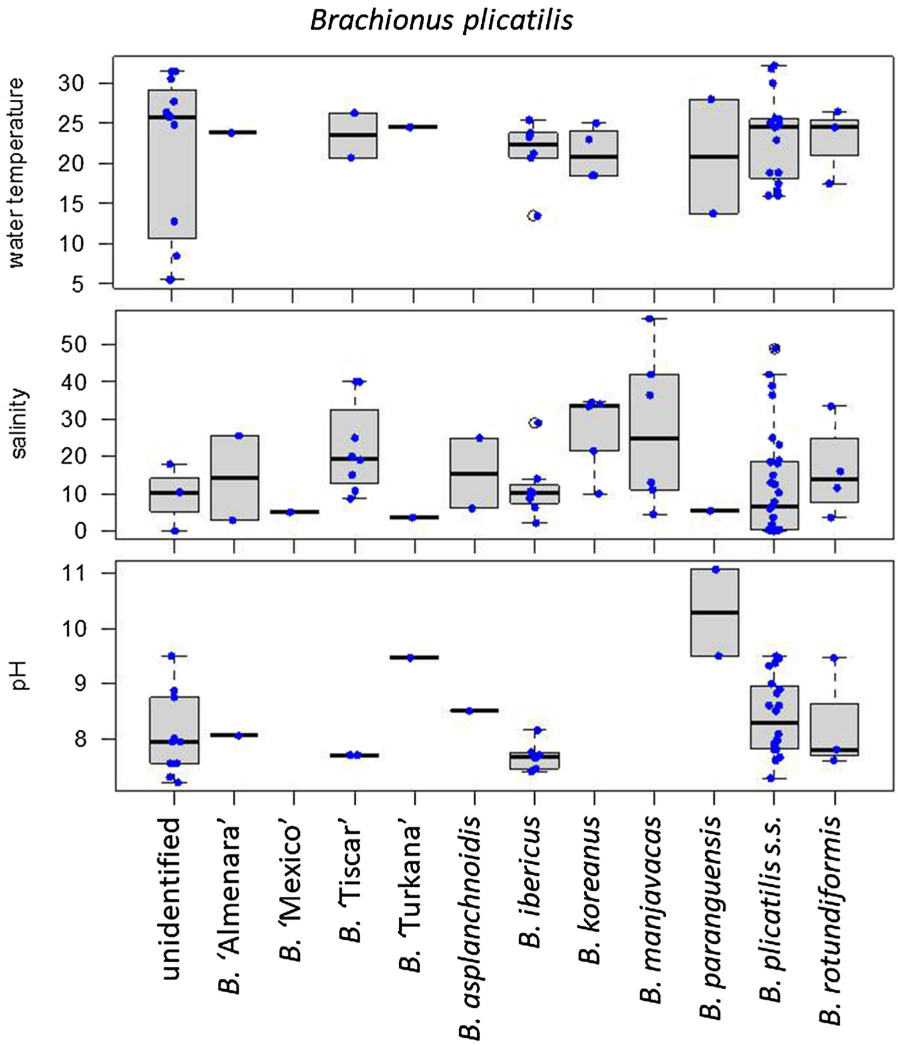


Fig. 2 Variability of environmental metrics (pH, salinity, and water temperature) in habitats where records of the *B. plicatilis* species complex are available. Records are visualized for eleven species in the complex and for those from studies that used DNA taxonomy but did not manage to identify the species, named 'unidentified'. The actual values of the observations are overimposed on the boxplots as blue dots to show sample size

available information on environmental characteristics retrieved from published papers, indeed confirmed that some of the cryptic species may be adapted only to a narrow range of values for some of the environmental features.

For the *B. calyciflorus* species complex, seasonal successions, potentially associated with differences in temperature adaptation, were already identified in the field in China (Zhang et al., 2018) and confirmed in laboratory experiments on life-history traits (Zhang et al., 2019; Paraskevopoulou et al., 2020) and on thermal tolerance (Paraskevopoulou et al., 2018). The results of our meta-analysis support that *B. fernandoi* is found in the field at lower temperatures than the other species in the complex. In a recent study, sequence divergence of the heat shock protein 40 gene (HSP40 kDa), a gene associated with thermal tolerance in *Brachionus* (Smith et al., 2013), was studied amongst the cryptic species within the *B. calyciflorus* species complex (Kiemel et al., 2022). The study revealed a divergent sequence evolution of HSP40kDa between the thermotolerant *B. calyciflorus* s.s. and the thermosensitive *B. fernandoi*. Selection analysis suggested that *B. calyciflorus* s.s. retained ancestral features in the HSP 40 kDa from which *B. fernandoi* diverged through positive selection (Kiemel et al., 2022). It is known that the HSP40 KDa is closely tied to thermal tolerance (Smith et al., 2013), thus it is likely that the most recently evolved trait is "thermotolerance loss". Given that hybridization has been observed between *B. calyciflorus* s.s. and *B. fernandoi* (Kiemel et al., 2022), it is plausible that the occupation of distinct temporally isolated niches based on different temperature tolerances may act as a pre-zygotic isolation mechanism, thereby promoting the integrity of species boundaries and facilitating the process of speciation (Kiemel et al., 2022; Kordbacheh et al., 2023). To further explore the role of temperature in shaping the occurrence and distribution of the species within the *B. calyciflorus* complex, it would be worthwhile to investigate the possibility of a biogeographical gradient associated with latitude, which could be connected to variations in water temperature.

Regarding the *B. plicatilis* species complex, the situation is more intricate, involving 15 different species (Mills et al., 2017). Furthermore, the complex was first identified as a group of separate species 30 years ago, in contrast to the *B. calyciflorus* complex, which was clearly identified as a cryptic species complex only within the past decade. Differential ecological responses between co-occurring species of the *B. plicatilis* complex are well known, with temperature and salinity identified as key factors already from the 1990s (Gómez et al., 1995, 1997). The crucial role of these two parameters was confirmed later in both laboratory and field studies (Ortells et al., 2003; Campillo et al., 2011; Montero-Pau et al., 2011; Papakostas et al., 2013; Gabaldón et al., 2015a, b). Additionally, predatory pressure was shown as a factor affecting the species coexistence and seasonal succession in three species from this complex (Lapesa et al., 2002). Recently, oxygen availability was suggested to play a role in species distribution and phenotypic plasticity in five *Brachionus* species representing the complex (Walczyńska & Serra, 2022). Finally, environmental unpredictability was found to be an important factor affecting the reproductive strategy in *Brachionus plicatilis* s.s. (Franch-Gras et al., 2014, 2017; Tarazona et al., 2017; Colinas et al., 2023), suggesting its possible role in ecological interactions between species. Another main difference between species in the complex is that, for example, *B. asplanchnoidis* has always been found only in continental saltwater bodies, like soda pans and never in marine waters (Michaloudi et al., 2017; Mills et al., 2017), with a potential adaptation to differences in salt composition. Our results of potential differences in adaptation to pH in the complex may be related to the same idea, with different ionic compositions of water driving speciation process. Yet, the results of our study of *B. paranguensis* being potentially adapted to a higher pH that the other species is weak: only one measurement is currently available for this species on pH and no measurements at all exist for other species. An alternative possible interpretation of our result on the role of pH is that pH is positively correlated with the rate of photosynthesis, and therefore also with oxygen concentration (Wetzel, 2001). Lack of sufficient information on oxygen conditions has prevented us from distinguishing the role of each of these factors separately. What is sure is that some hints exist on the occurrence of ecological differences between species in the *B. plicatilis* complex. Surprisingly, ecological differences between species, as analysed in this study, are not so strong as they are known in the cases when species co-occur (see Gabaldón et al., 2017 for a review). Such discrepancy could be explained as another case of niche displacement in rotifers (Marrone et al., 2023), with co-occurring species partitioning resources more strongly than when not co-occurring.

Temperature is amongst the most relevant variables affecting living organisms (Johnston & Bennett, 2008), and other parameters like oxygen concentration, pH, and salinity depend on temperature. The complexity of organismal interactions with the environment and limited information on the environmental reference of species distributions make identifying responsible environmental conditions challenging (Torres-Dowdall et al., 2013; Pociecha et al., 2016).

Another potential driver of speciation within a complex could be related to geographical isolation (Coyne & Orr, 2004). No review exists on the effect of geography on differentiation between cryptic taxa in rotifer complexes; yet, evidence from the most studied complexes, suggest that neither in *B. calyciflorus* s.l. nor in *B. plicatilis* s.l. each cryptic species could have a more limited distribution than that of the whole species complex (Mills et al., 2017; Michaloudi et al., 2018; Yang et al., 2022).

Our summary reveals that studies on ecological differentiation of cryptic species complexes in rotifers are biased towards abiotic factors. To gain a more comprehensive view, further research is also needed on the biological networks of interactions. For example, differences between cryptic species in a complex could occur in food composition, parasite–host interactions (Gorbunov & Kosova, 2001), and coadaptation with predators. Previous studies on predator–prey interactions found differentiation in life-history strategy (e.g. attached and free-swimming life forms of *B. dorcas* when exposed to *Asplanchna* kairomone by Jiang et al., 2021), morphology (e.g. spine length and angle differentiation of the same clone of *B. calyciflorus* s.l. against *Asplanchna* exposure by Gilbert, 2018), and behavioural responses (e.g. floating behaviour differentiation of *B. calyciflorus* s.l. against *Asplanchna* exposure by Zhang et al. (2021) and Gilbert (2023)). Very little data exist on these topics for comparative analyses within cryptic species complexes.

More data and analysis are surely needed before any reliable inference could be suggested on the drivers of the process of speciation within cryptic species complexes representing different groups of organisms. We are still far from understanding the patterns of ecological differences between species; only after a clear identification of the patterns found in the field between cryptic species within a complex we could start to speculate on the mechanisms involved in the speciation processes. Useful examples are coming from the differential thermal response of *B. fernandoi* in the *B. calyciflorus* complex analysed in the frame of gene expression (Paraskevopoulou et al., 2020; Kiemel et al., 2022), and more studies along this line would be welcome in the near future.

Species coexistence is driven by niche differentiation, which depends on the species-specific tolerances to all the environmental variables they experience and by species interactions, which describe how the species relate to each other within the environmental space they occupy. Both biotic and abiotic facets of niche differentiation need to be taken into account to understand species diversification and biodiversity patterns. In this study, we mainly focused on niche differences between species within cryptic species complexes in rotifers, based on the available published information. Although our main finding is that at the moment there is not enough data to perform any rigorous ecological analyses, yet, we provide hints that the topic could be interesting and worth developing. Also, we point where the major gaps are and therefore we would like to encourage other researchers to fill those gaps, not only for the case of rotifers but also for other cryptic species complexes.

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Data availability All raw data used for the study are available in the main document and in the Supplementary Tables.

Declarations

Competing interests The authors declare that they have no competing interests.

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