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REVIEW

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The effect of microplastics on *Daphnia* fitness – Systematic review and meta-analysis

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Abstract

1. Micro/nanoplastics pose a new environmental threat to aquatic ecosystems. The model organism *Daphnia* spp. has been used in many exposure studies to investigate the effect of micro/nanoplastics on organism fitness. However, owing to variation in experimental approaches, it is difficult to compare the findings. The aim of our study was to systematically review the research on the effect of micro/nanoplastics on *Daphnia* fitness, identify research gaps and offer recommendations for future studies.
2. We synthesised 121 studies and extracted data for numerous categories concerning study design, micro/nanoplastic characteristics and ecotoxicological endpoints. 32 studies were included in a meta-analysis on the effect of micro/nanoplastics on *Daphnia* reproduction.
3. Existing research exhibits several limitations. The majority of experiments have been conducted exclusively using *Daphnia magna*, neglecting other species and leading to an inherent bias in the representation of the broader *Daphnia* genus. Then, these studies have predominantly used a single genotype of *Daphnia*, disregarding potential clonal variation. In addition, most experiments investigated only a single *Daphnia* generation, although the limited number of multigenerational studies available suggest an increasing toxicity trend with subsequent generations, even if there was no impact on the F_0 generation.
4. Regarding the types of plastics tested, the majority of studies focused on pristine, spherical microplastic particles, primarily composed of polystyrene, with particle sizes of <100 μm, and at concentrations >0.1 mg/L. This narrow focus limits the applicability of the findings to environmentally relevant scenarios, where micro/nanoplastics can take various shapes and composition, undergo aging and usually occur at lower concentrations than those used in the studies reviewed.
5. The primary *Daphnia* response variable assessed was mortality, followed by variations in reproductive traits or body size. The meta-analysis focusing on reproductive traits unveiled a consistent and adverse influence of micro/nanoplastics exposure on the production of offspring by *Daphnia*.

6. Future studies should test environmentally relevant concentrations of micro/nanoplastics, focus on smaller, lake-inhabiting *Daphnia* species, incorporate clonal variation and extend the scope to include multiple *Daphnia* generations. Moreover, recognising the complexity of real-world scenarios, we recommend integrating assessments of micro/nanoplastic effects with multiple stressors. By simulating such conditions, studies can yield insights that better mirror the complexities of ecological systems and provide a more accurate representation of the potential consequences of micro/nanoplastic pollution.

KEYWORDS
cladocerans, intraspecific variation, meta-analysis, nanoplastics, toxicity

1 | INTRODUCTION

Plastic production has been increasing since 1950 resulting in ever increasing amounts of plastic waste; it is estimated that plastic production will reach 600 million tons in 2025 (Priyadarshini et al., 2022). Out of all that plastic, only 9%–11% has been recycled, as reported by a recent OECD study (2022). Commonly used plastics are not biodegradable which leads to their accumulation and fragmentation (Barnes et al., 2009). If left in the environment, plastic breaks down into smaller particles, referred to as microplastics (<5 mm; Thompson et al., 2004) and nanoplastics (<100 nm: based on the European Commission definition for nanomaterial size; Mech et al., 2020), producing a new environmental threat. In the majority of scientific literature nanoplastics are particles which are of ≤100 nm in size, and we will adapt this definition for our review. However, the definition is still under debate and sometimes a 1,000 nm cut-off is being used (see Hartmann et al., 2019). Other than fragmentation sources of micro/nanoplastics in the environment, there also are industrially manufactured plastic particles, which have an increasing demand in various sectors such as cosmetics and pharmaceuticals (Allan et al., 2021; Hernandez et al., 2017).

Micro/nanoplastics exhibit a widespread distribution, being present on land, in the air, and in freshwater and marine environments (reviewed in Horton & Dixon, 2018). Although these particles are dispersed across various habitats, a substantial portion ultimately end up in aquatic ecosystems, which mainly receive inputs of plastic particles through sewage discharge, rainwater scouring and atmospheric sedimentation (Du et al., 2021). Surprisingly, even pristine and remote habitats are not spared from the impact of micro/nanoplastics (e.g., González-Pleiter et al., 2020; Materić et al., 2022). To better understand the importance of this emerging threat, exposure studies are being conducted involving various aquatic organisms subjected to a range of concentrations of micro/nanoplastics. These studies compare the fitness variables of the exposed organisms in relation to their conspecifics raised under non-contaminated (control) conditions (reviewed in Al-Thawadi, 2020; Qu et al., 2023). By testing for potential adverse consequences of plastic exposure, these studies provide valuable insights into the ecological implications of micro/nanoplastics on aquatic life.

One of the frequently used model organisms in these experiments are the freshwater crustaceans *Daphnia* spp. This choice stems from their ecological significance and their exceptional suitability for experimentation purposes. Specifically, *Daphnia* spp. inhabit most standing freshwater bodies and play a key role in the trophic structure of aquatic food webs; they are the most common grazers of phytoplankton, and themselves provide food for planktivorous fish (Lampert & Sommer, 2007). Their amenability to experimentation as well as rapid responses to environmental changes elevated *Daphnia* as an iconic model in physiology, ecology, toxicology and evolutionary biology (reviewed in Ebert, 2022; Lampert, 2011). Some of these characteristics are:

- Cyclical parthenogenetic reproduction and the possibility to use genetically identical offspring, reducing experimental variation and allowing genetic and environmental effects to be disentangled,
- Short generation time enabling brief experiment durations and multigenerational experiments to study long-term effects,
- Small body size making them relatively easy to rear in large quantities,
- Generally high sensitivity to environmental stressors, including micro/nanoplastics, compared to other freshwater zooplankton species (e.g., Saavedra et al., 2019),
- Known genome enabling various -omics studies.

Moreover, *Daphnia* exhibit non-selective filter-feeding behaviour, consuming particles within a specific size range, typically up to 70 μm (this range can vary based on their body size; Burns, 1968), thereby rendering them susceptible to the ingestion of micro/nanoplastics.

Research on the effects of micro/nanoplastic on *Daphnia* has experienced significant growth over the past decade, with the first study published in 2013 (Lambert et al., 2013), marking the beginning of focused investigations in this area (Figure 1). The review article

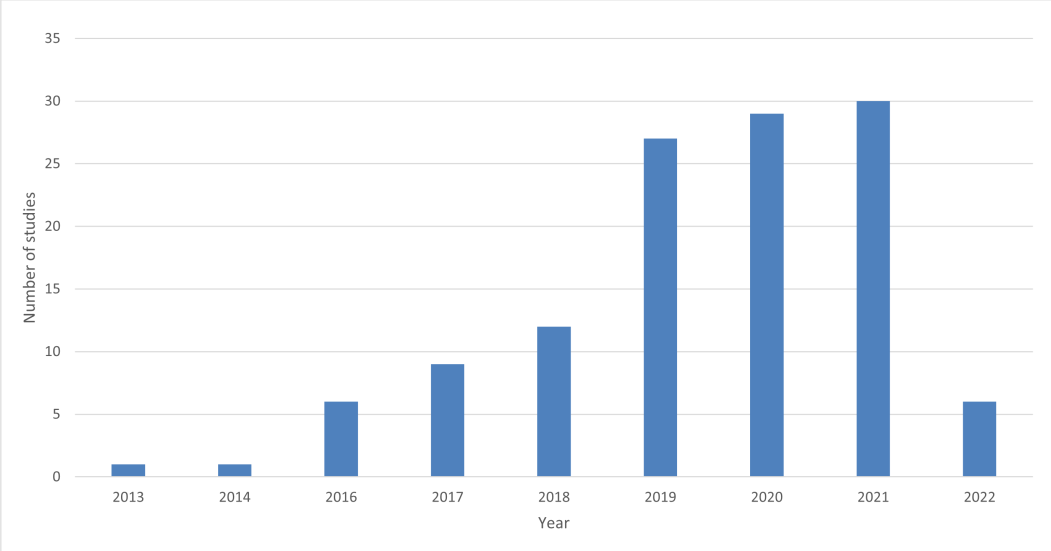

FIGURE 1 Annual distribution of experimental studies investigating the impact of micro/nanoplastics on *Daphnia* (up to 27 April 2022).

by Samadi et al. (2022) mentioned an even earlier study as the first one on the effect of micro/nanoplastics on *Daphnia*: (Rosenkranz et al., 2009). This 2009 article did not turn up in our literature search because it referred to the tested polystyrene particles as "nanoparticles" rather than explicitly using the term "micro- or nanoplastics". During the last five years, the number of experimental studies has notably increased (Figure 1), resulting in a substantial amount of available data on this topic. However, due to considerable variation in experimental approaches, it is difficult to synthesise the findings. Specifically, there is much diversity in respect to the tested response variables, as well as the types, sizes, shapes and concentrations of micro/nanoplastics used in the experiments. In addition, variation in the exposure conditions employed across the experiments adds to the difficulties in comparing findings across studies and identifying variables for future investigations.

Recently, four studies have already been published reviewing the toxicity of micro/nanoplastic or nanoparticle/nanomaterial towards *Daphnia* (Liu, Malinowski, & Sepúlveda, 2022; Reilly et al., 2023; Samadi et al., 2022; Yin et al., 2023). They summarise the ecotoxicological effects of micro/nanoplastics on *Daphnia* and partly provide systematic reviews on a few aspects. Two of these studies investigate the effect of nanoparticles/nanomaterials on *Daphnia* and rather briefly discuss nanoplastics as part of a higher-level particle category (Liu, Malinowski, & Sepúlveda, 2022; Reilly et al., 2023).

The present study offers a comprehensive and systematic review, examining the impact of micro/nanoplastics on *Daphnia* in-depth. By exploring various aspects, such as interspecific and intraspecific variation, multigenerational approaches, interactions with additional substances or stressors and a multitude of micro/nanoplastic characteristics, our study offers a holistic understanding of the effects of micro/nanoplastics on this keystone species. An important and innovative contribution of this study is an inclusion of a meta-analysis approach to investigate the effects of micro/nanoplastic on *Daphnia* reproduction, allowing for the generalisation of finding across multiple studies. The review concludes by identifying research gaps and offering future recommendations, with a specific emphasis on the ecological relevance of micro/nanoplastic effects on *Daphnia* and the comparability of studies.

2 | METHODS

2.1 | Literature search

We searched the literature using the search terms: Subject: Daphnia, Ceriodaphnia; intervention: microplastic*, nanoplastic*. The terms within each category ("subject" and "intervention") were combined using the Boolean operator "OR". The two categories were then combined using the Boolean operator "AND". An asterisk (*) is a "wildcard" that represents any group of characters, including no character. This resulted in the search string (*Daphnia* OR *Ceriodaphnia*) AND (microplastic* OR nanoplastic*). Firstly a Web of Science search (Basic Search: Topic, All Databases) was conducted from the year 1945 through 28 October 2020. In addition, a second search in Google Scholar (Title) was conducted on 28 October 2020 for the year 2020 to add more recent publications that were not yet included in the Web of Science databases. On 10 August 2021 and 27 April 2022 these searches were repeated to add new studies (second and third literature search, respectively). All articles were checked based on the abstract and full text and articles that did not discuss experimental studies about the effect of micro- or nanoplastics on *Daphnia* or *Ceriodaphnia* were excluded. Search duplicates were removed. All 121 papers included were primary literature in English from peer-reviewed scientific journals.

2.2 | Data extraction

Data from eligible studies was extracted in two different ways, to create: (a) a qualitative dataset (for an overview) and (b) a quantitative

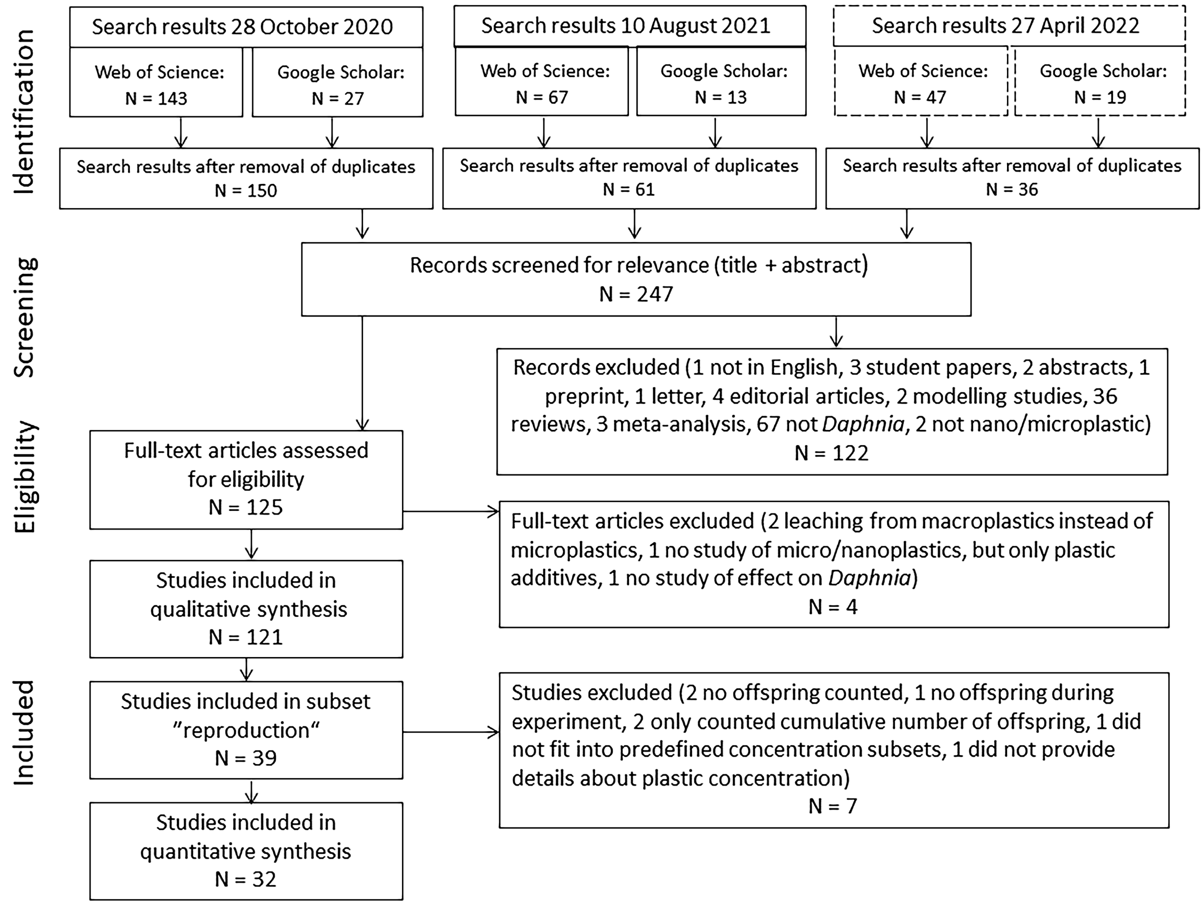

FIGURE 2 Flow diagram detailing the process of literature search and study inclusion.

dataset (needed for meta-analysis). From here on, we will use the terms "*Daphnia*" to refer to both *Daphnia* and/or *Ceriodaphnia* (unless we explicitly refer to *Ceriodaphnia*, under rare occasions).

2.2.1 | Qualitative dataset

Qualitative data was extracted from all 121 studies (84 from the first, 23 from the second and 14 from the third literature search) in the following categories:

- Tested species
- Number of tested genotypes (clones)
- Multiple generations (yes [number]/no)
- Additional treatment (e.g., temperature, food quality or quantity, humic acid, chemicals)
- Control particles (yes [type]/no)
- Description of micro/nanoplastic particles: polymer type, size, shape, charge/modifications, pristine versus aged
- Micro/nanoplastics concentration(s)
- Response variables: mortality, reproduction, body size adults, body size neonates, feeding rate, microplastic ingestion rate, additional response variable (e.g., gene expression, fatty acid analysis)

The list of 121 studies is provided as Supporting information Table S1.

2.2.2 | Quantitative dataset

The studies that investigated the effect of microplastics on the reproduction of *Daphnia* were combined in a "reproduction" subset. Thirty-nine such studies were identified (30 from first and nine from the second literature search; studies from the third literature search were not included into these analyses). The concentrations in the analysed studies were listed either in mg/L or particles/ml and they needed to be converted into one unit for comparability. As a concentration in mass per unit volume differs depending on particle size, shape and density, we chose the unit particles/ml. We recalculated the concentrations using the particle size and density, in the case of round particles (Leusch & Ziajahromi, 2021). The studies were then grouped into four concentration subsets (one study can fall into multiple concentration subsets):

1. <1,000 particles/ml (10 studies)
2. 1,000–10,000 particles/ml (12 studies)
3. >10,000-1,000,000 particles/ml (14 studies)
4. >1,000,000 particles/ml (12 studies)

The studies that fit into at least one of the four defined concentration subsets (32 studies) were included in the process of quantitative data extraction for a meta-analysis (seven studies were excluded as they either did not provide necessary information on microplastic concentration or did not provide the data needed for the analyses: Figure 2). In studies with multiple generations we only looked at F_0 because the majority of studies tested this generation only. In studies with different species we only looked at the genus *Daphnia* (as otherwise there were only few studies assessing *Ceriodaphnia*).

The following data was extracted for both the control and the micro/nanoplastic group(s): sample size (number of replicates; *N*); number of offspring (average value; AV); variation for number of offspring (standard deviation; SD). For "number of offspring" calculations, preferentially a "total number of offspring" (i.e., sum of all offspring from all clutches, per experimental unit) was considered. If this was not provided, "number of offspring in third clutch", "number of offspring in first three clutches", "number of offspring per clutch" or "number of offspring per day" was taken. When offspring number was only counted for first and second clutch, the second clutch was used (Trotter et al., 2021) or the first one, because more replicates were available for that one (Sadler et al., 2019). When number of offspring was only counted at certain time points, the time point that likely represented the third clutch was used (Day 15; Kelpsiene et al., 2020). As a measure of variation, standard deviation (SD) was extracted. If only values for standard error (SE) or confidence interval (CI) were provided, SD was obtained using the following formula: $SD = SE \times \sqrt{N}$, and $SD = \sqrt{N} \times$ (upper limit CI − lower limit CI)/(t value $\times 2$) (Higgins et al., 2023). Where it was not possible to specify whether figures showed SD or SE, we assumed SD (Lambert et al., 2013; Yin et al., 2020). In case of BoxPlots, median, 25th and 75th quartile as well as minimum and maximum values were extracted. We then calculated mean and SD values (see additional file 2, scenario 2 in Wan et al., 2014).

The data were extracted from tables, main text, figures (using WEBPLOTDIGITIZER version 4.4 and 4.5; Marin et al., 2017; Rohatgi, 2020), or the corresponding authors were contacted. The latter approach was employed for studies published no earlier than 2018, with a subsequent follow-up reminder issued two months later. When there was no response or a response without the data values, the studies were excluded from the meta-analysis (for details on study exclusion criteria see Figure 2 and Table S1).

2.3 | Meta-analysis

A random effects model, comparing the mean difference (MD) of number of offspring from the quantitative data set, was created using the "metacont" function of the R package *meta* (version 5.2–0) in R version 4.2.0 (R core development team). The data were analysed both pooled and within the concentration subsets, and visualised using the function "forest" of the package *meta*.

3 | RESULTS AND DISCUSSION

3.1 | Study design

3.1.1 | Tested species

Of the 121 analysed studies on the effect of micro/nanoplastics on *Daphnia* fitness, 104 studies (86%) have been conducted on *Daphnia magna* and 10 studies (8%) tested *Daphnia pulex*. Other tested species were: *Daphnia galeata*, *Daphnia carinata* and *Ceriodaphnia dubia*. Three studies compared the effect of microplastics on different species (Figure 3a). One of these investigated the effect of food supply and temperature on microplastic ingestion in *D. magna* and *D. pulex*. The ingestion of microplastics was generally faster and the increase of microplastic particle ingestion caused by higher temperatures was more pronounced in *D. magna* than in *D. pulex* (Hoffschroeer et al., 2021). Two studies compared *D. magna*, *D. pulex* and *C. dubia*. In the first one, the sensitivity to microplastics was comparable between *D. magna* and *D. pulex*, with a temperature-dependent increase in both species, whereas the sensitivity of *C. dubia* remained stable across temperatures. Consequently, *C. dubia* was the most sensitive species to microplastic exposure at 18°C and the least sensitive at 26°C (Jaikumar et al., 2018). In the second study (a chronic toxicity test), species sensitivity to microplastics varied with body size; the smallest *C. dubia* being the most sensitive and the largest *D. magna* the least sensitive species (Jaikumar et al., 2019).

3.1.2 | Number of genotypes (clones)

Only three of 121 studies (2.5%) tested more than a single *Daphnia* clone (Figure 3b). Chang et al. (2022) used six clones of *D. magna* sampled across differently temperature-adapted populations. Under standard ecotoxic test conditions (20°C) exposure to microplastic particles at an environmentally relevant concentration (5 μg/L) had almost no measurable effect. However, when combined with a higher temperature (24°C), microplastic exposure led to higher fecundity and higher intrinsic growth rates, but only in clones not adapted to higher temperatures, suggesting that thermal adaptation might buffer the effect of microplastics under warming. Then, when three *D. magna* clones were tested, each originating from a different population, two clones showed differences in gene expression patterns of stress response genes after microplastic exposure for 48 h and one clone did not (Imhof et al., 2017). Finally, eight clones from a single *D. magna* population were exposed to microplastics and two different temperatures. While microplastic exposure induced shifts in multivariate phenotypes in half of the clones, the other half was relatively resistant to microplastic effects (Sadler et al., 2019). Overall, the available multiple-clone studies indicated intraspecific differences in reaction to microplastics. This even concerned clones originating from a single population (Sadler et al., 2019), which presumable had a common microplastic exposure pattern and common

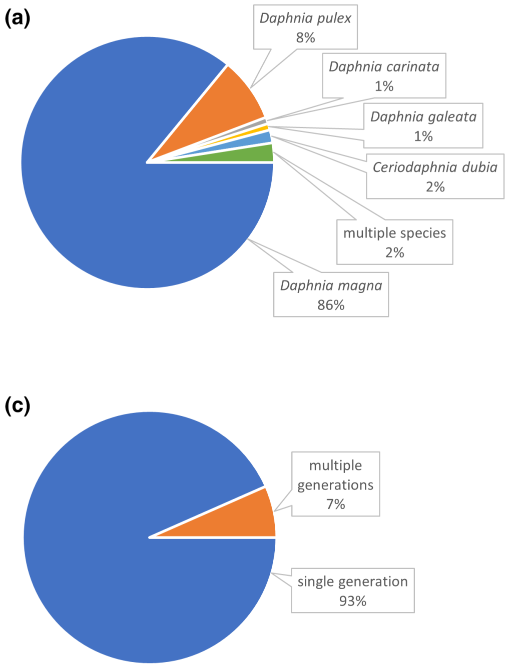

FIGURE 3 Study design overview. (a) type of tested *Daphnia* species; (b) number of clones (genotypes); (c) number of tested generations.

evolutionary history. This all demonstrates the importance of incorporating clonal variation into assessments of the impact of micro/nanoplastics.

3.1.3 | Multiple generations

The majority of reviewed studies tested only one *Daphnia* generation; only eight studies (7%) spanned two to four generations (Chang et al., 2022; Liu, Cai, et al., 2020; Liu, Jiao, et al., 2020; Martins & Guilhermino, 2018; Nogueira et al., 2022; Schür et al., 2020, 2021; Xu et al., 2020). Micro/nanoplastic toxicity generally increased with the number of generations even if there was no effect in F_0. In one study survival decreased steadily from 79% in F_0 to 55% in F_1, 35% in F_2 and 0% in F_3 at continuous exposure to microplastics. Furthermore, there was no effect on reproduction in F_0 and F_1, but >20% reduction in F_2 and F_3 generations, in comparison to the control (Schür et al., 2020). Liu, Cai, et al. (2020) investigated life-history variables and transcriptional responses through F_0 to F_2 generation, of *D. pulex* exposed to environmentally relevant concentrations of nanoplastics (1 µg/L). While survival was not affected and reproduction was only reduced in F_2, the transcriptional responses of stress defence and energy-related genes were induced in all generations; indicating a promotional effect of nanoplastics on F_0 and F_1 (hormesis effect), and toxic effect on F_2. Yet another study showed that even if the nanoplastic exposure only happens in F_0, there can still be a negative effect on reproduction in F_1 and F_2 (Nogueira et al., 2022). These results point out that single-generation studies are likely to be underestimating micro/nanoplastics toxicity, especially for short-lived species such as *Daphnia*.

3.1.4 | Additional treatments

More than half of all studies applied other experimental treatments in addition to micro/nanoplastics (n = 66, 55%). These treatments include: different temperatures, light intensities, pH, food limitation or quality, hydrodynamic conditions, varying exposure time, presence of biofilms and the addition of various substances such as chemicals, metals, humic substances, dissolved organic matter and aggregation agents. The inclusion of these treatments can help better simulate actual natural conditions where multiple stressors are ubiquitous. Similar to a study on other multiple stressors, which were shown to have either antagonistic, additive or even synergistic effects on *Daphnia* (Coors & De Meester, 2008), increased temperature, increased salinity or pesticides – as combined with microplastic contamination – also led to a synergistic effect (Felten et al., 2020; Serra et al., 2020). Ad/absorption of heavy metals to microplastics or the presence of antimicrobial agents in the water increased microplastic toxicity (Lin et al., 2020; Yin et al., 2020; Yuan et al., 2020; Zhang et al., 2019), whereas the presence of humic substances reduced the toxicity of nanoplastics (Fadare et al., 2019, 2020; Wu et al., 2019). Humic substances are an essential component of aquatic systems, and their effects on nanoparticle toxicity have been attributed to the mechanisms which modify the nanoparticle surface chemistry (Pokhrel et al., 2013; Zhang et al., 2015). Several studies combined the exposures of nanoplastic particles and humic substances and showed a detoxifying effect especially of humic acid (HA). Fadare et al. (2019) exposed *D. magna* to microplastic and nanoplastic particles under the presence of HA, and observed a dramatic decrease in the acute toxicity of nanoplastics, but also an efficiently diminished increase of antioxidant gene expression upon nanoplastic exposure.

This was attributed to the HA molecules adsorbing onto nanoplastic particles and forming an eco-corona which led to a complete change in the distribution pattern of nanoplastic particles to resemble that of larger microplastics, preventing entanglement and body burden. In another study, the acute toxicity of nanoplastics on *D. magna* was tested in the presence of three different types of humic substances; nanoplastic toxicity was reduced to varying degrees depending on their composition and corona formation, with an overall order HA > fulvic acid > natural organic matter (Fadare et al., 2020). Wu et al. (2019) used four polystyrene nanoplastics with different functional groups and charges. HA alleviated the nanoplastic toxicity towards *D. magna* which was attributed to the adsorption of HA onto nanoplastic particles, contributing negative charges. This reduced aggregation onto *Daphnia* and consequently reduced their entanglement and body burden.

3.1.5 | Use of control particles

Micro/nanoplastic particles share certain characteristics with natural particles in freshwater environments, such as size, shape, density and lack of nutritional value. Ingested natural particles (for example, suspended clay) can have adverse effects on *Daphnia*, like the reduction of feeding rate (Kirk, 1991). It is therefore important to distinguish the effects of plastic particles from those of natural particles. Surprisingly, only 9% of all studies ($n=11$) used some kind of control particle, mostly kaolin. In one of these studies, different kinds of control particles (kaolin, ground mussel shells, cellulose, glass) of different sizes and shapes (spherical, irregular, fibrous) were tested, next to respective types of polystyrene particles, to disentangle the specific microplastic-related effect from the effect of particle as such (Schwarzer et al., 2022). The impact of microplastic and control particles on the life history and morphology of *D. magna* exhibited notable differences. For example, reproductive success as well as body length of *Daphnia* decreased after chronic exposure to spherical plastic particles, but these effects were not observed in individuals exposed to spherical control particles composed of cellulose or glass. The authors concluded that the observed sublethal effects are polymer specific and not caused by the presence of particles per se.

3.2 | Microplastic characteristics

3.2.1 | Polymer type

The most commonly tested polymers in *Daphnia* studies were polystyrene (PS) ($n=75$; 62%) and polyethylene (PE) ($n=22$; 18%). Of the studies using PE, three studies aimed to compare the effects of primary (manufactured) and secondary microplastics, but only specified the polymer type of the latter (Jaikumar et al., 2018, 2019; Ogonowski et al., 2016). Twenty-five studies used other polymer types such as polyethylene terephthalate (PET), polymethyl methacrylate (PMMA), polyvinyl chloride (PVC), polyurethane (PUR), polypropylene (PP), polyamide, acrylonitrile butadiene styrene (ABS), polylactic acid (PLA) and polyisoprene, sometimes in plastic mixes with multiple polymers (Hiltunen et al., 2021; Imhof et al., 2017). Four studies did not specify which polymer type was tested. Then, 10 studies aimed to compare the effect of different polymer types on *Daphnia*. Some of these studies used a different particle shape, size and/or concentrations per polymer type, making a direct comparison difficult (e.g., Ziajahromi et al., 2017; Zocchi & Sommaruga, 2019). However, other studies using comparable types of plastic particles showed differences between the effects of polymer type on *Daphnia*. Specifically, irregularly shaped microparticles of PP and PE had stronger toxic effects on *D. magna*, in comparison to PVC particles (Renzi et al., 2019), whereas PET microfibres had stronger effect on immobilisation than PP microfibres (Kim et al., 2021). Then, irregular particles of polycarbonate (PC) caused higher immobilisation rates than PET and polybuthylene terephthalate (PBT) particles (Sonmez et al., 2022). When *Daphnia* were exposed to nanoplastic particles together with ionic silver, PS beads induced lethal toxicity, while PE beads did not. This observation led to the conclusion that the chemical composition of the plastic particle influences the sorption of silver ions (Monikh et al., 2020). Another study used irregular microplastics of the polymers PVC, PUR and PLA in different states (1, microplastics; 2, microplastics without their chemicals [removed by extraction]; 3, plastic chemical extracts; 4, plastic leachates). All three polymer types reduced the reproductive output of *D. magna* with an effect level specific to the plastic type (PVC > PLA > PUR). The effects of PVC were driven by chemical toxicity, while for PLA and PUR the physical toxicity dominated (Zimmermann et al., 2020). These results clearly show that different polymer types can induce various toxicity towards *Daphnia*. The chemical composition of micro/nanoplastics can influence whether or not they leach harmful substances or how they interact with additional substances in the environment. Different polymers exhibit distinct surface to volume ratios (Kooi et al., 2021). Generally, micro/nanoplastics have a relatively large surface area in relation to their volume, with the surface area increasing as particle size decreases. This increased surface area facilitates the adsorption and accumulation of contaminants from the surrounding environment (e.g., Kim et al., 2022) and promotes biofouling, affecting particle density and potentially leading to the sinking of plastic particles (Liu, Huang, et al., 2022). Different densities of polymer types also influence their buoyancy (Vermeiren et al., 2016) and therefore the chance for *Daphnia* to encounter them in the environment.

3.2.2 | Plastic size

Of all analysed studies, nearly three quarters ($n=89$; 74%) used microplastics, 22 studies (18%) tested nanoplastics, and 10 studies (8%) encompassed both particle categories (Figure 4a). The majority of studies ($n=104$; 86%) tested only one particle size whereas 17 studies (14%) used different particle sizes of the same polymer type and shape to compare their effect on *Daphnia*. *D. magna*, the largest *Daphnia*

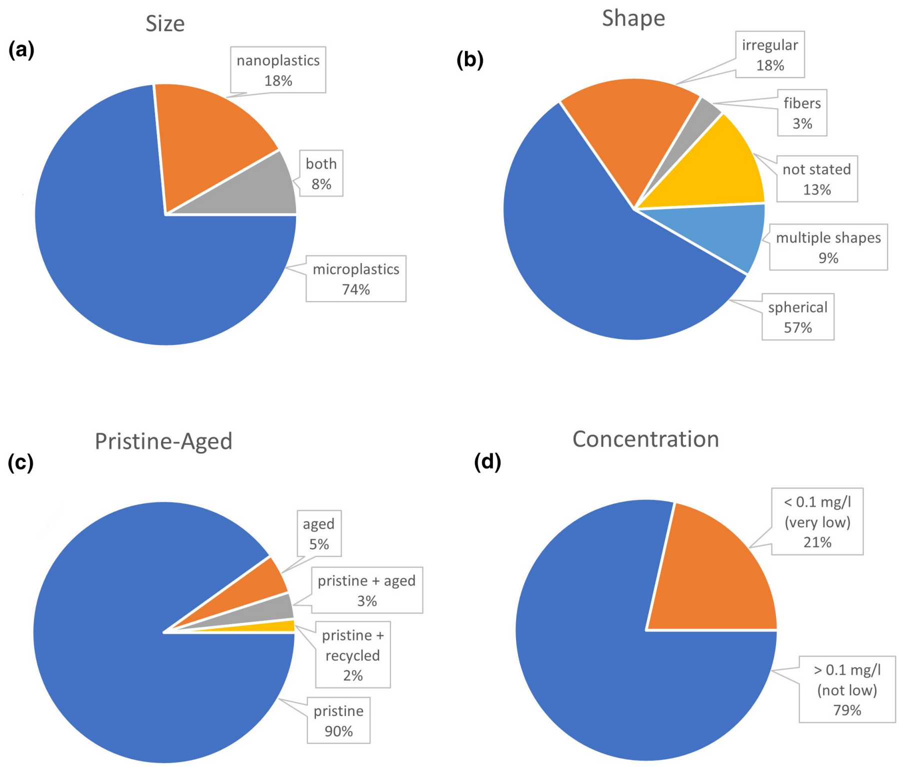

FIGURE 4 Micro/nanoplastic characteristics explored in analysed studies: (a) particle size; (b) particle shape; (c) pristine versus aged particles; (d) concentration.

species, can ingest smaller (1–10 µm) but not larger microplastics (90–100 µm) (Rehse et al., 2016; Scherer et al., 2017). This upper size limit for ingestion correlates with the *Daphnia* body size (Burns, 1968). Accordingly, the majority of studies used particle sizes of <100 µm, while 10 studies (8%) used larger particle sizes. Within the analysed studies tested particle sizes ranged from 0.02 to 354 µm for spherical and irregular micro/nanoplastics while fibre lengths of ≤1,400 µm were used. Across 17 studies that compared micro/nanoplastics toxicity of different particle sizes towards *Daphnia*, the tested particle sizes ranged from 0.02 to 230 µm. Three of these studies did not find any particle size-dependent differences (De Felice et al., 2019; Heinlaan et al., 2020; Kelpsiene et al., 2020). However, most studies concluded that smaller plastic particles are more toxic to *Daphnia* than larger ones (e.g., An et al., 2021; Liu, Zhang, et al., 2022; Rehse et al., 2016). For both acute and chronic toxicity of PVC microplastics on *D. magna*, 2-µm microparticles significantly reduced survival, growth and reproduction and caused oxidative damage, whereas 50-µm particles only reduced the offspring number at first brood (Liu, Zhang, et al., 2022). When the acute toxicity of 1-µm polystyrene microparticles and 0.1-µm nanoparticles (the latter one is a cut-off size, 100 nm, between micro- and nanoplastics, according to our definition) was compared, the larger particles did not show any toxicity even at the highest concentration of 400 mg/L. Contrary to that, the smaller nanoplastic particles caused 65% mortality at a concentration of 10 mg/L and 100% mortality at 200 g/L and 400 g/L (Fadare et al., 2019). Likewise, in another study 0.2-and 0.5-µm polystyrene microparticles did not cause any mortality whereas 50 nm (0.05 µm) nanoparticles as well as aggregates of 50-nm particles had a lethal effect (Frankel et al., 2020). Rist et al. (2017) showed that the ingestion of 0.1-µm polystyrene nanoparticles caused slower ingestion rates and decreased feeding rates compared to 2-µm microparticles. Another study found a significant dose effect in the toxicity of 50-nm polystyrene nanoparticles from 1 to 50 mg/L while no immobilisation was observed for larger microparticle sizes (0.5, 5, 10, 15 µm) at concentrations of ≤100 mg/L. The microparticles were ingested and egested without causing any physical damage to *Daphnia*. On the other hand, 50-nm nanoparticles at 10 mg/L caused severe damage to thoracopods, with accumulation of particles to the body surface, leading to 100% immobilisation (Ma et al., 2016). The acute toxicity of nanoplastics was size-dependent as well; smaller polystyrene particle sizes (20 and 40 nm) were more toxic than larger particles (60 and 100 nm, Pochelon et al., 2021). Lin et al. (2021) investigated the uptake mechanism of the polycyclic aromatic hydrocarbon pyrene as a model hydrophobic organic contaminant associated with microplastics of three different sizes. While immobilisation rates for microplastics alone were very low, they were higher for pyrene alone and in combination with microplastics (microplastics < pyrene < microplastics + pyrene). When pyrene and microplastics were combined, immobilisation rates increased with decreasing particle size. All three size classes were found in the intestine of *D. magna*, but only the smallest particle size (0–1.5 µm) was able to enter into the tissues through the carapace and intestine wall. The bioavailability of pyrene depended on the particle size (0–1.5 µm > 10–60 µm > 60–230 µm). These findings point out the importance of choosing the right particle size and especially the relevance of studies on the effect of nanoplastics on *Daphnia* fitness as their effect seems to be much more detrimental while their concentration in natural environments is increasing (e.g., Besseling et al., 2019; Entry, 2022).

3.2.3 | Plastic shape

More than half of all analysed studies ($n = 69$, 57%) used spherical (round) micro/nanoplastic particles which is the most common commercially available plastic shape. Twenty-two studies tested irregularly shaped particles which are usually produced by shredding or milling manufactured plastic beads or other plastic materials to mimic what happens to plastic material in the environment over time. Only four studies used fibres, and 15 studies did not state the shape of the used plastic particles. Eleven studies compared the effect of different particle shapes on *Daphnia* (Figure 4b). However, some of them used a different polymer type per plastic shape (Ziajahromi et al., 2017; Zocchi & Sommaruga, 2019) or only specified the polymer type for one shape type (Jaikumar et al., 2018, 2019; Ogonowski et al., 2016), making a direct comparison difficult. The few studies that also used comparable particle sizes mostly compared the effect of spherical and irregular plastic shapes on *D. magna* and concluded that plastic fragments exhibited a higher toxicity than plastic beads. Frydkjær et al. (2017) reported that both spherical and irregular polyethylene particles were rapidly ingested but the egestion of spherical particles was much faster than of irregular ones; after 24 h 49% of the individuals fed with microplastic beads had completely emptied their gut, whereas <1% of the individuals fed with microplastic fragments were able to do so. Also, immobilisation differed between both tested shapes; spherical particles caused very low immobility even at higher concentrations while irregular particles led to high immobilisation already at low concentrations. Na et al. (2021) showed that the acute toxicity of polyethylene microplastic fragments was more than 80-fold higher than that of microplastic beads. In another study, irregular polyethylene microplastics led to higher mortality, accumulation in the gut, and bioconcentration and a considerable decrease in carbohydrate and protein energy reserves in comparison with spherical microplastics (An et al., 2021). Only one study compared three different microplastic shapes: spherical, irregular fragments and fibres, all representing the same polymer type (Schwarzer et al., 2022). Here, the morphology and life-history traits of *D. magna* were negatively affected by small spherical microparticles, but not by other shapes. However, with larger particle sizes, no noticeable negative effects were observed, regardless of particle shape.

3.2.4 | Plastic surface charge/modifications

Twenty-one studies (17%) tested polystyrene micro/nanoplastics with surface modifications which can change the charge of the particle surface. Most commonly used were carboxylated particles resulting in a negative surface charge and aminated particles usually resulting in a positive surface charge. Eleven studies used only one kind of surface modification, two studies compared the effects of modified to unmodified particles on *Daphnia*, five studies compared different surface modifications and opposing surface charges, whereas three studies compared unmodified, carboxylated and aminated particles. Two of these studies used different particle sizes for the different modifications, preventing a real comparison (Lin, Jiang, Hu, et al., 2019; Wu et al., 2019). Most studies comparing modifications with different surface charges indicate that the positively charged aminated particles affected *Daphnia* negatively (Mattsson et al., 2017) or that they had a more toxic effect on *Daphnia* than the negatively charged carboxylated or sulfonated particles (Kelpsiene et al., 2020; Nasser & Lynch, 2016; Saavedra et al., 2019). This is in accordance with other studies that showed that positive charges enable particles to interact easily with negatively charged cell membranes (Nel et al., 2006) and that positively charged aminated polystyrene particles induced cell death in several in vitro cell systems (Anguissola et al., 2014). However, one study had opposite results, showing that carboxylated particles with negative charges were more toxic towards *Daphnia* than aminated particles with positive charges (Zhang et al., 2020).

3.2.5 | Pristine versus aged plastic

Once plastic particles get into aquatic environments they are exposed to abiotic factors such as sunlight and temperature, and interact with substances in the water, including HA or bacteria (Gewert et al., 2015). These aging processes can change the micro/nanoplastic properties. Biofilm formation on particle surface can lead to the alteration of particle density, morphology and physicochemical properties and facilitate the interaction between plastics and heavy metals or chemicals (Ma et al., 2020; Richard et al., 2019). Natural organic matter can adsorb to micro/nanoplastic particles leading to corona formation (Fadare et al., 2020; Schür et al., 2021). Nonetheless, most studies used only pristine particles ($n = 109$; 90%) which does not represent the situation in natural environments. Of the remaining studies, six tested aged particles, two used pristine and recycled ones, whereas four studies compared the effect of pristine versus aged particles (Figure 4c). Qi et al. (2021) compared the effect of virgin microplastics and microplastics that were aged in natural waterbodies for 4 weeks in summer. They showed that biofilms on aged microplastics enhanced the adsorption capacities of lead (Pb)(II) onto the plastics and increased the combined toxicity of Pb(II) and microplastics towards *Daphnia*. In another study, incubation of microplastic particles in stream water for 4 weeks resulted in biofilm formation which altered the particle density leading to a different distribution in the test medium. Biofilm-covered particles adsorbed 44% more silver ions than pristine ones, giving them a higher ecotoxicological potential (Kalčíková et al., 2020). Schür et al. (2021) exposed four generations of *D. magna* to pristine microplastics and microplastics that were incubated in filtered wastewater. Exposure to wastewater-incubated particles resulted in a lower *Daphnia* mortality than under pristine particles. They argued that the absorption of dissolved organic matter reduces the toxicity of microplastics.

For other life-history traits, the toxicity of the two particle types did not differ significantly (Schür et al., 2021). Another study showed that aged microplastics had a decreased adsorption of hydrophobic benzalkonium chlorides (BACs), but an increased adsorption of hydrophilic BACs compared to pristine microplastics. This resulted in lower mortality rates of *D. magna* in the presence of pristine microplastics for hydrophobic BACs and in the presence of aged microplastics for hydrophilic BACs (Kim et al., 2022).

3.2.6 | Plastic concentration

One quarter of all analysed studies ($n=32$, 26.5%) tested only a single micro/nanoplastic concentration while three quarters ($n=89$, 73.5%) used multiple concentrations. Eighteen studies compared the effects of two different micro/nanoplastic concentrations on *Daphnia*, 14 studies tested three different concentrations, and 51 studies used more than three concentrations. Six studies tested several concentrations but only specified the concentration ranges that were used. Several studies used different micro/nanoplastic concentrations or a different number of concentrations for different experiments; for example, a wide variety of concentrations for acute toxicity tests and only a concentration subset, a single concentration or completely different concentrations for chronic toxicity tests or other tests within the study (e.g., Liu, Zhang, et al., 2022; Vaz et al., 2021; Yin et al., 2020).

Plastic concentration may be the least comparable category of microplastic characteristics across analysed studies. This is because most studies (87%) measured micro/nanoplastic concentrations in mass per volume (i.e., mg/L) instead of particles per volume, although some give particles per volume as additional information. As mass per volume varies with changing particle size (and polymer density) it is hard to compare particle concentrations provided in mass, when different particle sizes and polymer types were used. Nevertheless, within single studies testing different concentrations of the same micro/nanoplastic particle size, toxicity typically increased with particle concentration, resulting in higher mortality and decreased reproduction in *Daphnia* (e.g., Besseling et al., 2014; Fadare et al., 2019; Nogueira et al., 2022). Studies deviating from this trend usually did not find toxic effects on *Daphnia* for any of the tested micro/nanoplastic concentrations (e.g., Jemec Kokalj et al., 2021, 2022; Kalčíková et al., 2020).

Within the analysed studies tested micro/nanoplastic concentrations ranged from as low as 0.001 mg/L (Liu, Cai, et al., 2020; Trestrail et al., 2020) or 4.3 particles/ml (Schrank et al., 2019) to extreme 10 g/L (Frydkjær et al., 2017; Gerdes et al., 2019) or 6.74×10^{10} particles/ml (Monikh et al., 2020). Twenty-six of all analysed studies incorporated relatively low micro/nanoplastic concentrations into the experimental design, such as <0.1 mg/L (Figure 4d), which is still mostly higher than what used to be considered environmentally relevant (≤15 µg/L for 50-nm, ≤1 µg/L for 100-nm, <0.5 µg/L for 5-µm particles; Al-Sid-Cheikh et al., 2018; Lenz et al., 2016). Recently, however, Materić et al. (2022) reported that across 11 sampled Swedish lakes and streams, the average nanoplastic concentration was as high as 563 µg/L. Most of these studies that had applied relatively low concentrations did not find any effects of these concentrations, especially the studies that only tested for acute toxic effects (e.g., Heinlaan et al., 2020; Lin, Jiang, Xiong, et al., 2019; Trestrail et al., 2020). By contrast, Pacheco et al. (2018) showed that 21 days of exposure to 0.02 mg/L of microplastic particles caused 10% mortality of *D. magna* in comparison to the control. Two other studies in which a single *Daphnia* generation was exposed to low concentrations of microplastics (i.e., 4.3 particles/ml, 500 particles/ml, respectively) also found negative effects on the reproductive output of *Daphnia* (Schrank et al., 2019; Schwarzer et al., 2022). The two studies that exposed multiple *Daphnia* generations to the environmentally relevant concentration of 1 µg/L of nanoplastics (75 nm) showed that, while there was no toxic effect in F_0 and F_1, reproduction was reduced in F_2 in comparison to the control (Liu, Cai, et al., 2020; Liu, Jiao, et al., 2020). Finally, two studies showed that microplastics at low concentrations of 50 or 5 µg/L, while having no detrimental effect alone, they did have an effect on *Daphnia* fitness when combined with other stressors, such as warmer temperatures/temperature fluctuations or warmer temperatures and ammonium (Chang et al., 2022; Serra et al., 2020). These findings emphasise that the experiments on the effect of micro/nanoplastics on *Daphnia* fitness should include environmentally relevant concentrations, and, if possible, should test multiple *Daphnia* generations and/or multiple stressors.

3.3 | Response variables

Throughout all studies an array of response variables has been assessed. Mortality was the most commonly tested ecotoxicological endpoint ($n=97$; 80%), followed by reproduction ($n=46$; 38%). Morphological responses such as the body size of adults ($n=41$; 34%) and neonates ($n=16$; 13%) or physiological responses such as feeding rate ($n=7$; 6%) and plastic ingestion rate ($n=14$; 12%) were less commonly tested. Many studies ($n=90$; 74%) assessed some additional response variables such as oxidative stress or general stress response, often using gene expression analysis, or evaluating behavioural traits, growth rates, interaction of microplastics with different substances (Figure 5).

3.4 | Meta-analysis: Effect of microplastics on Daphnia reproduction

A comprehensive analysis encompassing 32 distinct studies has been undertaken to assess the influence of micro/nanoplastics on *Daphnia* reproduction. In the aggregate dataset, a total of 158 effect sizes were compiled, capturing the comparison of offspring numbers between control groups and those exposed to micro/nanoplastics. Micro/nanoplastics had a consistently adverse impact on offspring production ($MD=-10.5129$, $z=-5.24$, $p<0.0001$).

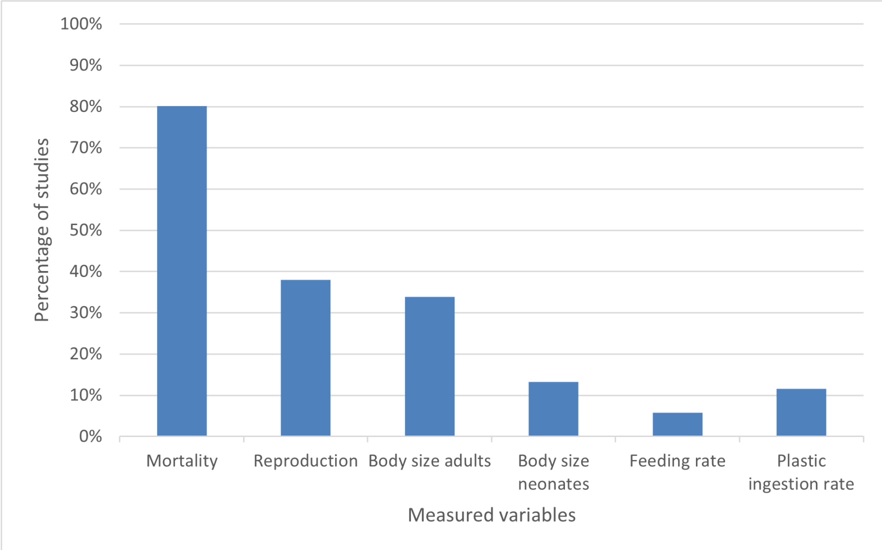

FIGURE 5 Distribution of measured *Daphnia* response variables as percentages of analysed studies.

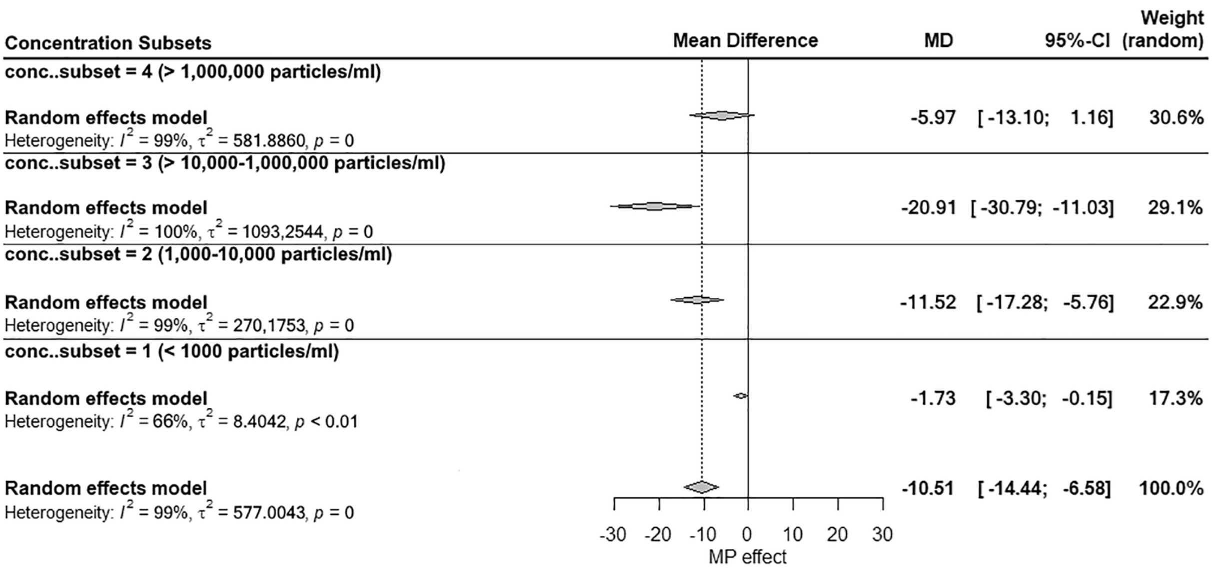

FIGURE 6 Meta-analysis forest plot of micro/nanoplastics (MP) effects on the average number of offspring using a random effects model. Centre of diamonds represents mean differences of subsets or the complete dataset (vertical dashed centre line) and edges show the 95% confidence intervals.

Upon categorising the effect sizes under the four concentration subsets, subset 1 (<1,000 particles/ml; MD = −1.7252, $z = -2.15$, $p = 0.0318$), subset 2 (1,000–10,000 particles/ml; MD = −11.5209, $z = -3.92$, $p < 0.0001$) and subset 3 (>10,000-1,000,000 particles/ml; MD = −20.9073, $z = -4.15$, $p < 0.0001$) each exhibited significant negative effects (Figure 6). Subset 4 (>1,000,000 particles/ml), which encompasses the highest concentration effect sizes, also showed a negative effect (MD = −5.9663, $z = -1.64$, $p = 0.1010$), although this is only a trend. The differences between the concentration subsets were significant ($Q = 24.21$, df = 3, $p < 0.0001$). In subsets 1, 2 and 3 there was a clear decline in mean offspring counts with increasing plastic particle concentrations. Strikingly, subset 4 presented an anomalous profile, displaying a mean difference in juveniles that is only slightly lower than that of subset 1 (Figure 6). It is intriguing, that even the most diminutive concentration subset (<1,000 particles/ml) manifests a substantial reduction in host fecundity, underscoring the remarkable sensitivity of *Daphnia* to micro/nanoplastic exposure.

3.5 | Research gaps and future recommendations

The majority of analysed studies (86%) were conducted on *D. magna* which is two to five times larger than other *Daphnia* species (Burns, 1969; Koivisto, 1995). This size difference makes *D. magna* generally less sensitive to contaminants compared to smaller *Daphnia* species (Gonçalves et al., 2007; Koivisto et al., 1992; Saebelfeld et al., 2017). As was found likewise for microplastics; Jaikumar et al. (2019) showed that in comparison to two other (smaller) *Daphnia* species, *D. magna* was the least sensitive species. Thus, the very low tested concentration of microplastics that are concluded to have no effect on *D. magna* might in fact be still toxic to other, smaller, species. Furthermore, *D. magna* occurs mostly in fishless habitats such as small ponds and rockpools, but not in lakes with fish; this is because its relatively large body size makes it strongly vulnerable to fish predation. Thus, the results obtained from the *D. magna* studies cannot be extrapolated to lake ecosystems. The latter are mostly inhabited by the very small species from the *D. longispina* complex, the most common members of lake zooplankton communities in the northern hemisphere (Keller et al., 2008; Ma et al., 2019). The lack of microplastic studies on this species complex (tested in one study only, Cui et al., 2017) creates a severe knowledge gap. As the tolerance to environmental contaminants is not similar for relatively large *D. magna* versus smaller *Daphnia* species, and given the differences between habitats of *D. magna* and those of other species, future studies should concentrate on smaller *Daphnia* species inhabiting lakes. Only this will allow an extrapolation of laboratory results to the lake ecosystems. In addition to lack of interspecific variation in the *Daphnia*-microplastic research, another important (and similarly unexplored) level of variation is intraspecific. Only 2.5% of the analysed studies used more than a single *Daphnia* clone. All these studies showed significant intraspecific differences in *Daphnia* reaction to microplastics, irrespective if the tested clones originated from multiple or from single populations. This illustrates the importance of incorporating clonal variation into future assessments of the impact of micro/nanoplastics.

While irregular microplastic shapes have been demonstrated to cause more adverse effects than spherical particles, attributed to a prolonged gut passage time (e.g., An et al., 2021; Frydkjær et al., 2017), the studies analysed here did not explore gut tissue damage as a possible cause for this observed difference in toxicity. Conversely, other research has indicated that microplastics can cause intestinal damage in zebrafish (Zhao et al., 2021) and, more recently, also in *D. magna* (Chen et al., 2022). Therefore, future studies could incorporate the histological analysis of intestines to explain the mechanisms of microplastic toxicity in *Daphnia*.

Another recommendation is the inclusion of environmentally relevant concentrations into experimental designs. Very few of the analysed studies (7%) tested micro/nanoplastic concentrations that are considered environmentally relevant (according to the thresholds applied in Al-Sid-Cheikh et al., 2018; Lenz et al., 2016): (Chang et al., 2022; Heinlaan et al., 2020; Jaikumar et al., 2019; Liu, Cai, et al., 2020; Liu, Jiao, et al., 2020; Ogonowski et al., 2016; Scherer et al., 2017; Trestrail et al., 2020). In order to mimic the conditions which *Daphnia* have to deal with in natural environments, it is indispensable for future studies to use environmentally relevant micro/nanoplastic concentrations. Here, it is important to consider that the larger the particle size, the lower the concentration needs to be. Fortunately, analytical methods for determining environmental particle concentrations are improving, especially on the level of nanoplastics where previously no method was available to detect their concentrations in environmental samples (Besseling et al., 2019). New methods enable a better assessment of what are environmentally relevant micro/nanoplastic concentrations. As micro/nanoplastic concentrations given in mass per volume can vary depending on particle size/shape/density, this is not a comparable unit across studies. Therefore, a standardisation of concentration units is necessary. Future studies should report micro/nanoplastic concentrations at least in particle number per volume (or both mass and particle number) for an easier and more impactful comparison between studies. In addition, only 7% of the analysed studies tested the multigenerational effect of micro/nanoplastics. However, these studies often showed that micro/nanoplastic toxicity increases with the number of exposed *Daphnia* generations; even if there was no effect in F_0, a micro/nanoplastic effect often only manifested in F_2 (Liu, Cai, et al., 2020; Liu, Jiao, et al., 2020; Schür et al., 2020). This was especially the case when very low, environmentally relevant nanoplastic concentrations were tested. Single-generation studies would miss these effects on *Daphnia* fitness and therefore underestimate micro/nanoplastic toxicity. For this reason, future studies should include multiple generations, ideally at least three. Finally, more than half of the analysed studies included various other experimental treatments to act as additional stressors. Several of these treatments showed antagonistic (e.g., humic acid), additive (e.g., heavy metals) or synergistic (e.g., temperature, salinity or pesticides) effects in combination with micro/nanoplastic contamination. Very low microplastic concentrations with no detrimental effect alone did decrease *Daphnia* fitness when combined with additional stressors (Chang et al., 2022; Serra et al., 2020). These findings point out the importance of including multiple stressors into future assessments on the effect of micro/nanoplastics to resemble natural environmental conditions, especially those caused by climate change.

AUTHOR CONTRIBUTIONS

Conceptualisation: Justyna Wolinska, Elisabeth Funke; *Developing methods*: Elisabeth Funke, Justyna Wolinska; *Conducting the research*: Elisabeth Funke, Lukas Webb; *Data analysis*: Elisabeth Funke, Lukas Webb; *Data interpretation*: Elisabeth Funke, Lukas Webb, Justyna Wolinska; *Preparation of figures and tables*: Lukas Webb, Elisabeth Funke. *Writing*: Elisabeth Funke, Justyna Wolinska, Lukas Webb.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.8315276.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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