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Experimental Studies with Nematodes in Ecotoxicology: An Overview

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Abstract: With respect to their high abundances, their role as intermediaries between microorganisms and higher trophic levels, and their ubiquitous occurrence in all habitats, nematodes are of strong potential interest as environmental indicators. Ecotoxicological methods to evaluate the risk of anthropogenic pollutants on ecosystems require both in vitro and in vivo toxicity tests to investigate either mechanisms or pathways of toxicity and to set accurate toxicity thresholds. For this, the interest in nematodes as model organisms in ecotoxicology increased over the past few decades and existing appropriate experimental methods are reviewed in this manuscript. An overview of the various existing ecotoxicological tools for nematodes, ranging from molecular laboratory methods to experimental model ecosystem approaches, and their role as indicator organisms is given. The reviewed studies, approaches that range from species-based to community-based methods, reveal exciting possibilities for the future use of nematodes in ecotoxicological studies. Suitable ecotoxicological tools and ecological indices for nematodes should be integrated in weight-of-evidence approaches for assessing the ecological risk of contamination.

Key words: chemicals, contamination, ecology, ecotoxicology, free-living, freshwater, marine, methods, microcosms, model ecosystems, molecular, NemaSPEAR[%] index, review, single species, soil.

Due to their high ecological relevance in freshwater, marine, and terrestrial habitats, nematodes are of strong potential interest as environmental indicators (Wilson and Kakouli-Duarte, 2009). Two symposia on "Nematodes as Environmental Bioindicators" 2007 in Edinburgh (United Kingdom) and 2012 in Gent (Belgium) helped to open avenues of communication between various scientists and stakeholders. In general, the interest in nematodes in the field of ecotoxicology is growing. If searching for the terms "nematode*" AND "ecotoxicology" in Google Scholar, the number of hits increased 10-fold within the last 20 years (which is above average of the overall increase in ecotoxicological papers). A considerable part (25%) of these papers on nematodes describes studies with the model nematode *Caenorhabditis elegans*.

Ecotoxicological methods to evaluate the risk of anthropogenic pollutants on ecosystems, must (i) assess the toxicity of single chemicals or chemical mixtures in water, sediment, and soil (European Commision, 2003; ECHA, 2008; EFSA, 2013) and (ii) evaluate the ecological status or quality of certain ecosystem compartments, such as soil or sediments that are potentially exposed to pollution (European Water Framework Directive [WFD]) (European Community, 2000). A prospective risk assessment requires both in vitro and in vivo toxicity tests to investigate mechanisms of toxicity and to set accurate toxicity thresholds, such as NOEC (no observed effect concentrations) and EC10 (the concentration at which 10% of the total effect occurs) for regulatory purposes (European Commision, 2003; EFSA, 2013). To refine toxicity thresholds (and reduce safety risks), higher-tier testing is required (Boxall et al., 2002). This can be achieved using (i) chronic toxicity endpoints (e.g., reproduction), (ii) realistic exposure scenarios (e.g., sediments for scarcely soluble substances), or (iii) ecologically more relevant multispecies test systems (model ecosystems), such as microsomes or mesocosms. Regulatory authorities have to rely on environmentally safe thresholds for chemicals in the process of chemical authorization and restriction of their release in the environment (e.g., European Regulation, Evaluation and Authorization of Chemicals [REACH]). In retrospective risk assessments, the ecological status or quality of an ecosystem is assessed by evaluating the in situ fauna or flora (WFD; European Community, 2000). Here, indicator systems can help to identify habitats with poor ecological status and to link this status to the presence of chemical pollution or other types of stress, including hydromorphological modifications and climate change (e.g., Von der Ohe et al., 2007; Von der Ohe and Goedkoop, 2013). Appropriate actions to improve the ecological status of ecosystems (as mandated by the European Union WFD) can only be taken if the causes of the deleterious effects on the ecosystem are known (De Zwart et al., 2009).

For all these challenges in ecotoxicology (or applied ecology), there exist appropriate experimental methods that use nematodes as a model or indicator organism. These methods are reviewed in this manuscript. Although many studies have examined the effects of chemicals on a single species (mainly using *C. elegans*), much less is known about the ecotoxicological impact on nematodes in multispecies set-ups or at the community level. Here, we provide an overview of the various ecotoxicological tools that already exist for nematodes, ranging from molecular laboratory methods to experimental model ecosystem approaches (Fig. 1). This review is divided into two parts: (i) the first part gives an overview of laboratory methods that were applied to study effects of chemicals on a single nematode species, as listed in Table 1. Due to the vast number of studies

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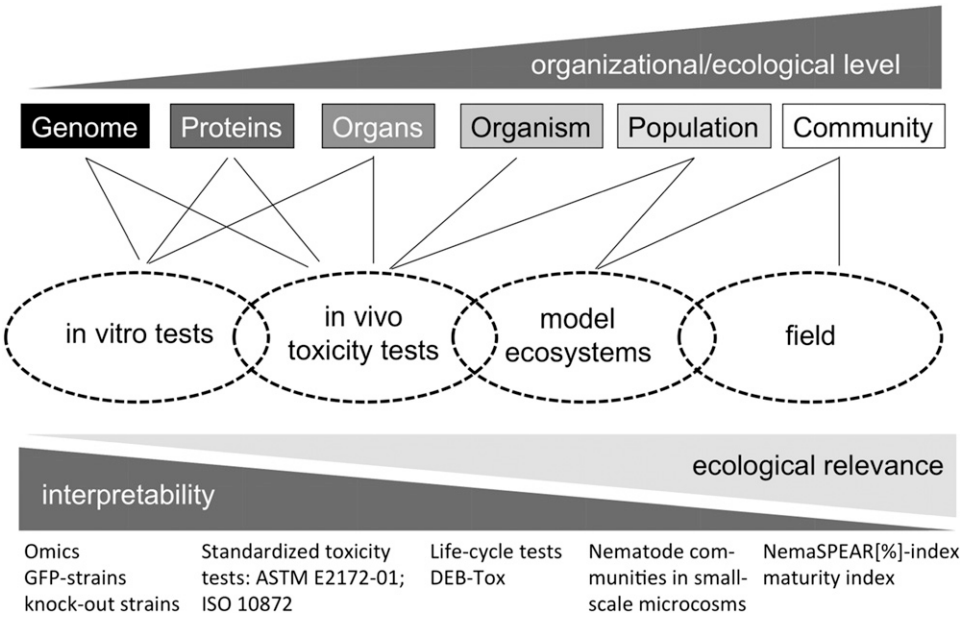

Fig. 1. Ecotoxicological methods at different organizational and ecological levels that can be applied using nematodes as test or indicator organisms. Omics stands for genomics, transcriptomics, proteomics, metabolomics. GFP = green fluorescent protein, DEB-Tox = dynamic energy budget theory applied to toxicological issues; NemaSPEAR = nematode species at risk.

with *C. elegans* in, e.g., medical research, this section is not claiming completeness. However, the reader can find a comprehensive compilation of examples for important environmental chemicals and links for continuative reviews on specific topics; (ii) the second part gives an overview of relevant studies on effects of chemicals on free-living nematode communities in experimental set-ups (model ecosystems). A comprehensive literature research was carried out in ISI Web of Science using the search term "nematode*" AND "ecotoxicology" AND ("microcosm*" OR "mesocosm*"), revealing more than 2000 hits. Based on this pool, studies dealing with community assessment parameters of free-living nematodes, as listed in Table 2, were categorized as relevant for our field of interest and reviewed, whereas publications concerning other fields of research, e.g., studies on genetic and metabolomic responses to chemicals as well as applications with parasitic nematodes as considered organisms, were excluded (NOT "gen*" or "metabolom*" or "parasit*"). The yielded ecotoxicological microcosm studies were screened on the use of a representative (nematode) community, an adequate description of the experimental set-up, and reported exposure concentrations of the used chemicals. Beside the mentioned nematode community assessment parameters, tested chemicals, type of microcosm, duration, and extraction methods were recorded (Table 2).

Laboratory Ecotoxicological Methods with a Single Species

Almost a century ago, the first toxicological studies were carried out with free-living nematodes as the test organism (*Rhabditis elegans*; Honda, 1924). Since then, various nematode species, mainly bacterial feeders, have been used for testing the toxicity of chemicals and environmental samples (e.g., *C. elegans*, *Panagrellus redivivus*, *Plectus acuminatus*, *Monhystera disjuncta*). Apart from *C. elegans*, which is by far the most commonly used nematode in single-species testing, various other soil and marine nematode species have been employed to assess the toxicity of (i) toxic compounds, such as heavy metals, pesticides, and pharmaceuticals, and (ii) contaminated natural samples (Table 1).

Due to the nearly ideal qualities of *C. elegans* as a model organism in genetics, developmental biology, and medical biochemistry (e.g. easy culture, simple body plan, and short generation and life cycle), the effects of chemicals on this nematode species at various organizational levels (molecular, organs, whole organism, and population) have already been described. Therefore, many molecular and biomedical methods exist for *C. elegans* that could be exploited for ecotoxicological purposes (for reviews see, e.g., Kaletta and Hengartner, 2006; Menzel et al., 2009a; Hulme and Whitesides, 2011). Also, for whole-organism toxicity testing the most mature and standardized test systems are those developed for *C. elegans* (ASTM E2172-01: ASTM, 2001; ISO 10872: ISO, 2010; for reviews see, e.g., Leung et al., 2008; Höss and Williams, 2009; Muschiol et al., 2009).

Effects at the molecular level: C. elegans is one of the most important nonmammalian model organisms, besides *Escherichia coli*, *Saccharomyces cerevisiae*, *Drosophila melanogaster*, *Danio rerio*, and *Arabidopsis thaliana*. As such, it has become a cornerstone of fundamental biological research and systems biology (Ideker et al., 2001) and a wide range of sophisticated methods are available for

Table 1. Nematode species (except *Caenorhabditis elegans*) used in toxicity testing.

Species	Tested chemical	Toxicity endpoint	Reference(s)
Acrobeloides nanus	Cd, carbendazim, PCP	DEB modeling	Alda Álvarez et al. (2006)
A. nanus	Cu, Zn	R	Hao et al. (2010)
Acrobeloides sp.	Bt toxin	D, M, R, S	Wei et al. (2003)
A. avenae	Bt toxin	G, S	Igonoffo and Dropkin (1977)
Bursilla monhystera	VOC	Chemotaxis	Höckelmann et al. (2004)
Caenorhabditis briggsae	Azasteroid	D, G, R	Bottjer et al. (1985)
(Caeno)Rhabditis briggsae	Antibiotics	Activity	Briggs-Gochnauer and McCoy (1954)
Diplolaimella spec 1	Co, Hg, Pb	D, S	Vranken and Heip (1986)
Heterocephalobus pauciannulata	Cu	Life cycle traits	Kammenga and Riksen (1996)
M. disjuncta	Cd	S	Vranken et al. (1985)
M. disjuncta	Cu, Hg, Ni, Zn	D, S	Vranken et al. (1988)
M. disjuncta	Cr	D, S	Vranken et al. (1989)
M. disjuncta	Metals, acid-iron waste, PCP, lindane	D, F	Vranken et al. (1991)
Monhystera microphtalma	Cd	S	Vranken et al. (1985)
Multispecies	Cd, PCP	S	Kammenga et al. (1994)
Multispecies	Cu	S	Bongers et al. (2001)
P redivivus	Metals, mutagens	D, Molt	Samoiloff et al. (1980)
P. redivivus	AMD, actidione, hydroxyurea	G, Gonad Dev	Boroditsky and Samoiloff (1973)
P. redivivus	Azasteroid	G, D, R	Bottjer et al. (1985)
P. redivivus	Sediments, extracts of sediments	G, Mat, S	Ongley et al. (1988)
P. redivivus	Lindane, PCP, fluorosurfactants	S	Debus and Niemann (1994)
P. redivivus	Bt toxin	G, S	Igonoffo and Dropkin (1977)
P. redivivus	Refinery effluents	G, Mat, S	Sherry et al. (1997)
P. redivivus	Contaminated sediment	G, S	Ross and Henebry (1989)
P. redivivus	Cu	Feed, Mov, R, S	Boyd and Williams (2003)
P. redivivus	Sediment extracts	Molt, S	Samoiloff et al. (1983)
P. silusiae	Cd, Cr, Cu	Phar Pump	Mudry et al. (1982)
P. silusiae	Metals	S	Haight et al. (1982)
Panagrolaimus cf. *thienemanni*	Cd, aldicarb, ivermectin	G, R	Brinke et al. (2011a)
P. acuminatus	Cd, Cu, PCP	R	Kammenga et al. (1996)
P. acuminatus	Cu	Life cycle traits	Kammenga and Riksen (1996)
Pristionchus pacificus	DAPG	Egg hatch, S	Meyer et al. (2009)
P. pacificus	Bt toxin	D, Morph, R, S	Wei et al. (2003)
P. pacificus	Ni	F, G, life span	Rudel et al. (2013)
P. pacificus	Cu	Feed, Mov, R, S	Boyd and Williams (2003)
P. pacificus	Pathogenic bacteria	R, S	Rae et al. (2010)
P. pacificus	Acetochlor	G, R, S	Zhang et al. (2013)
Rhabditis marina	Salinity, Cd	Popul Dev	Derycke et al. (2007)
R. marina	Cd	S	Vranken et al. (1985)
R. marina	Cd, Ba	Popul Dev	Lira et al. (2011)
R. rainai	DAPG	Egg hatch, S	Meyer et al. (2009)

PCP = pentachlorophenol, Bt = *Bacillus thuringiensis*, VOC = volatile organic compounds, DAPG = 2,4-diacetylphloroglucinol, AMD = actinomycin D, DEB = dynamic energy budget, D = development, F = fecundity, Feed = feeding, G = growth, Gon Dev = gonad development, Mat = maturation, Molt = molting, Morph = morphology, Mov = movement, Phar Pump = pharyngeal pumping, Popul Dev = population development, R = reproduction, S = survival.

studying molecular processes in *C. elegans* (Strange, 2006). Many of these have been used to study the molecular response of this nematode to environmental toxicants. In the following section, we provide several examples of toxicogenomic studies of *C. elegans*. For more exhaustive information on this topic we refer the reader to the reviews of Leung et al. (2008), Menzel et al. (2009a), Helmcke et al. (2010), and Caito et al. (2012).

Toxicogenomics can be defined as a study that investigate the response of a genome to hazardous substances by means of (i) genomic-scale mRNA expression analyses (transcriptomics), (ii) cell- and tissue-wide protein expression techniques (proteomics), or (iii) cell- and tissue-wide metabolite profiling (metabolomics) (Stürzenbaum et al., 2012). "Omic" techniques can be applied to identify novel genes involved for example in metal homeostasis, detoxification, and to unravel toxicological pathways and toxicity mechanisms (modes of action) by combining molecular with phenotypic responses. DNA microarrays have been used to profile the overall gene expression in *C. elegans* after its exposure to various types of chemical stressors, including endocrine disruptors (Custodia et al., 2001; Novillo et al., 2005), ethanol (Kwon et al., 2004), humic substances (Menzel et al., 2005), polychlorinated biphenyls (Menzel et al., 2007), phthalate (Roh et al., 2007), bacterial toxins (Huffman et al., 2004), metal ions and nanoparticles (Cui et al., 2007; Roh et al., 2009b), and complex chemical mixtures in contaminated sediments (Menzel et al., 2009b). Microarray studies helped to identify general and mode-of-action-specific stress-responsive genes that are involved in defense pathways (e.g., protection against oxidative stress), ion homeostasis, xenobiotic

metabolization, and hormone regulation. Combining gene silencing (RNAi; Fire et al., 1998) or gene knockout (mutant strains) methods with phenotypic effect screening, the functions of stress-responsive genes can be verified, which in turn confirms their use as biomarkers for specific toxic stresses (e.g., Roh et al., 2009a). By fusing green fluorescent protein markers with stress-responsive genes, gene expression can be monitored in vivo microscopically and the molecular response in specific tissues can thus be localized (Chalfie et al., 1994).

Effects on the whole organism: The easy culturing, transparent body, and short generation cycle of *C. elegans* offer advantages in the screening of the in vivo toxicity of chemicals with respect to various toxicity endpoints, such as the mortality, growth, reproduction, and behavior of nematodes. Testing can be done using low-tech or low-cost set-ups (incubator plus microscope) or with high-tech and high-throughput systems, such as the COPAS BioSorter (Union Biometrica, Holliston, MA) (Pulak, 2006; Boyd et al., 2010a; Hunt et al., 2012). For screening the toxicity of chemicals, high-throughput set-ups with *C. elegans* have been used to investigate the toxic effects of metals (Hunt et al., 2012), neurotoxicants (Boyd et al., 2010b), fluoridation compounds (Rice et al., 2014), and various water-soluble compounds toxic to mammals (Sprando et al., 2009). In the case of mammalian toxicants, these systems can be applied to initially screen toxicity using a nonmammalian toxicological model, thereby reducing testing with traditional mammalian animal models (e.g., rats).

Ecotoxicological chemical testing is required for assessing the risk to living organisms of industrial, agricultural, or household chemicals that are released into the environment, including nanoparticles, pesticides, and pharmaceuticals. Laboratory in vivo bioassays are appropriate tools for testing the toxicity of chemicals on intact organisms to establish reliable effect thresholds that help to evaluate the risk of these chemicals. Although *C. elegans* is still rarely used for regulatory chemical testing, it does appear in reports for REACH regulation (Cesnaitis et al., 2014; Versonnen et al., 2014). *C. elegans* toxicity tests in aqueous medium have been carried out for a variety of toxicants, such as metals (e.g., Tatara et al., 1997; Traunspurger et al., 1997b; Wang and Wang, 2008; Höss et al., 2011c), polycyclic aromatic hydrocarbons (PAH; e.g., Sese et al., 2009; Spann et al., 2015), pesticides (reviewed in Meyer and Williams, 2014), pharmaceutical compounds (e.g., Dengg and van Meel, 2004; Brinke et al., 2011a), endocrine disruptors (e.g., Höss et al., 2002; Höss and Weltje, 2007), and pesticidal bacterial toxins (e.g., Wei et al., 2003; Höss et al., 2013). Nanomaterials are a relatively new class of environmental toxicants and there are special requirements regarding their toxicity testing. *C. elegans* is a suitable organism for testing nanomaterials. In fact, a comparatively large number of studies have examined the toxicity of nanomaterials on this nematode with respect to toxicity endpoints, such as survival, growth, reproduction, movement, and life span (e.g., silver: Meyer et al., 2010; Yang et al., 2012; gold: Tsyusko et al., 2012; cerium oxide: Collin et al., 2014; Zhang et al., 2011; iron oxide: Höss et al., 2015; fullerene: Cha et al., 2012; titanium oxide: Angelstorf et al., 2014; Wu et al., 2013; zinc [Zn]: Ma et al., 2011). With sophisticated genetic techniques, such as gene expression and knockout strains, specific toxicity mechanisms have been investigated, including oxidative stress and phototoxicity (Roh et al., 2009a; Tsyusko et al., 2012).

A major advantage of *C. elegans* as the test organism is that testing can be carried out both in aqueous medium and on solid substrates, such that the risk of chemicals in soils as well as sediments can be determined (Traunspurger et al., 1997b; Höss et al., 2009). This is especially important for chemicals that bind to organic or mineral particles, such as metals and hydrophobic chemicals (e.g., Ingersoll et al., 1997). According to the Technical Guidance Document on Risk Assessment (Part II) of the European Commission, *C. elegans* is a possible alternative test organism to refine the predicted no effect concentration of biocides for the soil compartment (European Commision, 2003). For the sediment compartment, besides tests with *Lumbriculus variegatus* and chironomids, "long-term tests with a further benthic species using spiked sediments" are recommended (European Commision, 2003). *C. elegans* is a suitable alternative test species because there exist readily standardized sediment and soil toxicity tests (ASTM E2172-01: ASTM, 2001; ISO 10872: ISO, 2010). Moreover, *C. elegans* has been recommended as a suitable test organism for testing the toxicity of engineered nanoparticles in complex media, such as soil (Handy et al., 2011). In a round-robin exercise, toxicity testing using *C. elegans* according to ISO 10872 was shown to be a reliable and reproducible system for testing contaminated sediments and soils as well as spiked chemicals in water (Höss et al., 2012). This test system has already been used to assess the toxicity of spiked sediments (Höss et al., 2001; Comber et al., 2006, 2008; Rudel et al., 2013), contaminated soils (Black and Williams, 2001; Höss et al., 2009, 2011b; Huguier et al., 2013), contaminated sediments (Tuikka et al., 2011; Feiler et al., 2013), and complex aqueous samples, including waste water and pore water (Hitchcock et al., 1997; Harmon and Wyatt, 2008).

Toxicokinetic and toxicodynamic modeling approaches are gaining increasing popularity in ecotoxicology and environmental risk assessments (Ashauer and Escher, 2010). In this context, the short life span of *C. elegans* was exploited in its use as a model organism to observe the effects of chemicals on the various traits of this nematode over its whole life cycle. These data were then modeled to determine effects on population

dynamics (e.g., Brinke et al., 2013; Goussen et al., 2013) and dynamic energy budgets (DEB modeling) (Alda Álvarez et al., 2005; Swain et al., 2010; Wren et al., 2011; Jager et al., 2014). Although requiring further experimental effort for their confirmation, these models allow for an ecologically more relevant interpretation of toxicity data.

Experimental Studies on Model Ecosystems

Model ecosystems, e.g., microsomes and mesocosms, are useful tools to assess the fates and effects of environmental chemicals (e.g., Van den Brink et al., 2005). These test systems are an effective compromise between standard laboratory tests and outdoor studies. They are large enough to study natural communities under controlled conditions and small enough to provide sufficient replication and precise control over relevant experimental variables. As such, they provide insight into the mechanisms of the biotic responses of natural assemblages, such as abundance, biomass, and diversity (Lamberti and Steinman, 1993; Brinke et al., 2011b; Faupel and Traunspurger, 2012). Model ecosystems therefore provide a balance between interpretability and practicability on the one hand and ecological relevance on the other (Fig. 1). Community studies are a suitable tool to assess the potential hazard of contamination on fauna, with the structure of the inhabiting communities reflecting their response to environmental conditions over a period of time. This allows an ecologically more relevant risk assessment than laboratory bioassays with a single species (Höss et al., 2004). Although single-species tests provide valuable information for predicting effects of tested chemicals on individual organisms (e.g., toxicity thresholds and modes of action), the controlled laboratory conditions of model ecosystems allow the coincidental effects of pollutants to be demonstrated on the community level with respect to secondary production and in terms of the interactions between anthropogenic toxicants and complex ecosystems (Faupel and Traunspurger, 2012). These effects could be caused by changes in the food web and/or other indirect effects, such as changes in predator–prey relationships or competition (Landner et al., 1989; Culp et al., 2000; Fleeger et al., 2003; Clements and Rohr, 2009). Thus, model ecosystems are used in higher-tier studies to predict the effects of specific chemicals on ecosystems under more realistic conditions, while avoiding the safety-related issues associated with large-scale testing (Forbes and Calow, 2002).

Nematodes are the dominant organismal group in freshwater and marine sediments (Heip et al., 1985; Traunspurger, 2002; Traunspurger et al., 2006) as well as in soils (Yeates, 1981; Ferris et al., 2001). Even if their small size and their functional and structural diversity requires experience in the handling of these organisms, nematodes are very well suited for model ecosystem studies due to their short generation time, continuous reproduction, and high densities (Höss et al., 2006). Furthermore, nematodes represent different trophic levels, with species feeding on detritus, bacteria, algae, fungi, and higher plants, besides omnivorous and predatory species (Yeates et al., 1993; Traunspurger, 1997, 2002). Consequently, they occupy a significant position in the food web, between bacteria, protists, and macrofauna, and are important contributors to nutrient cycling (Ingham et al., 1985; Beare, 1997; Traunspurger et al., 1997a; Bergtold and Traunspurger, 2005). Within this taxon, the numerous species have evolved several life-history strategies, ranging from fast-reproducing species, i.e., the "colonizers" or *r*-strategists, which are regarded as relatively tolerant of disturbances and easily adapt to new environmental conditions because of their short generation times, to rather slowly reproducing species with long generation times; these "persisters," or *K*-strategists, categorized as much more sensitive to disturbances (Bongers, 1990).

Laboratory studies on nematodes in microcosms can be adapted to reproduce various habitats, such as soil and marine or freshwater sediments. The following sections provide examples of experiments with nematodes in model ecosystems that underline the suitability of this organismal group for risk assessment at higher ecological levels.

Extraction methods: For the quantitative separation of meiofauna from sediment and soil particles, special techniques have been developed. The preferred methods for extracting these small organisms from freshwater sediment particles are the silica gel centrifugation method with Ludox, following Pfannkuche and Thiel (1988), and the decantation method, according to Uhlig et al. (1973). For marine sediments, the resuspension–decantation method of Wieser (1960) and the modified centrifugation/flotation technique of McIntyre and Warwick (1984) and Austen and Warwick (1989) are most commonly used. In the experimental set-ups with soils, simple techniques such as the Baermann funnel (Baermann, 1917) or the Oostenbrink elutriator–cotton–wool filter method (Oostenbrink, 1960), both of which make use of the active emigration of soil-inhabiting meiofauna, have been applied. Centrifugation techniques, e.g., with Ludox, are rarely used as separation method for terrestrial microcosms (Table 2).

Nematode community assessment parameters: Microcosm studies have been carried out to determine the effects of different treatments based on changes in the abundance of nematodes (and other meiofaunal groups), their species and/or genus composition, biomass, secondary production, and the trophic structure of nematode communities as measurement parameters. Freshwater nematode species are morphologically identified following standard works (Andrassy, 1984; Loof, 2001; Eyualem et al., 2006) and/or classified in

TABLE 2. Studies on model ecosystems with nematodes.

Chemicals	Containers	Duration (d)	Nematode community assessment parameters	Nematode extraction method	Reference(s)
Freshwater sediment					
Cd	Boxes	218	AB, ID, FT, MI, H', J', PRC	CM	Brinke et al. (2011b)
Cd	Boxes	215	AB, ID, SP, PRC	CM	Faupel and Traunspurger (2012)
Cd	Boxes	215	AB, ID, BM, PRC	CM	Faupel et al. (2011)
Cd	Boxes	215	AB, ID, SP	CM	Faupel et al. (2012)
Isoproturon	Aquaria	56	AB, ID, FT	RDM	Traunspurger et al. (1996)
Ivermectin	Cylinders	224	AB, ID, FT, MI, H', J', PRC	CM	Brinke et al. (2010)
p-Nonylphenol	Cylinders	98	AB, ID, FT, MI, H', J', PRC	CM	Höss et al. (2004)
Tetracycline	Cylinders	28	AB	n. a.	Quinlan et al. (2011)
Marine sediment					
Cd	Cylinders	460	AB, BM	RDM	Sundelin and Elmgren (1991)
Cd, Cr, Cu, Hg, Pb	Cylinders	30	AB, ID, MDS	n. a.	Millward et al. (2001)
Cd, Cu, Zn	Cylinders	60	AB, ID, H', J', MDS	CM	Austen et al. (1994)
Cd, Cu, Pb, Zn	Cylinders	60	AB, ID, H', J', MDS	CM	Austen and McEvoy (1997a)
Co, Zn	Cylinders	30	AB, ID, H', J', MDS	RDM	Beyrem et al. (2011)
Cr	Cylinders	30	AB, ID, BM, H', J', MDS	RDM	Boufahja et al. (2011a)
Cu	Cylinders	40	AB	BF	Bogomolov et al. (1996)
Cu	Cylinders	77	AB, ID, H', J', MDS, PCA	CM	Warwick et al. (1988)
Cu, Fe, Pb, Zn	Cylinders	32	AB, ID, FT, MI, MDS	CM	Gyedu-Ababio and Baird (2006)
Cd, diesel	Cylinders	90	AB, ID, BM, H', J', MDS	RDM	Beyrem et al. (2007)
Diesel	Cylinders	28	AB, GE	n. a.	Carman et al. (1997)
Diesel	Cylinders	90	AB, ID, BM, H', J', MDS	RDM	Mahmoudi et al. (2005)
Diesel	Aquaria	60	AB, MDS	CM	Lindgren et al. (2012)
Hg	Cylinders	60	AB, ID, H', J', MDS	RDM	Hermi et al. (2009)
Lubricant oils	Cylinders	35	AB, ID, H', J', MDS	CM	Beyrem et al. (2010)
Ni	Cylinders	30	AB, ID, H', J', MDS	RDM	Hedfi et al. (2007)
Ni, Cu, Cr, diesel	Cylinders	30	AB, ID, BV, RVPL	RDM	Boufahja et al. (2011b)
Pb, Zn	Cylinders	60	AB, ID, H', J', MDS	RDM	Mahmoudi et al. (2007)
Permethrin	Boxes	25	AB, ID, H', J', MDS	RDM	Boufahja et al. (2011c)
Permethrin	Cylinders	30	AB, ID, H', J', MDS	RDM	Soltani et al. (2012)
PAHs	Cylinders	28	AB	n. a.	Carman and Todaro (1996)
PAHs	Cylinders	28	AB, GE	n. a.	Carman et al. (1995)
PAHs	Cylinders	30	AB	RDM	Louati et al. (2013)
Triclosan	Cylinders	21	AB (NGS)	NGS	Chariton et al. (2014)
TBT	Exp. streams	60	AB, ID, H', J', MDS	CM	Austen and McEvoy (1997b)
TBT	Cylinders	56	AB, ID, FT, BM, H', J', MDS	CM	Schratzberger et al. (2002)
Soil					
Benomyl, dimethoate	Cylinders	77	AB	WF	Martikainen et al. (1998)
Biochar	Boxes	184	AB, ID, FT, H', MI	OCWM	Zhang et al. (2013)
Carbendazim	Cylinders	56	AB	BF	Burrows and Edwards (2002)
Carbendazim	Cylinders	112	AB, ID, FT, MI	OCWM	Moser et al. (2004)
Carbofuran	Cylinders	28	AB, ID, FT	TM	Chelino et al. (2011)
Cd, Cu, Ni, Zn	Cylinders	14	AB, ID, FT, MI	OCWM	Korthals et al. (1996)
Cu, Zn	Cylinders	183	AB, ID, FT	OCWM	Korthals et al. (2000)
Cd, Cu, MT, PCB	Cylinders	56	AB, FT	BF	Parmelee et al. (1997)
Cu, p-NP, TNT	Cylinders	7	AB, FT	BF	Parmelee et al. (1993)
Cry proteins	Cylinders	84	AB, ID, FT, MI, PRC	CM	Höss et al. (2014)
Deltamethrin	Cylinders	123	AB, ID, FT, PC	TM	Griffiths et al. (2006)
Lindane	Cylinders	88	AB, ID, FT, MI, H', J', PRC	OCWM	Scholz-Starke et al. (2013)
Zn	Plots	730	AB, ID, MI, H', PRC	OCWM	Smit et al. (2002)
Zn	Cylinders	112	AB, ID, BM, FT, MI, PRC	OCWM	Van der Wurff et al. (2007)

AB = abundance, ID = identification, FT = feeding types, MI = maturity index, H'= Shannon-Wiener index, J' = evenness, PCB = polychlorinated biphenyl, PRC = principle response curve, SP = secondary production, BM = biomass, BV = body volume, MDS = multidimensional scaling ordination, PCA = principle component analyses, GE = grazing efficiency, RVPL = relative volume pharyngeal lumen, NGS = next generation sequencing, CM = centrifugation method, RDM = resuspension-decantation method, OCWM = Oostenbrink/cotton-wool method, BF = Baermann funnel, WT = wet funnel, TM = tray method, MT = malathion, PAH = polycyclic aromatic hydrocarbons, p-NP = para-nitrophenol, TBT = tributyltin, TNT = trinitrotoluene.

various feeding types according to Traunspurger (1997) and Moens et al. (2006). Taxon identification for nematodes from marine sediments is carried out following standard works and pictorial keys (Platt and Warwick, 1983, 1988; Warwick et al., 1998). The responses of soil inhabiting nematode communities to contamination are mainly assessed using classifications in trophic groups following the system of Yeates et al. (1993). Identifications to family level (rarely to genus or even species level) are done according to Bongers (1988). At the family level, nematodes of all habitats can be ranked with *c–p* values, following the colonizer–persister

scale of Bongers and Bongers (1998); the data are then used to calculate the maturity index (MI) (Bongers, 1990) (Table 2). This ecologically meaningful index is typically used in terrestrial studies but has been only rarely applied to investigations of freshwater and marine sediments (Beier and Traunspurger, 2001; Höss et al., 2004; Heininger et al., 2007; Brinke et al., 2010) (Table 2).

Multivariate analyses are suitable techniques to reveal chemically induced changes in nematode assemblages in spiked treatments compared to control communities over time. For species compositions in freshwater sediments and soils, the principle response curve (Van den Brink and Ter Braak, 1999) method is commonly applied. In marine sediments, multidimensional scaling (Clarke, 1993) ordination is the multivariate technique of choice. Univariate measure of effects include diversity indices, such as the Shannon–Wiener index (H') and evenness (J') (Neher and Darby, 2006). These assessment parameters are commonly determined in studies with freshwater and marine sediments (e.g., Austen et al., 1994; Brinke et al., 2010) but have only rarely been applied to terrestrial microcosms (e.g., Smit et al., 2002; Scholz-Starke et al., 2013).

Freshwater Sediments

So far, most freshwater microcosm and mesocosm studies have focused on macrobenthic invertebrates (macrofauna, such as snails, mussels, and insect larvae) in assessing the effects of chemicals on benthic communities (e.g., Fletcher et al., 2001; Wijngaarden et al., 2005). Only a few studies have used nematodes in microcosm tests focusing on freshwater sediments (Table 2), although the suitability of nematodes as test organisms in sediment toxicology is generally acknowledged (see the section Laboratory Ecotoxicological Methods with a Single Species and reviews by Traunspurger et al., 1995; Traunspurger and Drews, 1996; Höss and Traunspurger, 2003; Höss et al., 2006; Höss and Williams, 2009). Various environmental chemicals have been investigated in terms of their effects on nematode communities in freshwater microcosms, including heavy metals such as cadmium (Cd; Brinke et al., 2011b; Faupel et al., 2012; Faupel and Traunspurger, 2012), organic pesticides, such as ivermectin (Brinke et al., 2010) and isoproturon (Traunspurger et al., 1996), endocrine disruptors such as 4-nonylphenol (Höss et al., 2004), and pharmaceuticals such as the antibiotic tetracycline (Quinlan et al., 2011). In microcosm studies that focused on meiofauna, especially nematodes, the long-term effects of those chemicals were determined in experimental periods of 1 to 7 months. Only nematodes showed a tendency to recover from high-level exposure, based on an abundance of up to 90% of the meiofauna, such that they constituted the dominant taxon (Brinke et al., 2011b). Fairly neglected but ecologically important parameters are biomass and secondary production, which, to our knowledge, were first investigated in microcosms by Faupel and Traunspurger (2012). In their study, nematode secondary production was significantly influenced, as evidenced by a decrease of up to 95%, in highly contaminated microcosms compared to the control over the entire course of the experiment. In other experiments, strongly dose-dependent changes in the species compositions of nematode communities were observed (Höss et al., 2004; Brinke et al., 2010, 2011b; Faupel et al., 2011). The diversity of the nematode community, expressed as the Shannon–Wiener index, decreased significantly in microcosms treated with the highest Cd concentration ($H' = 0.6$), whereas diversity remained at a relatively constant high value ($H' = 1.8$–1.3) in control, low-level, and medium-level treatments (Brinke et al., 2011b). The results of a microcosm study with ivermectin supported these findings based on an even greater decrease of the Shannon–Wiener index, from 2.0 in control microcosms to 0.2 in high-level treatments (Brinke et al., 2010). Since nematodes are representative of all trophic levels in meiofaunal communities, a closer and differentiated examination of the different feeding types could be very valuable. In general, the dominance of bacterivorous taxa seems to increase under low and medium metal stress whereas that of predacious taxa decreases. In highly contaminated treatments omnivores and predators are the dominant feeding types (Brinke et al., 2011b; Faupel et al., 2012). Microcosms with a high concentration of Cd could be distinguished from those of the other treatments by the consistently greater dominance of predacious and omnivorous nematodes from the genera *Mononchus*, *Mesodorylaimus*, *Ironus*, and *Dorylaimus*, whereas species from the bacterivorous genus *Eumonhystera* almost disappeared. Bacteria-feeding nematodes, mainly represented by individuals of the genera *Daptonema* and *Eumonhystera*, were completely eliminated at the highest concentration of Cd but remained dominant in control treatments (Brinke et al., 2011b). Similar results were obtained for ivermectin-treated communities, where predacious and omnivorous species, especially those of the genus of *Tripyla*, were significantly more abundant in microcosms containing high concentrations of the organic pesticide, whereas the bacterivorous genus *Eumonhystera* decreased in abundance (Brinke et al., 2010). In further microcosm studies, both the sensitivity and the decrease in abundance of bacterivorous nematodes in highly contaminated microcosms were demonstrated (Traub-Eberhard et al., 1994). The initial communities in a microcosm study focusing on the effects of 4-nonylphenol were also dominated by species of bacterial feeders, which accounted for up to 96% of all nematodes (Höss et al., 2004). Over of the course of this study (14 weeks), the deposit-feeding species *Eumonhystera dispar* and *E. simplex* increased in relative abundance in treated microcosms

as did the epistrate-feeding species, *Chromadorina bioculata*. According to the MI theory, nematodes with a low *c–p* value, so called "colonizers" or *r*-strategists, should be more tolerant of sediment contamination than species with higher *c–p* values. The conflicting findings of the reviewed studies, however, are not explained by MI. The limited suitability of this index to reflect chemically induced changes in freshwater nematode communities motivated the development of a new stress index, the NemaSPEAR[%], which is based on a large field-derived dataset of nematode species sampled from German rivers with a pollution gradient (Heininger et al., 2007; Höss et al., 2011a). This index was developed using a co-occurrence approach (i.e., multivariate correlation of nematode species and environmental conditions in the same sample) aimed at identifying species that mainly occur in uncontaminated sediments (nematode species at risk = NemaSPEAR) and species that are ubiquitous or occur mainly in polluted sediments (nematode species not at risk = NemaSPEnotAR). The NemaSPEAR[%] index was validated for an independent dataset and for microcosm data (taken from Brinke et al., 2010, 2011b) and has proven to be a promising tool for assessing the ecotoxicological potential of fine sediments (Höss et al., 2011a).

Marine Sediments

The effects of contaminants have been more frequently studied on marine rather than on freshwater nematodes. In the following, we provide a brief overview of selected studies from marine environments. The effects of Zn, copper (Cu), and Cd, on marine or estuarine meiofauna communities have been intensively examined in several publications (e.g., Austen et al., 1994; Austen and McEvoy, 1997a; Beyrem et al., 2007) (Table 2), whereas less is known about the effects of cobalt (Co), iron (Fe), lead (Pb), nickel (Ni), mercury (Hg), and chromium (Cr) on nematodes in marine model ecosystems (e.g., Beyrem et al., 2011; Boufahja et al., 2011a) (Table 2). To reproduce the realistic conditions of multiple pollutions in marine and/or estuarine sediments, many studies have used mixtures of contaminants in their experiments. This includes metal mixtures as well as different combinations of PAHs (e.g., Carman et al., 1995; Louati et al., 2013). Microcosm studies on meiofauna/nematode communities have also considered the effects of other organic substances of environmental concern, including diesel or lubricant oils, tributyltin (TBT: a biocide in ship-bottom paints), and pesticides such as permethrin and triclosan (Table 2).

For the most abundant contaminants in aquatic ecosystems, which are the heavy metals Cu, Cd, Ni, Pb, and Zn (Hagopian-Schlekat et al., 2001), nematodes have been classified into sensitive and tolerant species. Due to its very clear response to contaminations with Zn (Mahmoudi et al., 2007; Beyrem et al., 2011), Pb (Mahmoudi et al., 2007), and a Cd/diesel mixture (Beyrem et al., 2007), *Calomicrolaimus honestus* is classified as a metal-sensitive species, whereas *Oncholaimus campylocercoides* is very tolerant toward Zn (Mahmoudi et al., 2007; Beyrem et al., 2011), Cd (Beyrem et al., 2007) and Ni (Hedfi et al., 2007), and mixtures of Zn/Cu (Beyrem et al., 2011), Cd/diesel (Beyrem et al., 2007) and Pb/Zn (Mahmoudi et al., 2007). For other marine nematode species, no clear relationship regarding sensitivity or tolerance of metal contamination could be determined. *Marylynnia stekhoveni* was sensitive against Zn, Cd (Beyrem et al., 2007, 2011), and Cr (Boufahja et al., 2011a) as single contaminant, but showed tolerance towards Co and the mixtures of Zn/Co (Beyrem et al., 2011) and Zn/Pb (Mahmoudi et al., 2007). Overall, the response of nematode species towards metal contamination appears to be much more substance specific than species specific. By increasing the mortality of most species in highly contaminated microcosms, metal contamination in general was shown to be responsible for a decrease in nematode abundance and diversity, expressed in terms of the Shannon–Wiener index (H') and evenness (J'), respectively.

Only a few studies have focused on the response of free-living marine nematode communities towards organic substance of environmental concern. Mahmoudi et al. (2005) and Lindgren et al. (2012) found significant increases in nematode abundances in diesel-contaminated environments, but these results were not confirmed by Beyrem et al. (2007). Both the Shannon–Wiener index and the evenness decreased significantly with increasing diesel concentrations (Mahmoudi et al., 2005). In the aforementioned study, the species *O. campylocercoides*, *Chaetonema* sp., and *Pomponema* sp. were shown to be sensitive to diesel contamination, whereas *Hypodontolaimus colesi*, *Daptonema fallax*, *Daptonema trabeculosum*, and particularly *M. stekhoveni* were more tolerant. Austen and McEvoy (1997b) and Schratzberger et al. (2002) examined the influence of TBT on nematode communities with varying results. Both studies found significant changes in those communities based on decreasing diversity indices (Shannon–Wiener, evenness). Nevertheless, no feeding-type-specific response was identified by Austen and McEvoy (1997b), whereas Schratzberger et al. (2002) demonstrated that the relative abundance of nonselective deposit feeders was significantly lower in the highly contaminated TBT treatments than in controls whereas for epigrowth feeders the trend was the opposite. Selective deposit feeders and predatory nematodes were not affected by TBT contamination in terms of relative abundance.

In microcosms treated with PAHs in different combinations, nematode abundance increased (Carman et al., 1995; Carman and Todaro, 1996; Louati et al.,

2013); moreover, nematodes were the single main taxon detected in high-level treatments (Louati et al., 2013). Beside their direct effects on nematode assemblages, chemicals may have indirect food web effects via direct impacts on sediment-associated natural communities, such as microbes, diatoms, ciliates, and protists (Austen and McEvoy, 1997a; Schratzberger et al., 2000).

Soils

Soil microcosm studies have focused on contamination with pesticides (e.g., Chelinho et al., 2011; Scholz-Starke et al., 2013; Höss et al., 2014) and metals (e.g., Korthals et al., 1996, 2000; Smit et al., 2002; Van der Wurff et al., 2007), especially the heavy metals Zn, Co, and Ni (Table 2). Summarizing the results of metal treatments in microcosm studies, the taxa *Acrobeles*, *Alaimus*, *Aporcelaimellus*, *Clarkus*, *Plectus*, and *Thonus* showed the highest sensitivity, whereas *Aphelenchoides*, Diplogasteridae, *Pratylenchus*, *Pseudohalenchus*, Rhabditidae, and *Tylenchorhynchus* were either less sensitive or tolerant (Korthals et al., 1996, 2000; Smit et al., 2002). In carbofuran-treated microcosms the sensitivities of Diplogasteridae and Rhabditidae were relatively high (Chelinho et al., 2011) unlike *Aphelenchoides*, which increased in abundance. In microcosms contaminated with the insecticide deltamethrin (applied as Decis), both Rhabditidae and *Pratylenchus* again showed the highest sensitivity, whereas Helicotylenchidae seemed to be quite tolerant of this insecticide (Griffiths et al., 2006).

Trophic analysis by (Parmelee et al., 1993, 1997) revealed that Cu contamination had significant, negative effects on omnivorous–predatory nematodes but herbivorous nematodes increased in abundance over the course of the treatments. Additionally, an increase in abundance of bacterial feeders in Cu-treated microcosms was demonstrated by Korthals et al. (1996). For the pesticides carbendazim (Moser et al., 2004), lindane (Scholz-Starke et al., 2013), and different insecticidal crystal proteins (Höss et al., 2014), negative effects on the abundance of omnivorous-predatory nematodes were shown. In the reviewed studies, the sensitivity of omnivorous-predatory nematodes to chemicals was assumed to have resulted in a disruption of the soil food web structure (e.g., Parmelee et al., 1997). Thus, indirect effects due to the loss of nematodes can be demonstrated in microcosm experiments. Microcosm studies have also confirmed that soil nematodes are sensitive indicators of environmental contaminants, such as heavy metals and organic pesticides, and that food web and community analyses are necessary to detect the more subtle, indirect effects of chemicals on soil meiofauna.

As measure of stress-induced changes in the nematode species composition, the MI has provided ambiguous results, although, as expected, the MI decreased with increasing chemical concentrations of metals (Korthals et al., 1996), carbendazim (Moser et al., 2004), and insecticidal Cry proteins (Höss et al., 2014). Smit et al. (2002) found a decrease of the MI in Zn-treated microscosms, but this effect was not dose dependent. Nematode communities exposed to lindane did not react with a shift in *c–p* groups (Scholz-Starke et al., 2013). Nonetheless, independent of the chemical, total nematode abundance appears as a measure to get a first insight into the effects of contamination (e.g., Burrows and Edwards, 2002; Smit et al., 2002; Chelinho et al., 2011).

Conclusion and Outlook

The findings of the reviewed studies reveal exciting possibilities for the future use of nematodes in terms of single-species and microcosm studies. The use of nematodes as test organisms in ecotoxicology has significantly increased over the past two decades. However, the most common tool to assess the toxicity of chemicals is represented by single-species testing, even though they do not assess effects at the community or ecosystem level. For nematodes it could be shown, that compared to single-species toxicity testing, experimental set-ups using entire communities offer a more sensitive measure of the effects of chemical pollutants in freshwater, marine, and terrestrial ecosystems. Model ecosystems, such as microcosms, could be effectively used to identify priority contaminant combinations or interactions. These set-ups were needed to show changes in trophic structure and enabled scientists to more accurately assess ecological damage to ecosystems.

For most of the meiofauna-/nematode-based assessment parameters, sound knowledge in morphological taxonomy is required, which might still be one of the obstacles for a broad routine application of meiofaunal taxa in ecotoxicology. However, current investigations use advances in DNA sequencing to provide a comprehensive view of benthic invertebrate diversity under the influence of a contaminant (Chariton et al., 2014) or use biochemical biomarkers of a single species from an entire nematode assemblage to show on first-phase responses of nematodes (Duarte et al., 2010; Boufahja and Semprucci, 2015). Next-generation sequencing, with high-throughput sequencing of target regions of 18 rDNA genes, offers a novel approach to monitor the responses of benthic assemblages, irrespective of the size and taxonomic demand of the organismal group. This could be realized by analysing communities or selected single species within microcosm studies. The obtained molecular data with respect to nematode responsiveness to the contaminant can be applied to generate taxonomic information on genus level for entire meiobenthic assemblages or show on first-phase responses by a single species. These findings can be

seen as a complementary rather than as a competing approach to the traditional endpoints and techniques for achieving ecotoxicological data that encompass the responses of the diverse biota used in microcosms (Chariton et al., 2014).

Overall, this literature overview confirmed that nematodes can be seen as a suitable organismal group for assessing the risk of anthropogenic contamination of marine, freshwater, and soil ecosystems in experimental set-ups. This conclusion is based on several arguments that have been repeatedly confirmed by the studies discussed in this manuscript:

(i) Ecological relevance is an important argument for considering certain taxa in environmental risk assessment: free-living nematodes represent one of the most abundant and species-rich organismal groups in marine and freshwater sediments, as well as in soils. Due to their high trophic diversity, they occupy key positions in the food web and are important contributors to nutrient cycling.

(ii) The ubiquity of nematode species is an advantage in comparing datasets between different parts of the world. Nematodes are found all over the world, such that experimental studies can be carried out over a wide range of geographic scales with comparable species assemblages.

(iii) For fine freshwater sediments, which often are hotspots of chemical contamination, conventional indices based on macrobenthic invertebrates cannot be applied, as in these habitats only few macroinvertebrates can be found. Here, meiobenthic organisms as nematodes are suggested to be used as bioindicators.

(iv) Small experimental set-ups reduce costs and allow for greater replication within one treatment. Regarding nematode communities, microcosm experiments can be carried out in containers as small as centrifuge tubes, which will still contain enough individuals and species to allow valid statistical analyses.

(v) Well-studied model organisms, such as the nematode *C. elegans*, allow precise and reproducible results in standardized toxicity tests. Moreover, deep knowledge of the genetics, physiology, and development of this species enables ecotoxicologists to dissect the principal toxicological mechanisms.

(vi) Standardized test methods are important for routine toxicity testing. This is especially true with respect to complex matrices, such as sediments and soils, where many disturbing factors lead to large variations in the test system. For *C. elegans*, two standards for toxicity testing of water, sediment, soil, and waste are available (ASTM E2172-01: ASTM, 2001; ISO 10872: ISO, 2010).

(vii) Toxicity-related bioindices are important tools for interpreting changes in the structure of communities. These indices can be used to distinguish chemical-induced community alterations from those caused by other (natural) environmental factors (e.g., habitat structure), even in controlled experimental set-ups (model ecosystems). For nematodes, specific (taxonomic and nontaxonomic) indices were developed to assess stress-related community changes in soil (MI and MI25: Bongers, 1990; Bongers and Ferris, 1999), freshwater sediments (NemaSPEAR[%] index: Höss et al., 2011a), and marine sediments (Vanaverbeke et al., 2003; Losi et al., 2013).

Combining sophisticated experimental tools with field observations allows for more accurate decision making in environmental risk assessment. Data on chemical concentrations, single-species and multispecies toxicity, and in-situ communities can be integrated as single lines of evidence in a weight-of-evidence approach (e.g., Chapman and Anderson, 2005). As suitable ecotoxicological tools and ecological indices for nematodes are already available, this organismal group should be used more often in weight-of-evidence approaches for assessing the ecological risk of contaminated habitats (Wolfram et al., 2012).

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