

PERSPECTIVE PAPER

Climate-change effects on the sex ratio of free-living soil nematodes – perspective and prospect**Carla Klusmann^{1,2}, Simone Cesarz^{1,2}, Marcel Ciobanu³, Olga Ferlian^{1,2}, Malte Jochum^{1,2}, Martin Schädler^{4,1}, Stefan Scheu^{5,6}, Marie Sünneemann^{1,2}, Diana H. Wall⁷ and Nico Eisenhauer^{1,2,*}**¹ German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103 Leipzig, Germany² Institute of Biology, Leipzig University, Puschstraße 4, 04103 Leipzig, Germany³ Institute of Biological Research, Branch of the National Institute of Research and Development for Biological Sciences, Str. Republicii Nr. 48, 400015, Cluj-Napoca, Romania⁴ Department of Community Ecology, Helmholtz-Centre for Environmental Research – UFZ, Theodor-Lieser-Str. 4, 06120 Halle, Germany⁵ J.F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany⁶ Centre of Biodiversity and Sustainable Land Use, Büsgenweg 1, 37077 Göttingen, Germany⁷ School of Global Environmental Sustainability and Department of Biology, Colorado State University, Fort Collins, CO 80523-1036 USA

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Abstract

Human-induced global environmental change is predicted to alter the stability and functioning of ecosystems worldwide. Most research in recent decades has focused on studying climate-change effects on aboveground systems, causing a poor understanding of belowground responses. However, gaining knowledge on environmental-change effects on soil biota is of crucial importance, as soil-ecosystem services are indispensable for human well-being and contribute fundamentally to the functioning of terrestrial ecosystems. Nematode communities play a central role in various soil ecosystem processes and are therefore commonly used as biological indicators to assess soil conditions and soil health. While causing overall shifts in community composition patterns, which are most often examined, climate change might also alter nematode population dynamics and the sex ratio (number of males per female). Previous studies on plant-parasitic nematode species suggest that changes to unfavorable environmental conditions trigger reduced development of females and favor sexual rather than parthenogenetic reproduction. Therefore, we are presenting the working hypothesis that predicted climate change causing reduced resource availability and enhanced environmental stress will lead to an increased proportion of males in soil nematode communities. Our systematic literature review revealed that climate- and environmental change effects on the sex ratio of free-living soil nematode populations are inconsistent, but heavily understudied. Data on sex ratios have been treated mostly as additional information, presented without any underlying theory and hypotheses, as well as limited discussion. In this perspective paper, we thus propose that future studies should include clear hypotheses and test if the sex ratio of free-living nematodes increases with climate change due to more stressful environmental conditions and low resource availability. Furthermore, we conclude that experimental studies investigating the specific roles of male and female nematodes are needed to better predict the implications of a changing climate on soil ecosystem functioning.

Keywords Climate change | human impact | nematode sex ratio | soil biodiversity

1. Introduction

As a consequence of anthropogenic activities in the recent decades, natural ecosystems across the globe are now facing a variety of rapidly accumulating environmental challenges, such as increases in atmospheric CO₂ concentrations, rising temperatures, and biodiversity change (IPCC 2021). However, the majority of research on global-change consequences for ecosystems has focused on aboveground flora and fauna rather than on belowground systems resulting in a limited understanding of soil-biodiversity changes (Cameron et al. 2019, Eisenhauer et al. 2020). Understanding environmental change effects on soil biota is highly important though, as soil organisms make up ~25% of all species on earth and provide a large set of fundamental soil ecosystem services, such as carbon sequestration, maintenance of soil properties, and the support of biogeochemical cycles (Bardgett & van der Putten 2014, Wall et al. 2012). Some of these, for example climate regulation, are indispensable for human well-being. Furthermore, soil biodiversity is directly linked to the functioning of both, above- and belowground systems, and plays a key role in mediating the impact of future environmental change on global terrestrial ecosystems (Bardgett & van der Putten 2014, Wagg et al. 2014).

Some of the most important threats to soil biodiversity are the loss of plant biodiversity, invasion of exotic species, environmental pollution, land-use intensification, and extreme climatic events (Orgiazzi et al. 2016, Veresoglou et al. 2015). Recent studies show that the magnitude of threat imposed by a global change driver or the interaction of several drivers depends on the focal group of organisms (Blankinship et al. 2011, George et al. 2019). For instance, Blankinship et al. (2011) demonstrated positive effects of increased levels of CO₂ on soil microfauna and -flora, but negative effects on soil mesofauna. Despite this variability of responses, recent studies highlighted the dominant role of climate (change) effects on different groups of soil organisms (Delgado-Baquerizo et al. 2020, Phillips et al. 2019, van den Hoogen et al. 2019). Most studies investigating global-change effects on soil communities focused on a relatively confined set of changes in community properties such as total abundance, biomass, functional community composition, or biodiversity indices. However, changes in such broad and integrated biodiversity indices can only be understood if there is knowledge about the climate change-induced shifts in community composition, biotic interactions, and population densities (Spaak et al. 2017).

Soil-nematode communities are often used as a biological indicator for the assessment of soil health and ecosystem functioning. Their community composition

and their central role in soil energy fluxes and cycling of organic matter allow drawing conclusions regarding the state of the soil ecosystem compartment (Neher 2001, Ferris et al. 2001). Nematodes are ubiquitous and very abundant animals, accounting for approximately 80% of all metazoans on earth (van den Hoogen et al. 2019) and an estimated global biomass of 0.02 Gt carbon (Bar-On et al. 2018). They play a central role in soil food webs and are functionally very diverse, including herbivores, bacterivores, fungivores, carnivores, and omnivores. Thus, soil nematodes take an active part in various ecosystem processes like root herbivory, nutrient cycling, and decomposition. Prior to seeing climate change drivers causing shifts in nematode abundance or taxonomic diversity, as analyzed by most previous studies, more subtle alterations within a population may occur, such as behavioral changes (Cohen et al. 2018, Eisenhauer et al. 2018) and changes of the sex ratio (Schwanz & Georges 2021, Wall et al. 2002). For example, environmental changes might influence sex ratios (Freckman & Caswell 1985, Scheu & Drossel 2007, Wall et al. 2002). Changes in nematode sex ratios have significant ecosystem implications. For instance, studies on the plant-parasitic nematode *Heterodera schachtii* have shown that, on average, females require 29 times more food compared to males due to the extended sedentary phase which is required for reproduction (Müller et al. 1981). Generally, plant-parasitic species with sedentary females, such as root-knot nematodes and cyst nematodes, are among the most detrimental agricultural pests (Jones et al. 2013). Thus, it may be assumed that nematode effects on a given ecosystem will depend on their sex ratio; for example, crop damage is suggested to be much higher when there are more females, as they require a lot of energy for reproduction (Anjam et al. 2020, Anwer et al. 2018, Triantaphyllou 1973).

Generally, changes in sex ratios might be due to females producing eggs of an unbalanced sex ratio, i.e. due to changes in the primary sex ratio. Further, unbalanced mortality of females and males, i.e., changes in the secondary sex ratio, may contribute to shifts in the sex ratios of populations (Stearns & Hoekstra 2005). It is important to note that nematodes may reproduce via different modes including facultative as well as obligatory amphimixis, meiotic as well as mitotic parthenogenesis, and hermaphroditism (Bird et al. 2009). Therefore, shifts in sex ratios towards females might be due to an increased number of females reproducing via parthenogenesis or being able to self-fertilize their eggs. Mechanisms responsible for variation in primary sex ratios are manifold and include infections of females by bacterial endosymbionts or changes in environmental factors experienced by females (Hardy 2002, Austin

et al. 2009). Each of these mechanisms as well as changes in secondary sex ratios likely contribute to variation in sex ratios in nematode populations (Morran et al. 2009, Thomas et al. 2012, Wall et al. 2002).

Overall, the majority of studies on the influence of environmental factors on sex determination and sex ratio of nematodes are lab studies which focused on plant and insect parasitic species (Ellenby 1954, Triantaphyllou 1960, Trudgill 1967). First experiments already showed that not only genetic but also environmental factors can influence sex determination (Triantaphyllou & Hirschmann 1964). One of the most-commonly studied environmental drivers tested in experiments is the availability of resources. Taken together, these studies show that nutrient deficiencies and manipulated concentrations of missing or strongly reduced essential minerals exclusively caused an enhanced proportion of males (Tyler 1933, Cryan & Hansen 1966, Grundler et al. 1991, Singh et al. 2013). Moreover, McClure & Viglierchio (1966) and Kahel-Raifer & Glazer (2000) concluded that the sex ratio was most dependent on the source of nutrition and its availability compared to other possible influencing factors, such as temperature or intensity of infection by parasitic nematodes. With the exception of an aquatic study by Schroeder et al. (2013), who found an increasing ratio of periphytic male nematodes to females (sex ratio) with ameliorated conditions (trophic state of the lake), studies on resource gradients, such as lake depth (Traunspurger 1998), also showed that the fraction of females was reduced when resources were scarce. These findings fit with resource-based theories on the evolution of sex predicting that parthenogenetic reproduction is favored if resources are plentiful (Scheu & Drossel 2007, Song et al. 2011). As most studies looked at parasitic species, ecological parameters such as nematode population density and therefore competition were often examined as additional, not focal, drivers. Nevertheless, the findings show that the higher the population density in a host, or the intensity of infection, the higher the percentage of developed males (Christie 1929, Ellenby 1954, Trudgill 1967). As elevated population densities often coincide with increased competition for resources, these findings also support the conclusion that resource shortage might generally increase the proportion of males over females, which likely is related to reduced parthenogenetic reproduction if resources become limiting (Scheu & Drossel 2007, Song et al. 2011).

Experiments that solely studied the effect of temperature on nematode sex ratios found that higher temperatures, representing a sudden environmental stress in those contexts, led to higher relative numbers of males (Hansen et al. 1972, Moens et al. 1996, Laughlin et al. 1969). These results suggest that, analogous to

resource-related drivers, overall stressful conditions have a ‘masculinizing’ effect on nematode populations. As suggested by Scheu & Drossel (2007), stressful conditions might be associated with resource shortage favoring sexual over parthenogenetic reproduction. Other, less-frequently studied drivers include elevated CO₂ (Hansen et al. 1972), age of host plant, immune response, and resistance (McSorley 2003), biodiversity (Michiels & Traunspurger 2005), size of the host animal (Golestaninasab et al. 2012), and succession (Pen-Mouratov et al. 2014). Due to the low number of studies, however, general conclusions are hard to draw. Nevertheless, except for a few cases, studies from 1929 to 2020 overall agree that unfavorable conditions increase the proportion of males relative to females (further described as sex ratio). As a consequence, a high percentage of males was even supposed to demonstrate unfavorable conditions for nematode populations (Anjam et al. 2020). Thus, the questions arise if similar patterns can be found in free-living nematodes and which underlying mechanisms are driving a shift towards male-dominated communities under adverse conditions.

Due to lower investment in reproduction, the development of male nematodes requires fewer resources than that of females. By shifting the sex ratio towards the less resource-consuming males, the few juveniles developing into high resource-demanding females may have a higher probability of surviving (Freckman & Caswell 1985). Similarly, reducing the female population when food is scarce may also reduce competition for available nutrients, as males are able to survive longer without them (Singh et al. 2013). Additionally, producing more males ensures an increased heterogeneity of the population, as sexual reproduction increases genetic diversity (Grunder et al. 1991, Bürger 1999, Maynard Smith 1978). Being highly genetically variable improves the ability to withstand adverse environmental conditions due to a rich portfolio of responses and the production of progeny with possible superior fitness (Kahel-Raifer & Glazer 2000). Lastly, plant-parasitic female nematodes are often sedentary, while the male nematodes are fully mobile, which allows them to leave areas of adverse conditions and still guarantee the persistence of the gene pool and/or fitness of the population (McSorley 2003, Bird 1971). However, it remains to be explored which sex ratio ensures highest genetic diversity under different environmental conditions.

Soil-ecological studies on the consequences of increased proportions of females are rare, although parthenogenetic reproduction is very widespread in soil (Castagnone-Sereno & Danchin 2014, Chahartaghi et al. 2009, Heethoff et al. 2009, Scheu & Drossel 2007). Since it is known that resource consumption is higher

for females and that there are further morphological and behavioral differences between males and females, a population shift towards females is very likely to influence nematode consumers and prey, soil nutrient cycles, and thereby alter relevant ecosystem functions. Thus, the consequences for food-web dynamics and related ecosystem services are still unknown, even though those questions are of fundamental importance when trying to predict ecosystem-scale consequences of climate change. Moreover, we currently lack a systematic and comprehensive synthesis of the available literature on climate-change effects on free-living soil nematode sex ratios. Taking existing studies on parasitic nematodes and other taxa into account (Triantaphyllou 1973, Kahel-Raifer & Glazer 2000, McSorley 2003), we introduce the working hypothesis that climate change leads to a higher proportion of males in soil-nematode communities, if it coincides with increased environmental stress. To address this research question and to inspire future studies, we performed a systematic literature search and compiled the available literature on climate-change effects on free-living soil nematodes. We discuss the ecological implications of this work and outline future research directions as well as prospects.

2. Methods

We ran a Web of Science Core Collection search on March 30th, 2020, using the following search string: nematod* AND 'climat* change' OR drought OR temperature* OR warming OR heat* OR precipitation* OR rain* OR flood* OR irrigation OR moisture OR watering OR fire OR 'carbon dioxide' OR CO2 OR 'global change' OR 'environmental change' OR disturbance* OR stress*. This search delivered 13,964 results. We screened the titles for keywords and phrases and also the abstract, when additional information was needed. Based on this initial screening, we selected 53 papers that we then studied in more depth. After thoroughly reading and removing studies that did not focus on soil nematodes or on environmental influences, or that did not report sex ratios, we were left with four studies that matched the scope of the present paper. From these, we derived information on the different study characteristics (location, type of biological system), environmental drivers (temperature, moisture, diversity), and soil nematode responses (population density, number of males per female, sex ratio change) which are displayed in Table 1. Moreover, we added unpublished data from four of our own experiments (Table 1). Due to the paucity of climate change studies on the sex ratio of soil nematodes,

we also considered additional studies with variation in soil resource availability and stress (e.g. plant diversity experiments). This resulted in a total of eight studies being considered in the following section. All of these studies used common soil nematode extraction methods and identification protocols.

3. Results and discussion

Notably, none of the studies examining the effects of environmental drivers on nematodes focused explicitly on the community's sex ratio, but they provided this information in addition to more common nematode community and diversity response variables. In the majority of studies, the focus of analysis was on changes in abundance of adults and juveniles and life cycle parameters such as mortality and number of juveniles per female. This finding is supported by the observation that none of the studies presented clear hypotheses on expected sex ratio responses to the environmental drivers studied. The paucity of studies on soil nematodes' sex ratios did not allow us to analyze the extracted data in a more quantitative way (i.e., in a meta-analysis), yet we reviewed the available information qualitatively. As mentioned above, we may see changes in the sex ratio due to switching reproduction modes. However, unless stated otherwise, the information on the species' reproduction mode and their ability to switch modes are not available from the literature. Therefore, we do not address these differences in the following and focus solely on the overall change in sex ratio. Nevertheless, such information will be critical to assess in future research.

Three out of eight experiments included in our review were conducted in the McMurdo Dry Valleys. These hyper-arid deserts in the Antarctic are known to be some of the coldest on Earth and comprise only a very low number of plant and animal species. In this region, the most dominant microfauna species in soils is the microbivorous-feeding nematode *Scottinema lindsayae*. This species reproduces exclusively sexually and has a relatively long life cycle (218 days at 10°C, Overhoff et al. 1993). It has not yet been reported if *S. lindsayae* switches its mode of reproduction. For field populations, a proportion of 63 % females is reported on the McMurdo LTER website (SD = 0.24, $n = 27$; Weicht & Moorhead 2004). This nematode species is adapted to dry soil conditions with soil moisture ranging from 0.9–2.9% (Adams et al. 2007, Bamforth et al. 2005) and has only been reported from Antarctica (Boström et al. 2011). Accordingly, it was found to be the most abundant and most widely distributed nematode species in the driest

soils. With increasing soil moisture, for example near streams and lakes, its abundance decreases significantly, while the occurrence of other taxa was not impacted (Ayres et al. 2007, Treonis et al. 1999). Both the McMurdo Dry Valleys ecosystem and the well-adapted nematode species are extreme in their characteristics. Therefore, insights based on *S. lindsayae* might not be representative for soil nematodes of other biomes/regions. However, due to the limited number of existing studies on climate change effects on soil nematodes and the qualitative character of our perspective paper, we decided to include all three experiments in our synthesis, despite the overrepresentation of the species and the ecosystem type.

As snowfall patterns and snow water contents are expected to be altered under the influence of climate change (Barnett et al. 2005, Mote et al. 2005), Ayres et al. (2010) tested the effect of increased snow accumulation on soil-nematode communities. A snow-fence set-up caused an increased accumulation of snow (+200%) over five years which resulted in increased soil moisture of approximately 5–9% and decreased soil pH. Year (date) had a significant effect on the sex ratio of *S. lindsayae* (Table 1, $P < 0.001$) which was 0.9 males per female at the beginning of the experiment (year 1). The second year after the experiment's establishment was the year with the highest soil moisture and was followed by the year with the highest ratio of males to females (1.5). In summary, the ratio of males to females increased as soil moisture increased. These examinations support our overarching hypothesis: for the nematode *S. lindsayae*, which is specifically adapted to dry soils, moist habitat conditions may represent adverse environmental conditions, and, accordingly, the ratio of males to females increased as a response to increasing soil moisture. It is important to note that the life cycle of *S. lindsayae* spans several years under the extremely low temperatures and that changes in abundance and primary sex ratio do not appear immediately. This could explain why a relative increase in males is not reported for the year with the highest soil moisture (year 2) but the year after. Furthermore, the shift in the sex ratio might have occurred due to higher mortality in females than in males, i.e. due to changes in the secondary sex ratio.

In a second study from the McMurdo Dry Valleys, Simmons et al. (2009) examined the consequences of predicted future warming for polar regions on soil-nematode populations. It is assumed that estimated increases in temperature enhance snow and glacial melt which leads to an overall increase in soil moisture and higher stream discharges (Barrett et al. 2008, Lyons et al. 2005). Simmons et al. (2009) experimentally increased soil surface temperature in the austral summer (+2°C between December and February) as well as soil-water

content once in December (+12.7 L/m²). The warming treatment reduced the nematode population significantly by 42% compared to the control. However, there was no significant difference between treatments regarding the sex ratio (Tab. 1). At one site (Lake Bonney), a natural flooding event occurred shortly after sampling in the summer of 2001/2002. As a result of the natural flooding, the abundance and sex ratio of soil nematodes decreased in 2002/2003 (the latter by 42%) resulting in a reduced number of males per female. In the years after the flood, the sex ratio increased again and reached its initial value. Especially because the flood occurred naturally and not experimentally, the results of this study are likely to be representative of climate-change consequences and climate-extreme effects on nematode communities. However, additional confounding factors such as reduced nutrient availability and physical disturbance might also have contributed to the observed differences further stressing the need for controlled experiments. At the two other sites, neither treatment nor year had a significant influence on the sex ratio.

The third McMurdo Dry Valley study, Porazinska et al. (2002), tested climate-change effects indirectly. The aim was to identify nematode-population dynamics across temporal and spatial scales and to connect these to different environmental conditions. Along an elevational transect, plots were established at three altitudinal levels (low, medium, and high) which differed in their soil-moisture contents, as increasing soil moisture is also predicted to be a consequence of future climate warming in Antarctica (Foreman et al. 2004, Wall 2007) with negative impacts on the local biodiversity (Andriuzzi & Wall 2018). Soil moisture decreased with elevation, indicating that the environmental conditions for the highly-abundant nematode *S. lindsayae* were most adverse at the lowest sites and most favorable at the highest. Consistently, nematode abundances correlated positively with dryness. However, elevation had no significant effect on the sex ratio, while sampling year did (Tab. 1, statistics unavailable). There were significantly more males per female in year six than in years one and three. Since the low-elevation habitat with its high soil-moisture content was the least favorable one for nematodes, we expected the sex ratio to be greatest at the low sites. This was only the case in the last year of sampling. Years one and three showed opposite trends. During these years, there were most males per female at the sites with suitable conditions and least males under adverse conditions. Thus, the data of year six are the only ones which match our hypothesis.

Wall et al. (2002) conducted a study to investigate changes in the nematode communities along a gradient of environmental conditions using five successional stages at a sand dune. The stages went from beach and fore dune

Table 1. List of studies considered. The reader should note that due to a paucity of climate change studies on the sex ratio of soil nematodes, we also considered additional studies with variation in soil resource availability and stress (e.g. plant diversity experiments). Experimental details are described in the Results and discussion section. Statistically significant factors are indicated by bold numbers. The reference to which sex-ratio change was calculated when an environmental gradient existed is indicated as control (ctrl.). The colors indicate environmental conditions: ● = favorable, ● = medium, ● = unfavorable.

Study	System	Driver of change	Cond./ Gradient	Year	Sex Ratio [males:females]	Sex Ratio Change	Abundance [# live ind./ kg soil]	Comments
Ayres et al. 2010	Antarctic Dry Valleys (hyper-arid) [Fryxell]	Snow accumulation (+200%)	●	2001	0.90 (ctrl.)		1,100	<ul style="list-style-type: none"> Species: <i>S. lindsayae</i> Snow accumulation increases soil moisture (+5–9%), decreases soil pH 2003: year with highest moisture Effect of date on sex ratio ***
			●	2003	0.60	-0.30 ***	600	
			●	2004	1.50	+0.60 ***	500	
			●	2006	0.80	-0.10 ***	500	
Simmons et al. (2009)	Antarctic Dry Valleys (hyper-arid) [Site Bonney]	Soil surface temp. (+2°C) water (+12.7 L/m ² once/year) increased temp. and water addition	●	1999/00	1.10 (ctrl.)		400	<ul style="list-style-type: none"> No differences in sex ratio among treatments Box = flooding event shortly after sampling 2001/2002 42% smaller populations in warmed plots Sex ratio decrease 2002/03; P < 0.05
			●	2001/02	0.80	-0.30	115	
			●	2002/03	0.25	-0.85 *	110	
			●	2004/05	0.55	-0.55	90	
			●	2006/07	1.30	+0.20	215	
Wall et al. (2002)	Sand dune system	Increasing successional stages: Beach Fore Dune Yellow D. Grey D. Dune heath	●		1.00 (ctrl.)		1,143	<ul style="list-style-type: none"> Sex ratio was significantly greater (***, P < 0.001) at the beach and fore dune sites than at the grey dune and dune heath. Organic carbon content increases → dietary substrate becomes less limiting with succession
			●		1.02	+0.02	3,502	
			●		0.75	-0.25	2,774	
			●		0.10	-0.90	8,921	
			●		0.05	-0.95 ***	7,667	
Porazinska et al. (2002)	Antarctic Dry Valleys (hyper-arid)	Elevational transect: Low (83 m a.s.l.) Med. (121 m a.s.l.) High (188 m a.s.l.)	●	Dec. 1993	low (ctrl.): med:	0.5 +0.15	83 369	<ul style="list-style-type: none"> Species: <i>S. lindsayae</i> Sex ratio significantly higher in year 6 than in 1 and 3, elevation had no effect Soil moisture decreases with elevation Sex ratio overall: 0.94, low: 0.79, medium: 1.15, high: 0.83
			●		high:	0.9 +0.4	230	
			●	Dec. 1995	low (ctrl.): med:	0.4 +0.15	64 318	
			●		high:	0.7 +0.3	348	
			●	Jan. 1999	low (ctrl.): med:	1.5 -0.3	32 175	
			●		high:	0.75 -0.75	182	
			●					
			●					

Study	System	Driver of change	Cond./ Gradient	Year	Sex Ratio [males:females]	Sex Ratio Change	Abundance [# live ind./ kg soil]	Comments
GCEF (unpubl.)	Grassland (Bad Lauchstädt)	Ambient climate (a) = ctrl. Future climate (f): -20% summer precipitation, +10% spring & fall precipitation, + 0.6°C	● ● ● ● ● ● ● ●	2019	Org. farm. a.: 0.13		1,400	
					Org. farm. f.: 0.21	+0.08	1,640	
					Conv. farm. a.: 0.44		2,760	
					Conv. farm. f.: 0.31	-0.13	2,560	• No significances
					Ext. meadow a.: 0.16		2,320	
					Ext. meadow f.: 0.22	-0.04	3,000	
					Int. meadow a.: 0.09		1,960	
					Int. meadow f.: 0.39	+0.30	2,440	
EcoWorm (unpubl.)	Forest (3 CAN, 1 USA)	Earthworm invasion (low invasion vs. high invasion)	● ● ● ● ● ● ● ●	2017	CAN 1 low.: 0.07		1,360	• Data generally dominated by juveniles (no sex determination possible), these are excluded here
					CAN 1 high.: 0.04	-0.30	820	
				2016	CAN 2 low.: 0.16		7,970	
					CAN 2 high.: 0.31	+0.15	3,060	• Ratios are not based on overall abundance counts, but on the subset of identified (and sex-identified) individuals
				2016	CAN 3 low.: 0.42		7,440	
					CAN 3 high.: 0.31	-0.11	2,810	
				2016	USA low.: 0.47		3,740	• No significances
					USA high.: 0.41	-0.06	1,260	
MyDiv (unpubl.)	Temperate forest plantation	Tree species richness	● ● ●	2019	1 sp.: 0.38 (ctrl.)		1,869	
					2 spp.: 0.23	-0.15	1,915	• No significances
					4 spp.: 0.20	-0.18	2,108	
Jena Experiment Global Change Experimental Facility Drought 2013 (unpubl.)	Grassland	Plant species richness (1,4,16,60) Drought Sep.: Ambient soil water content: 18 ± 3% Dry soil water content: 8 ± 2% Drought Nov.: Ambient soil water content: 21 ± 2% Dry soil water content: 20 ± 2%	● ● ● ● ● ● ● ● ● ● ● ● ● ●	Sep. 2013	Amb 1 sp. (ctrl.): 0.16		4,087	
					dry 1 sp.: 0.35	+0.19	9,062	
					amb 4 spp.: 0.35		7,448	
					dry 4 spp.: 0.46	+0.11	9,935	
					amb 16 spp.: 0.37		13,835	
					dry 16 spp.: 0.25	-0.12	11,303	• Data dominated by juveniles
					amb 60 spp.: 0.22		11,077	• No significances
					dry 60 spp.: 0.20	-0.02	11,142	
					amb 1 sp. (ctrl.): 0.17		4,087	
					amb 4 spp.: 0.39	+0.22	15,997	
					amb 16 spp.: 0.68	+0.51	13,835	
					amb 60 spp.: 0.21	+0.04	11,077	
				Nov. 2013				

over yellow and grey dune to dune heath, beach being the earliest and dune heath being the latest successional stage. Both salinity and soil moisture decreased with increasing successional stage and, thus, with distance from the beach. In contrast, organic carbon content in the soil increased with successional stage. Conditions for nematode communities thus were more stressful at early than at the later successional stages, as high salinity and moisture as well as lack of dietary substrate are major threats to nematode populations. This is supported by changes in nematode abundance, which increased along the environmental gradient of successional stages reaching 1,143 ind./kg soil at the beach and 7,667 ind./kg soil at the dune heath. In agreement with our hypothesis, the nematode sex ratio was significantly greater at the early (1.0 and 1.02 at the beach and fore dune, respectively) than at the later stages (0.1 and 0.05 at the grey dune and dune heath, respectively) (Tab. 1, $P < 0.001$). It correlated positively with pH ($P < 0.01$) and negatively with organic matter content ($P < 0.01$). Wall et al. (2002) argued that the male-dominated population at the beach is likely due to the combination of a stressed and resource-limited environment.

Due to the lack of studies on environmental-change effects on nematodes that also include sex ratio data, we decided to integrate additional unpublished data that we had access to. From these datasets, we extracted the information on sex ratios. As we were unable to focus on species composition, we cannot make any inferences on changing reproduction modes of nematodes from the following experiments. For instance, we had detailed soil nematode data from the Global Change Experimental Facility (GCEF), Bad Lauchstädt, Germany, from 2019 (i.e., 5 years after the establishment of the experiment; Schädler et al. 2019). In this experiment, the effects of a future climate scenario on five different agricultural land-use types were tested, while nematode data were only available for four land-use types (Siebert et al. 2020). The future climate consisted of a reduction in summer precipitation (-20%), an increase in spring and fall precipitation (each +10%), and a mean temperature increase of +0.6°C (Schädler et al. 2019). Ambient and future climate scenarios were crossed with different land-use types: intensively-used grassland (meadow), extensively-used grassland (meadow), conventional agriculture, and organic agriculture (extensively-used sheep pasture was not included in the nematode study). In three out of four cases (organic agriculture, extensively-used meadow, intensively-used meadow), the future climate scenario increased soil-nematode abundances. The sex ratio, however, did not respond significantly to the climate-change treatments (Tab. 1). In two of the land-use types (organic farming, intensively-used meadow),

the sex ratio was slightly increased, while in the other two (conventional farming, extensively-used meadow), it decreased. Given these opposing, non-significant trends, future long-term studies should explore if land-use intensity modulates soil nematode community responses to climate change (Siebert et al. 2020).

The EcoWorm project examines the effects of earthworm invasion on native forest ecosystems in northern North America (Eisenhauer et al. 2019). The invasion of non-native species is a common global-change driver and often causes local biodiversity change and loss (Murphy & Romanuk 2014, IPBES 2019). Earlier studies on ecosystem consequences of non-native earthworm invasion have shown that these invasive ecosystem engineers cause adverse environmental conditions for other soil organisms (Eisenhauer et al. 2007) and decrease soil biodiversity (Ferlian et al. 2018b). In 2016 and 2017, nematodes were collected from three Canadian forests and one US forest. In each forest, ten plots were sampled in an area without (or with few) invasive earthworms and ten plots in an area with many earthworms (Eisenhauer et al. 2019). Soil nematode abundances showed a clear response to the invasion of earthworms. In three out of the four invaded forests, the abundance was reduced by at least -50% compared to low-invaded forest areas (Jochum et al. 2021). However, the response of the soil nematode sex ratio was less clear. Similar to abundance, we expected a more male-biased sex ratio in the earthworm-invaded forest areas, as the conditions in the invaded areas were less favorable for nematodes (Jochum et al. 2021). Contrary to these expectations, nematode sex ratios generally did not change significantly and there was only one site where it declined in trend indicating more favorable conditions for females (Tab. 1).

The MyDiv Experiment, set up in 2015, investigates the impact of different mycorrhizal types on tree diversity-ecosystem functioning relationships (Ferlian et al. 2018a). It is located in Bad Lauchstädt, Germany. The species pool of the MyDiv Experiment contains ten deciduous tree species that are native to Central Europe, with five species only associating with ectomycorrhizal (EM) fungi and five species only associating with arbuscular mycorrhizal (AM) fungi (Ferlian et al. 2018a). Tree species were planted in monoculture, two-, and four-species mixtures. Further, these tree-diversity levels were established for AM trees only, EM trees only, and there were two-, and four-species mixtures of AM and EM trees. As biodiversity generally increases ecosystem functioning and stability (Duffy et al. 2017, Tilman et al. 2014, Isbell et al. 2017), biologically-diverse systems may be considered more favorable for soil communities than monocultures (Scherber et al. 2010, Eisenhauer et

al. 2013). Therefore, we expected the relative number of nematode females to increase along the tree-diversity gradient. First data from 2019 support this expectation. Nematode abundance increased from monocultures to four-species mixtures and in parallel the ratio of males to females declined (Tab. 1; unpubl. data). Even though these results were statistically non-significant, the trend suggests that plant diversity might ameliorate environmental conditions for soil organisms (Eisenhauer et al. 2010, Lange et al. 2014) and this is associated with an increased fraction of females in nematode communities. As plant-diversity effects on ecosystem functions (Guerrero-Ramírez et al. 2017, Reich et al. 2012) and soil communities (Eisenhauer et al. 2010, Thakur et al. 2015) may increase over time, long-term effects of plant diversity on nematode sex ratios need further attention.

The Jena Experiment located in the Saale river valley close to the city of Jena, Germany, was established in 2002 to study the effects of plant diversity on ecosystem processes with the focus on element cycling and trophic interactions (Roscher et al. 2004). In 82 plots, 60 mesophilic grassland species which are typical for Central European meadows are grown in 1, 2, 4, 8, 16, and 60 species mixtures comprising four functional plant groups (grasses, legumes, small forbs, and tall forbs). To account for changes in soil structure and texture on the 10-ha field site, the experiment was set up in a randomized block design, with the blocks accounting for different distances from the Saale river (Roscher et al. 2004). Beginning in 2008, an experiment was set up in subplots to simulate summer drought conditions for approximately 4.5 weeks by excluding natural rainfall (Vogel et al. 2013). The rain exclusion plots were equipped with rainout shelters; control plots also were equipped with shelters but received ambient rainwater (Cesarz et al. 2017). In 2013, a natural flood occurred at the site of the Jena Experiment lasting three weeks from May 30th to June 24th. The drought treatment started three months after the beginning of the flood when water had fully retreated from the plots. In September 2013, the drought treatment caused a 41% reduction in precipitation in comparison to the control treatment. While the soil-water content in the ambient ('control') subplot was 18%, the drought subplots' soil-water content was reduced to 8%. We expected nematode sex ratios to be higher under simulated drought than under ambient conditions. Contrasting these expectations, data from September 2013 did not show any clear trend with the differences generally being not significant (Tab. 1). In trend, the sex ratio was higher in the drought than in the ambient treatment in monocultures and 4 species mixtures, whereas the opposite was true for the 16 and 60 species mixtures. With increasing plant-species richness, soil-aggregate stability associated with water

infiltration (Pérès et al. 2013) and top-soil water content increases (Eisenhauer et al. 2010), suggesting that unfavorable abiotic conditions caused by drought may be ameliorated in high-diversity plots (Mulder et al. 2001, Vogel et al. 2013). Accordingly, Cesarz et al. (2017) found that high-diversity plant communities buffered negative effects of the prior flood on soil-nematode communities. Hence, stressful conditions imposed by the drought may have been reduced in the 16 and 60 species mixtures explaining why nematode sex ratios were not higher in the drought than in the control treatment.

Five months after the flooding, in November 2013, differences in soil-water content between drought and ambient subplots did not differ anymore, which is why we only analyzed nematodes of the control treatment for potential plant-diversity effects. As in the MyDiv Experiment, we expected nematode sex ratios to decrease with plant-species richness as high plant diversity is likely to be associated with more-favorable conditions for nematodes. In contrast to these expectations, the sex ratio was lowest in monocultures and highest in the 16 species mixtures, but these differences were not significant (Tab. 1). In future studies on nematode sex ratios, it may be important to differentiate the trophic guilds of nematodes, as plant diversity may have dissimilar effects on the functional composition of nematode communities, with higher abundances of plant-feeding nematodes in species-poor plant communities, but higher abundances of microbivorous nematodes, predators and omnivores at high plant diversity (Eisenhauer et al. 2011).

4. Conclusions and perspectives

While searching for studies that met the criteria for inclusion in our review, we made several observations that are critical for future research on nematode sex ratio change in response to global-change drivers. First, we found that there are almost no replicated studies investigating environmental drivers of nematode sex ratios. Similarly, the drivers investigated typically were not related to climate-change factors, but included other stressors or environmental gradients. Most studies focused on plant-parasitic nematodes, while almost no data is available for free-living soil nematodes (but see Kapranas et al. 2017; Tab. 1). Furthermore, most studies focused on nematode abundance, diversity, or functional/trophic group composition, but not on nematode sex ratios. Even if data on sex ratios were provided, they usually were treated as additional information presented without underlying theory and hypotheses, without any reference to the several potential underlying mechanisms

outlined in our introduction, as well as limited discussion (Simmons et al. 2009). We propose that future studies should include clear hypotheses and test if the sex ratio of free-living nematodes increases with climate change due to more stressful environmental conditions and low resource availability (Fig. 1).

Besides their different resource needs, little is known about differences in the ecological roles of free-living male and female nematodes. Therefore, consequences of potential shifts in nematode sex ratios under future climate change conditions remain unknown, i.e., their consequences for ecosystem processes and services are unclear. To address this knowledge gap, experimental studies are needed that manipulate the sex ratio of free-living nematodes under climate-change conditions and explore the ecosystem consequences for decomposition, nutrient cycling, and plant growth. Understanding the climate-change driven consequences of shifts in nematode sex ratios is expected to improve predictions on how climate change affects belowground processes and their consequences for the aboveground world.

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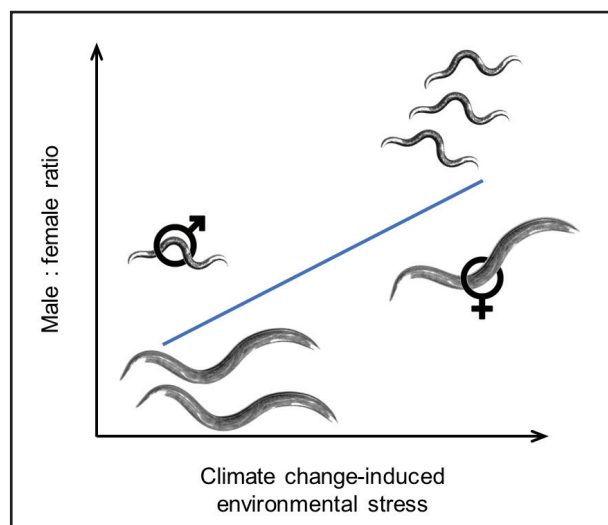


Figure 1. Hypothesized relationship between climate change-induced environmental stress and the ratio between male (depicted by the smaller nematodes) and female nematodes (depicted by the larger nematodes). While data availability and support in form of empirical evidence regarding free-living soil nematodes is still scarce and our general understanding is mostly based on research on phytopathogenic nematodes, future studies may test the hypothesis that the sex ratio increases with climate change due to more stressful environmental conditions and low resource availability.

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