The effects of changing temperature and precipitation on free-living soil Nematoda in Norway

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1. Abstract

The life cycle and behavior of free-living soil nematodes is highly dependent on environmental factors such as temperature and soil moisture, fluctuations leading to significantly lower development and activity rates, dormancy and/or mortality. This literature review summarizes present knowledge about free-living soil nematode temperature and moisture requirements, as well as the commonly accepted predictions about climate change-induced temperature and precipitation changes in Norway. The available information is analyzed and the potential effects of a changing climate on soil nematode communities are discussed. Finally, the influence of an altered nematode community the rest of the soil ecosystem including other soil organisms such as bacteria, fungi and plants is considered.

2. Introduction

Nematodes are ubiquitous members of the soil faunal community, and are principal contributors to key processes such as primary production and nutrient recycling in many ecosystems. At the same time, many species belonging to the Phylum Nematoda are known to infect other animals and plants, causing disease and even mortality in animals and affecting plant growth and vitality. Nematodes' varied roles within the global ecosystem are due to their remarkable diversity, with the Nematode phylum being composed of approximately 80,000 species.

As nematodes are such a vital part of the ecosystem, interacting with multiple other species throughout their life cycles and playing vital roles in nutrient cycling and primary production, a change in their population dynamics is expected to imbalance the rest of the ecosystem. Their study, then, is key to understanding and predicting the potential alterations in the soil ecosystem dynamics which may occur due to the ongoing climate change. Climate factors which are especially pertinent to the nematode life cycle and functions and which are expected to undergo changes include temperature and humidity.

Climate change is likely to significantly affect the higher latitudes, and Norway has been chosen as a region of interest for the change in population dynamics of free-living soil nematodes.

This literature review will examine and compile the information pertaining to the effects of temperature and moisture on nematode life cycle from the perspective of a changing climate. First, a hypothesis concerning the expected results will be offered. Then, a section discussing the investigation methods, namely modelling and experimental studies, most commonly applied in the reviewed literature will be provided. The results section is composed of two parts: the first part is an overview of nematode functions and roles in the ecosystem determined by their feeding mechanism, their life-cycle, and responses to temperature and humidity, and the second part is a review of the predicted temperature and precipitation changes that Norway is expected to undergo. A discussion of the potential changes in the free-living soil nematodes behavior and life-cycle as a result of the changing environmental conditions is offered next. Finally, a section offering final remarks, and a list of references is offered.

3. Hypothesis

The scientific hypotheses to be tested in the present paper are as follows:

Climate change induced temperature and precipitation changes will provide generally favorable living conditions to free-living soil nematodes, which will result in an increase in their development and reproduction rates.

The increase in development and growth rates will positively affect nutrient cycling rates and encourage plant growth.

Literature including biological, soil and climate science research papers, journals and books will be compiled, and the relevant information will be investigated. Conclusions supporting or opposing the proposed hypotheses will be drawn based on the available literature.

4. Materials and Methods

This study drew conclusions regarding the effects of climate change on Norwegian soil ecosystem dynamics from available literature in the form of research papers and scientific journals and books. In order to determine whether there is an overlap in the predicted temperature and soil moisture conditions in Norway and free-living nematodes' life requirements, studies examining the population dynamics of free-living nematodes as a result of changed temperature and precipitation were compiled and analyzed. Predictions of future climate changes affecting the region of Norway were also investigated. Lastly, the pattern in nematode requirements and responses to temperature and humidity conditions was compared with the climate predictions, and an analysis of the potential change in free-living nematode population dynamics as a response to climate change in the 21st century was presented. Finally, an assessment of the potential consequences on the rest of the soil ecosystem was suggested.

The studies analyzing nematode temperature and humidity requirements were categorized based on the investigation method that was applied, and a short description of the methodology used was noted. Sections 4.1 and 4.2 below give an indication of the possible ways in which one could assess the effects of a change in environmental conditions on soil nematodes population dynamics.

4.1 Lab studies

One way of estimating a potential response of nematode communities to changing climate factors is by measuring nematode response to a range of artificially induced environmental conditions. Sohlenius and Bostrom investigate the effects of a warmer climate and increased moisture conditions on the microfauna in a Swedish tundra soil by experimentally transferring soil blocks from a tundra soil in Abisko to nine warmer places in the country. In doing so, the potential climate change effects on microfauna, microbial biomass and nitrogen mineralization may be analyzed (Sohlenius and Boström 1999).

The experiment was conducted by transplanting 18 blocks of peat from the Stordalen mire to nine sites along temperature and moisture gradients in Sweden, as indicated by Figure 1 below.
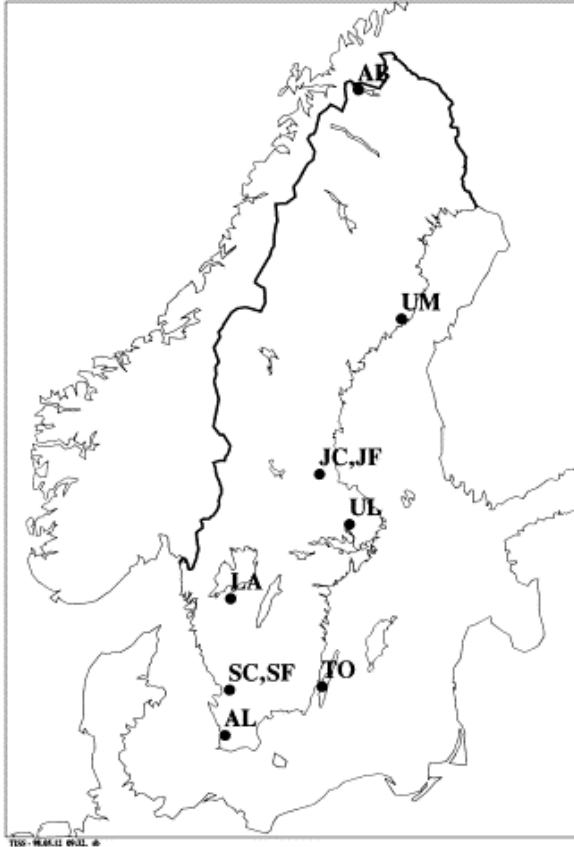
Figure 1: Map of the transplantation sites in Sweden. AB- Abisko, AL-Alnarp, JC – Jädraås clearing, JF – Jädraås forest, LA – Lanna, SC – Skogaby clearing, SF – Skogaby forest, TO – Torslunda, UL – Ultuna, UM – Umeå (Sohlenius and Boström 1999)

After transplantation, the soil blocks were sampled between day 2 and 11 of each month from July to December 1996 by taking cores out from each block. Subsamples of peat were taken from each core by a wet funnel method, and the % soil moisture content of the peat was determined. Microbial and fungal biomass was determined by the Department of Animal Ecology at Justus Liebig University in Giessen, Germany via chloroform, fumigation and extraction procedures. Inorganic nitrogen was determined at the Department of Ecology at Aristotle University in Thessaloniki in Greece.

All the animals from each subsample were fixed in triethanolamine and formalin and counted in dishes under low magnification (40x), after which suspensions from three or four extractions were combined for subsequent analysis of faunal structure. The pooled suspensions were analyzed under higher magnification (125-200x) and about 150-250 randomly selected nematodes were identified in each suspension.

The nematode fauna was classified into semitaxonomic feeding groups according to Yeates (Yeates et al. 1993). The diversity of the nematode community was calculated with the Shannon-Wiener information function H' (Shannon 1948) and using the evenness factor J' (Pielou 1966). The maturity index MI was calculated as a means to indicate the degree of disturbance. The coefficient of variation CV was calculated to compare the variability of different parameters. Finally, the relationships between the different parameters investigated in this study were analyzed by multiple linear regression, and the

possible causal relations and covariations were tested with linear regression analysis. (Sohlenius and Boström 1999)

4.2 Modeling

Predicting climate-driven changes in the availability of free-living nematodes via modelling is another one of the available tools in evaluating the effects of a changing climate on the soil biota. In the case of infective nematodes, modeling population dynamics is a valuable step which can be taken for assessing and preparing for the possible damage which may be caused by a potential increase in nematode population size as a result of favorable warmer and moister conditions. A simulation model of the effects of climate change on the free-living stages of nematode parasites is proposed by Rose et al., which attempt to quantify the infection pressure of three species of Trichostrongyloid gastrointstestinal nematodes (GIN) by building on previous models of GIN populations (Grenfell et al. 2009) (Smith 2009) and incorporating the responses of nematodes to climate change. The simulation reveal a potential increase in annual infection pressure of two (*H. contortus, T. circumcincta*) of the three species of nematodes, as increased temperatures accelerate development and remove temperature constraints during the winter months (Rose et al. 2015). The third (*O. ostertagi*) species' rapid development is predicted to be offset by the high mortality at high temperatures.

The model described in Rose's study is based on the free-living stages of the GINs' life cycle, and it is assumed that a similar one can be applied to nematodes which spend their entire life as free living organisms, as the difference between free living and infective nematodes is that the latter spend some of their life stages within the host.

The model considers the individual life stages and estimates the life history parameters based on analysis of data in literature, and suggests temperature- and moisture-dependent development rates from egg to larvae, as well as stage- and substrate- specific mortality rates using data from past experiments analyzing proportions of individuals which developed or survived at discrete intervals and at a range of constant temperatures (Rose et al. 2015).

5. Results

5.1 Nematoda functions/roles in the ecosystem

In order to determine the potential consequences that might result from a disturbance in environmental conditions, knowledge of the roles and functions of free living nematodes is of vital importance. Studies analyzing the soil fauna's contribution to the underground food web suggest that N mineralization is one significant function performed by the nematodes, annelids, arthropods and mollusks in the soil. It is of interest to assess the contribution made by nematodes only, so studies quantifying the amount of N that is mineralized by each group composing the soil fauna were analyzed. It was concluded that the taxonomic group which made the greatest contribution to nutrient mineralization depended on the ecosystem, with no one phylum having the greatest contribution in all studied regions (Griffiths 1994).

For example, in a North American grassland, bacterial-feeding nematodes account for most of the N excreted by fauna (Hunt et al. 1987), while in fungal dominated food webs in coniferous forests the soil animals mainly responsible for mineralization were those belonging to the subclass Collembola (Verhoef and Brussaard 1990) Studies in the German Black Forest indicate that the protozoa and earthworms contributed 25% of the total litter decomposition (Beck 1989). The fact that each group belonging to the

soil fauna may influence soil processes to a different degree depending on local conditions is important to take into consideration when making statements about altered soil ecosystem dynamics as influenced by a change in temperature and humidity.

According to Banage, the role of free-living nematodes in the ecosystem is dependent on their feeding biology (Banage 1963). In his study examining the nematode content of soil samples, Banage concludes that the nematode group which affects soil processes the most is the plant feeding group, irrespective of vegetation or soil properties. The next groups of importance were the microbial feeders, followed by the predatory and the miscellaneous feeders, respectively (Banage 1963).

It is important to note that, although classification by feeding habits is the norm in the scientific community, Yeates suggests that feeding-habit groupings may not be as sharply delimited as previously thought. Studies analyzing *Aphelenchoides, Tylenchus, Tylencholaimus and Ditylenchus* populations indicate that, despite being classified as "root/fungal feeding nematodes" (Sohlenius et al. 1977), they may also feed on bacteria (Yeates 1987). Yeates also notes that the feeding habits of nematodes have been inferred rather than confirmed by maintenance over many generations under biologically confirmed conditions. Furthermore, Yeates brings attention to the fact that, when cultured in laboratory conditions, the potential interactions between members of the soil fauna that would occur under field conditions, as well as their consequences are reduced, making it difficult to extrapolate the results to field conditions. (Yeates et al. 1993)

These inaccuracies will affect the certainly with which it can be said the following nematode categories may affect the soil microclimate, so caution should be used when drawing conclusions. However, as this method of categorizing nematodes is the standard used in the reviewed journals, it shall be followed in this literature review as well.

5.1.1   Plant feeders

Plant feeding nematodes usually subsist on vascular plants, and can be identified by the ever-present tylenchoid stomatostyle or dorylaimoid odontostyle, a stylet or spear shaped mouth part that enables tissue extraction (Yeates et al. 1993). Studies analyzing the relationship between plant-feeding nematodes and plant biomass in regions where nematodes are the most abundant group of multicellular soil animals, namely in grasslands, suggest that these nematodes are a major factor affecting net primary production. (Scott et al. 1979) (Stanton 1988) (Verschoor 2002)

Plant feeding nematodes may have a beneficial role in nutrient recycling in the soil by excretion of ammonia and organic N by defecation, and by causing increased root exudation as a response to root herbivory (Verschoor 2002). Despite the root herbivory not having been quantified, Yeates found a measurable increase in ^{14}C in the soil compartment after root herbivory, as early as within 15 days after pulse-labelling of the host plant (Yeates et al. 1993). Verschoor's study suggests that plant-feeding nematodes contribute to approximately 2-5% to the total N mineralization. Despite the relatively low direct contribution of plant-feeding nematodes to N mineralization, the functional contribution of plant-feeding nematodes to N mineralization may be considerably more than the estimated 2-5%, as mentioned later and exemplified in section 5.1.2.

In addition, in his study analyzing the carbon and nitrogen budgets of plant-feeding nematodes in grasslands of different productivity, Verschoor stresses that the reduced productivity resulting from the

time which had passed since the last fertilization time is likely to have affected the amount of nitrogen which was mineralized. The contribution of plant-feeding nematodes to N mineralization may decline with time since last fertilizer application (Verschoor 2002). This fact is likely to have affected the values for mineralized nitrogen that were obtained in the study, resulting in an underestimation of the nitrogen contributed to the soil by nematodes.

The increased nitrogen and carbon levels may stimulate bacterial populations, which are then consumed and further recycled by microbial feeders, as discussed in section 5.1.2. (Denton et al. 1998) This may contribute to a positive feedback mechanism as the increase in microbes leads to an increase in the bacterial-feeding nematode population, leading to enhanced nutrient mineralization rates and greater plant growth as a result of high soil nutrient content (Bardgett et al. 1999a) (Bardgett et al. 1999b).

5.1.2 Microbial feeders

Bacterial-grazing and omnivorous nematodes often dominate soil nematode communities, comprising as much as 90% of the total soil nematode community (Yeates 1979) It has been suggested that these nematodes have developed a commensal or mutualistic relationship with plants by making resources in short supply more available.

Earlier observations suggest that microbivorous nematodes have a positive effect on plant growth through enhanced nutrient mineralization (Ingham and Coleman 1983). The contribution of microbial-feeding nematodes to nutrient recycling is their high consumption of bacteria, which, when coupled with low nutrient assimilation rates results in high return of nutrients to the soil. This, connected with plants' exudation of low-molecular weight carbon compounds as a result of root herbivory which stimulates bacterial populations, leads to significant amounts of bioavailable nutrients in the soil benefitting plant growth (Anderson et al. 1981). This is likely to lead to an increase in the turnover rate and increase primary production.

In Ingham's study measuring primary production in soils containing different types of biota, it was concluded that shoot and root production was significantly higher in the ($pbfn_bn_f$) soils: the plants grown in the soils enriched with bacteria, fungi, bacterial-feeding nematodes and fungus-feeding nematodes produced significantly more shoot and root biomass than those grown in all other types of soils. This can be attributed to the nematode excretion of N, previously sequestered in bacterial biomass (Ingham et al. 1985) which is then used by plants for primary production.

The presence of bacteriovorous nematodes in soil has thus been linked by some studies to an increase in microbes in the soil, increasing turnover rate. In addition to the processes described earlier, Ingham attributes the bacterial population growth in the presence of bacterivorous nematode to three mechanisms. Firstly, up to 60% of the bacteria passing through the gut of a nematode is defecated alive (Smerda et al. 1971), obtaining nutrients while in the gut of the nematode, which results in a growth spurt in the bacteria population. Secondly, the nematode may transport the live bacteria in its gut to new, unexplored microsites, which may provide new untapped sources of nutrients, which the bacteria may not be able to access via its own mode of transportation (Gould et al. 1981). Lastly, the excretion products of nematodes may provide immediate, concentrated substrates, rich in nutrients like amino acids, which the defecated live bacteria may consume (Anderson et al. 1983).

However, it is important to note that the effects of bacterial-feeding nematodes on microbial populations in soils seem to be variable, with some studies suggesting that the presence of microbial-feeding nematodes reduces the numbers of microbes in soil (Santos and Whitford 1981), (Santos et al. 1981) (Elkins and Whitford 1982), and others indicating the opposite, with higher bacterial numbers in soils with bacteriophagic nematodes (Abrams and Mitchell 1980).

In conclusion, there is a positive feedback mechanism involving bacteria and bacteriophagic nematodes, with bacteria populations potentially increasing in the presence of bacteria-consuming nematodes, leading to more nutrients absorbed by the bacteria and then recycled by the nematodes, ultimately resulting in increased primary production and turnover rate.

5.1.3   Fungal feeders

Similarly to plant feeding nematodes, fungal feeders have a specialized mouth part with which they pierce the cell wall of the fungus and extract the contents. The effect of mycophagic nematodes on the growth of soil fungi has been studied, but appears to vary depending on the species of fungus and perhaps the species of nematode (Ingham et al. 1985)

In Ingham's study comparing N and P mineralization in soils containing bacterial feeding and fungal-feeding nematodes, it was found that soil treatment with fungi and fungal-feeding nematodes did not increase plant growth or N uptake because fungal-feeding nematodes excreted less NH_4 than bacterial-feeding nematodes, and because the N mineralized by the fungus alone was sufficient for plant growth. (Ingham et al. 1985) In the control study with only the (p) plant and (pb) plants and bacteria treatments, there was net N immobilization, and the plants took up the little N that was available, leading to limited plant growth.

Fungi's roles in the soil ecosystem include, but are not limited to decomposition of lignin and other soil organic matter, which are then further decomposes by the soil microbial community and made bioavailable to plants. Furthermore, approximately 80 to 90% of all plants form symbiotic mycorrhizae fungi relationships by forming hyphae networks. The hyphae are about 1/60 of the diameter of plant root hairs and assist the plant in acquiring water, nitrogen, phosphorus and other micronutrients by releasing enzymes into the soil which break down complex molecules which the hyphae then reabsorb and redistribute to plant roots.

5.1.4   Predatory

Predatory nematodes feed on other soil microorganisms, including plant parasitic nematodes, which reduces the parasites' detrimental effect on plant growth and leads to the release of nutrients in plant-available forms. Studies analyzing predation by the four major orders *Mononchida, Diplogasterida, Dorylaimida* and *Aphelenchida* were conducted so as to assess their effectiveness as biocontrol agents and consequent value to agriculture. It was found that displogasterids are most suited for parasitic nematode control due to their short life cycles, easy culture, prey-specificity, chemotaxis sense and resistance to adverse conditions (Khan and Kim 2007).

The order Mononchida is characterized by its strongly sclerotized buccal cavity, often armed with one or more puncturing teeth, with its life cycle duration ranging from 45 days for some species to 15 days at 25 C for others (Grootaert and Maertens 1976). Mononchids have been used to control plant parasitic nematodes in sugar beet fields, citrus nematodes, potato cyst nematodes, with varying levels of success.

Overall, monochids have efficient predatory abilities and provide natural control or plant parasitic nematodes in the soil if their populations can be manipulated in the field. However, their flaws include their intolerance to environmental fluctuations, low rate of reproduction, long life cycle and cannibalism (Khan and Kim 2007).

Dorylaimids possess a hollow stylet that they use to puncture the prey organisms and to disorganize the internal organs of the prey, rendering it immobile. Dorylaimids are the most ubiquitous of all predatory nematodes, occurring in all types of soils, climates and habitats, and feeding on other microorganisms in additions to other nematodes (Khan and Kim 2007).

The life cycle of the Dorylaimids may last between 3-6 months to 36 days at 25 C depending on species They are extremely efficient predators due to their acute prey searching ability, attraction and aggregation activities at feeding site and wide range of predation on plant parasitic nematodes (Khan and Kim 2007).

Diplogasterids have a comparatively smaller buccal cavity than other taxas, ad are the most readily cultured nematodes, completing their life cycle in 8-15 days. They appear to be more prey selective than other groups, which renders their biological control agents ability less useful than that of other nematode groups, though their advantage lies in their chemotaxis sense and easy culture.

Lastly, Aphelenchid predators have a feeding apparatus in the form of stylet, which they use to inject digestive enzymes in the body of their prey, which paralyzes it almost instantly, (Hechler 1963) permitting representatives of this taxa to feed on nematodes larger than themselves. Their life cycle is complete in 3-6 days (Hechler 1963), and their reproductive potential is high, making them and efficient biocontrol agent.

Khan suggests that much of the available information on predatory nematodes is based on laboratory experiments, rendering it incomplete and likely to be inaccurate as field interactions might play a role in nematode behavior. However, recent studies demonstrate that predatory nematodes substantially reduce the population of migratory stages of root-knot and citrus nematodes in pot and field conditions (Khan and Kim 2007).

Biocontrol potential and efficacy of predatory nematode vary with species, diplogasterids being the most efficient. Prey susceptibility to predation play a role, with the migratory stages of endoparasitic nematodes being the most vulnerable (Small and Grootaert 1983). In addition, prey nematodes may have characteristics providing resistance to predation, for example thick cuticle, course body annulations, gelatinous matrix, toxic body secretions and rapid ondulatory body movement (Small and Grootaert 1983).

5.1.5   Omnivorous

Omnivorous nematodes are able to feed on different food sources depending on environmental conditions and food availability, functioning as predators if protozoa or other nematodes are available, or as bacteria- and fungal-feeders when its primary food source is no longer available.

Omnivorous nematodes may also change their feeding habits throughout its life, preferring a different food source as a juvenile as opposed to adulthood.

A description of the effects on the rest of the soil ecosystem that nematodes falling into the individual feeding classification have is included in the previous subsections.

5.2 Nematoda life cycle

Despite the remarkable diversity of the phylum Nematoda, most can be related to the same basic life cycle pattern. In order to give an indication of the general development pattern for nematodes, studies analyzing the growth and development of the small nematode *Caenorhabditis elegans* have been used. The C. elegans is a free-living, non-parasitic, bacteriovorous soil nematode living in temperate soil environments and can thus be used as a representative for most free-living soil nematodes.

This basic life cycle consists of seven stages: the egg, the four larval stages (L1, L2, L3, and L4) and the two adult stages. Sometimes an extra stage called L5 is included, which describes the sexually immature adult. The dauer larva of C. elegans is a developmentally arrested stage induced by unfavorable conditions such as starvation, high or low temperatures or overcrowding (Wang et al. 2009). Free-living nematodes don't spend any time inside a host, instead passing through all of their life stages in the external environment. This characteristic makes them very sensitive to changes in environmental conditions and a good candidate for a study analyzing the effects of climatic changes on the life cycle of nematodes.

A major study analyzing the growth and reproduction of *C. elegans* has been conducted by Byerly et al. Their study supports the idea that nematode growth at favorable conditions follows a smooth sigmoidal pattern with time, linear growth being most rapid around the time of the fourth molt and nearly ceasing by the start of the adult stage. Egg-laying occurs shortly after the fourth molt, the rate rising rapidly at first, then more gradually to a peak followed by a relatively rapid fall.
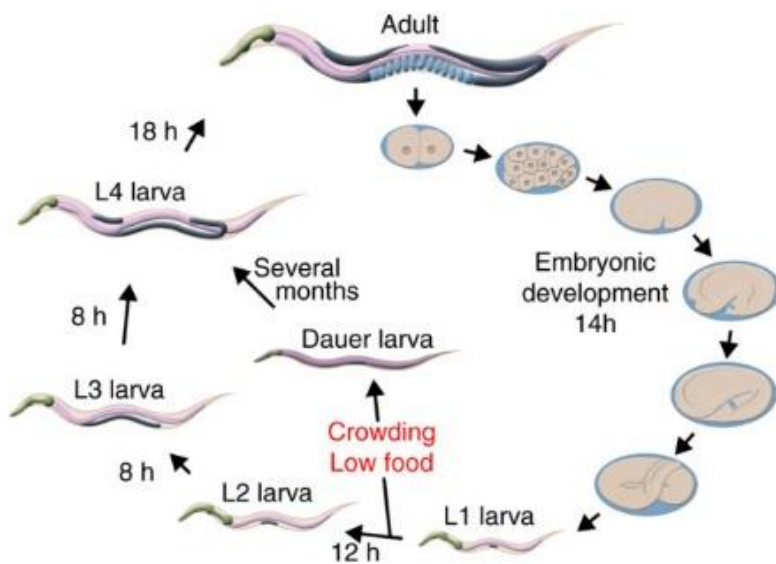

Figure 2: Common life cycle of free-living soil nematode (Altun and Hall 2017)

In addition to investigating the *C. elegans* life cycle, Byerly's study also analyzed the nematode population's development at 20 degrees C, their usual growth temperature, and compared it to nematode development and at 16 degrees C and 25 degrees C, noting the differences in the rate of growth and reproduction. According to Byerly et al., the development of free-living nematode is significantly impacted by external factors including temperature and humidity levels. Only when the environmental conditions are favorable the enclosed larvae is stimulated to secrete the enzymes which digest the surrounding egg membrane and exert pressure against the weakened membrane to rupture it and escape. The nematodes grown at 16 degrees C and 25 degrees C were found to follow the normal development pattern, though the size of the nematodes and the egg yield was significantly reduced (Byerly et al. 1976), which indicates that despite 16 degrees C and 25 degrees C are not ideal thermal conditions, it is possible for nematodes to develop at these temperatures. The noted differences between nematode development at 16 degrees C and 25 degrees C, though incomplete, offer an indication of the nematode response to the climatic conditions changes which will be discussed in further sections.

5.3 Nematoda responses to temperature and humidity

Despite there not being sufficient evidence to accurately and confidently predict the response of nematode populations to changing climate conditions, there are some studies which attempt to investigate the effects which changing temperature and moisture may have on nematode survival, development, fecundity and life cycle, in addition to the relationships and functions within the soil system.

Overall, higher soil temperature may induce a greater reproduction rate and result in a higher population density as observed in present experiments, with nematode densities twice as high in warmed soils, particularly when combined with increased soil moisture content. Studies suggest, however, that too high soil temperatures induce mortality in nematodes.

Nematodes are poikilothermic animals, meaning that their metabolic rate, activity level and behavior follows the temperature in the environmental without much delay. Environmental temperature, then, is one of the most important factors in nematode biology (Dao 1970). Wallace and Oostenbrink indicate that nematological thermograms are similar to other biological optimum curves, demonstrating successive areas of kill, cold stupor, limited activity, optimum, limited activity, heat stupor and kill in a gradient from low to high temperature (Wallace 1963). Despite a lack of experimental data relating the stipulated thermogram to a large number of nematode species, the assumption is that nematodes are similar to other organisms when it comes to relating survival rates to temperature and follow the aforementioned thermogram (Dao 1970).

It appears that soil nematodes normally thrive at temperatures between 15 degrees and 30 degrees C and become motionless from 5-15 degrees C and 30-40 degrees C. However, some species are able to conduct essential activities at low temperatures; Heterodera avenae (hatch at 2 degrees C), H. trifolii (hatch at 4 degrees C), Ditulenchus dipsaci (invade at 5 degrees C), H. schachti (active at 5-10 degrees C). These are plant parasites found in temperate climates. Others, on the other hand, only become active at relatively high temperatures; Hemicycliophora arenaria (hatch at 21 degrees C), Tylenchulus semipentrans (hatch at 15 degrees C, reproduce at 21-22 degrees C), Trichodorus christiei (reproduce at >16 degrees C), Scutellonema arenaria (reproduce at 18 degrees C), H. glycines (hatch at 16 degrees C) and Meloidogyne spec. (reproduce at 15-16 degrees C). These, on the other hand, are nematodes found

in warmer regions (Dao 1970). Overall, however, the temperature range nematodes generally thrive at is 15 to 30 degrees C.

The maximum temperatures for activity are generally between 30 C and 35 C, at which point nematodes generally attempt to escape the unsuitable conditions (Clapham 1931). Regarding the lower end of the spectrum, nematodes can sustain under temperatures below 5 C for quite a long time by entering an anabiotic state (Dao 1970).

There isn't much available literature quantifying the point at which increased soil humidity can hurt nematodes, if such a point even exists, as soil nematodes are technically water organisms, living in soil water. It is known that soil moisture content, greatly determined by precipitation levels, is an overarching factors for nematode activity levels, as they live in water films between soil particles and feed on directly or indirectly plant-derived resources. Elevated precipitation, in addition to making nematode dispersal in the soil possible, leads to higher rates of primary production, resulting in increased availability of nutrients for nematodes.

5.3.1 Temperature

Temperature has been shown to affect factors including rate of development (Bergeson 1959), generation time (Evans and Fisher 1970), egg production and hatching (Bergeson 1959) (Greet 1978), size (Evans and Fisher 1970) movement (Dusenbery et al. 1978) and respiration (Elliott et al. 1980). The effects of temperature on these responses varies, and thus the best way to assess optimum temperature for a species is by measuring the population response, as it reflects the summation of several processes affected by temperature.

Bakonyi and Nagy analyze the impact of temperature and moisture changes on the nematode fauna in a semiarid grassland (Bakonyi and Nagy 2000). Their findings suggest that both temperature and soil moisture content influenced nematode population density. Ruess et al. also investigate the potential effects of climate change on soil microorganisms, including nematodes, in subarctic soils. Their study measures microorganism biomass before and after treating soils to passive greenhouses and nutrients, and suggests that the temperature enhancement, with or without the fertilizer, leads to a doubling of the bacterial and fungal-feeding nematode population density and a greater microbial and fungal biomass. The study indicates that collectively, the effects result in an enhanced net N and P mineralization rates due to increased soil fauna (Ruess et al. 1999). Ruess' study also suggests that the simulation affected the nematode species composition, with the different species responding differently.

In Richard V. Anderson and David C. Coleman study analyzing the population dynamics of six bacterial-feeding nematode species when exposed to different temperatures, three types of responses are observed. The most common response, as indicated by Anderson's and Coleman's study, is the independent growth curve and significantly different population density for each temperature, exemplified by the *Caenorhabditis* and the two *Pelodera* species, a response which results in a bell-shaped curve when plotted. The second response type is population development over a narrow temperature range, as exemplified by a single species, the *Mesodiplogaster*, whose populations only developed at 20-24 degrees C. The third response population growth and development over a relatively wide temperature range, as exemplified by *Acrobeloides* and *Rhabditis*, which can develop at a temperature range of 15-20 degrees C.

According to Anderson's and Coleman's study, the temperature significantly affects the amount of time required for population development, with maximum population density requiring more time at low temperatures (<24 degrees C) and population developing occurring relatively more quickly at higher temperatures.

Michael R. Klass' study concerning the effect of the biological and environmental factors influencing the life span of the free-living *Caenorhabditis elegans* supports the idea that temperature and life span is indirectly related, with the life span being greatly reduced at temperatures above 25.5 degrees C. The study also suggests that the reproductive phase is most sensitive to temperature change relative to life span.

5.3.2 Precipitation and soil moisture

Soil water is one of the major factors influencing nematodes, as they are soft-bodied, water dwelling creatures which live in the soil water films in the spaces between soil particles, quickly entering a dormant state when soil water becomes scarce. In addition, nematodes largely rely on plant-derived resources for sustenance. Water is then a majorly important factor determining their activity rate and food provisions, and consequently changes in its availability may directly impact soil nematode development and community composition (Yeates 1999)

It has been suggested that, under climate change scenarios, changing precipitation may occur simultaneously with atmospheric N deposition and may act interactively rather than cumulatively (Song et al. 2016). Observed effects of precipitation include increased soil N leaching and mineralization (Schimel et al. 1997), as well as stimulated plant growth leading to enhanced photosynthesis and transpiration, and soil moisture. The effects of changing precipitation regime on soil fauna abundance is still poorly understood, however, there are some studies which attempt to investigate soil microorganisms' response to a change in water availability.

It has been demonstrated that elevated precipitation may increase BNPP (belowground net primary productivity) (Bai et al. 2010), stimulate soil microbial and fungal biomass, and thus providing more resources for soil fauna like microbivorous and fungal-feeing nematodes (Liu et al. 2009)

The study of Song et al. suggests that water addition significantly increases soil nematode abundance and generic richness but does not affect the relative abundance of different trophic groups (Song et al. 2016) These conclusions were drawn by studying nematode population dynamics under experimental conditions of added nitrogen (N), added water (W) and added nitrogen and water (NW). It was found that water addition stimulated plant density by 130% and increased root biomass by 48%, but had no influence on species richness. The favorable conditions for plant growth was stipulated to provide better microenvironments for nematodes , as plant roots and root-derived C compounds are recognized as important resources for soil food-webs (Pollierer et al. 2012). As Landesman suggests, increased water availability can significantly impact soil fauna abundance (Landesman et al. 2011). Lastly, enrichment of resource availability could also alleviate the intensity of interspecific competition and increase soil nematode generic richness (Song et al. 2016).
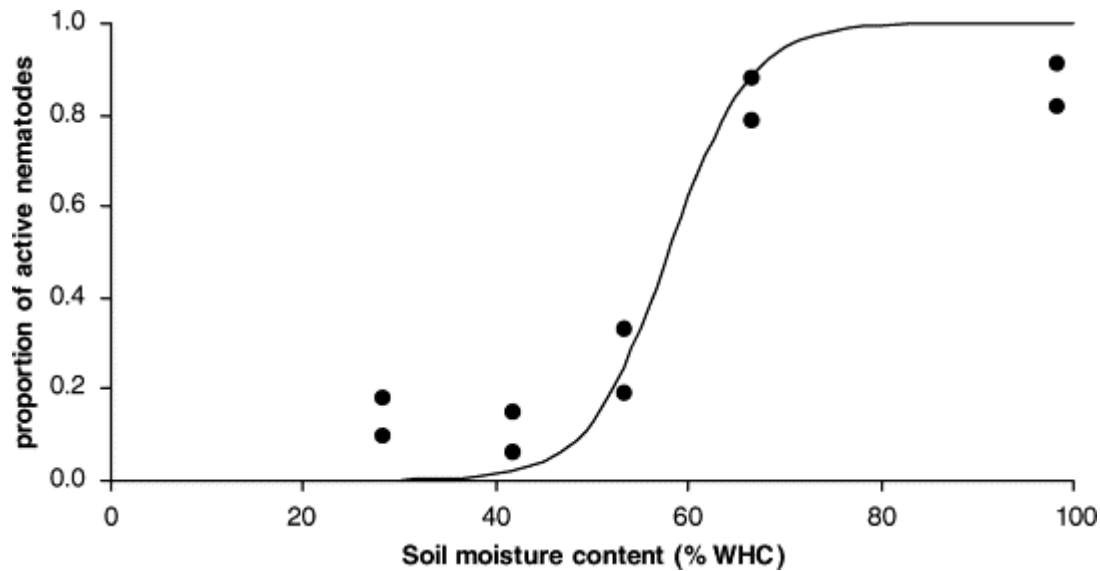
Fig 3: The relationship between soil moisture content and proportion of active nematodes, expressed as the percentage of the soil water holding capacity (WHC) (Demeure et al. 1979).

Soil moisture content as illustrated as % of soil Water Holding Capacity (WHC) leads to a dramatic increase in nematode activity levels as it increases from 40% to 65%, after which it plateaus. Nematodes, then, thrive at a WHC of a given soil of 65% or more.

5.4 Climate change in Norway

There is growing evidence that the climate is undergoing significant changes as a result of multiple factors, the most important being the increase in atmospheric greenhouse gases resulting from human activity, as concluded by the Intergovernmental Panel on Climate Change (IPCC). (IPCC 2013c) Anthropogenic climate change is having a significant impact on physical and biological systems globally, with consequences including, but not being limited to shrinking glaciers, melting permafrost, shifts in spring peak of river discharge and species distribution and community structure (Rosenzweig et al. 2008).

During the 20th century, Europe experienced an increase in average annual surface temperature of 0.89 degrees C (0.69 C-1.08 degrees C) for the period of 1901-2012 and about 0.72 degrees C (0.49 C-0.79 degrees C) for the period of 1951-2012 (IPCC 2013b) Positive annual temperature trends are found over most land areas, particularly since 1981. An increase in the frequency of warm extremes as opposed to cold extremes has also been observed. IPCC also reports that the Northern Hemisphere mid to high latitudes show a likely increasing trend in warming (medium confidence prior to 1950, high confidence afterwards) (IPCC 2013a). Observed precipitation trends show a high degree of spatial and temporal variability, with both positive and negative values.

Despite the multitudes of studies making projections about the future of climate, it is important to note that there is a number of uncertainties in the scientific community's understanding of the future of the climate, which can be summarized in terms of three questions: 1) how will the external forcing of the climate system change in the future? 2) how will changes in external forcing factors influence climate? 3) to what degree is climate change signals masked or amplified by natural variability? (Kjellström et al.

2011) Furthermore, it is uncertain the degree to which anthropogenic activity will continue to interact with and affect the environment. IPCC developed a series of emission scenarios coupled with corresponding potential expressions of climate change. The projections are based on long term trends on greenhouse gas emissions resulting from different economic and social trends with varying degrees of concern for sustainability and the environment. The scenarios range from a free trading environmental with high capital turnover but little concern for the environment (A1) to a world of increased care for the ecosystem (B2) (IPCC 2013a). These uncertainties may influence the extent to which climate will change in the future, the different scenarios corresponding to different degrees of change. Moreover, climate is thoroughly influenced by local geographical features such as mountain ranges, valleys, fjords, distance from the coast, altitude and lake, and most of these features are not accounted for in climate models (Benestad 2002) In conclusion, predictions should be taken into account but viewed critically.

Syntheses and assessments of state-of-the art climate research conclude that the main changes at high northern latitudes will include increasing temperatures and precipitation, as well as increased frequency of certain types of extreme weather events (IPCC 2013a).

The research of specific regions permits the development of smaller scale models which is more likely to take into consideration the conditions particular to the area of interest and thus result in more accurate prediction. Uleberg et al, for example, investigated the impact of climate change for six municipalities in Northern Norway by developing downscaled temperature and precipitation projections for the 21st century. Ensembles of climate simulations (72 for temperature and 22 for precipitation) were developed for different Norwegian regions based on multiple emission scenarios, namely B2, A1B and A2), several global climate models and downscaling methods (Uleberg et al. 2014).

Figure 4: Municipalities studied by Uleberg in his study *Impact of climate change on agriculture in Northern Norway and potential strategies for adaptation* (Uleberg et al. 2014)

5.4.1 Changes in temperature

The Norwegian climate is characterized by large gradients both in the east-west and in the north-south direction due to topographic heterogeneity and the presence of both coastal and continental climate. The continental parts of Norway experience mean monthly winter temperatures below -15 degrees C compared to coastal regions in southern Norway where mean summer temperature are between 0-2 degrees C. High mountain areas in the south normally have a mean monthly summer temperature between 6-8 degrees C, while coastal south-eastern parts normally experience 14-16 degrees C. Mean monthly summer temperature in the lower parts of northern Norway is normally around 10-12 degrees C, and the seasonal temperature decreases with latitude and altitude.

A multitude of studies examining the potential effects of climate change on Norway's climate support the idea that an increase in temperature is inevitable, especially in winter, and that warming rates will increase with both altitude and latitude.

Overall, the annual mean temperature in Norway has been observed to increase by about 0.09 degrees C per decade between 1900 and 2008, depending on the geographical region, with some areas warming by 0.5 degrees and others warming by 1.1 degrees (Førland et al. 2011). Projections for two periods - 2021-2050 and 2071-2100 have been calculated using simulations based on statistical and dynamic downscaling of global climate model results from IPCC between 1961 and 1990 (IPCC 2013a)The results suggest that the northernmost Norway will undergo the greatest change in temperature, and that western Norway temperatures will change the least. Specifically, northern Norway is likely to warm by 1.5-2.2 degrees C by 2050, with the largest increase concerning autumn and winter temperatures.

The simulations indicate that summertime changes are likely to be 30% smaller than wintertime changes in northern and middle Norway and 10% smaller in southern Norway while springtime changes are comparable to wintertime changes in southern Norway and slightly smaller in northern Norway. Projections for 2071-2100 suggest that the maximum temperature in summer will increase most in the south-east by 3 degrees C, with the rest of the country facing a warming of up to 2 degrees C. The number of hot summer days will increase, mostly in the northeast, and the winter season will be milder and shorter, with minimum temperatures between 2.5-4 degrees C above present values. Consequently, the growing season is projected to increase by 1-2 months over large parts of the country.

Benestad's study investigating local climate scenarios for various locations in Norway using different global climate model scenarios supports the general consensus regarding a general warming in the future for all locations, with strongest trends during winter. The regions expected to undergo the most warming are those with a continental climate, specifically Nesbyen and Karasjok, marked with an N and a K in Figure 5 below.
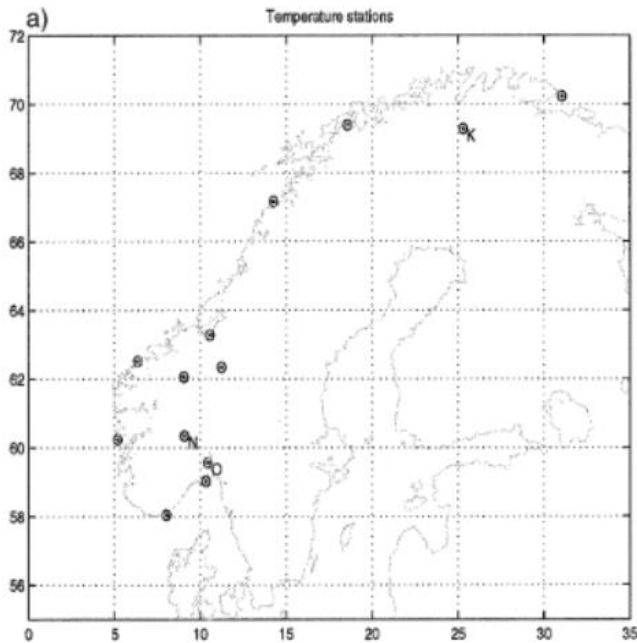
Figure 5: Map illustrating the stations network for temperature. The climate stations measuring the temperature include Oslo (marked with "O"), Nesbyen ("N"), Ferder, Oksøy, Bergen, Ona, Røros, Dombås (Kjøremsgrende), Værnes, Bodø, Tromsø, Karasjok ("K"), and Vardø. The precipitation measurements are made at Halden, Moss, Oslo, Røros, Verma, Hemne, Namdalseid ("N"), Dunderlandsdal ("D"), Sulitjelma ("S"), Barkestad ("B"), Tromsø, Geilo, Bjåen, Sviland, Bergen, and Lavik (Benestad 2002)

In the spring, the multimodel ensemble used by Benestad suggests higher median values for northern Norway (Tromsø, Karasjok and Vardø) but these estimates are also associated with a larger spread. (Benestad 2002) The spring warming is predicted to be less than that during other seasons, except in northernmost locations, which are predicted to undergo the smallest temperature change in the autumn.

Uleberg's study concerning Northern Norway, the analyzed regions mentioned in Section 5.4, suggests that the average projection displays a considerable increase in temperature for all municipalities, especially during winter, and most pronounced in the Finnmark (Northeastern) area. Figure 6 below indicates the observed and predicted temperatures suggested by Uleberg et al for the studied regions.
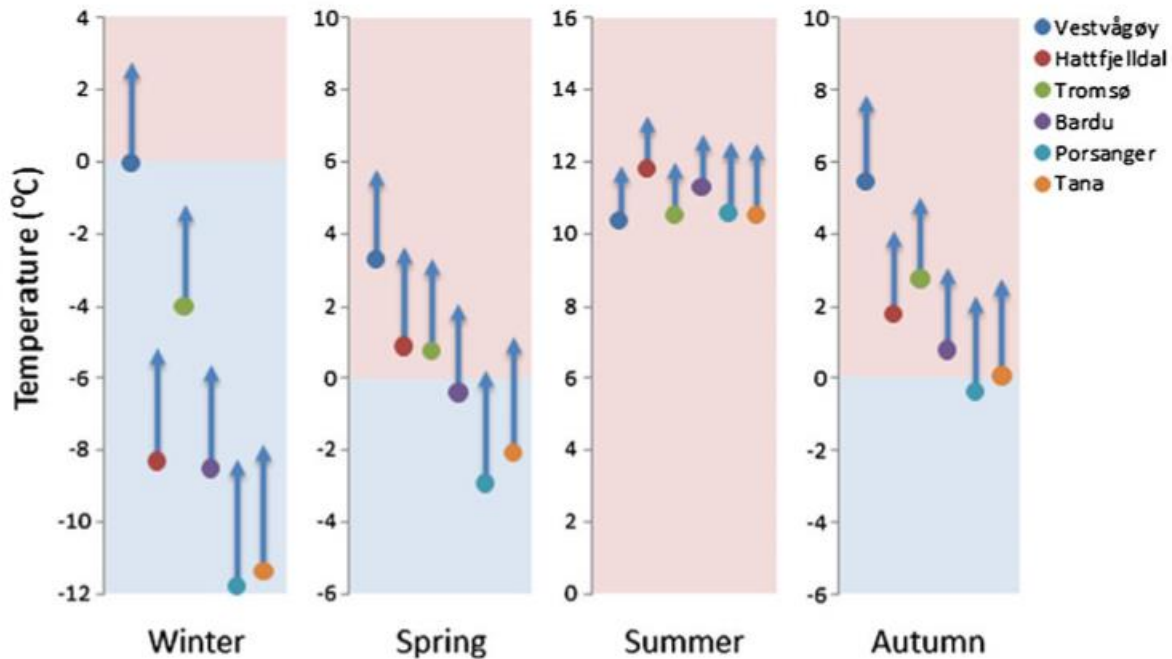
Figure 6: Average seasonal temperatures observed during 1961-1990 (points) and projected for 2021-2050 (arrows) in the municipalities of interest (Uleberg et al. 2014).

According to Figure 6 proposed by Uleberg, the winter temperature in the Vestvågøy area is predicted to raise above freezing temperature before 2050, while the other regions are likely to remain under 0 degrees C, while still warming up quickly. Spring and autumn temperatures are likely to raise above 0 degrees C for all regions of interest. As supported by IPCC predictions discussed earlier in the section, the change in summer temperatures will be the least pronounced, the studied regions likely warming up less in the summer than in winter.

The temperature predictions were used by Uleberg to calculate the change in the growing season, defined by Engen-Skaugen as the number of days per year with an average temperature above 5 degrees C (Engen-Skaugen et al. 2007). For the period 1961-1990, the mean growing season for the regions of interest varied between 90 and 150 days, with Vestvågøy having the smallest growing season range of 150-180 days. Uleberg predicts that the growing season is likely to increase by 7-28 days for the investigated municipalities for 2021-2050. The largest increase is predicted for the inland, northernmost municipalities due to their mountainous character, which currently have the shortest growing season, and the lowest is predicted for Vestvågøy.

Karlsen et al. suggested that the onset of the growing season is gradually delayed from lowland to mountains while the ending of the growing season in autumn is more heterogeneous. Spring frost and frozen are likely to be lowest in coastal municipalities, as those will experience mean winter temperatures above 0 degrees C toward the end of the century (Karlsen et al. 2005).

Engen-Skaugen et al. analyzed the potential effects of climate change on Norway's temperatures using two global medium resolution models, the ECHAM4/OPYC2 from MPI and the HadAM3H from the Hadley centre, and the IPCC SRES emission scenarios B2 and A2. The analyzed time period was 2071-

2100, with the control time period of 1961-1990 representing the current climate. The researchers analyzed three locations – Oslo in the southeast, Bergen-Florida in the southwest and Karasjok in the northeast. According to the A2 scenario, the mean temperature increase from west to east is somewhat stronger (<3 degrees C west to >3.5 degrees C east and >4.5 degrees C northeast) than the mean temperature increased according to B2 (<2.5 degrees C west to >3 degrees C east and >4 degrees C northeast). Oslo-Blindern is predicted to undergo the largest temperature increase, and Bergen-Florida is projected to have the smallest future warming. Karasjok, on the other hand, is projected to experience the largest wintertime temperature increase (Engen-Skaugen et al. 2007). Engen-Skaugen suggests that the warmest daily winter temperatures will increase, but the temperature of the coldest winter days will increase the most, especially in the coldest areas. Thus, the coldest days in winter are likely to experience far warmer temperatures in the future compared to the present, and the warmer summer days will be warmer, though there is a large spread in these results. Furthermore, the models suggest that climate change may lead to smaller regions with cold climate in the winter and the warm coastal regions in southwest are likely to move further inland and eastwards. Mean summer temperatures will increase, especially in southeastern regions (Engen-Skaugen et al. 2007).

5.4.2 Changes in precipitation

Observations suggest that the total annual precipitation in North Norway, except for the Varanger Peninsula, has increased with approximately 2% per decade during the past century. (Førland et al. 2011) IPCC states that an increase in the amount of precipitation at high altitudes is very likely, with the increase being largest in winter and smallest in summer (IPCC 2013a). The AIA climate scenarios suggest that the regions over the Arctic (60-90 degrees) will increase by roughly 12% from 1981-2000 to 2071-2090. Some parts of Norway will receive more precipitation than others in the future, specifically Northern Norway is projected to undergo an increase of 20-30% in annual precipitation between 2021 and 2050, and the Northeastern part is likely to receive up to 40% more. The seasonal precipitation is projected to increase over the whole region during all seasons, with the largest increase during winter and spring.

The intensity of strong precipitation events is also likely to increase in most parts of the country, the pattern being most noticeable for longer-duration rainfall events. The frequency of moderate to strong precipitation events has increased by 10-30% in most parts of the country since 1957, particularly in the wetter regions. This pattern is likely to continue and be exacerbated over time. According to Official Norwegian Reports, the number of days with enhanced precipitation will increase in all of Norway and for all seasons (Bardalen and al. 2010)

Some studies have been conducted which analyze specific regions of Norway and propose potential scenarios regarding those areas only. According to Uleberg's study concerning Northern Norway municipalities, the average precipitation of his studied areas, mentioned in section 5.4, is predicted to increase for the period of 2021-2050, as illustrated in Figure 7 below.
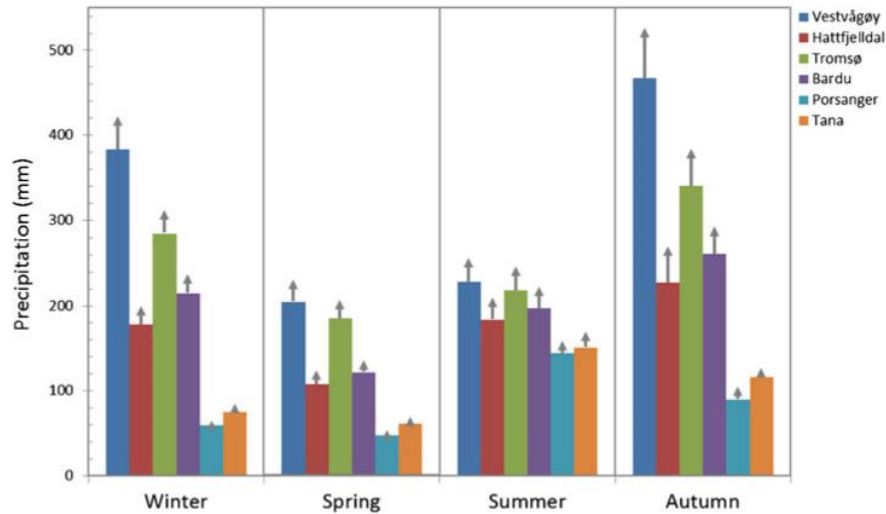
Figure 7: Average seasonal precipitation observed during 1961-1990 (columns) and projected for 2021-2050 (arrows) in the municipalities of interest (Uleberg et al. 2014)

At the moment, the municipalities with the lowest precipitation are Porsanger (350 mm/year) and Tana (400 mm/year), while Vestvågøy (1,300 mm/year) and Tromsø (1,000 mm/year) have the most precipitation (Uleberg et al. 2014).

As Figure 7 suggests, autumn precipitation is predicted to increase the most for all municipalities except Tana, a region where summer rainfall is likely to increase more than its autumn rainfall.

6. Discussion

Climate is the average weather conditions over a period of time, and includes atmospheric conditions, temperature, precipitation and humidity, air pressure, wind velocity and direction, sunlight and other radiation. Whether directly or indirectly, climate significantly determines the distribution and diversity of organisms.

As opposed to other organisms, whose populations' survival or extinction is clearly influence by the climate, studies analyzing the climate effects on nematode populations are contradictory, some suggesting that some climatic components are instrumental in determining nematode dynamics, and other maintaining that established populations are persistently present in a high density regardless of the climate. However, the consensus among the majority of soil scientists and biologists, as exemplified in a multitude of studies performed via experimentation or modelling, is that free-living soil nematodes are highly dependent on water and that temperature plays a vital mode in the activity levels of these soil organisms.

Despite the name, soil nematodes live within water films between soil particles, and are dependent on soil moisture for dispersion, as well as protection from desiccation to which they are vulnerable due to their soft bodies and the thin epidermis. In addition, irrespective of the feeding mechanism, nematodes feed on organisms which are also greatly affected by water availability or lack thereof.

As described in section 5.1, soil nematodes obtain their nutrients from other organisms cohabiting the soil ecosystem, such as plants, microbes, other nematodes, fungi, or a mixture of the above. These soil

organisms are similar to most other organisms on earth in that they require water to survive. Due to its chemical configuration resulting in high solvency, water can carry substances into and out of the cell, allowing the most basic cell functions and processes to take place. Plants require water in order to conduct photosynthesis and process CO_2 into carbohydrates, as well as maintain tissue turgidity and transport nutrients throughout the plant body. Bacteria break down complex polymers such as starch, cellulose and protein via hydrolyzation, which requires water. Fungi release enzymes into their surrounding environment to break down complex compounds into simpler ones that are then available for absorption, water being a necessary component which allows these enzymes to leave the fungus, remain functional and break down the substances. All organisms which nematodes feed on need water for respiration, metabolism and/or reproduction. Therefore, water scarcity influences nematodes not only due to their dependence on water for their own functional processes, but also because it may lead to a decline in the organisms they rely on for sustenance.

Nematodes generally seem to thrive at a soil moisture content of 60% WHC and upwards, at which the proportion of active nematodes reaches a value of 1, as illustrated by Figure 3 in Section 5.3.2. It is assumed that enhanced rainfall, whether characterized by an increase in the mean precipitation or an increase in extreme rainfall events, is not likely to negatively affect free-living soil nematode, as none of the investigated studies mention conditions ever being too wet for nematode survival. As nematodes thrive when soil moisture reaches maximum values, it is predicted that an increase in rainfall in Norway will positively affect nematodes' development and growth rates.

The effects of temperature are more diverse as nematodes are sensitive to temperatures falling outside specific ranges they are comfortable at, which is generally 15-25 degrees C. However, it is important to note that the optimum temperature for population development is different for cohabiting nematode species, which facilitates coexistence of related species in the same habitat. Nematodes have survival strategies which allow them to exist at temperature falling below their preferred range, such as entering a dormant state called Dauer, mentioned in Figure 2 in section 5.2. This mechanism is helpful in that it reduces the affected nematode's metabolism and slows down internal processes until conditions are restored to normal. However, nematodes are not able to sustain at temperatures exceeding the upper end of their comfort range, generally attempting to flee when temperatures reach, or exceed 30 C, or otherwise facing mortality.

The aforementioned responses apply to extreme temperature conditions only, the studied literature suggesting that nematodes are similar to other organisms in that higher temperatures (which stay within their preferred range) may lead to enhanced development, growth and reproduction rates, as well as higher egg yield. The nematodes' response to increased temperature depends on species, as well as the rest of the conditions which influence these processes. Studies suggest that an increase in temperature leads to a significant increase in the population size of bacterial and fungal-feeding nematodes, as well as faster development.

The increased temperature is predicted to happen as a result of human-induced climate change, specifically the increase in the greenhouse gases released in the atmosphere which trap longwave radiation emitted by the earth, warming it up. Precipitation is expected to increase as warmer air can hold more water vapor, the warmed atmosphere retaining enough energy for water molecules to maintain their gaseous state. The resulting water vapor is released as precipitation when the moisture cools and reaches saturation point, which may happen due to cold or warm fronts, convective lift,

convergence or orographic lifting. The latter mechanism is particularly relevant to the region of interest, as Norway's geography is dominated by mountain ranges broken up by valleys and fjords, resulting in highly identifiable regions which are likely to undergo increased precipitation. Furthermore, the mountainous character of Norway contributes to the heterogeneous climate as determined by its both continental and coastal conditions. These characteristics make Norway a particularly interesting and challenging region to study and determine a potential climatic future for.

Generally, climate change predictions concerning Norway suggest that an increase in temperature is imminent, with the most likely affected regions lying in the northernmost part. Predictions also indicate that wintertime temperatures are likely to change at a higher rate than summertime temperatures, which may lead to an increased growing season. As discussed in previous sections, nematodes have a wide range of preferred temperatures, but most of them are not comfortable at temperatures above 30 C or under 5 C. It is unlikely that climate change in the next 50 to 100 years will lead to temperatures of over 30 C in Norway, or a decrease in temperature. It is likely that the intensity and/or frequency of extreme events including heat waves and rainfall events will increase, with the latter being most probable for a high-latitude region such as Norway.

As discussed in section 5.4.1, Norway's temperatures vary significantly throughout the country due to the presence of both continental and coastal climate, as well as the mountainous character. Studies analyzing the potential effects of climate change in specific regions have quantified the change as ranging from 1-3.4 degrees C depending on region and season. The temperature change effects on soil nematodes are likely to vary as a function of the original temperature. Figure 5 in section 5.4.1 suggests a potential change in temperatures in six regions in Northern Norway as quantified by Uleberg. It is likely that these changes will lead to higher levels of activity of nematodes in the spring and autumn in Vestvågøy, as climate change would shift temperatures from a seasonal average of 3 degrees C to almost 6 degrees C, thus surpassing the 5 degrees C point at which most nematodes enter a dormant state. The change in summer temperatures in Northern Norway is smaller than the changes in other seasons, but the increase in temperature in nevertheless likely to lead to an increase in the metabolic rate of some nematodes, potentially resulting in greater growth, reproduction rates and metabolism. These effects are due to the small (1-1.5 degrees C) increase in temperatures, shifting summer average temperatures from around 10 degrees C to 12-13 degrees C. Assuming that the initial temperature is within the preferred range for some nematodes, this shift will lead to more favorable conditions, especially when paired with an increase in soil moisture.

Soil moisture, largely determined by precipitation is also predicted to increase. Some models suggest that the North and Northeastern region, especially, will undergo a significant increase in precipitation, especially in the winter and spring. Others propose that summer precipitation will increase the most in the northernmost region. In general, the areas which are expected to undergo the most significant increases in precipitation are those located on the coast, which are already very precipitous as a result of the frequent weather fronts and mountainous character leading to orographic lifting.

As nematodes live in the water films between soil particles, soil characteristics play an important role in determining how the precipitation translates into soil moisture. The coastal soils are composed of silt, clay and sand as a result of the coast being flooded by sea water in the melting periods between ice ages. Silt and clay covered areas are likely to hold on to more water than sandy soils due to the soil particle large surface area, and so the high precipitation is likely to translate into high soil moisture in

those regions, which may be beneficial to soil nematodes. The widely cultivated eastern Norway soils are rich in mineral content; an increase in temperature and precipitation is likely to improve environmental conditions for nematodes.

The higher development and metabolic rates may lead to increasingly efficient soil processes that nematodes contribute to, as described in section 5.1. According to the investigated literature, greater temperatures (remaining within the preferred range) coupled with higher precipitation rates may lead to higher litter decomposition rates resulting in greater nutrient mineralization. This increase in bioavailable nutrients such as nitrogen and phosphorus is likely to enrich the soil, making it more favorable for plant growth and thus increasing primary productivity, as well as enriching subsoil biodiversity. In addition, an increase in the population of certain predatory or fungal-feeding nematodes may contribute to population control of parasitic nematodes, arthropods, insects or fungi which contribute to disease and mortality of plants and crops in cultivated areas. Better temperature and moisture conditions may elevate survival probability of nematodes used for pest control in agricultural settings and thus contribute to an increase in crop production.

However, it is possible that, coupled with the higher temperatures, the enhanced precipitation rates will lead to freeze-thaw cycles and possibly to a frozen crust instead of a snow cover. The frozen crust will keep soil temperatures low despite air temperatures giving the impression that conditions would be favorable for soil fauna. Milder winters may counteract the effect, but this is an important potential factor that may result in stagnant, or even decreased soil nematode activity levels. Furthermore, climate change may challenge the competitive ability of some species, with population composition becoming modified as a result of raising temperatures. The increasing temperatures may also allow certain species to extend their occurrence northward and may desynchronize predator-prey interactions in the soil.

Overall, the ecology of soil fauna is complex and it is difficult or impossible to predict behavioral changes by considering temperature and moisture only, as other factors, external or not, will likely play a role and affect the outcome. Climate change is definitely expected to affect soil system interactions in complex ways, potentially altering soil biodiversity.

7. Conclusion

Free-living soil nematodes are important members of the soil fauna community, contributing to vital soil processes including but not being limited to litter decomposition and nutrient mineralization. Despite being found in most types of soil and climate, nematodes have a range of environmental conditions at which they thrive.

This paper analyzed the temperature and moisture conditions in relation to nematode survival and developmental rates. It was concluded that the temperature ranges at which nematodes thrive vary among species, with nematodes generally carrying adaptations allowing them to survive at temperatures characteristic for the region they inhabit. However, the temperature range at which nematodes are generally comfortable was found to be 15-25 degrees C. The soil moisture expressed as WHC of 60% and above was concluded as preferable for soil nematodes.

Climate change predictions suggest that temperature will increase throughout Norway in the next 50 to 100 years, particularly in the northernmost part in the winter. It is also suggested that precipitation rates will increase, and that extreme rainfall events may become more frequent and/or intense. Climate

change-induced temperature and precipitation increases in Norway are predicted to positively impact local free-living soil nematodes, leading to enhanced development and metabolism rates and consequently an increase in litter decomposition and nutrient mineralization, and ultimately increased primary production.

State of the art tools are used to predict future changes in climate conditions, yet uncertainties regarding future emissions and the accuracy of applying global models to small scale regions result in an unclear image of the future. In addition, it is important to take into consideration the fact that temperature and soil moisture content are only two of the many factors which may determine nematode development and activity levels, and drawing conclusions based on those conditions only may be erroneous. It would be valuable to investigate the effect of other environmental conditions which may undergo changes as an effect of climate change. Further researching investigating the effects of a potential change in wind speed and intensity, as well as an altered soil community composition on soil nematodes may be of interest. Alternatively, it may be valuable to compare and contrast the effects of changing temperature and precipitation in Southern Europe on local nematode communities, as climate is expected to undergo a different set of changes in the lower latitudes and nematode response to climate change may be entirely different in Southern Europe than in Northern Europe.

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