

Climate change effects on terrestrial parasitic nematodes: Where are the knowledge gaps?

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Review Article

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Abstract

Climate change is expected to affect parasitic nematodes and hence possibly parasite–host dynamics and may have far-reaching consequences for animal health, livestock production, and ecosystem functioning. However, there has been no recent overview of current knowledge to identify how studies could contribute to a better understanding of terrestrial parasitic nematodes under changing climates. Here we screened almost 1,400 papers to review 57 experimental studies on the effects of temperature and moisture on hatching, development, survival, and behaviour of the free-living stages of terrestrial parasitic nematodes with a direct life cycle in birds and terrestrial mammals. Two major knowledge gaps are apparent. First, research should study the temperature dependency curves for hatching, development, and survival under various moisture treatments to test the interactive effect of temperature and moisture. Second, we specifically advocate for more studies that investigate how temperature, and its interaction with moisture, affect both vertical and horizontal movement of parasitic nematodes to understand infection risks. Overall, we advocate for more field experiments that test environmental effects on life-history traits and behaviour of parasitic nematodes in their free-living stages under natural and realistic circumstances. We also encourage studies to expand the range of used hosts and parasitic nematodes because 66% of results described in the available studies use sheep and cattle as hosts and 32% involve just three nematode species. This new comprehension brings attention to understudied abiotic impacts on terrestrial parasitic nematodes and will have broader implications for livestock management, wildlife conservation, and ecosystem functioning in a rapidly warming climate.

Introduction

Parasitic nematodes are a group of multicellular organisms infecting and occupying a diverse range of hosts and ecosystems (Chung & Boeri 2012; Aleuy & Kutz 2020). They are a cause of animal disease (Charlier *et al.* 2009; Mehlhorn 2016) and can potentially impact the dynamics of wild populations (Tompkins *et al.* 2002), food webs (Lafferty *et al.* 2006), and prey–predator interactions (Hudson *et al.* 1992; Hatcher *et al.* 2006). Parasitic nematodes and their development, survival, and distribution/migration in and on the herbage are sensitive to abiotic factors such as moisture and temperature (Crofton 1965; Stromberg 1997; O’ Connor *et al.* 2006; Gyeltshen *et al.* 2022). Thus, changing environmental factors associated with climate change are expected to affect parasitic nematodes, with possible consequences for parasite–host dynamics (Kutz *et al.* 2009; Molnár, Kutz *et al.* 2013; Dobson *et al.* 2015). However, there has been no recent review of the knowledge gaps about the effect of temperature and moisture on direct life cycle parasitic nematodes in birds and mammals. Highlighting the knowledge gaps about abiotic effects, and particularly the interaction of moisture and temperature (O’ Connor *et al.* 2006) on parasitic nematodes, could guide future research and provide a better understanding of the implications for livestock health management, wildlife conservation, and ecosystem functioning in a rapidly warming climate.

In this review, we focus on parasitic nematodes with a direct life cycle. This group of parasites has one definitive host and a free-living stage outside the host where they occupy highly diverse habitats (e.g., faeces and herbage; Figure 1) and may be vulnerable to changes in abiotic conditions (Molnár, Dobson *et al.* 2013; Molnár, Kutz *et al.* 2013). In an attempt to understand environmental effects on parasitic nematodes with a direct life cycle, many studies have focused on the seasonal correlation between environmental factors and nematode abundance (Chaudary *et al.* 2008; van Dijk *et al.* 2010; Halvorsen 2012; Holand *et al.* 2019) and behaviour (Langrová *et al.* 2003; Kuzmina *et al.* 2006; Santos *et al.* 2012). Although seasonality studies are important in shedding light into the role of annual environmental change, the underlying mechanisms influencing the parasite dynamics often remain unknown (Altizer *et al.* 2006) and need to be disentangled with experimental studies. Therefore, to tease apart the diverse factors and mechanisms that affect parasite–host dynamics, we have focused on reviewing experimental field and laboratory studies on the effect of

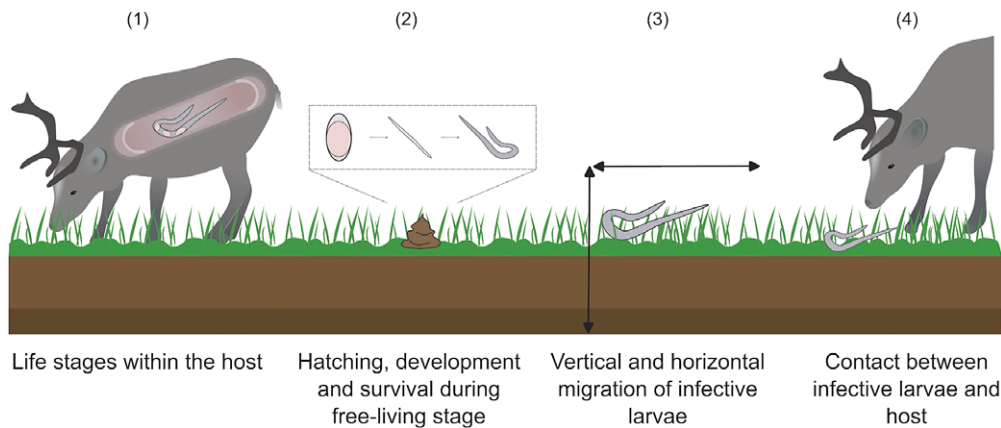


Figure 1. Schematic figure of the life cycle of parasitic nematodes with a direct life cycle that occupy highly diverse habitats (faeces, herbage, and inside the host) during the different life stages. 1) Parasitic nematodes with a direct life cycle have one definite host, in which exsheathment, reproduction, survival and egg production occurs. 2) In the free-living stage outside the host, eggs develop into infective larvae. 3) Infective larvae move out of the faeces and 4) are ingested by the host again.

abiotic conditions on parasitic nematodes with a direct life cycle in birds and mammals. Our primary aim is to identify the knowledge gaps by reviewing the literature describing studies that manipulated the effects of temperature, moisture, and precipitation on hatching, development, survival, and behaviour of parasitic nematodes in the free-living stage.

Methods

For this review, we researched articles in *Web of Science* (© Copyright Clarivate 2021) on the effects of temperature, precipitation, and moisture on parasitic nematodes, with the last search date on 5 December 2022. The search string employed was (Parasit*) AND (nematod* OR roundworm) AND (temperature OR moisture OR humidity OR precipitation). This search resulted in 1,391 papers. From this total, only studies that fulfilled all the following criteria were included in the subsequent analysis: a) parasite with direct life cycle, b) parasite of terrestrial mammal or bird, c) effect of temperature, moisture, precipitation, or humidity on life-history traits (hatching, development, or survival) or behaviour of parasitic nematodes in the free-living stage, and d) experimental study under laboratory or field conditions. We specifically excluded studies on the effect of abiotic factors on the soil nematode community and studies not written in English. Most of the excluded studies were on plant and insect parasitic nematodes, soil communities, or observational studies without experimental manipulation. Finally, we added one relevant study (PhD thesis) that was missed by the literature search but that was previously known (Hoar 2012) to give a total of 57 relevant papers to review. In the next section, we synthesize the results of the reviewed papers. When findings are based on evidence from three or more papers, we only refer to the oldest (first documentation) and most recent relevant paper in the text here. In parentheses, we indicate the number of papers on the specific topic with n_p , while n_r refers to the total number of results described in the different papers (as some papers describe results of multiple species or life stages). We refer the reader to the references of the reviewed studies provided in the Supplementary Material.

Results

The main findings are described below and summarized in Table 1. A complete overview of the results can be found in the Supplementary

Materials available at the journal's website (Tables S1–S13 in Appendix 1). In addition, we would like to point out that the majority of results described in the available studies use sheep and cattle as hosts (66%), and consequently, 32% of the results on environmental effects on parasitic nematodes are obtained from just three nematode species: *Teladorsagia circumcincta*, *Trichostrongylus colubriformis*, and *Haemonchus contortus* (Figures 2 and 3).

1 What are the effects of temperature and moisture on life-history traits of free-living parasitic nematodes?

1.1 Temperature effects on parasitic nematode life-history traits

Temperature effects (studied in laboratory) on hatching ($n_p = 8$, $n_r = 18$, Table S1) (Crofton 1965; Melville *et al.* 2020), development ($n_p = 14$, $n_r = 29$, Table S2) (Ciordia & Bizell 1963; Gyeltshen *et al.* 2022), and survival ($n_p = 15$, $n_r = 19$, Table S3) (Gardner *et al.* 2004; Wang *et al.* 2022) are generally well known. All three traits have an optimum temperature and a minimum and maximum temperature in which the trait functions. Moreover, the temperature effect is dependent on the trait (van Dijk & Morgan 2008; Gyeltshen *et al.* 2022), the species (Crofton, 1965; Gyeltshen *et al.* 2022), larval stage (Peacock *et al.* 2022), and sometimes substrate (Knapp-Lawitzke *et al.* 2016; Wang *et al.* 2022). Thus, conclusions on the effect of temperature cannot be drawn based on one trait or stage only, but it is important to consider the different life-history traits, larvae stages, substrates, and the corresponding temperature ranges, simultaneously. However, a minority of the studies ($n_p = 5$, $n_r = 14$, Table S1–S3) (Ciordia & Bizell 1963; Gyeltshen *et al.* 2022) cover both the optimum temperature and the upper and lower temperature threshold in which the trait functions.

In addition, some species (e.g., *Nematodirus follicollis* and *Nematodirus battus*) require 'chilling' before hatching (van Dijk & Morgan 2009; Oliver *et al.* 2016) and/or show higher hatching rates after chilling (van Dijk & Morgan 2008). Some parasitic nematode species develop to infective larvae within the eggs before they hatch. Interestingly, within this group of nematodes there are species that need a minimum of 'chilling units' before hatching can occur, as, for example, in *Nematodirus filicollis* (Oliver *et al.* 2016). Chilling experiments aim to study these specific chilling requirements, (e.g., specific chilling temperature and chilling duration). Temperature could also impact developmental paths, for instance,

Table 1. The main findings of the reviewed literature on temperature and moisture effects on life-history traits and behaviour of parasitic nematodes of birds and mammals. For more detailed results, we refer the reader to the corresponding text and the supplementary Tables S1–S13 in Appendix 1

| | | Life-history traits | Behaviour |
|-------------------------------------|-------|---|--|
| Temperature | Lab | Hatching, development, and survival occur within a range with an optimum (Table S1–3). | There is a temperature range and optimum for L3 larvae migration (Table S10). |
| | | Some species require a chilling treatment before hatching (Table S1). | Temperature did not affect migration out of faeces in a greenhouse setting and non-significantly affected migration into soil and grass (Table S10). |
| | | Temperature could change developmental paths (Table S4). | Light, temperature, and vegetation type might have interacting effects on migration of L3 larvae (Table S10). |
| | | Fluctuating temperatures could yield different outcomes compared to constant temperatures (Table S5). | Temperature is important for thermokinetic behaviour and olfactory responses of skin-penetrating nematodes (Table S11). |
| | Field | The few studies showed development threshold and positive effect of thermal energy accumulation on L3 larvae recovery from faeces (Table S6). | |
| Precipitation & moisture | Lab | Positive effects of simulated rainfall & faecal moisture content on development and recovery rate of L3 larvae (Table S7). | There was a minimum and optimum faecal moisture content and required minimum of simulated rainfall for migration out of faeces, with increased migration with increasing rainfall (Table S12). |
| | | Low relative humidity (in salt solutions) resulted in high egg mortality, but drought stress had no significant impact on the recovery of L3 larvae from soil or grass (Table S7). | Simulated rainfall and evaporation affected migration of L3 larvae to deeper soil layers, but drought stress had a non-significant negative effect on L3 larvae migration in soil (Table S12). |
| | | | Larvae needed water to migrate out of faeces but not to move into herbage (Table S12). |
| | Field | The few studies showed variable results: 1) confirmed importance of soil moisture, 2) no long-term effect of wetting of pasture on infection in host, 3) no relation between egg viability and soil texture, moisture, and sun exposure (Table S8). | Lack of movement of eggs on dry soils, and slow and limited movement on wet sandy soils, but limited nr. of studies (Table S13). |
| Temperature & moisture | Lab | The limited number of studies that tested for interacting effects suggested a lack of interaction between temperature and moisture on life-history traits of parasitic nematodes (Table S9). | The limited number of studies that combined moisture and temperature did not test for interacting effects. |

to the infective larval stage or adult stage ($n_p = 4$, $n_r = 4$, Table S4) (Viney 1996; Aleuy *et al.* 2019).

Most laboratory studies keep each temperature treatment level constant over time (all above mentioned and Table S1–S4). However, the effects of fluctuating temperatures (which is more representative of the natural environment) on life-history traits yield different, but nonuniversal, outcomes compared to constant temperatures ($n_p = 5$, $n_r = 6$, Table S5) (Saunders *et al.* 2000b; Hernandez *et al.* 2013) and thus require more attention. Also, only a limited number of studies were conducted in the field with contrasting climatic conditions ($n_p = 2$, $n_r = 3$, Table S6) (Hoar 2012; Hernandez *et al.* 2013). These studies confirmed a temperature threshold of development of a parasitic nematode in the lower central Canadian Arctic (Hoar 2012) and a positive effect of thermal energy accumulation on the recovery of infective L3 larvae from faeces in Scotland with a temperate climate (Hernandez *et al.* 2013). Since recovery was not specified in this last study, we assume Hernandez *et al.* (2013) used recovery as a proxy for the result of hatching, development, and survival combined.

1.2 Precipitation and moisture effects on parasitic nematode life-history traits

The effect of moisture on life-history traits under laboratory conditions ($n_p = 10$, $n_r = 29$, Table S7) (Rossanigo & Gruner 1995; Gyltshen *et al.* 2022) has been less extensively studied compared

with the effect of temperature. Nonetheless, these studies showed positive effects of simulated rainfall (O'Connor *et al.* 2007; Khadijah, Kahn, Walkden-Brown *et al.* 2013), faecal moisture content (FMC)/soil moisture (O'Connor *et al.* 2007; Gyltshen *et al.* 2022), and the ratio of precipitation to evaporation rates (O'Connor *et al.* 2007) on development and recovery rate (here used as proxy for developmental success) of L3 larvae from soil. FMC was also positively correlated with body length of L3 larvae (of four different nematode species; Rossanigo & Gruner, 1996). Larvae recovery was also affected by simulated rainfall timing (Khadijah, Kahn, Walkden-Brown *et al.* 2013a, 2013b) but in opposite ways according to the distribution (split vs. single) of simulated rain (O'Connor *et al.* 2007, 2008). Low relative humidity resulted in high mortality of eggs of *Nematodirus battus* (van Dijk & Morgan 2012), but drought stress had no significant impact on the recovery of L3 larvae (*Cooperia oncophora*) from soil or grass (proxy for survival; Knapp-Lawitzke *et al.* 2016). As with temperature, only limited studies were conducted in the field ($n_p = 3$, $n_r = 4$, Table S8) (Khadijah, Kahn, Walkden-Brown *et al.* 2013c; May *et al.* 2022). These field studies showed differing results but were also conducted in the field under different climatic conditions. Soil moisture was identified as important for translation (a term used by the authors to describe the process of development and transition from egg to parasite stage within the host) of parasitic nematodes in sheep in New South Wales (NSW), Australia (Khadijah, Kahn,

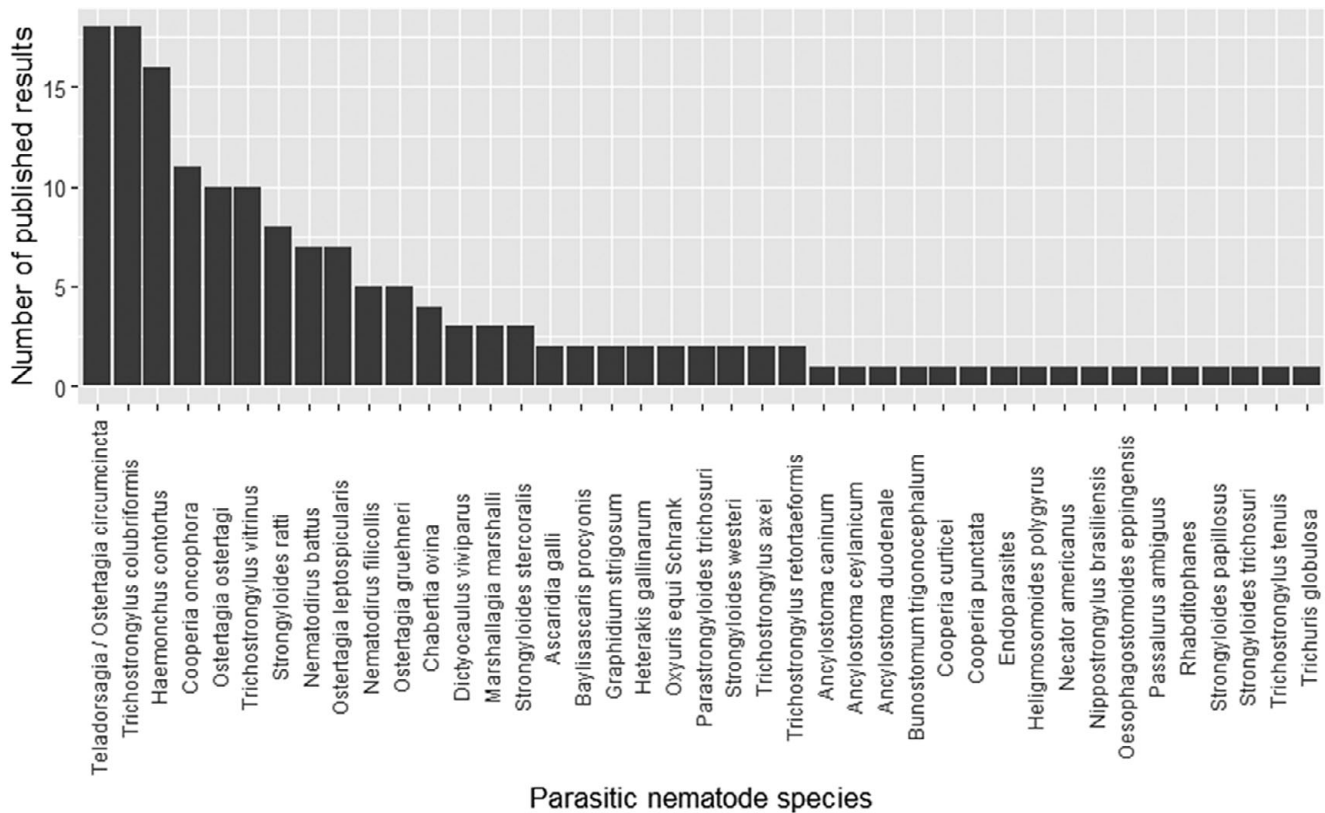


Figure 2. Bar graph of the parasitic nematode species that were used in the reviewed studies on the x-axis. On the y-axis, the number of published results on environmental effects on parasitic nematodes that were obtained from the corresponding parasitic nematode species, ordered from most studied to least studied species.

Walkden-Brown *et al.* 2013c). Nonetheless, wetting of pasture did not have long-term effects on infection of endoparasites (including nematodes) in sheep and cattle (measured by larvae and egg count in faeces) in Germany (May *et al.* 2022). In addition, a field study in Texas showed that viability of eggs (of *Baylisascaris procyonis* that can have both direct and indirect life cycle with racoon as host) was not related to soil texture, moisture, and sun exposure (Ogdee *et al.* 2016).

1.3 Interacting temperature and moisture effects on parasitic nematode life-history traits

Only two studies ($n_p = 2$, $n_r = 5$, Table S9) (Rossanigo & Gruner 1995; McCarthy *et al.* 2022) tested for an explicit interaction effect between temperature and moisture, and neither found one. McCarthy *et al.* (2022) found that lungworm (*Dictyocaulus viviparus*) L3 larvae mortality was similar in paired wet and dry conditions measured at three different temperatures; so, by inference, the effect of moisture on L3 larvae mortality did not depend on temperature. A study of strongyles in sheep, cattle, and deer found that the optimal faecal moisture content for development was independent of temperature (Rossanigo & Gruner 1995). Thus, a limited number of studies report a lack of interacting abiotic factors on life-history traits of parasitic nematodes. Three other studies focused on the combination or additive effects of abiotic factors on life-history traits without testing for possible interactions (Table S2, S3, S7; Rossanigo & Gruner 1996; Knapp-Lawitzke *et al.* 2016; Gyeltshen *et al.* 2022). For instance, an extensive laboratory study on the effect of temperature and faecal water content (FWC) on development averaged FWC across the different temperatures, instead of considering the interaction

between FWC and temperature, and merely suggested that temperature negatively affected FWC (Gyeltshen *et al.* 2022). Rossanigo & Gruner (1996) found that L3 larvae body size increased with faecal moisture content (FMC) in all three temperature regimes in four species of strongyles, but apparent interacting effects between temperature and moisture (visual assessment of their Figure 1) were not formally tested. Finally, a study of temperature (spring versus summer scenarios), drought (adequate water versus none), and exposure duration on the overall recovery of L3 larvae (proxy for survival) showed negative effects of temperature (on recovery from soil) and exposure duration (on recovery from grass), but possible interactions were not tested (Knapp-Lawitzke *et al.* 2016). Thus, more information on interacting factors might exist in the present literature, and this data could possibly be acquired to analyze interacting factors specifically.

2 What are the effects of temperature and moisture on the behaviour of free-living parasitic nematodes?

2.1 Temperature effects on parasitic nematode behaviour

The effect of temperature on parasite behaviour and movement (out of faeces and in soil) is not conclusive ($n_p = 6$, $n_r = 8$, Table S10) (Saunders *et al.* 2000a; Gyeltshen *et al.* 2022). For example, some laboratory studies showed migration declined over time (days) stored at a constant high temperature of 30°C (Hamilton *et al.* 2022) and an optimum temperature for L3 larvae migration out of faeces (Gyeltshen *et al.* 2022). However, temperature did not affect migration out of faeces in a greenhouse setting (Wang *et al.* 2018) and had no significant effect (but a positive trend) on vertical

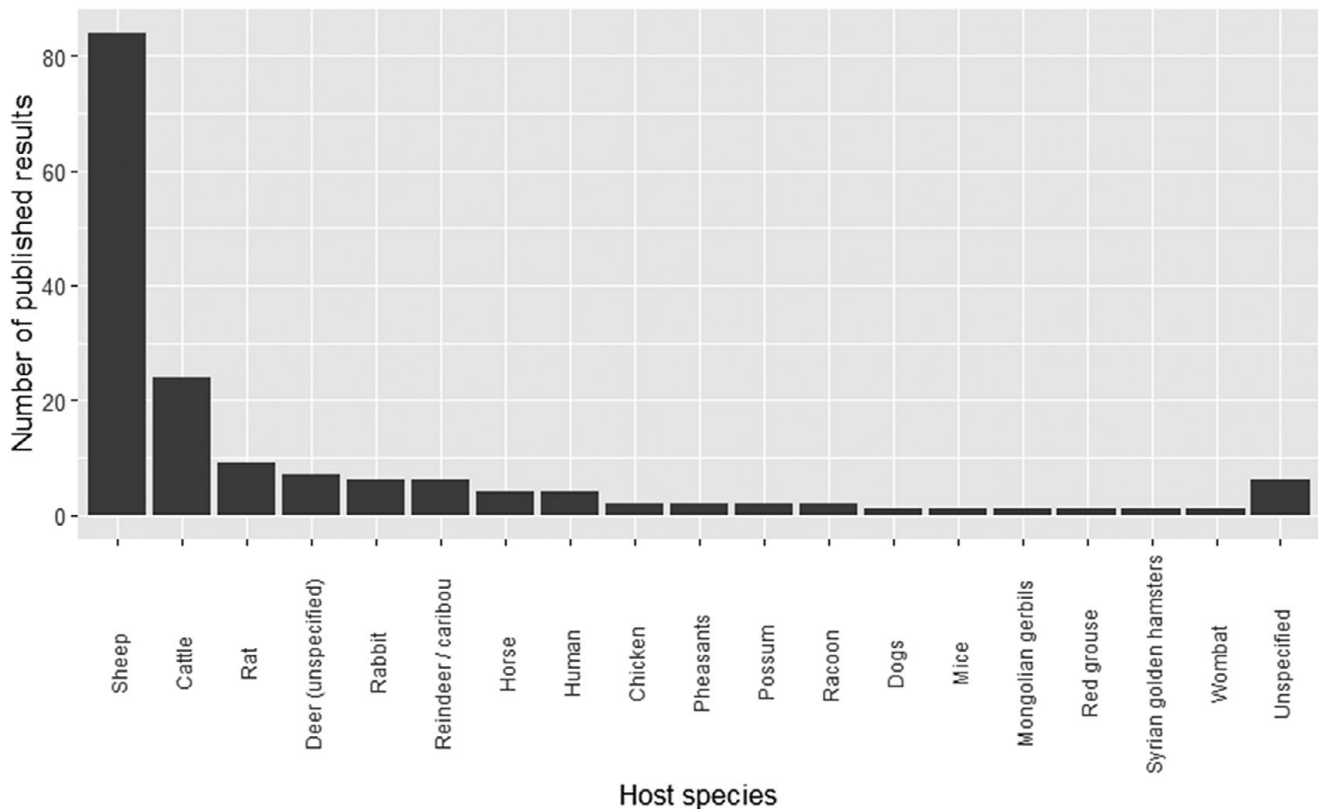


Figure 3. Bar graph of the host species that were used in the reviewed studies on the x-axis. On the y-axis, the number of published results on environmental effects on parasitic nematodes that were obtained from using the corresponding host species, ordered from most studied to least studied species.

migration of L3 larvae in soil (Knapp-Lawitzke *et al.* 2016). Moreover, the effect of temperature on parasite behaviour is complex, as temperature might interact with light and vegetation type (Saunders *et al.* 2000a). Studies under laboratory conditions conclusively indicated that temperature is important for thermokinetic behaviour and olfactory responses of skin-penetrating nematodes ($n_p = 10$, $n_r = 15$, Table S11) (Stankiewicz 1996; Dulovic *et al.* 2022; and for a more extensive review, see Bryant & Hallem 2018; Mendez *et al.* 2022; Takeishi 2022). We could not find field studies on the effect of temperature on parasitic nematode behaviour.

2.2 Precipitation and moisture effects on parasitic nematode behaviour

Studies under laboratory or greenhouse conditions ($n_p = 7$, $n_r = 19$, Table S12) (Rossanigo & Gruner 1996; Gyeltshen *et al.* 2022) showed that water is required for infective larvae to migrate out of faeces (van Dijk & Morgan 2011; Wang *et al.* 2014), with both a minimum and optimum faecal water content (FWC) value for migration of infective larvae out of faeces (Gyeltshen *et al.* 2022). Similarly, there was increased migration under increasing simulated rainfall, again with a required minimum for migration to occur (Wang *et al.* 2022). In contrast to migration out of a faecal pat, it has been suggested that parasitic nematodes do not need water to move from the soil surface into the herbage (van Dijk & Morgan 2011). Simulated rainfall and evaporation also affected migration of L3 larvae to deeper soil layers. Recovery of L3 larvae in deeper soil layers increased with lower evaporation rates, with increasing simulated rainfall, and over time (O'Connor *et al.* 2008). In contrast, drought stress had no significant effect (but a negative trend) on L3 larvae migration from grass to soil

(Knapp-Lawitzke *et al.* 2016). Moreover, it was suggested that migration can be mediated by individual differences in body length. Short L3 larvae (collected from dry faeces) migrated more slowly than long L3 larvae collected from wet faeces (Rossanigo & Gruner 1996). There is only one field study on the effect of rain and moisture on the behaviour of parasitic nematodes in Texas ($n_p = 1$, $n_r = 1$, Table S13) (Ogdee *et al.* 2016). This study indicated no (passive) movement of nematode eggs on dry soils and minor movement on wet soils (dependent on the soil type but remained within the top 10 cm in the soil column) over the course of two years (Ogdee *et al.* 2016).

2.3 Interacting temperature and moisture effects on parasitic nematode behaviour

None of the reviewed studies explicitly tested for an interaction effect of temperature and moisture on parasitic nematode behaviour. In the discussion we will elaborate on three studies (also described in paragraph 1.3) that included a combined effect of moisture and temperature and thus had a study design capable of testing for possible interacting effects, but which were not explicitly done (Table S10, S12; Rossanigo & Gruner 1996; Knapp-Lawitzke *et al.* 2016; Gyeltshen *et al.* 2022).

Discussion

In this review, we identified the knowledge gaps in research on abiotic effects on terrestrial parasitic nematodes in birds and mammals (Figure 4). While much is known about the separate effects of temperature and moisture on parasite life history (Figure 4, lines 1a, 1b), knowledge about the interactive effects

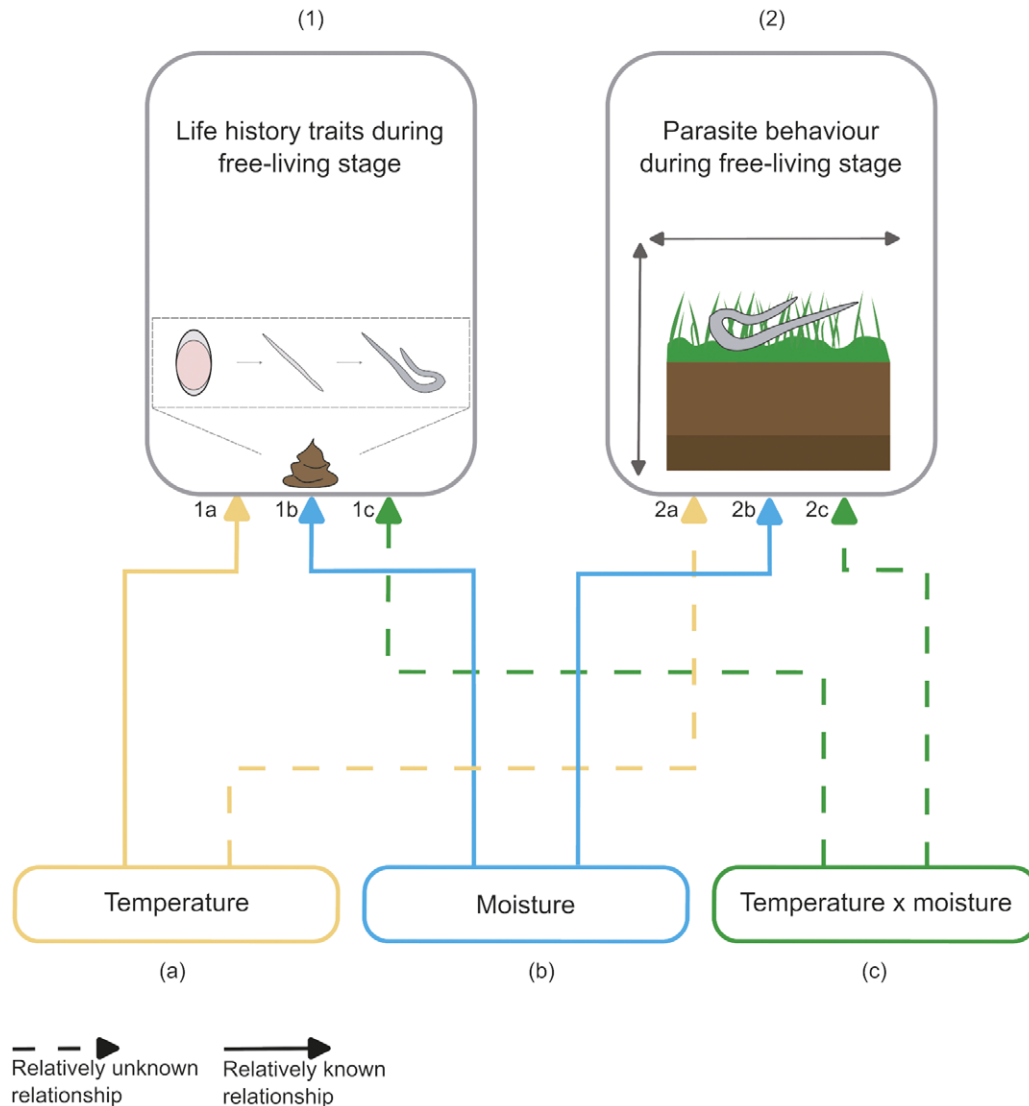


Figure 4. Visualization of the relatively known (solid arrows) and relatively unknown (dashed arrows) effects of temperature (yellow, a), moisture (blue, b), and temperature and moisture combined (green, c) on 1) life-history traits and 2) behaviour of parasitic nematodes of birds and mammals during the free-living stages.

of both temperature and moisture on parasitic nematode life-history traits is scarce (Figure 4, line 1c) even though this has long been recognised as important (see O' Connor *et al.* 2006). We highlight this as the first major knowledge gap, especially given recent climate change (IPCC 2021). Although positive moisture effects have been documented on parasite motility (Figure 4, line 2b), there is little known about temperature effects (Figure 4, line 2a) or the interaction of moisture and temperature (Figure 4, line 2c). This is the second major gap and is important because these interactions could influence transmission into the host (Silva *et al.* 2008). Also, we advocate for more experimental field studies that test the effects of multiple environmental factors on life-history traits and behaviour under more natural and realistic circumstances. Moreover, we encourage studies to expand the range of used hosts and parasitic nematodes. Future studies targeting these knowledge gaps should improve our understanding of how environmental change will affect parasitic nematodes and, consequently, influence parasite–host dynamics. Such research has broader implications for identifying infection risks,

which is highly relevant to livestock managers and wildlife conservationists, and for an improved understanding of ecosystem functioning in a rapidly warming climate.

1 Parasitic nematode life-history traits

Although temperature effects on hatching, development, and survival are generally well known (Figure 4, line 1a), we wish to encourage future research to focus on three issues. First, additional studies should calculate complete temperature dependency curves for all the different vital rates of a variety of species (see, for example, van Dijk & Morgan 2009). Insight into the full range of temperature dependency curves could be used for projecting parasite–host dynamics under changing climates with mathematical models (Fox *et al.* 2012; Molnár *et al.* 2017). Determining temperature dependency curves of different life-history rates will also allow the search for general patterns within and across species (Vineer *et al.* 2016; Phillips *et al.* 2022). Discovering general patterns (by using meta-analysis) would provide insight into the reliability

of translating findings to different study systems. Second, future studies should investigate how fluctuating temperatures, more representative of the increased variance observed under climate warming (IPCC 2021), affect life-history traits – therefore better representing natural circumstances. Third, studies should test which species require pre-hatch chilling and how a warming climate will affect and possibly reduce hatching rate of species that require chilling. For example, warming could delay accumulation of ‘chilling units’, which could delay hatching by one year (Oliver *et al.* 2016), with possible consequences for infectivity patterns. Thus, although temperature effects on life-history traits are generally well known, specific knowledge is still needed.

Most of the studies we reviewed that tested effects of moisture focused on the overall recovery of L3 larvae under different moisture conditions (Figure 4, line 1b). However, measuring total recovery of L3 larvae from faeces or soil is sometimes used as a proxy for developmental success (O’Connor *et al.* 2007) or survival (Knapp-Lawitzke *et al.* 2016), or is not specified (Hernandez *et al.* 2013). Nonetheless, true recovery is composed of hatching, development, larval survival, and possibly motility. This means that the effects of rain and moisture on the separate rates of hatching, development, and survival are still poorly known. To disentangle this, (laboratory) experiments are needed that sample frequently and differentiate between the different life stages and between dead and live larvae to separate survival and migration processes (for instance, by using extracting methods that are not based on motility and counting living and dead individuals). Studying the moisture response curve for separate instead of composite processes would also improve predictive models as advocated by Molnár and colleagues for thermal response curves (Molnár *et al.* 2017).

The effect of interacting environmental factors on parasitic nematodes is identified as an important knowledge gap because it is more representative of variation in the natural environment than the effect of the separate abiotic factors in isolation (Figure 4, line 1c). In addition, under the current climate change projections, more extreme weather events are expected (IPCC 2021), and therefore, experiments that test interacting effects of moisture and temperature across large gradients, even beyond the current norm, are increasingly valuable. Only two studies formally investigated the possible interaction between temperature and moisture and indicated an absence of interactive effect of temperature and moisture on parasite life history (Rossanigo & Gruner 1995; McCarthy *et al.* 2022). Among three other studies which focused on additive effects of abiotic factors on life-history traits without testing for possible interactions (e.g., Rossanigo & Gruner 1996; Knapp-Lawitzke *et al.* 2016; Gyeltshen *et al.* 2022), one presented a figure suggesting apparent interactions (Figure 1 in Rossanigo & Gruner 1996). When reanalysing the data provided in their Table 2, there is a statistically significant interaction between moisture and temperature on L3 larvae body size in all four species studied: the temperature regime leading to the largest larvae differed as faecal moisture content varied from 30 to 80%, reflecting that optimal development temperatures are modulated by moisture (Supplementary Materials – Appendix 2). Testing for interactions among multiple environmental factors (Rossanigo & Gruner 1995; Tarbiat *et al.* 2018; Shifaw *et al.* 2022) will advance our understanding of parasite–host interactions under increasingly variable conditions.

2 Parasitic nematode behaviour

Parasite motility influences contact rates between parasite and host, and hence potentially transmission rates. Also, parasite motility could modulate the effect of environmental change on life-history traits, by, for instance, the ability to ‘escape’ adverse environments. Nevertheless, there is limited knowledge on how temperature alone, or in combination with moisture, affect behaviour, especially the vertical migration of parasitic nematodes (Figure 4, lines 2a, c). Therefore, we advocate studies on temperature, moisture, and their combined effects on parasite behaviour and highlight two specific angles. First, how does temperature (Figure 4, line 2a) and soil moisture (Figure 4, line 2b), and their interaction (Figure 4, line 2c), affect vertical migration of parasitic nematodes in vegetation and in soil, especially under natural conditions? For instance, an entomopathogenic nematode (infecting insects) that poorly tolerates desiccation migrated towards the bottom soil layer with decreasing moisture content, while another species of nematode that is desiccation tolerant remained in the top layer (Salame & Glazer 2015). Whether parasitic nematodes of birds and mammals show similar migration behaviour is unknown. In addition, parasitic nematodes face a trade-off between avoiding adverse environmental conditions and opportunities enhancing the probability of being ingested by the host. For example, L3 larvae recovered from soil were considered fitter (measured with migration assay) than the individuals recovered from the grass (Knapp-Lawitzke *et al.* 2016). Migration behaviour might also vary between individuals with, for instance, longer nematodes (grown at optimal conditions), migrating more than shorter individuals and possibly increasing infection probability (Rossanigo & Gruner 1996). In addition, insight is needed on how parasitic nematodes are distributed among different vegetation types and possible interactions with abiotic factors (Saunders *et al.* 2000a). These insights could be provided by experiments that test vertical migration under different environmental factors on different vegetation types. Second, how do temperature and moisture levels affect the distance of horizontal dispersal (Figure 4, lines 2a, b, c), and do parasitic nematodes predominantly disperse actively or passively (for instance, rain splashes might be a major factor for translocation; Grønvold & Høgh-Schmidt 1989)? We advocate experiments that test dispersal range away from faeces under various environmental factors, including extreme temperature and moisture levels. Although rainfall is required for migration out of faeces (van Dijk & Morgan 2011; Wang *et al.* 2014), heavy precipitation could also have negative effects. For instance, irrigation of the pasture facilitated migration of larvae, but mortality was high, and fewer larvae were recovered from the herbage on irrigated plots compared to dry plots, possibly due to mortality or dispersal to wider areas (Young & Anderson 1981). Studying horizontal dispersal distances is especially relevant in relation to faecal avoidance by hosts (Hutchings *et al.* 1998; van der Wal *et al.* 2000). Understanding the factors that affect both vertical and horizontal movement and linking this to the contact place with the host will help in understanding transmission patterns and infection risk of the host. In addition, the availability of vegetation (in relation to environmental conditions) is potentially an important factor in understanding the link between contact rates with the host and transmission. For example, vegetation growth (due to high levels of rainfall) could lead to a dilution effect with a decreased density of nematodes in the environment and possibly result in fewer encounters with parasites by the host (Grenfell 1988; Grenfell 1992; Shearer & Ezenwa 2020).

3 Translation from laboratory to field conditions

We advocate more field studies, in addition to laboratory studies, because microclimate differences and soil structure might alter the relationships between environmental factors and parasites only documented under laboratory conditions. For example, solar radiation might cause mortality at temperatures lower than the threshold temperature determined in the laboratory (van Dijk *et al.* 2009), and snow layers could benefit parasite survival (Rossi *et al.* 2019). Moreover, air temperature might be an insufficient proxy for temperature conditions near or in soil (Lembrechts *et al.* 2022), especially during times with snow cover (Convey *et al.* 2015). Surface or soil temperature might be more important and could have different effects on life-history traits of nematodes (Jenkins *et al.* 2006; Kutz *et al.* 2014). Also, in the field, biotic interactions may affect parasite life history and behaviour in several ways. For example, the presence of earthworms can reduce the number of recovered larvae in the field (Waghorn *et al.* 2011). The presence of nematophagous fungus was associated with a reduction in the number of infective parasite larvae (Kuzmina *et al.* 2006), but fungus can also play a role in and facilitate migration of parasitic larvae (McCarthy *et al.* 2022). Moreover, in some species, contact between bacteria and embryonated eggs is required for hatching within the host (Hayes *et al.* 2010). These biotic interactions add complexity beyond simple relationships between weather variables and parasite life-history traits and behaviour. Thus, field experiments and laboratory experiments are complementary. Lab experiments will continue to provide mechanistic links between the environment and parasite traits, but they need to be scrutinized in real-world settings to investigate if relationships hold. By doing so, we can more reliably draw conclusions on how changing climates affect parasites and hence their interaction with hosts.

4 Expanding the range of parasitic nematode and host species studies

In addition, we would like to stress that the majority of results described in the available studies use sheep and cattle as hosts (66%), and 32% of results describing environmental effects on parasitic nematodes are obtained from just the three nematode species: *Teladorsagia circumcincta*, *Trichostrongylus colubriformis*, and *Haemonchus contortus* (Figures 2 and 3). These species are the most abundant gastrointestinal nematodes in sheep and cause major production losses (O'Connor *et al.* 2006). However, we envisage that the nematode–host interaction could be different for livestock and free-living hosts. For example, wild animals generally live in lower population densities and do not receive (anthelmintic) treatments or supplemental food. Also, parasitic nematodes of livestock hosts might encounter different selection pressures due to rotational grazing or other treatments, which might result in differences in environmental effects on parasitic nematodes of wild compared to livestock animals. Because there is limited data on wildlife hosts and their parasitic nematodes, we encourage future studies on the parasitic nematodes of wild host species under natural conditions. Moreover, few of the reviewed studies involve the environmental effects on parasitic nematodes infecting humans. However, infection of soil-transmitted helminths in humans is a major cause of human disease (Brooker *et al.* 2006; Weaver *et al.* 2010), especially in places where sanitation facilities are limited but population densities are high (Brooker *et al.* 2006; Weaver *et al.* 2010). To limit infection by

soil-transmitted helminths, insights are needed on how these parasites are affected by environmental changes (Weaver *et al.* 2010).

5 Link to life stages within the host and parasite host dynamics

The scope of this review was to identify the knowledge gaps in research about the abiotic factors impacting hatching, development, survival, and behaviour of direct life-cycle parasitic nematodes in their free-living stages. However, we have not considered how environmental factors experienced in these free-living stages might affect parasites once they are within the host – for example, when they need to exsheath, develop, survive, and reproduce (Figure 1) (Kutz *et al.* 2009; Morley & Lewis 2014; Cizauskas *et al.* 2017). Also, environmental factors can affect parasitic nematodes during the stages within the host through effects on homeostasis of the host, for instance (see for a review, but not specifically on parasitic nematodes, Morley & Lewis 2014). It is also suggested that rainfall could affect parasite infection levels through changes in host susceptibility, with low rainfall levels (compared to high rainfall levels) increasing susceptibility of the host to parasite infection (Shearer & Ezenwa 2020). This could possibly be explained by reduced food availability and quality under low rainfall conditions, and hence changes and reduction in body condition of the host, but this mechanism needs to be tested (Shearer & Ezenwa 2020). Also, we need to consider the abilities for adaptation to changing conditions by the host and by the parasites (reviewed by Aleuy & Kutz 2020) to get a full comprehension of the environmental effects on parasitic nematode.

6 Implications

In this review, we have focused attention on understudied abiotic impacts that could improve our insights into how environmental factors affect parasitic nematodes in their free-living stages, and hence the likely impact of climate change. Addressing these knowledge gaps will also have implications for identifying infection risks, of high relevance to livestock managers and wildlife conservationists, as well as improve our understanding of ecosystem functioning under a rapidly warming climate. First, experiments on the temperature and moisture (and their interaction) dependency curves of parasitic life-history traits and behaviour could better guide livestock managers about parasite dynamics and epidemiology (considered as an important knowledge gap according to the research community in livestock helminthology; Morgan *et al.* 2019) and infection risks under changing climates. For instance, improved knowledge on how abiotic factors influence parasite life history and behaviour can help improve models that project infection pressure under various climate change scenarios (Rose *et al.* 2016). Moreover, data from these experiments could refine infection risk maps and calendars estimating when and where infection risks are high (Navarre 2020; McFarland *et al.* 2022) and provide insights about pasture management strategies (Morgan *et al.* 2019, Navarre 2020), such as fencing off risk areas and drainage (Beltrame *et al.* 2021). For instance, experiments on the effect of temperature and moisture (and their interaction) on the vertical and horizontal distribution of parasitic nematodes could provide information on infection hotspots in the herbage and might guide management of forage heights (Navarre 2020). Second, knowledge (obtained by additional experiments on temperature and moisture effects on parasites) could provide insights benefiting wildlife conservation, such as disease risk frameworks and optimal timing of intervention, particularly in areas with a co-existence of livestock and

wildlife (Khanyari *et al.* 2022). Moreover, the presence of parasites might be, in some cases, beneficial to population health (Thompson *et al.* 2010). For instance, parasites could possibly act on delayed density dependent mechanisms, which could dampen host population fluctuations and hinder population crashes resulting from rapid increases. Thus, understanding environmental effects on parasites and if and how parasite species should be conserved (Thomas *et al.* 2005) will have indirect benefits for wildlife and ecosystem conservation. Third, knowledge about environmental effects on parasitic nematodes (based on experiments that test the effect of a broad range of moisture and temperature regimes on life-history traits and behaviour of a wide range of parasites) might improve the understanding of ecosystem functioning. Parasites play a role in ecosystem engineering processes, either by modifying hosts that are ecosystem engineers or as engineers themselves (Thomas *et al.* 1999). They can also impact intraspecific species interaction (Hudson *et al.* 2006) such as predator–prey interactions (Hudson *et al.* 1992; Hatcher *et al.* 2006) and hence energy flow through the system (Hudson *et al.* 2006). Understanding which functions in the ecosystem will be lost if a parasite species disappears might result in the realization that parasite species need to be conserved in order to maintain an ecosystem and its functions (Thomas *et al.* 2005). Parasites could also cause cascading effects on other (trophic) species in the ecosystem (Thomas *et al.* 2005). For instance, it was suggested that lethal and sub-lethal effects of a parasitic nematode on an herbivorous host could result in trophic cascades (in terms of lower herbivore host biomass and increased producer biomass) (Koltz *et al.* 2022). Thus, changes in the environmental effects on parasitic nematodes might have larger consequences on the ecosystem than just on the parasite and host. In conclusion, addressing and hence filling the knowledge gaps about abiotic impacts on parasitic nematodes could have broad implications for livestock managers and wildlife conservationists and improve our fundamental understanding of parasitic nematodes and ecosystem functioning under a rapidly warming climate.

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