

A REVIEW OF THE IMPACT OF EXTREME ENVIRONMENTAL FACTORS ON EARTHWORM ACTIVITIES AND THE FEEDBACK ON THE CLIMATE

OPUTE, P. A.^{1,2*} – MABOETA, M. S.¹

¹*Unit for Environmental Sciences and Management, North-West University, Private Bag X6001, Potchefstroom 2520, South Africa*

²*Department of Animal and Environmental Biology, Faculty of Life Sciences, University of Benin, Benin City, Nigeria
(ORCID: 0000-0003-3324-0206)*

**Corresponding author
e-mail: ashibudike.opute@uniben.edu*

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Abstract. Soils support a diverse range of organic life and provide several ecosystem functions and services that allow terrestrial life to thrive. Earthworms influence greenhouse gas (GHG) emissions from the soil both biologically (via respiration and litter modification) and physically (via increased macroporosity and altered air and water movement pathways). They improve soil carbon sequestration but also actively contribute to the release of major greenhouse gases. Shifting geographical ranges of earthworms due to changes in climatic conditions might affect the composition, structure and function of the soil ecosystem. This review examines the possible effects of the projected change in climate on earthworm communities and resulting implications for soil GHGs due to changes in environmental endpoints such as temperature and moisture. Earthworm activity, abundance, and biomass increase as soil moisture content increases, but drought and flooding reduce earthworm productivity. Climate change is likely to exacerbate earthworm invasions at higher latitudes and altitudes. However, because higher temperatures inhibit earthworm activities during droughts, anticipated warmer and drier climates may impede earthworm invasions. Climate change may disrupt the delicate balance between carbon sequestration and greenhouse gas emissions from soil in the coming century, but there are currently insufficient field studies to back up these prognostications.

Keywords: *temperature, precipitation, soil moisture, drought, flooding, ecosystem engineers, carbon sequestration*

Introduction

Climate change is becoming a significant problem with potentially far-reaching global consequences. Emissions of greenhouse gases (GHG) have increased significantly in recent years and will continue to increase over time, owing to global industrialization. According to projection models, by 2100, air temperatures would have risen from 1.1 °C to 6.4 °C, possibly altering species' spatial distribution, phenotypic and phenological variations, extinction, and consequently, environmental degradation (Múgica et al., 2015). Most importantly, the projected possibilities for climate change (high atmospheric CO₂, temperature, precipitation, ultraviolet radiation, and frequency of extreme events) will have significant implications for the structure and function of the soil ecosystem (Grimm et al., 2013). The most plausible effects to occur in soils, as indicated by the Intergovernmental Panel on Climate Change (IPCC), are those associated with temperature increases, fluctuations in moisture content, hypoxia phenomena, and acidification, as well as soil feedback to the atmosphere via the release of more GHGs (IPCC, 2014).

One of the primary fields of ecology, sustainable agriculture, and global change studies, among others, is the influence of soil fauna on organic matter decomposition (van Groenigen et al., 2014). Earthworms act as ecosystem engineers, regulating microbiota activities in the soil and associated carbon cycling through multiple processes on different time scales and at different spatial scales. Earthworms contribute to the organic matter dynamics in agroecosystems by ingesting 2 to 15 Mg ha⁻¹ year⁻¹ of residual organic materials and processing up to 10% of the topsoil each year (Medina-Sauza et al., 2019). After consumption, soil and organic materials are mixed with intestinal mucus and digested with the aid of enzymes produced from earthworms, indigenous gut microbiota and ingested microbes. Several physical, chemical, and biological changes occur in the soil as it goes through the earthworm's gut until undigested elements are egested as casts (Abail et al., 2017). These processes describe the differences between the many niches available for earthworms in cycling ecosystem carbon. Earthworms are referred to as "predators" when they have a top-down effect on carbon C, cycling through controlling the microbiota population. When they modify C cycling via the bottom-up processes of supplying microbiota with simple inorganic substrates, they are called "primary decomposers." Anthropogenic greenhouse gas emissions tend to increase long-term radiative forcing, resulting in global warming with the levels of atmospheric carbon dioxide (CO₂), nitrous oxide (N₂O) and methane (CH₄) growing by approximately 41%, 20% and 160%, respectively in 2012, compared to 1850–1900 (IPCC, 2013). Earthworms play significant roles in the global greenhouse gas balance, affecting both the biotic and abiotic soil characteristics that affect the soil's GHG emissions, carbon sequestration, and plant growth. Climate change dramatically influences ecosystems' biodiversity (Bardgett and van der Putten, 2014) which include shifts in ecosystem dynamics, habitat selection, species abundance and distribution, phenology, and invasiveness (Eisenhauer et al., 2014). While some efforts have been made towards integrating data on soil organisms' possible response to climate change, there is still insufficient research on soil community responses and their most important drivers, especially for large soil invertebrates. Furthermore, despite the known significance of the role earthworms play in ecosystems and the evident threats posed by climatic change scenarios, there is scarcely any comprehensive research on climate change impact on earthworms and the possible implications for soil greenhouse balance. More recent reports (including Blume-Werry et al., 2020; Phillips et al., 2019; Singh and Singh, 2019; and Singh et al., 2019) have indicated that the impact of earthworms will increase in the coming years. These effects, they claim, will boost not only carbon sequestration in the soils but also greenhouse gas emissions such as CO₂, N₂O, and CH₄. Singh et al. (2019) established a baseline for predicting earthworm distribution in the coming decades, however, they identified a knowledge gap in the interacting effects of the various climate change drivers on earthworms. Therefore, this review seeks to assess how distal climate change drivers, such as temperature, moisture, drought, and floods, affect earthworms and how this might affect the delicate balance between earthworms' positive contribution to soil health and greenhouse gas emissions from the soil.

This paper systematically reviewed a range of scientific literature to analyze the possible impacts of climate change drivers on earthworm populations and their probable implications for soil greenhouse balance. The climate change drivers focused on include temperature and precipitation changes and extreme events such as drought and flood. A Web of Science (WoS) search was conducted (June 2021) focusing on literature published between 1991 and 2020, using the search syntax: ('climate change' OR

‘warming’ OR ‘flood’ OR ‘precipitation’ OR ‘moisture’ OR ‘temperature’) AND (‘lumbric*’ OR ‘earthworm*’) AND (‘GHGs*’ OR ‘emission’ OR ‘soil’). We streamlined the search to the WoS categories: Zoology and Ecology and WoS document type: Articles, returning 336 publications. The published articles from the restricted search were between 1991 and 2020, with the highest number of publications (7.14% of 336) occurring in 2015 (Fig. 1). The majority of the studies were from temperate countries like the United States (25.30%), England (12.20%), and Germany (10.42%) and very few studies from tropical areas such as Nigeria (0.89%), South Africa (2.98%) and Zimbabwe (0.30%) (Fig. 2).

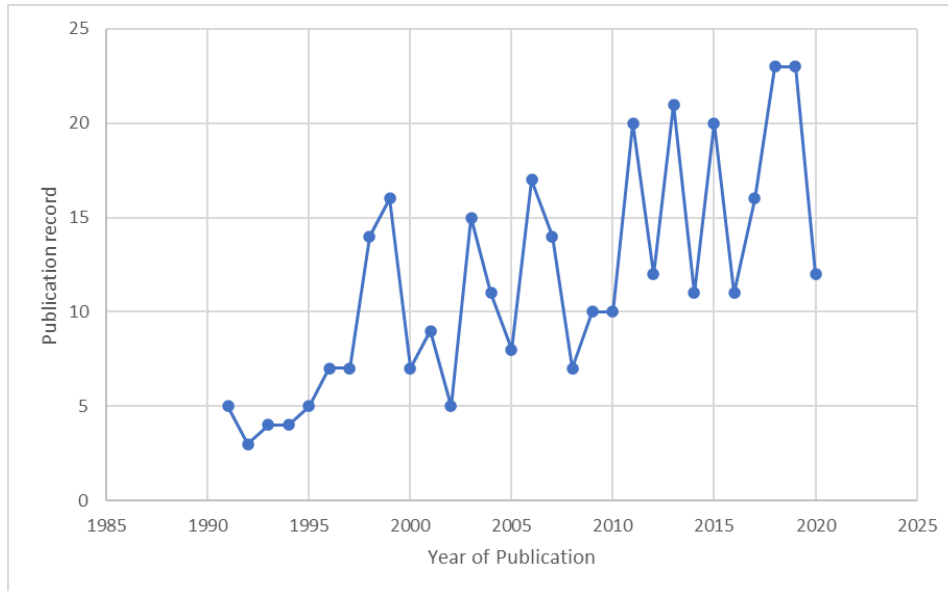


Figure 1. Publication output by year based on WoS search criteria

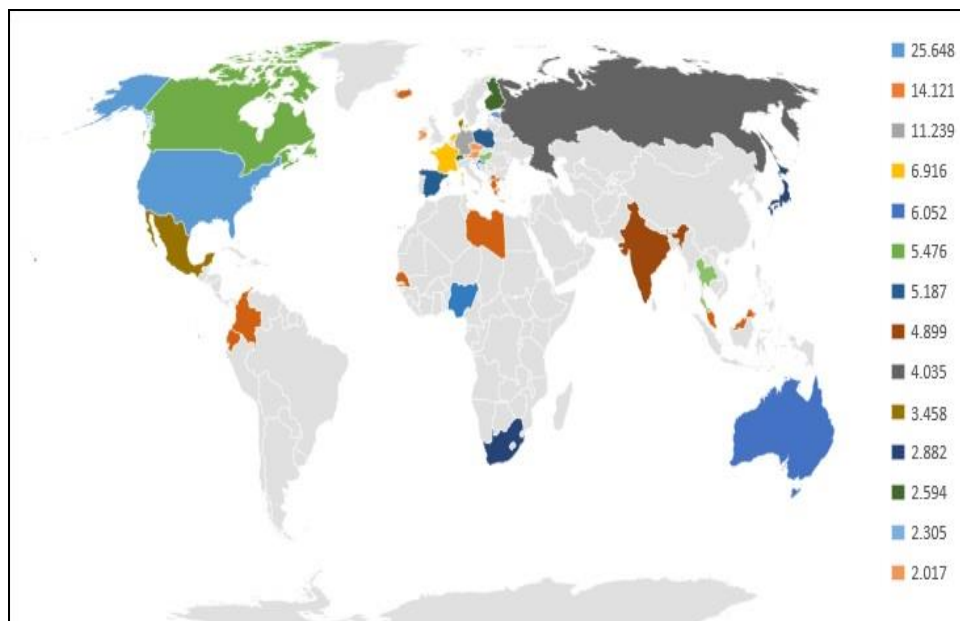


Figure 2. Percentage distribution of publications across countries/regions based on WoS search criteria

Climate change projections

Climate change will become one of the greatest threats to biodiversity in the coming years, with most ecosystem functions and services at risk (Siebert et al., 2019). As evidenced by changes in the unpredictability of its drivers, for instance, temperature, moisture or precipitation, and wind, climate change will persist for a prolonged period, and its effects will be difficult to reverse. It is likely to coincide with an increased probability of extreme climatic events, such as flooding and drought (IPCC, 2013). Many climate change models anticipate that extreme precipitation events will become more often (Singh et al., 2019), while average precipitation will remain steady but with a great deal of variability. Although changes in rainfall may appear to show considerable variability on a small scale, the projected rise in global mean air temperature remains undeniable. The overall global surface temperature increases for 2016–2035 will be similar across the four representative concentration pathways (RCP) with a range of 0.3 to 0.7 °C for the medium confidence (IPCC, 2014). This prediction rests on the assumption that no significant events such as volcanic eruptions, alterations in nitrogen and carbon dioxide concentrations will occur or sudden increases in energy balance following changes in anthropogenic climate forcing agents such as greenhouse gases. A global mean surface temperature increase of 0.3 °C to 1.7 °C is predicted under RCP2.6, 1.4 °C to 3.1 °C under RCP6.0, 1.1 °C to 2.6 °C under RCP4.5 and 2.6 °C to 4.8 °C under RCP8.5 (Fig. 3a).

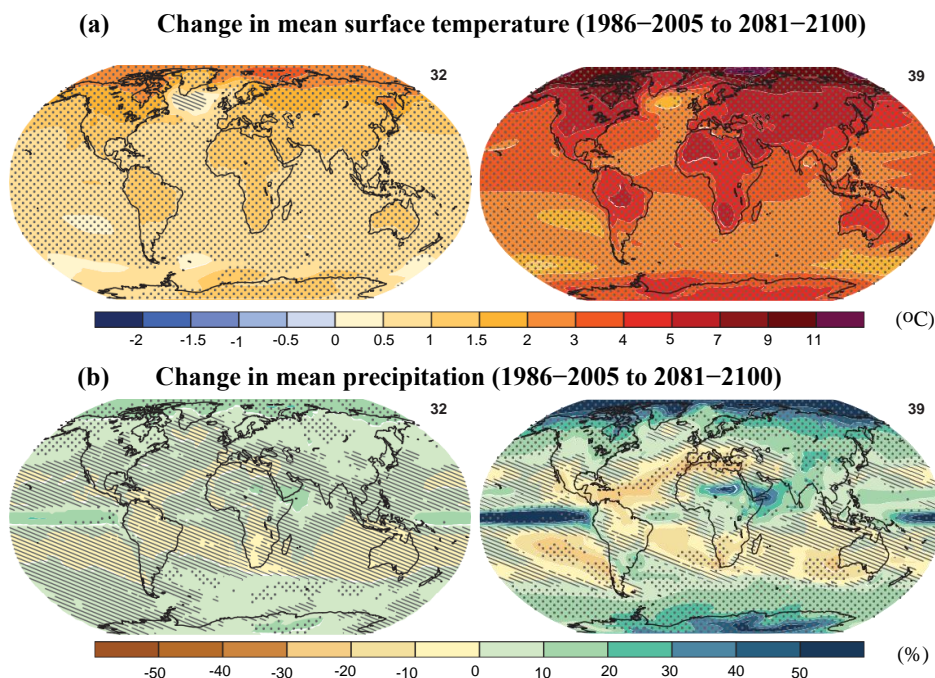


Figure 3. Change in mean surface temperature (a) and change in mean precipitation (b) based on multi-model mean projections under RCP2.6 (left) and RCP8.5 (right) scenarios for 2081–2100 relative to 1986–2005. In the upper right corner of each panel, the number of models used to determine the multi-model mean is indicated. Stippling (dots) illustrates regions where the projected alteration is significant compared to natural internal variability and where the sign of change is correlated by at least 90% of models. Hatching (diagonal lines) indicates regions where the expected change is less than one standard deviation from natural internal variability (Adapted from IPCC SPM, 2014)

Temperature extremes (hot/cold) will inevitably be more frequent as the global mean surface temperature increases, e.g. heatwaves become more frequent and intense. The occasional winter weather will continue to occur (IPCC, 2014). However, precipitation changes are not going to be homogenous. The high latitudes and equatorial Pacific are likely to increase the mean annual precipitation under the RCP8.5 scenarios. Also, under the RCP8.5 scenario, mean precipitation in arid environments will decline, while mean precipitation in wet areas will increase (*Fig. 3b*).

Europe's mean temperature has steadily increased over the years, with more significant warming occurring in its higher latitudes (IPCC, 2014). The warming in Scandinavia in the 1980s was the strongest, while warming in the Iberian Peninsula was most remarkable in summer (EEA, 2012). The decadal mean land surface temperature is 1.3 ± 0.11 °C for 2002–2011. This temperature is far above the projected average for 1850–1899 based on the analysis of the gridded surface temperature from Hadley Centre/Climatic Research Unit (data set 3), Merged Land-Ocean Surface Temperature and Goddard Space Studies Institute (GISS) (Brohan et al., 2006; Smith et al., 2008; Hansen et al., 2010). Different climate change models agree significantly with each other for all warming scenarios within Europe. The highest warming rate is predicted during summer in Southern Europe and Northern Europe during winter. Even if the current global warming is assumed to be limited to 2 °C in comparison to 1850-1899 (preindustrial times), European climates will differ from what they are today in the next few decades (Jacob and Podzun, 2010). During the summer, rainfall may likely decrease in the south of Sweden and increase in winter. Near the end of the 21st century, a reduction in the mean long-term winter snowfall in Northern Europe is expected (Räisänen and Eklund, 2012). Alterations in severe precipitation will be on the high confidence range for high rainfall in Northern and Continental Europe for all seasons besides summer.

Africa's temperatures will rise higher than the worldwide 21st-century average (James and Washington, 2013). Under the RCP4.5 and RCP8.5 frameworks, the global average surface air temperature will most likely rise above the range observed during the twentieth century by 2069. However, these unprecedented climates will come between 1-2 decades sooner than the average global events across the tropics. Insignificant climatic changes can push tropical West Africa's narrow climatic boundaries (Niang et al., 2014). Projections suggest that African regions will reach increases of 2 °C in the preceding two decades towards the end of this century compared to the annual mean temperature for the late 20th century and the whole of Africa under the high emissions scenario. Based on RCP prediction, the exceedance of the critical global average temperature rise of 2 °C would occur in much of Africa by mid-21st century. Southern Africa's mean land surface will experience higher-than-average mean global land warming across all seasons (James and Washington, 2013). Additionally, the projected warming of between 3.4 °C and 4.2 °C by the year 2100 would be at the high end of the natural variability of the climate (Moise and Hudson, 2008). The projected elevated warming of semi-arid regions of the southwestern subregions will encompass South Africa, Botswana and Namibia (Engelbrecht et al., 2009). Projections for precipitation have higher geographical and seasonal variability than projections in temperature, although rain tends to be more unpredictable than temperature. Still unclear are the projected changes in rainfall across sub-Saharan Africa in the middle part of the 21st century (James and Washington, 2013). In countries with high or complex topography, downscaled projections suggest that rainfall and rainfall extremes will intensify near the end of the 21st century.

Effects of climate change drivers on earthworms

Globally, ecosystems are under unprecedented stress due to climate change (Masson-Delmotte et al., 2018). The soil ecosystem provides critical services and sustains the high biological diversity on which terrestrial life depends. Earthworms, along with other organisms, are essential parts of terrestrial ecosystems. Phillips et al. (2019) compared earthworm communities sampled from a variety of regions around the world. They discovered that species richness and abundance were higher at high latitudes, thus, contradicting previous reports for organisms above ground. They found that climate variables also influenced earthworm communities despite the effects of habitat cover and soil parameters. Climate change also significantly reduces soil moisture (Poll et al., 2013). Earthworms are at a disadvantage because of the permeability of their integuments and the fact that they rely on moist habitats for survival (Siebert et al., 2019). The diversity, abundance and richness of many earthworm groups decline with increasing drought and rise in temperature due to the deleterious impacts on their physiology, development, and reproduction caused by global climate change (Geisen et al., 2014). Distal climate change drivers that affect earthworms with possible influence on soil GHG emissions on larger scales include temperature, moisture or precipitation, flooding and drought (*Table 1*).

Effects of temperature

Temperature is a significant climate change driver contributing to global warming and influencing soil species' activity and decomposition processes. Thus, many researchers have studied the effects of temperature on individual soil-dwelling micro- and macro-organisms. Earthworms are poikilothermic; therefore, temperature affects them, influencing their activity, growth, density, metabolism, respiration, and reproduction (Eisenhauer et al., 2014). When exposed to the ideal environment for their metabolic processes, high and low temperatures trigger the same set of behaviours. Lower extreme temperatures are less documented than upper-extreme temperatures, ranging from 25 °C to 35 °C and differ significantly between species. Tropical species become more adapted to higher temperatures in time than temperate species, while temperate species become more resistant to lower temperatures (Singh et al., 2019). Earthworms may have profound seasonal variation in their occurrence and activity patterns, especially in areas with dry or cold climates.

Earthworm abundance increases during summer and decreases during winter due to soil conditions and climate change (Singh et al., 2019). The activity of decomposer organisms will be affected by future increases in soil temperatures, potentially increasing the cycling of elements and emission of greenhouse gases. Marhan et al. (2015) studied the effects of incorporating *Phacelia tanacetifolia* Benth. (a nitrogen-rich green manure litter) in arable soil by introducing *Aporrectodea caliginosa* coupled with increasing soil temperatures (+3.5 °C) on carbon and nitrogen cycling for 42 days in a three-factorial microcosm experiment. They found that higher CO₂ emissions increased with increasing soil temperatures, although emission was stronger in litter-free treatments. This result implies that as temperature increases, resulting in drought and reduced litter, endogeic earthworms' CO₂ emissions will increase. Earthworm activity significantly increased N₂O emissions by 70–90%. They concluded that there is a higher risk of N losses in the form of leaching or N₂O emission in earthworm-populated arable soils with warmer climatic conditions. In a Hohenheim climate change experiment,

Siebert et al. (2019), suggested that reduced earthworm density and warming alter ecosystem functions and services in the soil simultaneously, owing to changes in soil biota diversity and density which would likely result in inefficient belowground food webs. Findings from this research emphasize the need to maintain a higher population of earthworms to mitigate the negative consequences of climate change in agriculture. Climate change, on the other hand, has been observed to lower earthworm density and biomass. In the context of a field experiment, earthworm density and biomass exhibited strong negative correlations with temperature, with densities across all sites lower than the global average, according to Mcinga et al. (2021). The study found that earthworm diversity and density were highest in sub-humid habitats and that temperature influenced earthworm distribution, diversity, and density.

According to González-Alcaraz and van Gestel (2016), *Eisenia andrei* loses weight at higher temperatures than at lower temperatures. Similarly, Lima et al. (2015), observed that *Eisenia andrei* lost more weight at a higher temperature of 26 °C than at 20 °C, thus, confirming the effects of warming on earthworms. Both studies, however, focused on earthworms' responses to contaminated environments. Therefore, global warming may be less severe in temperate and wet areas (Berman and Meshcheryakova, 2013). In contrast, a steady rise in temperature across tropical and arid regions can put earthworms in these soils under significant water and metabolic stress, especially during year-round intermittent rainfall (Hughes et al., 2019). Hughes et al. (2019) employed climatic niche modelling to estimate the distribution of *Rhinodrilus alatus*, a species that has been historically harvested and sold as fishing bait in Brazil. According to their findings, climate change will alter the breadth of earthworm distribution and cause severe dispersion outside of the already defined geographical boundaries of the worms. Climatic conditions are significant determinants in the diversity of earthworms and their geographical distribution. Thus, earthworm populations continue to decrease during the dry or cold season and reach their most incredible abundance in a favourable environment (Singh et al., 2019). Generally, for plants and other animal species, a warming climate will have a negative impact in equatorward and low elevation populations but a positive impact in poleward or high elevation populations of a given species range. Furthermore, even if the effects of rising climate are entirely negative for a given species, other species function better in the new, warmer climate, so it is a matter of mismatch of climate and species, as well as species' ability to migrate to stay in an optimum climate.

Effects of soil moisture

According to IPCC (2013), the likelihood of severe rainfall and flooding events is on the rise globally. The report further stated that more places experienced higher frequencies of heavy precipitation events than those experiencing lower frequencies; for instance, precipitation events have increased considerably over the last 50 years across North America and Europe. However, confidence in trends is at a low level in other countries. Under the SRES A1B and A2 scenarios, in the 21st-century, precipitation is likely to decrease in North Africa and South Africa (medium to high confidence). There is uncertainty surrounding rainfall predictions across sub-Saharan Africa from the middle to the later part of this century (Niang et al., 2014). Soil moisture content is a significant factor affecting water and heat energy exchange between the surface of the earth and atmosphere via plant transpiration and the process of evaporation, essential for the survival of earthworms, growth, and population increase. Bessolitsyna (2012)

evaluated the abundance and distribution of earthworms in southern-middle Siberia and found that soil moisture and soil types changed their richness and distribution. Andriuzzi et al. (2015) demonstrated that earthworms are affected by altered rainfall patterns; thus, they may alter their burrowing behaviour. Poorly drained soil can also be disadvantageous to earthworm survival, such as in the case of anaerobic conditions. However, when earthworms, such as *Lumbricus Terrestris* are present, soil moisture drops much faster after heavy rainfall (Eisenhauer et al., 2014; Andriuzzi et al., 2015). Earthworms' survival in arid environments is contingent upon having adequate moisture in the soil, which is unlikely to be an issue in more temperate climates. Many earthworm species can enter diapause, para-diapause, or aestivation to survive in dry soil. *Aporrectodea trapezoides*, for example, might be able to withstand reduced moisture conditions by aestivation and remaining dormant pending improvement in soil moisture (McDaniel et al., 2013). Soil moisture influences microbially mediated nitrogen (N) cycle reactions by regulating redox potential (Chen et al., 2014). The nitrifier denitrification pathway is a significant contributor of N₂O fluxes from soil and a function of moisture content (Kool et al., 2011). Previous drying-rewetting research found that the rate of the drying and recovery cycles could affect N₂O emissions (Chen et al., 2014).

Effects of flooding

Flood-prone areas have a complex topsoil composition, which provides a diverse range of habitats for earthworms (Bullinger-Weber et al., 2012). Flooding has a profound impact on the soil's physical and chemical qualities. Water diffuses oxygen at a far slower rate than air, roughly 104 times slower (Schlesinger, 2013). Thus, during flooding in soils, oxygen demand quickly exceeds the supply (Wilshire-Kiss, 2019). Microorganisms and plant roots absorb oxygen shortly after flooding, leaving a depleted level of oxygen near the air-water interface; as a result, the soil becomes anoxic within 24 h (Tanji et al., 2003) and remaining at a low ebb throughout the inundation period (Unger et al., 2009). Endogeic species is the most commonly found earthworms in agricultural soils, followed by anecic and epigeic earthworms (Pelosi et al., 2009). In aerated water, earthworms can live for extended periods and are capable of surviving flooding, but their survival and behavioural responses vary between species (Zorn et al., 2008). To avoid drying and maintain hydrostatic pressure, all soft-bodied organisms such as earthworms need moist conditions. Therefore, moisture is an essential element of earthworms' survival. Their high abundance and high frequency of occurrence in floodplains of temperate regions are therefore not surprising. On the other hand, flooding and torrential rain can make earthworms hard to find, and many earthworms die after being exposed to heavy rain (Zorn et al., 2005). *Lumbricus rubellus* (Epigeic species) are the first to colonize floodplains within the first five years of a severe flooding event, even with the poor soil quality of such habitats (Fournier et al., 2012). According to Zorn et al. (2005), the number and biomass of *L. rubellus* declined to near-zero in flooded areas but recovered quickly within six months to pre-flood levels. Furthermore, epigeic species in a frequently flooded habitat attain maturity faster than those in less frequently flooded habitats (Klok et al., 2006). However, the breakdown of soil structure is the most common devastating physical effect of flooding in soils. It dissolves soil cementing agents and biological films, causing soil particle cohesiveness to decrease. Soil organic matter content increases as a result of regular floods. Once the ecosystem is impacted by a flood, returning to the previous state takes several years (Gerisch et al., 2012).

Table 1. Effects of climate change drivers on earthworms and greenhouse gas emission from soil

Earthworm species	Climate change drivers				Experimental period (days)	Type of experiment	Earthworm diversity, abundance and ecosystem function	Effect on CO ₂ emission	Effect on N ₂ O emission	Effect on CH ₄ emission	C/N ratio of soil	References
	Temperature	Precipitation/soil moisture	Flooding	Drought								
<i>Dendrobaena octaedra</i> ; <i>Aporrectodea caliginosa</i> ; <i>Pontoscolex corethrurus</i> (Rhinodrilidae); <i>Allolobophora chlorotica</i> <i>Amyntas aspergillum</i> , <i>Lumbricus terrestris</i> and <i>Fimoscolex sporadochaetus</i>	Increased temperature	Increased rainfall	-	-	-	Field	7 exotic earthworm species present; Earthworm density and biomass decreased with temperature; Earthworm density and biomass increased with rainfall	-	-	-	-	Mcinga et al. 2021
<i>Eisenia fetida</i>	20 ± 0.5 °C	12, 25, 50 and 75% WHC	-	-	20 days	Laboratory	-	Increased CO ₂ flux at 75% WHC	-	Detectable CH ₄ emissions 50 and 75% WHC	-	Gorbunova et al. 2020
<i>Eisenia fetida</i>	20 °C	60 % WHC	-	-	35 days	Laboratory	-	Increased emission	Increased emission	-	-	Zhu et al. 2018
<i>Aporrectodea caliginosa</i>	Elevated	-	-	-	42 days	Field	Increased nitrification activity in warmed soils; increased NO ₃ ⁻ leaching	Warming significantly increased cumulative CO ₂ emission by 14.9%	Strongly increased by 70–90%	low	-	Marhan et al. 2015
<i>Lumbricus terrestris</i>	-	Increased soil moisture	-	-	105 days	Field and laboratory	-	Increased by 13%	Increased by 27%	-	-	Nieminen et al. 2015

<i>Lumbricus terrestris</i> , <i>Aporrectodea longa</i> , <i>Aporrectodea caliginosa</i> , <i>Aporrectodea icterica</i> and <i>Aporrectodea rosea</i>	Elevated temperature	-	-	-	-	Field	Lower species richness and modify ecosystem functions	-	-	-	-	Siebert et al. 2019
<i>Lumbricus terrestris</i>	Increased temperature	-	-	Dryer conditions	-	-	Exacerbate the effects of deep ploughing on <i>L. terrestris</i> population declines	-	-	-	-	Johnston et al. 2018
<i>Eisenia fetida</i>	Increased air temperature	Reduced soil moisture content	-	-	21 days	Laboratory	Increased weight loss	-	-	-	-	González-Alcaraz and van Gestel (2016)
<i>Amyntas agrestis</i>	Increased temperature	Reduced moisture	-	-	-	Laboratory	Increased weight loss and reduced survival and	-	-	-	-	Richardson et al. 2009
<i>Eisenia fetida</i>	-	-	-	-	139 days	Laboratory	-	Increased emission	Increased emission	-	-	Tejada et al. 2014
<i>Eisenia fetida</i>	Increased temperature	-	-	-	14 days	Laboratory	Increased weight	-	-	-	-	Lima et al. 2015
<i>Lumbricus rubellus</i>	-	-	-	-	83 days	Field	-	Increased CO ₂ emission by 33%	Increase N ₂ O emission 42%	-	-	Lubbers et al. 2013
<i>Eisenia foetida</i>	-	-	-	-	15 days	Laboratory	-	Increased emission	-	Increased emission	-	Majumdar et al. 2006
<i>Eisenia nordenskioldi nordenskioldi</i> and <i>Eisenia nordenskioldi pallida</i>	Reduced temperature (-3 to -25 °C)	50-60 % WHC	-	-	14 days	Laboratory	Worms & cocoons of <i>Eisenia n. nordenskioldi</i> withstand temperatures of -34 & -40°C, and those of <i>E. n. pallida</i> , -28 & -23°C, respectively.	-	-	-	-	Berman and Meshcheryakova (2013)

<i>Aporrectodea caliginosa</i>	-	-	-	Average soil water matric potentials of -0.061, -0.085, -0.13, and -0.19 MPa	21 days	Laboratory	Drought did not affect earthworm mass, but drought lasting 2 or 3 wk increased the number of <i>A. caliginosa</i> in estivation. Three weeks of drought resulted in a mortality rate of 14%	-	-	-	-	McDaniel et al. 2013
<i>Aporrectodea turgida</i> and <i>Lumbricus terrestris</i>	-	33% water-filled pore space (WFPS), constant 97% WFPS	-	-	69 days	-	-	-	Earthworms increased N ₂ O emissions by 50% in the 33% WFPS soil but decreased N ₂ O emissions by 34% in the 97% WFPS soil	-	-	Chen et al. 2014
<i>Allolobophora chlorotica</i> , <i>Aporrectodea caliginosa</i> and <i>Lumbricus rubellus</i>	-	-	35%, 45% (field capacity), 55%, 65% (saturated) to 65%+ (saturated and an extra water layer) (% , w/w)	-	42 days	Laboratory	<i>A. chlorotica</i> was tolerant to water; <i>A. caliginosa</i> showed little response to flooding; <i>L. rubellus</i> was sensitive towards flooding	-	-	-	-	Zorn et al. 2008

Effects of drought

Water availability and low levels of organic matter in the soil limit the distribution of earthworms in many regions; however, they adapt to reduced moisture by entering aestivation to survive the harsh conditions occasioned by the low level of soil moisture (McDaniel et al., 2013). During severely reduced soil moisture, the soil becomes harder, severely reducing soil animals' mobility. There is a likely loss of plant diversity due to drought-induced changes in the soil's functioning, altering ecosystem services. Earthworms sustain critical ecological services such as litter decomposition and nutrient cycling, both of which may be affected by climate change. Drought stress directly affects earthworms by reduced soil moisture and indirectly by the decline of the quality plant supply on which they feed (Mariotte et al., 2016). Endogeic earthworms, for example, *Aporrectodea caliginosa*, living in horizontal burrows, are often very susceptible to drought (Bayley et al., 2010). Their ability to survive short droughts is because they can burrow into the soils and from aestivation chambers. Anecic earthworms may enter into diapause in dry periods and maintain dormancy for a few months (Jiménez and Decaëns, 2004). Several physiological mechanisms help earthworms survive prolonged periods of drought. Holmstrup et al. (2016) recently discovered the adaptive significance of the amino acid, alanine, in three species of earthworms (*Aporrectodea tuberculata*, *Aporrectodea icterica*, and *Aporrectodea longa*). They suggested that alanine accumulation sufficiently protects against the adverse effects of desiccation in earthworms. The findings of the study prove that earthworms respond to dry conditions by changing their metabolism and physiology

Climate change: earthworms and soil greenhouse emission

Earthworms play a significant role in the greenhouse gas balance of soils globally, and their impact will increase in the coming next decades (Lubbers et al., 2013). Earthworms are soil ecosystem engineers, triggering and responding to soil structural changes by feeding, burrowing, and casting activities. In a review by Lubbers et al. (2013), their findings unequivocally indicate a positive contribution to the net soil GHG emissions from soils in the presence of earthworms, suggesting that earthworms increase net soil-GHG emissions of nitrous oxide by 42% and carbon dioxide by 33%. According to Singh and Singh (2019), earthworms increased CO₂, N₂O, and CH₄ levels; however, emission rates vary depending on the physicochemical properties of the soil, organic matter incorporation, and earthworm feeding strategy.

An average of 20% of global carbon dioxide emissions are from soils (Rastogi et al., 2002), and approximately 33% of CH₄ and 67% of nitrous oxide (N₂O) emissions originate from soils globally (Lubbers, 2013) as shown in *Figure 4*. The production of greenhouse gases in soil ecosystems is the outcome of several biological processes. Carbon dioxide originates naturally from respiratory activities in soil (faunal, microbial, root respiration). Methane is produced through methanogenesis, while N₂O is by a combination of microbial activities. These processes thrive with the availability of carbon, soil temperature, moisture, and diffusivity, all of which influence microbial processes (Lubbers et al., 2013).

Furthermore, with the presence of earthworms, several investigations have indicated enhanced CO₂ and N₂O fluxes from the soil (e.g., Charpuis-Lardy et al., 2010; Nieminen et al., 2015). Few studies, on the other hand, revealed that earthworms elevated soil C stock, reduced CO₂ emissions, and contributed to soil C stability

(Bossuyt et al., 2005; Pulleman et al., 2005; Lubbers et al., 2013); no soil CO₂ efflux (Fisk et al., 2004) and lower N₂O emissions from soils (Lubbers et al., 2013). However, earthworms' effect on CH₄ fluxes has received less attention. Lubbers et al. (2013) concluded that the increasing emission of CO₂ by earthworms was insignificant during short experiments but significant after 200 days. Earthworms most likely accelerate initial C decomposition, but they may not affect the total amount decomposed over time. The reverse was the case for N₂O as well as earthworm-induced fluxes increased over time. These can be attributed to the anaerobic conditions in the earthworms' gut and the labile carbon and nitrogen present there. Soil greenhouse gas balance is best defined in the context of agroecosystems as the rate of carbon influx into soil carbon pools compared to the rates of carbon outflow and other GHG emissions from the soil (Lubbers et al., 2013). If the outflow rates equal inflow rates, then the C stock will be said to be stable. However, soil carbon stocks have decreased in recent decades due to the lower rates in the return of crop residues in soils.

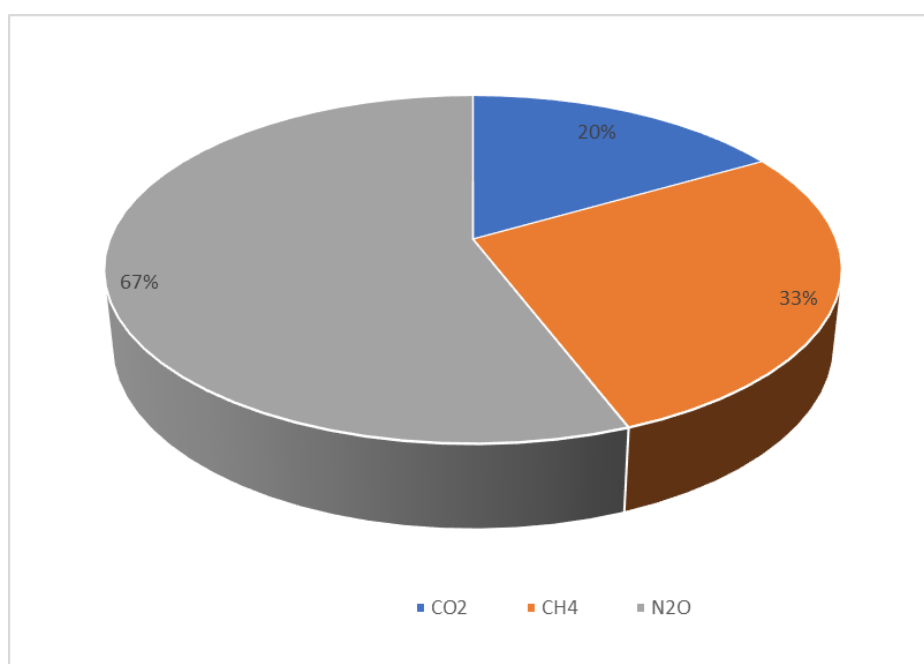


Figure 4. Percentage of global GHG (CO₂, N₂O and CH₄) emissions from the soils (Rastogi et al., 2002; Lubbers, 2013)

Earthworms increase soil carbon sequestration, which elevates greenhouse gas emissions. Soil activities that contribute to greenhouse gas emissions are dependent on the availability of substrates such as nitrogen (N) and carbon (C) for N₂O and physicochemical variables of the soil that ultimately determine microbial activity. The earthworm gut promotes anaerobic conditions by retaining moisture, carbon and mineral N during the denitrification process (Drake et al., 2006). When soil containing earthworms, their castings, mucus, and burrowing activities compared to soils without them, the outcome was a threefold emission of N₂O from the latter (Lemtiri et al., 2014). Earthworms ingest plant residues, and the microorganisms in their gut provide an ideal environment for mucus formation, thus, increasing the absorption of carbon and nitrogen in the foregut. Nitrogen fixation occurs in this region through clostridium, and

the ammonification process enhances N₂O production; at the same time, other microorganisms digested the organic substrate by enzyme action (Singh and Singh, 2019) (Fig. 5). The hindgut is an area where carbon is re-assimilated, increasing CO₂ percentage (Lubbers et al., 2013). Earthworms digest crop residues, thus, increasing the availability of organic nutrients in soils (Blouin et al., 2013). Thus, nitrous oxide comes from denitrification, nitrate, and nitrite processes which starts in the digestive system of earthworms. Earthworms are essential denitrifiers and significantly impact soil N₂O and N₂ emissions (Giannopoulos et al., 2010). Earthworms are responsible for over 50% of the soil-emitted nitrate (Drake et al., 2006). While earthworms hardly generate any GHGs, they can significantly impact the availability of substrates and physicochemical characteristics of the soil and indirectly affect emissions. The question of whether earthworms contribute to the soil sink or a source soil-GHGs emission has remained debatable. However, this review discusses how climate change drivers including, increased temperature, precipitation/moisture, flooding and drought, affect the distribution and biodiversity of earthworms and how that affects GHG emissions. Based on the findings from the reviewed literature, there is a strong indication that with the increasing impact of climate change, GHG emissions from the soil could increase (Fig. 5).

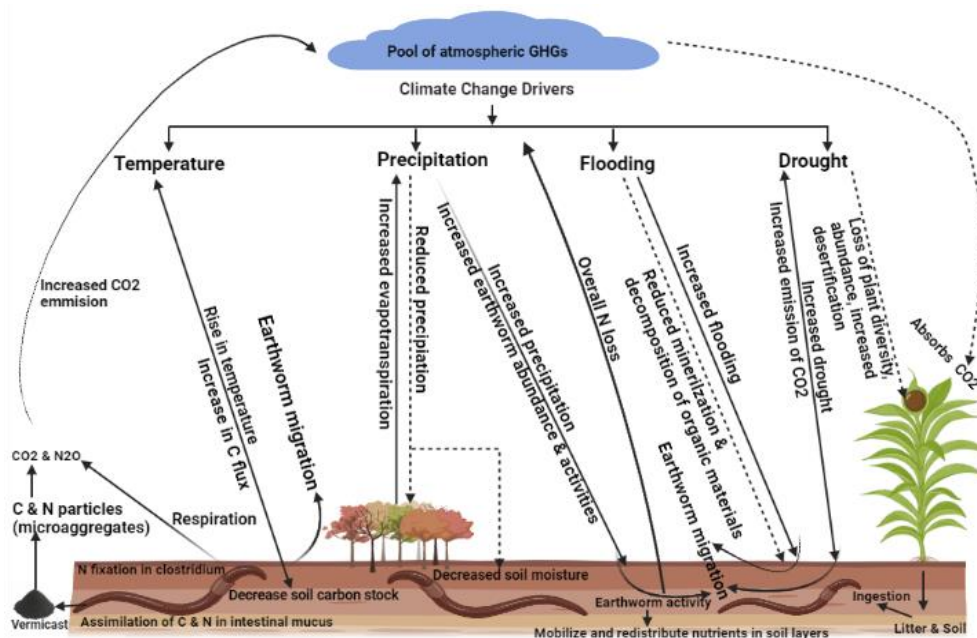


Figure 5. Simple representation of the impact of climate change on earthworms and the potential impacts of global warming on soil greenhouse gas balance (Solid lines indicate an increase while dotted lines signify a decrease in parameters)

In a bid to project the trends in the diversity, biomass and abundance of earthworms, Phillips et al. (2019) collected samples of earthworms from 6928 sampling locations across 57 countries, comprising temperate and tropical regions. They provided global, local, and regional abundance and biomass maps. They collected 180 published articles and several unpublished field study datasets from the 57 countries covering all continents except Antarctica. They studied the community patterns and determined the climatic factors that influence the abundance of earthworms. They added soil properties

into the earthworm model, which may play a role in earthworm population decision making (Rutgers et al., 2016). Their result demonstrated a strong association between climate variables and earthworm metrics. Although the link between the identified climatic factors and the evaluated community metrics is consistent with other studies, climate change will continue unabated because of increased anthropogenic activities. Their findings further highlighted the effects of temperature and precipitation on the diversity of earthworms, distribution and abundance, with consequences for their function and ecosystem services. When invasive earthworms impact ecosystems due to climate change, such as in parts of North America, distribution shifts may be problematic (Craven et al., 2017). Climate change may influence earthworm dispersal before it affects earthworm abundance and biomass since dispersal capabilities are relatively low in earthworms. Several terrestrial species ranges have recently moved to higher elevations and higher latitudes, and the rate of movements have tripled previously observed movement in the last few decades (Chen et al., 2020).

Earthworms will become more prevalent in ecosystems globally over the next few decades, as more organic fertilizers are applied to agricultural soils to feed the burgeoning population, which will provide more food for earthworms. Earthworm activity is likely to be stimulated as the world turns away from traditional land management techniques toward zero- or sustainable tillage. Both forms of tillage decrease the disturbance of the soil, which is beneficial to earthworms. Furthermore, several studies (Butterbach-Bahl et al., 2013; Lubbers et al., 2013) have improved our understanding of soil CO₂ and N₂O emission dynamics over the past decades. However, there are many considerable uncertainties and limitations in knowledge; for instance, soil biodiversity, physicochemical characteristics, and organism functions impact soil-GHG gas emissions. Among these gaps in knowledge, soil fauna's effects will be very significant in reducing, accelerating, or slowing down the emissions of CO₂ and N₂O from soils, most especially from agricultural soils subjected to different regimes of tillage. Over the next century, climate change will be one of the main drivers in altering the delicate balance between carbon sequestration in the soil by earthworms and soil greenhouse gas emission. In addition, invasive earthworms are spreading into new ecosystems due to global warming, causing soil disturbances and ecosystem transformation. This accelerated movement of earthworms into new territories has the potential to alter the climate and significantly release large chunks of stored carbon in these otherwise undisturbed soils. Thus, it has become expedient to understand the link between climate change, earthworms, and soil greenhouse gas balance.

Conclusions

This article puts the projected climate change data in context. We assessed how climate change drivers, such as temperature, moisture, drought, and floods, affect earthworms and the potential to affect the delicate balance between earthworms and greenhouse gas emissions. The structure, diversity, ecosystem function, the spread and success of invasive species of earthworms will be affected by climate change. The activity, abundance, and biomass of earthworms will increase when the soil is sufficiently moist. Additionally, climate extremes like drought and flooding are likely to impact earthworms negatively. Most of the data reviewed in this paper come from the world's temperate regions due to lack of data from other parts of the globe, such as Africa, the Mediterranean, and Antarctica. However, regardless of this gap in published

research data between regions, we expect all these climate change drivers to have nearly the same effects. Available scientific literature has shown that earthworms are likely to increase in environmentally diverse ecosystems in the future. Over the last few decades, we have gained a lot of knowledge about the dynamics of carbon dioxide (CO₂) and nitrous oxide (N₂O) emissions from agricultural soils. Conclusively, earthworms can influence CO₂ and N₂O release from arable soils, especially as the effects of climate change continues unabated. However, the number of earthworms that will significantly stimulate the overall emission of soil greenhouse gases is unclear. Therefore, we recommend that long-term studies of earthworms in natural systems or controlled climate chambers combined with field studies are required. This aspect of earthworm ecological studies will establish and improve our understanding of the significant fraction of the total soil GHG emissions (feedback) due to earthworms' activity influenced by climate change.

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Conflict of interests. The authors declare that they have no competing interests.

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