

Climate change effects on earthworms - a review

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Received 22 October 2019 | Accepted 26 November 2019

Published online at www.soil-organisms.de 1 December 2019 | Printed version 15 December 2019

DOI 10.25674/so91iss3pp114

Abstract

Climate change can have a plethora of effects on organisms above and below the ground in terrestrial ecosystems. Given the tremendous biodiversity in the soil and the many ecosystem functions governed by soil organisms, the drivers of soil biodiversity have received increasing attention. Various climatic factors like temperature, precipitation, soil moisture, as well as extreme climate events like drought and flood have been shown to alter the composition and functioning of communities in the soil. Earthworms are important ecosystem engineers in the soils of temperate and tropical climates and play crucial roles for many ecosystem services, including decomposition, nutrient cycling, and crop yield. Here, we review the published literature on climate change effects on earthworm communities and activity. In general, we find highly species- and ecological group-specific responses to climate change, which are likely to result in altered earthworm community composition in future ecosystems. Earthworm activity, abundance, and biomass tend to increase with increasing temperature at sufficiently high soil water content, while climate extremes like drought and flooding have deleterious effects. Changing climate conditions may facilitate the invasion of earthworms at higher latitudes and altitudes, while dryer and warmer conditions may limit earthworm performance in other regions of the world. The present summary of available information provides a first baseline for predictions of future earthworm distribution. It also reveals the shortage of studies on interacting effects of multiple global change effects on earthworms, such as potential context-dependent effects of climate change at different soil pollution levels and across ecosystem types.

Keywords Biodiversity | Climate change | Climate drivers | Cocoons | Earthworm invasions | Soil organisms

1. Introduction

Climate change is recognized as one of the greatest threats to biodiversity over the next century with significant consequences for the functioning and service provisioning of many ecosystems (Sala et al. 2000, Maxwell et al. 2016, IPBES 2018). In general, climate change refers to an alteration in the state of the climate,

reflected by changes in the mean and/or the variability of its properties like temperature, precipitation, and wind, and that persists for an extended period (typically decades or longer), and that coincides with an increased likelihood and/or intensity of extreme climate events, such as drought and flooding (IPCC 2013). Climate models project an increase in the frequency of extreme precipitation events (Bates et al. 2008), whereas the total

amount of rainfall is predicted to remain about the same as at present but with increasing variability (Wuebbles & Hayhoe 2004). While changes in precipitation may show substantial small-scale heterogeneity and may thus be challenging to predict, there is no doubt regarding the expected increase in global mean surface air temperature. Depending on CO₂ emission levels, the predicted temperature increase ranges between +1.1 and +6.4°C by the year 2100 (Nakicenovic et al. 2000) or between +1.4°C and +5.8°C over the period 1990 to 2100 (IPCC 2013).

Climate change may affect the functioning of ecosystems by altering the biodiversity and species composition of communities (Bates et al. 2008, Bardgett & van der Putten 2014). The impacts of climate change on biodiversity are likely to include changes in ecological interactions, habitat preference, species abundance and distribution, phenology and increases in invasive species (Eggleton et al. 2009, Lurgi et al. 2012, Eisenhauer et al. 2014). Despite some attempts to synthesize information on potential responses of soil organisms to climate change (Blankinship et al. 2011, Coyle et al. 2017), soil community responses as well as their most important drivers are still insufficiently studied, especially for large soil invertebrates (Veresoglou et al. 2015, Eisenhauer et al. 2017). Climate change effects on soil food webs can be caused by altering the activity and mortality of soil organisms. Increasing temperature (enhancing metabolic demands), frequency of extreme precipitation events and droughts may additionally cause mortality by changing the life cycle and nutrition of soil animals (Bates et al. 2008, Thakur et al. 2018). Increases in the frequency and intensity of extreme rainfall together with changes in land use make soils more vulnerable to erosion (Nearing et al. 2004) and impair their function as habitat for soil fauna.

Soil biodiversity is vital to humans as it supports a wide range of ecosystem processes, functions, and services (Blouin et al. 2013, Skubala 2013, Bardgett & van der Putten 2014, Jouquet et al. 2014, Wall et al. 2015) and includes different types of organisms, ranging from micro-flora and fauna, such as bacteria, algae, fungi, and protists, to macro- and mega-fauna like earthworms, insects, small vertebrates, and plants (Orgiazzi et al. 2016). Biodiversity loss has been reported worldwide (IPBES 2018), and this rapid loss has become one of the most important global environmental issues (Millennium Ecosystem Assessment 2005, Maxwell et al. 2016). The evidence of current extinction caused by climate change is very limited, but the rate of species loss is predicted to increase considerably over the next 50 years (Leadley et al. 2010, Bellard et al. 2012). However, reported and predicted biodiversity changes are mostly based on aboveground biodiversity observations (Eisenhauer et al.

2019). Despite many interactions between aboveground and belowground communities (Wardle 2002, Wardle et al. 2004), biodiversity patterns in one compartment may not necessarily represent those in the other (Cameron et al. 2019), highlighting the need to further explore biodiversity of above- and belowground communities simultaneously (Eisenhauer et al. 2019). Many anthropogenic activities are likely to accelerate the loss of biodiversity and ecosystem services in soil (Veresoglou et al. 2015, Wall et al. 2015), and approximately 60% of these services are likely to be degraded, because soil is not used in a sustainable way (Black et al. 2003, Skubala 2013).

Earthworms are important soil organisms of temperate and tropical regions (Lee 1985) and constitute approximately 40–90% of soil macro-faunal biomass in many terrestrial ecosystems (Fragoso et al. 1999). Earthworms are divided into 23 families, and over 700 genera and > 7,000 species have been described worldwide (Csuzdi 2012, Orgiazzi et al. 2016), but the expected number of species is much higher (Orgiazzi et al. 2016, Phillips et al. 2017). They are considered as keystone species (Power & Mills 1995, Lavelle & Spain 2001), especially due to their role as ecosystem engineers (Jones et al. 1994). Earthworms have the capacity to create, modify, and maintain habitats for other soil organisms as well as plant communities through the physical and chemical modification of their environment (Byers et al. 2006, Eisenhauer 2010, Bernard et al. 2012; Blouin et al. 2013). Earthworms influence ecosystem functions through litter fragmentation, burrowing, and casting activities, and thereby drive nutrient cycling, soil aggregate stability, water infiltration, plant growth, and soil carbon storage (Coleman et al. 2004). Moreover, they are often used as bio-indicators and model organisms in eco-toxicological studies due to their role in various ecosystems and the simple identification in comparison to other soil taxa (Fründ et al. 2011).

Earthworm diversity has been studied by many biologists throughout the world (e.g., Tsai et al. 2000, Blakemore 2003, Blakemore 2006, Sautter et al. 2006, Phillips et al. 2019). A recent global analysis highlights the importance of climate changes like increasing air temperature and altered mean annual precipitation on earthworm diversity (Phillips et al. 2019). However, these drivers may not only directly impact earthworms, but rather, they frequently alter soil properties like moisture, temperature, pH, and texture (Burke et al. 1989, Ruiz-Sinoga & Diaz 2010) which then affect earthworm communities (Tiunov et al. 2006, Nieminen et al. 2011). Moreover, climate-induced changes in vegetation biomass and composition may also affect earthworm populations (Eisenhauer et al. 2009). Finally, management at the field and landscape scale also influences earthworm diversity

and could alter belowground biological processes (Curry & Schmidt 2007, Johnston et al. 2014). For instance, reduced earthworm communities in intensively-used agricultural fields might be the result of pesticide and fertilizer applications as well as physical disturbances (Johnston et al. 2014, Pelosi et al. 2014, Singh et al. 2016; Briones & Schmidt 2017). Such disturbed communities in degraded soils may be particularly vulnerable to climate change effects (Siebert et al. 2019a).

Climate change will affect soils and soil processes mainly through changes of temperature and rainfall patterns. Increasing temperature, drought, and winter rainfall will affect soil moisture and temperature regimes, which have been reported to have variable impacts on earthworm populations (Carroll et al. 2000, Wever et al. 2001, Perreault & Whalen 2006, Staley et al. 2008). However, in order to develop and improve models of the effects of climate change on soil fauna distributions and predict potential impacts on ecosystem processes, more ecological research into the climatic tolerances of these important soil invertebrates is required (Sutherland et al. 2006, Moreau-Valancogne et al. 2013, Eisenhauer et al. 2017). Despite the widely acknowledged important role of earthworms for ecosystems and the obvious threats from climate change phenomena (e.g., Cock et al. 2013, Eisenhauer et al. 2014, Hughes et al. 2019, Siebert et al. 2019b), there is still no comprehensive overview of the effects of climate change on earthworm communities.

In this review paper, we present a systematic review of the scientific literature and synthesize the potential climate change effects on earthworm communities (Section 2), focusing on changes in temperature and rainfall, as well as on extreme climate events like drought and floods. We focus on responses of earthworm communities, abundance, biomass, and activity, while further physiological responses of earthworms were beyond the scope of this study. We conducted a search in Web of Science on July 2, 2019, using published literature between 1945 and 2019, applying the following search string: ('climate change' OR 'warming' OR 'flood' OR 'drought' OR 'precip*' OR 'temperature') AND ('lumbric*' OR 'earthworm*'). We restricted the search to the Web of Science Categories 'Ecology' and 'Articles', which returned 264 papers. Review, opinion, and perspectives papers were excluded from the list, which resulted in 177 papers. As usual, most of the studies reported were from earthworms living in temperate regions (Cameron et al. 2018, Maestre & Eisenhauer 2019), with few of them involving species present in the tropics or other climatic zones (e.g., Mediterranean). We screened for appropriate studies that tested climate change effects on earthworm communities and report their findings in Table 1–3. Given the relatively low

number of studies and high variability in the design, we did not perform a meta-analysis but present a review of the overall trends. Moreover, we provide perspectives for future research (Section 3) and conclusions.

2. Effects of climate change on earthworm diversity

2.1 Temperature

2.1.1 Effects of increasing temperature and context-dependencies

Temperature is one of the most important climate change drivers determining the activity of soil biota and decomposition processes. As a consequence, temperature effects have been studied on activities of soil microorganisms (Insam & Domsch 1988) and soil invertebrates (Byzova 2007). Warming has been shown to cause range shifts in many plant and animal species, with range expansion being strongly influenced by biotic interactions (Chen et al. 2011, Gilman et al. 2010). Several studies have stressed the possibility of warming-induced northward range expansions of some macro-detritivore species, including earthworms (Bohlen et al. 2004, Berg et al. 2010, Eisenhauer et al. 2014).

Earthworms are poikilothermic, i.e., their body temperatures are variable and fluctuate with the temperature of their environment. Hence, the activity, growth, density, metabolism, respiration, and reproduction of earthworms are affected by temperature (Edwards & Bohlen 1996). Both high and low temperatures cause a direct response, with earthworms tending to congregate in areas where conditions are optimal for their metabolism. Lower lethal temperatures tend to be less known than upper lethal temperatures, which typically range between 25 and 35°C, but vary substantially among species, with tropical species often being more resistant to higher temperatures than temperate species, and vice-versa for lower temperatures (Lee 1985). Below 10°C, earthworms generally reduce feeding activities, and above 40°C, cocoon production and development of young earthworms ceases completely (Edwards & Bohlen 1996, Satchell 1967). The lower temperature limit for earthworm activity may be at ~5°C or lower, depending on species and the population/genotype. Many common earthworm species from cooler climatic regions are typically active at temperatures above 2–4°C (Nordström & Rundgren 1974). Temperature and moisture interactions are also important: Presley et al. (1996) observed the maximum growth rate of *Eisenia fetida* at high moistures and moderate temperatures, but

after reproductive maturity, the maximal growth and survivorship occurred in moderate/high moistures and low temperatures. Eisenhauer et al. (2014) found lower earthworm densities (mainly of *Lumbricus rubellus*, *Aporrectodea caliginosa*, *Dendrodrilus rubidus*, and *Dendrobaena octaedra*, with a smaller proportion of *Aporrectodea rosea*, *Allolobophora chlorotica*, and *Octolasion lacteum*) with increasing soil temperature, unless rainfall increased as well. Many earthworm species enter into diapause or become quiescent, frequently migrating to deeper soil layers, if higher temperature causes soil water limitation (Jiménez et al. 2000). The ability of the anecic or large-bodied species to migrate vertically in the soil (some to more than 3 m depth; Buck & Abe 1990) ensures survival during dry and/or warmer condition on the soil surface (Gerard 1967, Eisenhauer et al. 2009, Drumond et al. 2013, 2015).

According to the soil moisture-dependent effect of increasing temperature, previous studies on earthworm performance reported inconsistent and partly contradictory results (Table 1). It was previously reported that a moderate increase in soil temperature could positively affect earthworm biomass and activity (Boström & Lofs-Holmin 1996). Particularly for *Aporrectodea caliginosa*, growth rates of juveniles (Eriksen-Hamel and Whalen 2006) and burrowing activity were higher at 20°C than at 15°C (Perreault & Whalen 2006). The metabolic, burrowing, and casting activity of endogeic earthworms typically increases with increasing soil temperature (Table 1), up to a point, often displaying a slightly bell-shaped curve pattern with rapid increases or decreases at very low and high temperatures, respectively, and smaller increases or decreases closer to the metabolic optima (e.g., Satchell, 1967, Lavelle et al. 1987, Berry & Jordan 2001, Wever et al. 2001). Hence, in colder and temperate regions, endogeic earthworm activity is likely to increase under elevated soil temperatures in the future, if soil moisture levels are sufficiently high. A study by Marhan et al. (2015) also indicated a higher loss of N in the form of N₂O emission from soil with high earthworm populations and warmer climate. González-Alcaraz & van Gestel (2016) reported higher weight loss of earthworms when kept at 25°C than at 20°C, and Lima et al. (2015) also found higher weight loss of *Eisenia andrei* at 26°C compared to 20°C, stressing the context-dependency of temperature effects (with both studies evaluating earthworm behavior in polluted environments). Effects of increasing temperature can therefore be expected to be positive mostly in colder and moist environments (Berman & Meshcheryakova 2013; Table 1). On the other hand, temperature increases in warmer tropical and particularly seasonally dry regions may cause additional water and metabolic stresses to earthworms inhabiting these soils,

especially if accompanied by changes in rainfall intensity and distribution throughout the year (Hughes et al. 2019).

Changing temperature is likely to affect the spatial and temporal habitat use by earthworms both at local and regional scales. At the local scale, temperature changes may change the vertical and horizontal distribution, while at the regional scale, it may impact species distribution patterns. If earthworms stay closer to the soil surface at higher temperature, they may be more susceptible to detrimental conditions like heat produced by UV radiation (Chuang et al. 2006). Moreover, several studies reported seasonal variations in the growth and activity of earthworms with respect to a change in temperature and soil moisture (Domínguez & Edwards 1997, Eisenhauer et al. 2009).

As a consequence, climatic conditions are major determinants of earthworm distribution and diversity (Fisichelli et al. 2013, Phillips et al. 2019). It is expected that future warmer and drier climates will decrease the spread of earthworm invasions, because the activity of earthworm is limited by higher temperatures under drought stress (Curry 2004, Eggleton et al. 2009, Zaller et al. 2009), while the opposite might be true if warming coincides with sufficiently high soil moisture levels. For instance, the ability of *Amyntas* species to respond quickly to winter warming has been shown to have positive consequences for invasiveness and range expansion (Görres et al. 2018; Table 1). Eisenhauer et al. (2014) also concluded that warming limits the invasion of earthworms in northern North America by causing less favorable soil abiotic conditions, unless warming is accompanied by increased and temporally even distributions of rainfall sufficient to offset greater water losses from higher evapotranspiration.

Earthworms may show very pronounced seasonal dynamics in their occurrence and activity patterns, particularly in seasonally dry or cold climates. Earthworm abundance tends to decline in the dry or very cold season and reaches highest densities and biomass when climatic and soil conditions are more favorable, e.g., conditions typically occurring in spring and autumn in temperate regions when temperature is modest and soil water content is high (Satchell 1967, Lavelle 1983, Jiménez et al. 1998, Walsh & Johnson-Maynard 2016). Notably, the interaction effects of temperature and soil moisture on earthworms were shown to differ from species to species. *Allolobophora chlorotica* and *Dendrobaena octaedra* were reported to respond more positively to an increase of temperature at lower soil moisture levels, while *Aporrectodea caliginosa* and *Lumbricus rubellus* showed negligible responses (Eggleton et al. 2009). Zaller et al. (2009) found that moderate experimental warming significantly reduced the density and biomass

Table 1. Summary table of studies on effects of temperature and/or precipitation/soil moisture as climatic drivers on earthworm species abundance and biomass, earthworm populations, and earthworm activity. t: effects of temperature; m: effects of moisture; tm: effects of temperature and moisture.

Study	Climatic drivers		Earthworm species*	Earthworm biomass	Earthworm population		Earthworm activity and additional comments and details
	Temperature	Precipitation/ Soil moisture			Density/ abundance	Cocoons/ juveniles	
Satchell (1967)	Below 10°C	NA	<i>Eisenia fetida</i>		↓ _t	↓ _t	Reduced feeding activity.
	25-30°C	NA			↑ _t	↑ _t	Increased feeding activity.
Daugbjerg (1988)	Below 10°C	Wide range of soil moisture conditions	<i>Lumbricus terrestris</i>	NA	NA	↓ _{tm}	Reduced feeding and juvenile activity.
	Below 5°C	Soil moisture below 16%	<i>Aporrectodea caliginosa</i>	NA	NA	↓ _{tm}	
	Below 5°C	Soil moisture below 10%	<i>Aporrectodea longa</i>	NA	NA	↓ _{tm}	
Edwards & Bohlen (1996)	Below 10°C	NA	<i>Eisenia fetida</i>	↓ _t	↓ _t	↓ _t	Reduced or little feeding activity. Cocoon production and development of young earthworms ceased completely.
	40°C			↓ _t		↓ _t	
Boström & Lofs-Holmin (1996)	Low (5°C) to high temperature (15°C)	Moderate soil moisture	<i>Aporrectodea caliginosa</i>	↑ _t	↑ _t	↑ _t	Earthworm aestivated at low humidity and high temperature.
Bennour & Nair (1997)	15°C	32.5%	<i>Aporrectodea caliginosa</i>	↑ _m	↑ _m	↑ _m	Earthworm numbers/ biomass showed positive relationship with soil moisture $p < 0.1$ for number/biomass and temperature.
	31°C	21%		↔ _t	↔ _t	↔ _t	
Daniel et al. (1996)	7.5-25°C	-10 kPa	<i>Lumbricus terrestris</i>	↑ _m ↓ _t	↑ _m ↓ _t	NA	Body weight of <i>L. terrestris</i> increased faster at optimum temp. (15-17.5°C). The mortality increased with increasing temperature.
Zaller & Arnone (1999)	0-25°C	25 to 45 vol.1%	<i>Nicodrilus longus</i> , <i>Nicodrilus nocturnus</i> , <i>Lumbricus terrestris</i> , <i>Nicodrilus caliginosus</i> , <i>Allolobophora chlorotica</i> , <i>Aporrectodea rosea</i> , <i>Octolasion cyaneum</i> , <i>Lumbricus castaneus</i> , <i>Dendrobaena mammalis</i>	↔ _m	↔ _m	NA	Increased soil moisture after rain did not significantly affect earthworm activity at any earthworm density level.
Wever et al. (2001)	5, 10, 15, and 20°C	Juveniles were cultured in soil with moisture levels 10, 15, 20, and 25%, dry weight basis	<i>Aporrectodea tuberculata</i>	↑ _{t+m}	↑ _{t+m}	↑ _{t+m}	Earthworm weight was increased in soil incubated with 25% moisture at 15 and 20°C. Lowest survival at soil moisture levels lower than 10%.

Continued table 1.

Study	Climatic drivers		Earthworm species*	Earthworm biomass	Earthworm population		Earthworm activity and additional comments and details
	Temperature	Precipitation/ Soil moisture			Density/ abundance	Cocoons/ juveniles	
Perreault & Whalen (2006)	5-20°C	Soil water matric potential	<i>Aporrectodea caliginosa</i> , <i>Lumbricus terrestris</i>		NA		<p>a) Burrow length increased with increasing temperature and in a drier soil (-11kPa) than in wetter soil (-5kPa).</p> <p>b) Surface casting activity increased at higher temperature and wetter soil.</p> <p>c) Feeding activity increased in wetter soil.</p> <p>d) Activity of juveniles increased with increasing temperature and drier to wetter soil.</p>
		a)-5kPa (wetter) or 30% b)-11kPa (drier) or 25%				NA	
Eriksen-Hamel & Whalen (2006)	20°C	a)-5 kPa	<i>Aporrectodea caliginosa</i>				<p>The instantaneous growth rate (IGR) was significantly affected by soil moisture, temperature, and the temperature×moisture interaction.</p> <p>Optimum growth conditions for <i>A. caliginosa</i> were at 20°C and -5 kPa water potential.</p> <p>Earthworm lost weight when the soil water potential was -54 kPa for all temperatures.</p>
	5-20°C	b)-54 kPa					
Millican & Lutterschmidt (2007)	8 to 26°C	Less than 80%	<i>Amyntas corticis</i> , <i>Diplocardia invecta</i>				<i>A. corticis</i> reproduced more successfully at higher temperatures than <i>D. invecta</i> .
Briones et al. (2009)	Increase of 3.5°C from 8°C (control)	NA	<i>Allolobophora chlorotica</i> , <i>Aporrectodea caliginosa</i> , <i>Aporrectodea longa</i>			NA	Four times fewer worms were recorded in the warmer treatment than in the control.
Eggleton et al. (2009)	Less than 6°C More than 16°C	Less than 11% and More than 40%	<i>Dendrobaena octaedra</i> , <i>Dendrobaena attemsi</i> , <i>Allolobophora chlorotica</i> , <i>Aporrectodea caliginosa</i> , <i>Lumbricus rubellus</i>	NA		NA	Dry summers had the strongest negative effect on epigeic species. Wetter month increased earthworm abundance. <i>A. caliginosa</i> and <i>L. rubellus</i> both were unaffected by a wide range of soil temperature levels because of high tolerance.
Richardson et al. (2009)	12°C and 25°C	24% and 54%	<i>Amyntas agrestis</i>			NA	<p>Earthworm <i>A. agrestis</i> survived at temp. of 12°C and 25°C. Earthworm survival was not observed at temperatures of -5, 5, or 35°C at any soil moisture level. Maximum survival plus fresh-weight maintenance occurred at 12°C and 24% soil moisture.</p>
	-5, 5, and 35°C	24% and 54%					

Study	Climatic drivers		Earthworm species*	Earthworm biomass	Earthworm population		Earthworm activity and additional comments and details
	Temperature	Precipitation/ Soil moisture			Density/ abundance	Cocoons/ juveniles	
Zaller et al. (2009)	5.5°C	Reduced water availability	<i>Dendrobaena octaedra</i>	↓ _t	↓ _t	NA	Epigeic earthworm density and biomass was decreased by 36% by warming.
Lima et al. (2011)	20°C	40% WHC of soil	<i>Eisenia andrei</i>	↻ _m	NA	NA	Mortality and weight loss in earthworms were not significantly affected by moisture.
Uvarov et al. (2011)	10-15°C	NA	<i>Lumbricus rubellus</i> , <i>Dendrobaena octaedra</i>	↑ _t	↑ _t	↑ _t	Smoothed temperature fluctuations than ambient temperature condition beneficially affected earthworm population.
Greiner et al. (2011)	18°C 1.5°C	NA	<i>Dendrobaena veneta</i> , <i>Eisenia fetida</i>	NA	NA	↑ _t ↓ _t	Adult earthworms exhibited near 100% survival in the room temperature treatment, but survivorship varied among species in the low temperature treatment. Number of hatchlings decreased in the low-temperature treatment relative to the room-temperature treatment for <i>D.veneta</i> and <i>E. fetida</i>
Bessolitsyna (2012)	Moderate temperature	Increased soil moisture	<i>Eisenia nordenskioldi nordenskioldi</i> , <i>Eisenia nordenskioldi pallida</i> , <i>Eisenia atlavinyteae</i> , <i>Eisenia sibirica</i> , <i>Dendrobaena octaedra</i>	↓ _m	↓ _m	NA	Over-moistened soils were unfavorable for earthworms. They could survive long-term flooding (provided air supply is sufficient) but avoided areas with waterlogged peaty soils.
Berman & Meshcheryakov 2013	-3 to -25°C	50-60% moisture	<i>Eisenia nordenskioldi nordenskioldi</i> , <i>Eisenia nordenskioldi pallida</i>	↓ _t	↓ _t	↑ _t	Water content in tissue of <i>E. n. nordenskioldi</i> and cocoons was lower in winter than in late summer. Cocoons could withstand cooling below -40°C. <i>E.n. pallida</i> was less cold hardy than <i>E. n. nordenskioldi</i>
Fisichelli et al. (2013)	Moderate temperature	Increased precipitation	Multiple earthworm species	↑ _{tm}	↑ _{tm}	NA	Moderate temperature and annual precipitation had a positive impact on earthworm abundance.
Eisenhauer et al. (2014)	About 3.57 and 4.23°C increases	Decrease soil moisture less than 21%	<i>Lumbricus rubellus</i> , <i>Aporrectodea caliginosa</i> , <i>Dendrobaena rubidus</i> , <i>Dendrobaena octaedra</i> , <i>Aporrectodea rosea</i> , <i>Allolobophora chlorotica</i> , <i>Octolasion lacteum</i>	NA	↓ _t	NA	The detrimental warming effects on earthworm densities and biomass could be due to warming-induced reductions in soil water content (SWC); warming may limit earthworm invasion by decreasing earthworm performance.
Marhan et al. (2015)	Increase from 15°C to 18.5°C	NA	<i>Aporrectodea caliginosa</i>	↻ _t	NA	NA	Increasing risk for N losses in the form of nitrate leaching and/or N ₂ O emissions from earthworm populated arable soils with a warmer climate in the future.

Continued table 1.

Study	Climatic drivers		Earthworm species*	Earthworm biomass	Earthworm population		Earthworm activity and additional comments and details
	Temperature	Precipitation/ Soil moisture			Density/ abundance	Cocoons/ juveniles	
Rajkhowa et al. (2015)	Varied between 17-26°C	Soil moisture 28-39%	<i>Drawida nepalensis</i> , <i>Eisenia</i> sp., <i>Amyntas diffringens</i> , <i>Perionyx</i> sp., <i>Lampito mauritii</i> , <i>Drawida</i> sp., <i>Perionyx excavatus</i> , <i>Eisenia fetida</i> , <i>Glyphidrilus gangeticus</i> , <i>Drawida</i> sp., <i>Pontoscolex corethrurus</i> , <i>Eutyphoeus</i> sp., <i>Gordiodrillus elegans</i> , <i>Metaphire posthuma</i> , <i>Dichogaster saliens</i> , <i>Perionyx anandalei</i> , <i>Amyntas alexandri</i>	↑ _m	↑ _m	NA	Density of the earthworm species varied under different soil habitat conditions. In open grassland, it was positively correlated with soil moisture, temperature and humidity, while biomass correlated only with moisture.
Gonzalez-Alcaraz & van Gestel (2016)	a) 20°C	50% and 30% WHC	<i>Eisenia andrei</i>	↓ _t	NA	NA	Earthworms exposed at 25°C and 30% WHC showed significantly higher weight loss than those at 20°C, both at 50% and 30% WHC. Earthworm weight loss was more pronounced in the polluted study soils and greater than 20% after 14 days of exposure of climatic condition.
	b) 25°C	30% and 50% WHC					
Görres et al. (2018)	Above 10°C	NA	<i>Aporrectodea agrestis</i> , <i>Aporrectodea tokioensis</i>	NA	↑ _t	↑ _t	Hatching during warming periods in winter resulted in high mortality. Such winter hatching, and loss, may increase with climate warming in the region.
Johnston et al. (2018)	Less than 20°C	.20 KPa	<i>Lumbricus terrestris</i>	↑ _m	↑ _m	↑ _m	Increased biomass at higher soil moisture levels.
				↓ _t			Mortality observed at higher temperatures.
Johnston & Herrick (2019)	a) 55°C	NA	<i>Amyntas tokioensis</i> , <i>Amyntas agrestis</i>	NA	NA	↓ _t	Cocoons became non-viable at high temperature.
	b) < 40°C 20-55°C	NA		NA	NA	↑ _t	The threshold of tolerance of cocoons was between 27.1°C and 38.1°C for <i>A. tokioensis</i> and <i>A. agrestis</i> .

*Earthworm species names given are the ones in the publication and do not necessarily reflect current taxonomic opinions as to their actual species status (particularly problematic for some of the cryptic species).



Climate change factor increases earthworm performance, ○ Non-significant effect of climate change factor on earthworms



Climate change factor decreases earthworm performance

of epigeic earthworms (*Dendrobaena octaedra*) in a *Carex* fen ecosystem in southern South America. Briones et al. (2009) examined the effect of soil warming on the abundance and diversity of different earthworm species in temperate grassland ecosystem in a plant-soil mesocosm experiment. Earthworms were sensitive to artificial warming, and substantially fewer worms were found in the warmed treatments than in the control mesocosms. Species richness was also significantly reduced by increased temperature, with only three species (*Allolobophora chlorotica*, *Aporrectodea caliginosa*, and *Aporrectodea longa*) retrieved in the warmed systems, whereas four additional species were retrieved in the control (*Lumbricus castaneus*, *Dendrobaena octaedra*, *Dendrodrilus rubidus*, and *Octolasion cyaneum*). The temperature rise of 3.5°C resulted in the total disappearance of epigeic species due to warmer conditions at the soil surface. Such a loss of epigeic earthworms could potentially result in alterations of the carbon cycle, as these surface dwellers produce casts more enriched with litter carbon than endogeic earthworms (Zhang & Hendrix 1995). Moreover, the earthworm community under a warmer scenario consisted of smaller populations of two endogeic species (*Allolobophora chlorotica* and *Aporrectodea caliginosa*) and one anecic species (*Aporrectodea longa*). Only this latter species significantly increased its population size in response to warming. Such changes in the diversity and abundances of earthworms are likely to have important implications for longer-term soil organic matter dynamics (Blouin et al. 2013) and probably other soil organisms (Eisenhauer 2010).

Notably, temperature may interact with other environmental drivers and disturbances in affecting earthworm communities. However, there have been few studies on such potential interactions (Table 1), which makes a comprehensive understanding of temperature effects on earthworms elusive. For instance, temperature has been shown to modulate effects of pesticides on earthworm communities. In an experiment with *Eisenia fetida*, it was observed that temperature and soil moisture affected soil enzyme activities, and caused a different response of earthworms to pesticides. Specifically, earthworms showed a different toxicity response when exposed to the same pesticide concentration at different temperature conditions: an increase in exposure temperature mostly increased the toxicity, whereas toxicity decreased at lower temperature (Pelosi et al. 2014, Velki & Ečimović 2015). These results highlight that further studies are needed to explore the mechanism underlying such complex interaction effects of climate changes and other environmental factors on the toxicity effect of pesticides and other chemical stressors on earthworms.

2.1.2 Frost tolerance of earthworms

Frost tolerance, generally assumed to be restricted to a few species of lumbricid earthworms (Lee 1985), may be a more common phenomenon than previously thought (Holmstrup et al. 2007). For instance, the desiccation tolerance of cocoons plays an important role for population sizes of the epigeic earthworm species *Dendrobaena octaedra* (Bouché 1972). The ability of earthworms to survive freezing is brought about by polyol and glucose synthesis from reserve glycogen that help to survive during summer diapause and reach 20–30% of dry tissue weight during autumn (Byzova 2007, Holmstrup et al. 2007, Overgaard et al. 2007, Overgaard et al. 2009, de Boer et al. 2017). Glycogen reserves are of great importance for winter survival in *Dendrobaena octaedra*, since they provide glucose that is used both as a cryo-protectant (Rasmussen & Holmstrup 2002) and as energy source for basal metabolism during winter (Calderon et al. 2009). Shekhovtsov et al. (2015) found that the epigeic earthworm species *Eisenia nordenskioldi* can accumulate up to 0.3% of glycerol and survive, if temperature goes down to -35°C. Moreover, the cocoons of *Eisenia nordenskioldi nordenskioldi* were observed to be tolerant to lower subzero temperatures compared to other earthworm species. All cocoons were reported to survive after 24 h exposure at -28.5°C, and 13.3% survived after exposure at -40°C (Berman & Leirikh 1985, Berman & Meshcheryakova 2013). Overall, earthworms belonging to five out of 13 species were found to withstand below zero temperatures, whereas cocoons of five species survived in the state of cryo-protective dehydration (Meshcheryakova & Berman 2014). However, the cold hardiness of earthworms may be more important for the broad distribution of a species than the hardiness of the cocoons (Meshcheryakova & Berman 2014). Alternatively, endogeic and anecic species may avoid freezing by hibernating in deep soil layers. Interestingly, both *Dendrobaena octaedra* (Opisthopora, Lumbricidae) and *Drawida ghilarovi* (Gates 1972) (Moniligastrida, Moniligastridae) can overwinter in a frozen state and have a similar lethal temperature of about -16°C (Berman et al. 2002, 2010). Conversely, species like *Allolobophora chlorotica* are very frost-sensitive, even as cocoons (Holmstrup & Zachariassen 1996).

Temperature may restrict the range expansion of earthworm species. Berman et al. (2016) reported that *Eisenia sibirica* tolerates temperature not lower than -12°C, and the limited capabilities for overwintering at low temperatures prevent this species from expanding its range to the North. Similarly, increasing winter severity from the west to the east prevents invasion of the cosmopolitan species *Dendrobaena octaedra* in Siberian

tundra and Taiga and control the northward expansion of *Drawida ghilarovi* from the south of Khabarovsk Territory (Berman et al. 2002, 2010). Many of the European earthworm species colonizing the Great Lakes region in the Northern USA (*Aporrectodea rosea*, *Lumbricus rubellus*, *Lumbricus terrestris*) are not frost-tolerant, and hibernate in deeper soil layers (Tiunov et al. 2006). Moreover, the cold winter climate of the region may have prevented the expansion of *Eisenia fetida* and Asian species of the genus *Amyntas* (Tiunov et al. 2006). Taken together, these findings indicate that a changing climate is likely to alter the geographic distribution of earthworms in a species-specific way and may be modulated by local environmental conditions, such as soil type and texture, pH, vegetation type, and chemical stressors.

2.2 Precipitation

According to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2013), the chance of heavy rain events and flooding is increasing globally, as precipitation will be concentrated into more intense events with longer periods and little precipitation in between such events. So far, drought has been given more attention in the ecological literature than intense rainfall (Beier et al. 2012), but both can have major effects on earthworms.

2.2.1 Effects of precipitation and precipitation seasonality

Generally, earthworm communities respond positively to precipitation at the local, regional, and global scale (Table 2; Satchell 1967, Lavelle 1983, Phillips et al. 2019). Many studies have shown maximum abundance of earthworms in the rainy/moist season(s) of the year (e.g., Bennour & Nair 1997, Jiménez et al. 1998, Eisenhauer et al. 2009, Rajkhowa et al. 2015). Hence, Tondoh (2006) reported that the monthly abundance of earthworms was significantly related to rainfall amount, and Lavelle (1983) observed a close relationship between rainfall and earthworm casting (indicating earthworm activity). Furthermore, greater accumulation of litter on the soil surface of agricultural and mixed forest systems during the wet season could provide more space, food, shelter, and protection from predation, and thereby contribute to enhancing earthworm populations and diversity (Ruan et al. 2005). The increase in earthworm density during humid periods follows reproductive peaks, resulting in enhanced growth of individuals. Therefore, in the humid periods, some earthworm species can accomplish most of their life cycle (Jiménez et al. 1998).

Earthworm communities gradually decrease in abundance as the annual rainfall decreases and the dry season becomes longer, so that in western Africa, for instance, earthworms were observed to disappear when the mean annual rainfall was less than 800–1000 mm/year and the dry season exceeded 3–5 months (Lavelle 1983, 1987). Extended dry seasons often lead to a drastic decrease in the density of earthworms (Lavelle 1971). Accordingly, Walsh & Johnson-Maynard (2016) reported that all sampled sites in southeastern Washington (Pacific Northwest USA) with a mean annual precipitation below 330 mm were free of earthworms. The same trend was observed in the Iberian Peninsula of Europe, a region with dry summers and wet winters that also restricted survival of some earthworm species (Fernandez et al. 2011). Morón-Ríos et al. (2010) conclude that inter- and intra-annual variability in precipitation is a key environmental factor for earthworms in Mediterranean ecosystems, and the capacity to migrate vertically into the soil may determine the earthworms' responses to precipitation.

2.2.2 Effects of precipitation and soil moisture

Soil moisture is a key variable controlling the exchange of water and heat energy between land surface and the atmosphere through evaporation and plant transpiration, and it is thus considered to be critical for the survival, growth, and reproduction of earthworms (Zorn et al. 2008). Accordingly, Diehl & Williams (1992) reported that both moisture and food availability had significant effects on the growth and burrowing rate of earthworms. Low soil moisture caused a reduction in aerobic metabolism and growth, and aerobic metabolism varied in earthworm species exposed to air versus water (Saroja 1964). Bessolitsyna (2012) studied the effect of soil moisture and different soil types in the landscape of southern middle Siberia and found that the abundance and distribution of earthworms were mainly affected by soil moisture. Forest and meadow ecosystems with high soil moisture and moderate temperature in the upper soil layer and litter were reported to be most favorable for earthworm communities, but over-moistened soils can also be unfavorable for the survival of earthworms, e.g., in the case of anaerobic conditions. Although, earthworms can live under submerged conditions for a certain period of time, particularly if the oxygen content of water is high enough, most species will die when exposed to excessive water logging conditions.

Similar to the context-dependent effects of temperature, precipitation and soil moisture effects on earthworms are variable and depend on temperature (Table 1). Thus, a significant correlation was observed between earthworm

density and biomass with soil moisture and temperature (Fournier et al. 2012). Moreover, positive interaction effects between temperature and soil moisture have been found to result in high earthworm population densities at locations with lower precipitation due to higher reproductive rates (Wever et al. 2001). Soil moisture content generally decreases with higher temperature due to increased evapo-transpiration, but it was shown to drop even faster in the presence of earthworms (*Lumbricus terrestris*) after intense rainfall (Ernst et al. 2009, Eisenhauer et al. 2014, Andriuzzi et al. 2015, Gonzalez-Alcaraz & van Gestel 2016). This finding indicates that the presence of particular earthworm species can also modulate the interacting effects of precipitation and temperature on ecosystem, for instance by changes in soil water content and litter layer (Eisenhauer et al. 2012).

In addition to variations with temperature, the sensitivity and effects of soil moisture depend on other environmental conditions like biogeographical zones and the hydrological conditions of the soil (Huhta et al. 1998). In arid ecosystems, the survival of earthworms is highly dependent on soil moisture, while in temperate zones their survival is unlikely to be at stake, unless the soil dries out. Several studies reported seasonal variations in the growth and activity of earthworms in response to changes in soil moisture (Lavelle 1983, Lavelle et al. 1987, Eriksen-Hamel & Whalen 2006, Perreault & Whalen 2006, Eggleton et al. 2009, Fisichelli et al. 2013). However, earthworm responses vary with life-history traits, and some earthworm species (e.g., *Pontoscolex corethrurus*, *Amyntas gracilis*, *Amyntas hupeiensis*) have a remarkable ability to withstand desiccation (Grant 1955, Ayres & Guerra 1981, Caballero 1979). As mentioned earlier, many species can also survive under dry soil conditions by entering diapause, para-diapause, or aestivation (Jiménez et al. 2000). For instance, *Aporrectodea trapezoides* is able to survive dry conditions by aestivating in the soil, and it is able to remain dormant, conserving moisture, until soil conditions are favorable again (Lee 1985, McDaniel et al. 2013). Baker et al. (1993) reported that lumbricid earthworms in Australia remained active in the top 10 cm of the soils only in the autumn-spring months when the soil water potential was above 150 kPa. *Aporrectodea longa* was found to start losing water below a soil water potential of 35.5 kPa and to enter diapause below 20 kPa (Kretzschmar & Bruchou 1991). In a similar study, Holmstrup (2001) also found that decreasing soil water potentials had a negative effect on the life cycle of *Aporrectodea caliginosa*. The change of soil moisture was found to affect earthworm growth and cocoon production, but it did not show any significant effect on cocoon development (Holmstrup 2001). However, other studies have shown that cocoons hatch

only when soil moisture becomes adequate for earthworm survival (Parmelee & Crossley 1988, Holmstrup 2001), underlining the need to explore species- and development stage-specific responses of earthworms to soil moisture.

2.3 Effects of drought

Drought has both direct and indirect impacts on the soil environment (Coyle et al. 2017). Water content in upper soil layers is reduced quickly, but deeper soil layers may not be immediately impacted (Nepstad et al. 2002). Lower soil water content increases soil hardness (Anh et al. 2014), and reduces the extent of water films (Coleman et al. 2004), compromising the movements of many soil fauna. Moreover, drought can result in reduced vegetation cover (Franklin et al. 2016, Garssen et al. 2014), which can lead to increased temperatures, altered microclimate on the soil surface, and reduced resource availability. Taken together, these direct and indirect drought effects typically reduce the biological activity and earthworm biodiversity in soils.

Despite the increasing frequency and growing importance of droughts in many regions of the world (Dai 2013), only a few studies have explored the effects of drought on earthworm communities (Zaller & Arnone 1999, Holmstrup 2001, Holmstrup & Loeschcke 2003, Plum & Filser 2005, Petersen et al. 2008, Owojori & Reinecke 2010, Morón-Ríos et al. 2010, Holmstrup et al. 2016) (Table 2). Earthworms have only very limited morphological or physiological means for reducing water transport through the cuticle (Carley 1978), and they are active only if free water is available in the soil (Lee 1985). Accordingly, the growth rate of adults and juveniles as well as the production of cocoons were shown to decline dramatically in response to drought, and the percentage of diapausing in earthworms increased between -20 to 30 kPa of water potential in soil (Holmstrup 2001). Earthworms often lose weight, decrease their burrowing activity, and may also enter diapause or become quiescent when soils become too dry (Rundgren 1975, Booth et al. 2000, Owojori & Reinecke 2010).

Moreover, differences in plant community composition can modulate earthworm community responses to drought (Mariotte et al. 2016). However, a more nuanced perspective on drought effects on earthworm communities may be required, as earthworm species were shown to respond differently to drought (Eisenhauer et al. 2014). Epigeic species living at the soil surface are strongly affected by dry and hot conditions during summer, because these species dwell in and feed on the litter layer and have limited ability to move down into the soil (Eggleton et al. 2009). The drought

Table 2. Summary table of studies on the effects of drought as climatic driver on earthworm species abundance and biomass, earthworm populations, and earthworm activity. p: effects of precipitation.

Study	Climatic driver Drought	Earthworm species	Earthworm biomass	Earthworm population Density/ abundance	Cocoons/ juveniles	Earthworm activity and additional comments and details
Zaller & Arnone (1999)	Low soil moisture	<i>Lumbricus terrestris</i> , <i>Allolobophora chlorotica</i> , <i>Nicodrilus longus</i> , <i>Nicodrilus nocturnus</i> , <i>Aporrectodea rosea</i> , <i>Nicodrilus caliginosus</i> , <i>Octolasion cyaneum</i> , <i>Dendrobaena mammalis</i> , <i>Lumbricus castaneus</i>	↔	↔	↔	Increased soil moisture, with additional rain, did not affect earthworm activity at any earthworm density level.
Holmstrup (2001)	-2 kPa and -300 kPa.	<i>Aporrectodea caliginosa</i>	↓	↓	↓	Cocoon development was less sensitive to water potential than growth and cocoon production when drought exposure was for 14 days. Cocoon production decreased below -10kPa. At -6 kPa, the growth of juveniles was significantly lower.
Holmstrup & Loeschcke (2003)	91.6% relative humidity	<i>Dendrobaena octaedra</i>	NA	NA	↓	Cocoons showed different sensitivity at different geographic regions. Epigeic species produced drought-resistant cocoons.
Plum & Filser (2005)	Drought Marsh soil	<i>Octolasion tyrtaeum</i> , <i>Octolasion cyaneum</i> , <i>Allolobophora chlorotica</i> , <i>Lumbricus rubellus</i>	↓	↓	↓	Drought reduced earthworm population size.
	Peat soil		↑	↑	↑	Soil-dependent effect in peat soil, highest earthworm density was found during the drought.
Petersen et al. (2008)	Gradual drought	<i>Dendrobaena octaedra</i>	NA	NA	↑	Gradually dehydrated cocoons showed an increased tolerance to extreme drought compared to acutely dehydrated cocoons.
Owojori et al. (2010)	Less rain	<i>Aporrectodea caliginosa</i>	↓	NA	NA	Toxicity of pollutants was more pronounced in the dry period than the wet winter period.
Morón-Ríos et al. (2010)	Reduced precipitation and drought	No species information provided	↓	NA	NA	Reduction of inter-annual precipitation variability and reduced summer drought in autumn and spring increased earthworm abundance. Earthworm density was higher in irrigated plots, i.e., the effects of drought were negative.
Lima et al. (2011)	Drought stress 10-40% WHC	<i>Eisenia andrei</i>	↔	↔	↔	Mortality and weight loss in earthworms were not significantly affected.
Friis et al. (2004)	1.5 pF-5 pF (wet to very dry)	<i>Aporrectodea caliginosa</i>	↓	↓	NA	Drought in combination with copper caused an increase in mortality. With increasing drought level, the effect of copper increased from about 40 microg Cu/g dry weight to about 90 microg Cu/g.
Mariotte et al. (2016)	18% reduction of mean summer precipitation	<i>Lumbricus terrestris</i> , <i>Aporrectodea caliginosa nocturna</i> , <i>Aporrectodea caliginosa caliginosa</i> , <i>Aporrectodea longa longa</i> , <i>Aporrectodea rosea</i>	↑	↔	↓	Drought significantly increased the biomass of earthworms in plots where subordinate plant species were present. The ratio of the number of juvenile earthworms significantly decreased in plots where subordinate plant species were removed during drought.
			↓			
Walsh & Johnson-Maynard (2016)	Precipitation increases	<i>Aporrectodea trapezoides</i>	↓ _p	↓ _p	NA	No earthworms were detected below 330 mm mean annual precipitation. Earthworm density showed a negative correlation with increasing precipitation.

↑ Climate change factor increases earthworm performance, ↔ Non-significant effect of climate change factor on earthworms,

↓ Climate change factor decreases earthworm performance

resistant cocoons produced by epigeic species could thus represent a main strategy (Bouché 1972, Petersen et al. 2008) of these species to persist during summer drought perturbations (Holmstrup & Loeschke 2003), and they may recover very rapidly in abundance after the end of drought conditions (Eggleton et al. 2009). Also the cocoons of the peregrine species of endogeic category *Microscolex dubius* were reported to survive hot and dry summer periods and hatch when placed in a more favorable environment (Doube & Auhl 1998).

Similar to earthworm abundances, the biomass response of earthworms during and after droughts varies according to different ecological strategies. For instance, the biomass of *Lumbricus terrestris*, *Aporrectodea caliginosa nocturna*, and *Aporrectodea caliginosa caliginosa* increased significantly, while that of *Aporrectodea rosea* was reported to decrease after drought (Mariotte et al. 2016). *Aporrectodea rosea* has low assimilation efficiency and forms aestivation chambers close to the soil surface (Edwards & Bohlen 1996, Gerard 1967), while *Aporrectodea caliginosa nocturna* forms aestivation chambers below 10–20 cm depth (McDaniel et al. 2013), which makes them less vulnerable to drought conditions. Anecic earthworms form permanent vertical burrows in the soil, enter into a diapause during dry periods, and can stay in a dormant stage for several months (Jiménez & Decaëns 2004). Endogeic earthworms (such as *Aporrectodea caliginosa*), by contrast, form non-permanent horizontal burrows in the top soil and are able to survive for short periods of drought by burrowing to soil depths of 10–20 cm and by forming aestivation chambers covered with mucus and gut content to protect themselves against water loss (Bayley et al. 2010). These dissimilar ecological strategies are thus likely to cause changes in earthworm community composition in response to pronounced and/or repeated droughts. Moreover, during long-lasting drought, some physiological mechanisms were shown to promote dehydration tolerance in earthworms. Various earthworm studies reported that glucose is an important osmolyte governing freeze tolerance (Holmstrup et al. 1999, Holmstrup & Overgaard 2007), whereas sorbitol is the main osmolyte in dehydrated eggs (Holmstrup 1995, Petersen et al. 2008). Spectroscopic analysis of compatible osmolytes in gradually dehydrated cocoon/embryos revealed the presence of more free amino acids like sorbitol, glucose, betaine, alanine, and mannitol than in acute desiccated embryos (Petersen et al. 2008). Bayley et al. (2010) also reported an increased concentration of alanine in the dehydrated adult individuals of *Aporrectodea caliginosa*. Recently, Holmstrup et al. (2016) discovered the presence of the free amino acid alanine in three earthworm species *Aporrectodea tuberculata*, *Aporrectodea icterica*, and

Aporrectodea longa. This increase in the concentration of free amino acids in desiccated earthworm reduced the rate of water loss from the body. Moreover, results of this study suggested that the accumulation of alanine provides protection against deleterious effects of desiccation in earthworms. Taken together, these observations indicate the importance of physiological responses of earthworms to dry conditions, which merits further research and synthesis.

In addition to differences in drought effects with respect to earthworm life-history traits, earthworm responses to drought were reported to further depend on other environmental conditions like chemical stressors, oxygen supply, and food availability in the soil (Diehl & Williams 1992). For instance, Friis et al. (2004) observed that drought in combination with heavy metals (copper) caused an increase in mortality of *Aporrectodea caliginosa*. Moreover, Plum & Filser (2005) recorded that soil water holding capacity and organic matter content are important factors modulating earthworm responses to drought conditions. In fact, high water holding capacity of the soil and artificially raised groundwater table were shown to favor earthworms during drought periods. These context-dependent effects might explain the high variability in earthworm responses to drought in previous studies (Table 2), and should be considered in future work and meta-analyses on this topic.

2.4 Effects of flooding

Floods lead to rapid changes in soil conditions and can cause the loss of existing plant biomass (Williamson & Wardle 2007, Wright et al. 2014, Zhang et al. 2015, Schomburg et al. 2018), but the deposition of nutrient-rich sediments make floodplains some of the most productive ecosystems around the globe (Tockner & Stanford 2002). During the flood, however, mineralization and decomposition processes of dead organic material and ultimately soil nutrient availability are reduced due to limited soil gas diffusion and low oxygen availability (Schoor & Matson 2001). Consequently, anaerobic conditions develop fast in flooded soil, which have significant effects on the composition of soil food webs, microbial biomass, and soil microbial community structure (Schoor & Matson 2001, Visser & Voesenek 2005, Unger et al. 2009, Plum 2005). Once an environment has been disturbed by a flood, it can take several years for the invertebrate community to return to its pre-disturbance state (Pearce & Pearce 1979, Gerisch et al. 2012). A meta-analysis of terrestrial invertebrates in flooded grassland concluded that flooding reduced the diversity, abundance, and biomass

of all groups of soil macrofauna, including earthworms, and the detrimental effects increased with the duration of flooding and rising temperature (Plum 2005). However, the ability of soil invertebrates to survive during flooding was shown to depend on their behavioral, morphological, and physiological traits (Plum 2005). In the present review (synthesized in Table 3), several studies showed that earthworm abundance was reduced in flood plain areas, and periodical flooding also had species-specific effects on earthworm populations. The reported absence of anecic earthworms indicates more erosion and sedimentation processes in flood plains, while the higher biomass of epigeic earthworm species may be positively correlated to topsoil texture and organic matter quality (Bullinger-Weber et al. 2012).

Many species of earthworms can survive long periods submerged in water (Roots 1956, Edwards & Bohlen 1996), and Zorn et al. (2008) suggested that earthworms are able to survive in flooded soil, but there are important differences among species (Ayres & Guerra 1981). Furthermore, the time period between two flooding events determines the earthworm population size and their maturity. In fact, it was shown that earthworms mature at a younger age at sites that are frequently flooded (Klok et al. 2006a). Earthworm numbers may also be reduced by floods, because cocoons cannot develop into reproductive adults and enhanced exposure to soil contaminants after flooding may further suppress earthworms (Klok et al. 2006b, Thonon & Klok 2007).

On the other hand, land-use change of floodplains may also have diverse effects on earthworm communities. For instance, Ausden et al. (2001) found hardly any *Aporrectodea caliginosa* in flooded grassland in Western Europe, while *Eiseniella tetraedra* (a species adapted to flooded soils) was more abundant in flooded grassland in England. However, Ivask et al. (2007) found that *Aporrectodea caliginosa* was less abundant in flood plain meadows than in non-flooded meadows, and Keplin & Broll (2002) found similar results with lower numbers of this species in flooded grasslands in Germany. In contrast, Pizl (1999) observed an increase in the relative abundance of *Aporrectodea caliginosa* after summer flooding. These inconsistent results suggest that the same species can show dissimilar responses in different environments, and further studies are needed to investigate which conditions may help buffer flooding effects.

One important factor that certainly plays a role is the duration of flooding. Short flooding periods followed by long recovery periods can benefit certain earthworm species (*Lumbricus rubellus* and *Allolobophora chlorotica*), which showed increased abundance and biomass in intermittently flooded areas (Schütz et al. 2008), and led to compositional shifts favoring epigeic

earthworms (Bullinger-Weber et al. 2012). Plum & Filser (2005) also noted that controlled flooding should be kept short, especially in winters following natural summer floods, and a recovery time of about six months was sufficient for the re-establishment of earthworm populations.

Various behavioral responses of earthworms can help them to escape from the flooded site, such as horizontal migration and climbing onto trees or other vertical structures like wooden poles of fences (Adis & Righi 1989, Pizl 1999, Plum 2005). In a field experiment, the earthworm species *Allolobophora chlorotica*, *Aporrectodea caliginosa*, *Aporrectodea longa*, and *Lumbricus castaneus* were observed to move upwards in soil samples when the lower parts of the samples were flooded (Ausden et al. 2001, Plum 2005). In addition to behavioral responses, earthworms have developed several physiological adaptations to overcome the lack of oxygen during flooding. For example, *Eiseniella tetraedra* and *Octolasion tyrtaeum* retain contact to the aerated zone by holding the tail vertically upwards and moving it within the water to maintain gas exchange (Pizl 1999, Beylich & Graefe 2002). The prospects of these responses depend on the severity and duration of the flood.

3. Conclusions, implications, and outlook

The present review highlights the effects of different climatic drivers (temperature, precipitation, drought, and flood) on the abundance, survival, and distribution of various earthworm species and ecological groups in different habitats and land-use types. Overall, we note that extreme climate events like droughts and floods are likely to have the most detrimental effects on earthworm communities. However, most of the results discussed and synthesized (in Tables 1–3) are based on studies of earthworm communities in temperate climate regions of the world (mainly composed of lumbricid earthworm species), although we have attempted to incorporate some of the very limited literature from the tropics and other climatic regions (e.g., Mediterranean). Hence, many of the principles presented here, in terms of the potential impacts are in dire need of further verification for these lesser-known earthworm communities. Although we suspect many of the climate drivers may have similar impacts in these regions, differences in soil types, vegetation, climate, and earthworm communities present therein (where lumbricids are not the main family) must be taken into consideration, in order for a more global synthesis to be conducted in the future.

Table 3. Summary table of studies on the effects of flooding on earthworm species abundance and biomass, earthworm populations, and earthworm activity.

Study	Climatic driver Flooding	Earthworm species	Earthworm biomass	Earthworm population		Earthworm activity and additional comments and details
				Density/ abundance	Cocoons/ juveniles	
Plum & Filser (2005)	High flood	<i>Octolasion tyrtaeum</i> , <i>Octolasion cyaneum</i> , <i>Allolobophora chlorotia</i> , <i>Lumbricus rubellus</i>	↓	↓	↓	Earthworms were less affected by shorter duration of the flood, but prolonged flood reduced earthworm population size.
Klok et al. (2006)	High flood	<i>Lumbricus rubellus</i>	↓	↓	↓	At frequent flooding sites, earthworms matured at lower weight and a younger age.
Ivask et al. (2007)	High flood	<i>Aporrectodea rosea</i> , <i>Lumbricus rubellus</i> , <i>Lumbricus terrestris</i> , <i>Aporrectodea longa</i> , <i>Allolobophora chlorotica</i> , <i>Lumbricus castaneus</i>	↓	↓	↓	Cocoons could not hatch, if period between two floods was short.
Thonon & Klok (2007)	High flood	<i>Lumbricus rubellus</i>	↓	↓	↓	Flooding reduced earthworm numbers.
Schütz et al. (2008)	Short-term flooding	<i>Lumbricus rubellus</i> , <i>Allolobophora chlorotica</i>	↑	↑	NA	Total earthworm numbers and biomass in flooded sites exceeded those of non-flooded sites (+51% and +71%, respectively). Short-term flooding (max.10days) interrupted by long recovery periods favor earthworm populations.
Zorn et al. (2005)	Flooding events (3-8 weeks) once per year	<i>Lumbricus terrestris</i>	↑	↑	NA	<i>L. terrestris</i> was found more often after the flooding period.
		<i>Allolobophora chlorotica</i>	↔	↔	↓	<i>A. chlorotica</i> : low populations of juveniles after flooding events, no effect on biomass or adults.
		<i>Lumbricus rubellus</i>	↓	↓	↓	<i>L. terrestris</i> was negatively influenced by flooding.
Zorn et al. (2008)	Soil moisture 35%, 45% (field capacity), 55%, 65% (saturated) to 65% with an extra water layer).	<i>Aporrectodea caliginosa</i>	↔	NA	NA	It was observed that <i>A. caliginosa</i> avoided 65% and 65%+ soil moisture. In the experiment, the effects were not significant.
		<i>Allolobophora chlorotica</i>	↓	NA	NA	<i>A. chlorotica</i> avoided the 65%+ treatment and escaped to the 65% compartment.
		<i>Lumbricus rubellus</i>	↓	NA	NA	More <i>L. rubellus</i> were found in the dryer compartments.

Continued table 3.

Study	Climatic driver	Earthworm species	Earthworm biomass	Earthworm population		Earthworm activity and additional comments and details
	Flooding			Density/ abundance	Cocoons/ juveniles	
Lima et al. (2011)	Flood stress 8-120%WHC	<i>Eisenia anderi</i>	↔	↔	↔	Mortality and weight loss of earthworms were not significantly affected.
Fournier et al. (2012)	High flood	<i>Allolobophora chlorotica</i> , <i>Allolobophora georgii</i> , <i>Aporrectodea caliginosa</i> , <i>Aporrectodea caliginosa nocturna</i> , <i>Aporrectodea caliginosa tuberculata</i> , <i>Aporrectodea giardi</i> , <i>Aporrectodea longa</i> , <i>Aporrectodea rosea</i> , <i>Dendrodrilus rubidus</i> , <i>Eiseniella tetraedra</i> , <i>Lumbricus castaneus</i> , <i>Lumbricus meliboeus</i> , <i>Lumbricus rubellus</i> , <i>Lumbricus terrestris</i> , <i>Octolasion tyrtaeum tyrtaeum</i>	↓	↓	NA	More epigeic species in the flood plain as pioneer community and dominance of anecic species indicated low flood intensity and good soil development.
Andriuzzi et al. (2015)	520 mm rainfall	<i>Lumbricus terrestris</i>	↔	↔	NA	Earthworms dug more burrows under intense rainfall.
Emets (2018)	High flood	<i>Aporrectodea caliginosa</i>	↓	↓	↑	After heavy flood, population increased by mass emergence of juveniles from cocoons.
Rodríguez et al. (2019)	Long-term spring flood at 15°C for 2 months	No further species information provided	↓	↓	NA	Flooding reduced earthworms, but the presence of flood-resilient plants could mitigate some of the negative impacts of flooding on soil functioning.



Climate change factor increases earthworm performance,



Non-significant effect of climate change factor on earthworms,



Climate change factor decreases earthworm performance

Nonetheless, this synthesis may also have important implications for the management of agricultural fields and future research directions. First, there is empirical evidence that agricultural practices that stimulate soil biodiversity, such as increased crop diversity, reduced tillage, and continuous soil cover, could help mitigate the effects of climate change on earthworm communities (de Vries et al. 2012, Scherr & McNeely 2008, Singh et al. 2016). Management practices that increase residue inputs to the soil may increase earthworm densities independently of tillage, and the quality of residue inputs may also be a driving factor of earthworm communities (Reich et al. 2005, Thomason et al. 2017). Enhancing plant diversity, productivity, and litter quality (e.g. high N content) might mitigate detrimental climate change effects, such as by drought, as subordinate plant species might also maintain high quantity and quality food for earthworms and potentially mediate drought effects on the earthworm community (Mariotte et al. 2016).

Second, we emphasize the importance of context-dependent climate change effects that are currently underexplored. For instance, the toxicity of pesticides (and other chemical stressors like heavy metals) for earthworms may increase with increasing temperature and after flooding (Klok et al. 2006a, Hackenberger et al. 2018). Such findings may have important management implications, as the toxicity of pesticides for earthworm might be reduced by changing the timing of pesticide use in agriculture fields after a time interval of water irrigation or precipitation event. Further implications might be the increased exposure of worms to higher temperatures and pesticide applications in agricultural fields after heavy precipitation events, when many earthworm species come out of the soil or closer to the surface. Hence, to reduce side effects of pesticides on earthworms, applications should not be performed directly after such rainfall events. However, more research is needed to test these proposed applied prospects.

Third, given the strong context-dependency of climate change effects on earthworms, future research needs to test such effects across different ecosystems and land-use types. Integrated measures of water availability accounting for both precipitation and temperature, such as the aridity index or the Standardized Precipitation-Evapotranspiration Index (SPEI), as well as soil abiotic conditions that determine water-holding capacity, can help to consistently identify and quantify wet and dry climate events and may be useful for future projections of earthworm distributions. As earthworms are involved in many ecosystem services and represent common bio-indicators, we argue that these three research lines may provide significant insights into the response of soil biodiversity to climate change.

4. Acknowledgements

Jaswinder Singh thanks the Alexander von Humboldt foundation, Germany for providing financial assistance for doing research work in the Department of Community Ecology, Helmholtz-Centre for Environmental Research-UFZ, Halle and at the German Center for Integrative Biodiversity Research (iDiv), Leipzig, Germany. G. Brown and W. Demetrio thank the CNPq for fellowship support. We are also grateful to the Helmholtz Association, the Federal Ministry of Education and Research, the State Ministry of Science and Economy of Saxony-Anhalt and the State Ministry for Higher Education, Research and the Arts Saxony for funding the Global Change Experimental Facility (GCEF) project. This research also received support from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement no. 677232 to NE) and from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118).

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