

Is soil biodiversity threatened by anthropogenic environmental changes?

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Dates:

Received: 11 May 2018
Accepted: 20 August 2018
Published:

How to cite this article:

Adriaan J. Reinecke and
Sophia A. Reinecke, Is soil
biodiversity threatened
by anthropogenic
environmental changes?,
*Suid-Afrikaanse Tydskrif
vir Natuurwetenskap en
Tegnologie* 37(1)

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Soil is a service-providing asset under growing pressure but it is also home to an array of soil-dwelling species encompassing virtually all terrestrial invertebrate phyla. The impact human-induced changes are having on the rich endemic soil biodiversity in many parts of the world is hardly known in spite of the fact that they play an important role in soils where they can influence chemical, physical and biological processes. Our literature search showed that although much has been written on the influence of global environmental changes on natural and managed terrestrial ecosystems, less than 3% of articles published in ecological journals dealt with belowground organisms or processes. Very few of these address the drivers of transformation such as rising CO₂ levels, warming, land use, pollution and changing precipitation in relation to the very soil food webs underpinning human food production.

In this review we highlight some of the main drivers of environmental change that are evidently impacting on soil ecosystems and posing a threat to soil biodiversity and processes. We examined the available evidence of such changes, their causes and possible impacts. We conclude that the evidence is mounting that the growth of land use, the increase in built-up areas, the physical and chemical impact of mining and other industrial activities, the landfarming of toxic wastes, the invasion of exotic species and shrub encroachment are also transforming the soil environment with consequences for soil biodiversity. The extent and severity of this impact and its long-term implications are not always very clear because much of the evidence is based on association rather than causation. A better understanding of the diversity and its role is needed before the environmental risks can be assessed reliably and goals of sustainability and conservation of soil biodiversity can be realised.

Keywords: soil biodiversity; environmental changes; effects

Introduction

Natural soil is home to a rich biodiversity of soil organisms and in some areas this includes a rich variety of endemic species (Hendrix and Bohken 2002; Janion-Scheepers et al. 2016). Although many species of soil organisms have over almost two centuries been described taxonomically, our knowledge of their ecological roles, requirements and ecophysiology is still limited. We know little about their tolerance for environmental change. This knowledge will in future become increasingly important as environmental conditions change as a result of climate and other changes. Soil is a service-providing asset under growing pressure (vdM Louw et al. 2014). It is home to an array of species of soil invertebrates which is enormous, encompassing virtually all terrestrial invertebrate phyla. The soil invertebrate meso- and macrofauna include a variety of surface litter and soil-dwelling (belowground) arthropods such as insects, soil mites, millipedes, centipedes and isopods. Also velvet worms (onychophorans), molluscs, annelids, nematodes and several others. With microorganisms (Botha 2010) they play an important role in soil ecosystems (Lavelle et al. 1997; Wall and Virginia 2000; Lavelle et al. 2006). However, larger animals and the equally "glamorous" aboveground arthropods, seem to catch the attention while the (in Charles Darwin's words) "lowly" subsurface animals and microorganisms have received comparatively little attention in spite of their diversity and importance. Many studies have already shown how important the role of soil biota is in soil formation and soil fertility. Macro-invertebrates have considerable impact on soil functions (Lavelle et al. 2006) by influencing chemical, physical and biological processes. They may also be the best possible indicators of soil quality. However, knowledge of their distribution and functional role in many parts of the world seems poor.

As for the terrestrial ecosystems evidence is mounting of irreversible change in their composition due to human activity and natural changes that will continue to alter their structure and function.

This is especially true for the vegetation where biological invasions are well documented and useful predictive models have been developed (Higgins and Richardson 1998).

All terrestrial ecosystems consist of aboveground and belowground components that interact to influence community- and ecosystem-level processes and properties. These components are closely interlinked at the community level. This is further supported by a greater degree of specificity between plants and soil organisms than has been previously appreciated (Wardle et al. 2004). These authors suggested a combined aboveground-belowground approach to community and ecosystem ecology to obtain a better understanding of the regulation and functional significance of biodiversity.

Many human-induced changes affect the aboveground components directly but to what extent and by what are belowground biota and their functions being threatened or transformed? What is the impact of anthropogenic activities such as the introduction of alien species, industrial activities and mining, agriculture and chemical pollution? The immediate biodiversity consequences seem obvious but is there hard scientific evidence of the actual impact and causality of the interaction, also for life in the soil and soil processes? What about the longer term, evolutionary impact of these drivers of change?

While conservation of biodiversity is currently receiving much attention, invertebrates, which may comprise as much as 95 % of biodiversity, are generally excluded (Hamer and Slotow 2002), even more so the subsurface dwellers. It is often assumed that vegetation types and patterns of floral diversity will adequately reflect those of the underlying diversity, i.e. invertebrates (Hamer and Slotow 2002), but substantiation is weak. As for nematodes, springtails, isopods, mites and several other invertebrate groups, a lack of adequate data for many parts of the globe as well as a shortage of expertise are often the main reasons why soil-dwelling invertebrates have been neglected.

In this review we focus on the role of the main drivers of change that are impacting on terrestrial ecosystems with the specific aim to highlight our current knowledge of effects on the soil-dwelling biota, with special emphasis on southern Africa. A literature survey was undertaken to establish whether the available soil zoological information addresses the question of major environmental changes. Is there significant and reliable evidence of such changes, their causes and effects for soil biodiversity? Which drivers of change may require closer scrutiny from soil biological researchers?

Major drivers of change affecting soil invertebrates

Land use and habitat transformation

The way land is used and managed can have a considerable impact on the soil fauna (Baker 1998). Agricultural activity

has a major impact on soils through practices resulting in chemical and organic matter input, tillage or no-tillage, soil compaction (Beylich et al. 2010), wind erosion and salinisation (Rengasamy 2006). Van Capelle et al. (2012) have shown that for certain functional groups, the tillage-induced impacts differed depending also on local soil characteristics which should be considered when deciding on a tillage system. Intensive land use reduces the diversity and abundance of many soil biota (De Vries et al. 2013). This affects soil processes and the ecosystem services that they maintain. These authors quantified, across four countries of contrasting climatic and soil conditions in Europe, how different land use systems, that caused differences in soil food web composition, influence the functioning of soils and their ecosystem services. Their assessment of the contribution of soil organisms to processes of C and N cycling across land use systems and geographic locations showed that soil biota need to be included in C and N cycling models and highlights the need to map and conserve soil biodiversity across the world.

The management practices of land use can be very important. In a recent review Mugerwa (2015) concluded that loss of termite predators and anthropogenic influences are the principal drivers of subterranean termites' destructive behaviour that is threatening the functioning and sustainability of selected African savannah ecosystems in Uganda. The author blamed inappropriate savannah management practices (overgrazing, indiscriminate tree cutting and overhunting) by humans for altering the feeding group composition of termites' assemblages, favouring grass harvesters and polyphagus termite feeders that forage on more abundant food items. According to this author overhunting results in decline in termite predators, which eventually enhances the proliferation of termite populations, escalates the density of termite nests, particularly epigeal mounds and intensifies consumption of herbaceous savannah vegetation.

Few wild areas remain where soil has not been affected in one way or another by land use. Also in many parts of the world agricultural and forestry transformations have taken place over hundreds of years resulting in the creation of croplands and rangelands that have entirely different characteristics in terms of floral and faunal composition and soil conditions (Biggs and Scholes 2002). Substantial differences in richness, abundance and diversity of invertebrate biota in general are already evident between unspoiled, protected regions compared to areas where the changes have taken place (Gebeyehu and Samways 2002; Witt and Samways 2004). Although most of these studies have dealt with surface- or detritus-dwelling arthropods and not much with subsurface biota, Dlamini and Haynes (2004) concluded that land use has major effects on the size, composition and diversity of earthworm communities.

Daniels and Van Wyk (2011) studied the critically endangered velvet worm species *Opisthopatus roseus*, endemic to the Ngele mistbelt forest in South Africa where

the habitat of the worms has been severely impacted by anthropogenic activities such as logging of indigenous trees, construction of a national highway, commercial timber plantations and introduction of alien plant species. This resulted in habitat fragmentation and potential range contraction for the species.

Some of the longest running ecology experiments (Van Wilgen et al. 2003) have provided important insight into the influences of management regimens in conservation areas, pointing to the major role land use plays in large scale transformation. Seymour and Dean (1999) compared invertebrates on a heavily grazed communal farm to moderately grazed farms and showed that arthropod abundance was consistently higher in the heavily grazed areas but species richness was greater on the moderately grazed areas while the Shannon diversity was higher at all three moderately grazed localities. Considerable differences in arthropod assemblages were projected where habitat degradation was severe. Soft-bodied, soil-dwelling invertebrates were however not reported on in their study.

Considering the importance of the belowground-aboveground link between soil fauna and vegetation, it seems reasonable to assume that drastic effects of land use on vegetation types can also impact on the soil fauna. In a vulnerability assessment of vegetation types in South Africa, Jonas et al. (2006) took various land use pressures into consideration such as land capability, afforestation, mining potential and population growth. They concluded that 19 vegetation types out of several hundred are critically endangered and ecosystem functioning was disrupted by habitat transformation. How this relates to soil fauna diversity and activity constitutes a clear gap in our knowledge of the impact of such transformations.

An important way forward was suitably demonstrated in the report of an extensive study programme of 109 sites (Cluzeau et al. 2012) in France. These authors found that most of the soil biological groups (except Collembola) exhibited lower abundance and community richness in croplands than in meadows, which provided a first, substantial reference database for soil biological data for France covering microflora and fauna. It has the potential to be used to calibrate future research results and to develop management baseline values for assessing the status of soil biodiversity under several different policies and practices. Application of this approach in other parts of the world and mirroring soil fauna data against vegetation mapping can provide a more scientifically sound way of demonstrating the effects of transformations and illustrate the importance of soil organisms for sustainable land use.

Land use practices can, however, also have a positive influence on soil biodiversity as was demonstrated by Sileshi and Mafongoya (2007) in Zambia. They showed that both quantity and quality of organic inputs were important in the maintenance of a diverse soil macrofauna in maize

crops. Also irrigation, mulching and organic farming practices in former dry areas can create favourable moisture conditions for soil-dwelling species. Reinecke et al. (2008) used the bait lamina test and found that the activity of soil organisms in vineyard soil was affected differently by different management practices. Organic management practices resulted in higher soil faunal feeding activity over the short term compared to conventional practices. Quantification of such effects by means of long-term field studies is needed.

With sustainable agriculture in a changing world in mind, the concept of soil ecological engineering forwarded by Bender et al. (2016) holds promise but it can hardly be implemented successfully without a basic knowledge of the diversity and role of soil organisms in soil processes in many parts of the world.

Fire as driver of change

Large parts of the world's terrestrial ecosystems burn on a regular basis and have done so for hundreds of millions of years (Bond and Keeley 2005). The earlier studies of Ahlgren (1974) and Abbott (1984) on the short-term effects of forest fires on soil fauna were not later extended to include grasslands where natural and prescribed fires are a regular phenomenon. The extent to which fire determines global vegetation patterns by preventing ecosystems from achieving the potential height, biomass and dominant functional types expected under the ambient climate was demonstrated by Bond et al. (2005).

It is generally accepted that fire presents a significant evolutionary force and plays a key role as an ecological process. It has been shown to affect insects severely (Swengel 2001; Parr et al. 2004). Collett et al. (1993) showed that prescribed low intensity fires caused a reduction in Collembola activity, up to one year, while earthworm populations also declined substantially, but recovered within three years of each fire. However, information on the long-term effects on soil-dwelling invertebrate diversity and their assemblages is mostly lacking in spite of several previous studies on the effects of fire (Parr and Chown 2003; Uys and Hamer 2007) and its use as a management tool. Abbott (1984) showed that while some taxa recovered in density within three years of a moderate intensity fire in the Jarrah forest in Australia, the relative abundance and/or activity of three other taxa remained depressed.

The majority of studies so far were observational reports with only a few experimental studies involving subsurface invertebrates. The impact of fire regimens on biodiversity and productivity have long been in the focus of land managers in southern Africa (Van Wilgen et al. 1990; Van Wilgen 2009; Bond and Keeley 2005). Fire causes a change in tree structural diversity. By contrast, ant assemblage structure is influenced only by whether a plot has burned or not, and not by the specifics of the burn treatment, although landscape productivity clearly also has effects on richness (Parr and Chown 2003; Parr et al. 2004). Sileshi

and Mafongoya (2006) provided field results from Zambia indicating that diversity and abundance of several major groups of soil-dwelling invertebrates were lower under burnt forest patches compared to unburnt ones. They concluded that fire can alter the structure of soil invertebrate communities through direct mortality or by its effect on availability of food resources. Somewhat different findings were made by Uys and Hamer (2007) who examined the impacts of different burning regimens (fire frequency and season) and fire history on invertebrate morphospecies richness and abundance. Morphospecies richness was consistently highest in blocks burnt in autumn, and higher for biennial burns or two years since last burn for epigeic, winged and wingless invertebrates, but this was not the case for soil invertebrates which showed limited response to fire.

More longer-term field studies, especially in grassland and savannah biomes, of the effects on populations and assemblages of earthworms, mites, collembolids, isopods and several other invertebrate groups are still needed. The question of resilience and long-term recovery of soil fauna where the vegetation has been changed as a result of fires, needs to be addressed. This will inform on future fire management strategies that would take the role of soil fauna in soil formation and sustaining of soil fertility (Wall and Virginia 2000; Lavelle et al. 2006) into account. Lack of expertise on the taxonomy of many of these groups may be a problem, but there is clearly no lack of opportunity for such investigations, given the frequency of managed or natural fires in southern Africa and elsewhere.

Change posed by chemicals reaching the soil

Chemicals used for crop protection, pest and vector control

The impact of chemicals entering the soil has received much attention since the 1960s but the last word is not yet spoken. Is this impact a major driver of change, transforming the soil environment irreversibly? Although much progress has been made in many countries to implement stricter control over what enters the soil through agricultural and industrial activities, soil ecotoxicological research is continuously revealing new frontiers of concern about new manmade substances among which pharmaceuticals, plastics and nanoparticles.

Many chemicals of different kinds are released into the environment by agricultural activities aimed at feeding plants or protecting crops against pests and weeds. Even irrigation practices may lead to salinisation of soil, with detrimental effects for the soil fauna (Owojori et al. 2009). Control of disease vectors requires vast amounts of chemicals as well, while manufacturing and mining industries are dumping wastes containing different kinds of chemical cocktails in the environment.

Among the organic chemicals entering the environment, the notorious persistent organic pollutants (POPs) were and are of major concern (Fiedler 2008). The development of

scientifically sound criteria is crucial for identifying further POPs as the current list is not exhaustive and persistence in different environmental compartments such as biota, fatty tissue, water, sediments and soil types can vary considerably. Soil ecotoxicological research, in contrast to aquatic research, has not received as much attention since Rachel Carson's well-known book *Silent Spring* stimulated research and awareness of the impact of chemicals on the biological environment in the nineteen sixties. A literature survey indicated that no soil ecotoxicological studies for purposes of regulatory compliance were reported on in several African countries that seem to be relying on assessments undertaken in Europe and the USA where conditions are vastly different (Eijsackers et al. 2017).

Pesticides of different kinds are widely used for crop protection and combatting disease vectors such as malaria mosquitoes. South Africa uses the most pesticides in sub-Saharan Africa (Dalvie et al. 2003) with more than 500 active ingredients legally registered for the country. Pesticides mostly end up in the soil and water due to spray drift and water run-off (Dabrowski et al. 2002; Reinecke and Reinecke 2007) of which almost half are organophosphates that are designed to be biologically active and therefore have the potential to cause negative side-effects to non-target organisms. They are supposed to have a relatively short half-life. Although environmental quality guidelines may seldom be exceeded, this may however, not be the case for soils in specific areas where malaria control is taking place (Van Dyk et al. 2010). Moreover, the setting of such general guidelines or limits may have limited value (Reinecke and Reinecke 2010) due to the complexity and heterogeneity of the soil environment. Variability of environmental factors such as physical, chemical, microbiological and textural characteristics can influence mobility of chemicals adsorbed in the soil matrix and therefore affect bioavailability and uptake. Ragnarsdottir (2000) suggested that organophosphates can persist in the environment for long periods of time and were detected in soils years after application. Reinecke and Reinecke (2007) also detected organophosphates in orchard soil six months after the last spraying event. These pesticides can drift from agricultural lands to pristine areas where they affect the beneficial soil macrofauna detrimentally (Reinecke and Reinecke 2007). The latter authors found significantly lower earthworm population densities in orchards where organophosphates were sprayed compared to an adjacent uncultivated field.

Also fungicides can have a negative effect on soil organisms. Maboeta et al. (2002, 2003) investigated the effects of the widely used fungicide copper oxychloride on field populations of an exotic (*Aporrectodea caliginosa*) and an indigenous earthworm (*Microcheatus* sp.) and monitored changes in worm density, biomass, copper concentrations in soil and earthworms, and, as a biomarker, neutral red retention times of coelomocytes, which measure cellular damage in an organism. For *A. caliginosa* there was a significant impact on worm density and biomass on the

treated plots six months after spraying with the fungicide had stopped although copper levels in both soil and earthworm tissues had declined significantly. The effects manifested at a much later stage at the population level than with the biomarker response, suggesting that the biomarker may have predictive value. For the indigenous *Microcheatus* sp. the impact of the fungicide was sooner and much more severe. This species' response was more sensitive. More than a year after spraying had stopped the worm biomass and numbers were still significantly lower compared to control plots. The important question that needs to be addressed is what the effect of long-term, regular spraying will be on the populations.

Chemical waste disposal via landfarming and landfills

Many different organic compounds, apart from agricultural chemicals, also enter the soil and groundwater via landfills (Daso et al. 2013) and landfarming of oil refinery sludge (Reinecke et al. 2016a). The specific chemical threats to beneficial soil organisms and soil processes are difficult to pinpoint because most contaminants entering the environment consist of cocktails of different chemicals in variable ratios depending on the sources. Determining their hazard potential for soil organisms is also difficult because the amount of each compound entering the environment and their interactions are seldom known, even if their individual toxicity scores may be known.

Landfarming is considered a low-technology method of dealing with solid waste and is advocated for effective remediation and sanitation of soils. It is widely used but its sustainability is uncertain (Reinecke et al. 2016a) because it requires large areas of land, is time consuming and there are risks of soil and groundwater pollution (Hu and Zeng 2013). The total land surface being used for landfarming is unknown and is probably much smaller than that used for mine tailings and landfills. However, the hazardous nature of the chemicals involved and the fact that soil and groundwater may be affected is reason for concern.

The contaminants in the oil sludge being landfarmed may be toxic not only to soil microorganisms, as research on bioremediation suggests, but also to a variety of beneficial soil organisms such as mites, earthworms, springtails and potworms which inhabit healthy soils (Wahl et al. 2012). The concentrations of Al, Mn, Pb, S and Zn were higher in site soil where landfarming had taken place for several years than in the sludge itself indicating that accumulation had taken place over time from this supposedly "organic" waste and posing a potential threat to the soil fauna (Reinecke et al. 2016b).

The refinery sludge as well as soil from a landfarming site were toxic to earthworms, potworms and springtails (Reinecke et al. 2016a; 2016b; 2016c). The refinery waste, therefore poses a threat to beneficial soil organisms and soil ecosystems but the actual risk involved will remain uncertain until the extent of the practice is comprehensively

and thoroughly investigated and suitable risk assessment and monitoring systems are implemented. Although very few of the earlier recommendations of Cortet et al. (1999) on the indicator role and utilisation of soil organisms' responses to pollutants have been followed up as yet, it is clear that the presence of chemicals in many soils is constituting a driver of transformation with long-term implication for the soil fauna and their functional role in soil processes.

Mining and industrial activities as agents of change

Mining plays an important role in the economies of several countries such as Australia, South Africa, Russia, Zambia, Zimbabwe and many others where both physical and chemical environmental impacts on ecosystems are evident (Rösner and Van Schalkwyk 2000). Acid and metal contamination of soil due to mining activities and industrialisation have come under increasing scrutiny. A study by Ikenaka et al. (2010) indicated that heavy metal pollution in Zambia is still increasing. Gold mining in South Africa resulted in vast volumes of tailings being deposited in impoundments and poor management of some tailings dams resulted in seepage, adversely affecting soils and water quality (Roesner and Van Schalkwyk 2000). The impact on soil biodiversity has not been studied in depth. Van Collier-Myburgh et al. (2014) used soil enzymatic analyses and earthworm (*Eisenia andrei*) responses to determine the effect of chromium mine waste on the activity of a soil microbial community and soil invertebrates. Chromium mining had a toxic effect on enzymatic activity. Maboeta and Fouche (2014) used bioassays to show the impact of copper ($\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$) on earthworms exposed to soils from a Cu production site.

Mining of Cu, Pb, and Zn causes the greatest degradation of the environment and copper mining produces extensive mine wastes and tailings. Soil contamination with trace metals is considered a serious problem related to mining and smelting (Dudka and Adriano 1997).

Efforts to rehabilitate mine dumps have achieved mixed results. Mine dumps in various temporal stages of re-vegetation establishment can provide an ideal opportunity to study the temporal succession of plants as well as the soil-dwelling fauna. This could provide information within a short period of time, covering successive changes that would otherwise have required decades to follow.

Given the extent of mining activities in many countries, future plans for expanding coal mining to pristine areas and fracking for gas, the need to develop a risk assessment procedure that would include the soil fauna seems important.

Biological invasions as driver of change

Plant invasion may impact on soil-dwelling invertebrates although most studies have so far concentrated on vertebrates or aboveground invertebrates. Indigenous

plants can hold soil to prevent erosion and maintain moisture but alien plants may disturb these functions and even affect soil chemistry differently. Pryke and Samways (2009) investigated invertebrate response to alien pine plantations, their removal in comparison with natural vegetation, recovering indigenous forests and a botanical garden. Their findings strongly support removal of alien pines in an urban context, and also emphasise that an urban botanical garden of indigenous plants has major invertebrate conservation value. This may also be valid for subsurface invertebrates but needs to be investigated.

Woody plant encroachment happening in savannahs in Africa may alter carbon and nitrogen pools over the long term, with potential regional or wider biogeochemical implications, given the widespread encroachment (Hudak et al. 2003; O'Connor et al. 2014). This will, in turn, influence the soil conditions for its faunal inhabitants and could lead to changes in species composition, especially if the changes favour introduced species more. According to Wolfe and Klironomos (2005), immigration of plant species into novel habitats may change the function of the soil food webs by (i) changing the quality, quantity and timing of litter input and rhizodeposition; (ii) causing release of novel antimicrobial compounds; (iii) altering nutrient relations by introducing alternate modes of nutrient acquisition; or (iv) by altering soil structure or physical properties.

The indications are that exotic plants can alter the distribution and success of various beneficial and plant-pathogenic fungi by releasing toxins into the soil or by changing patterns of decomposition as a result of altered quality of detritus (Van der Putten et al. 2009).

Examples of the introduction of alien belowground species into soils can be found in many countries such as, for example, the United States (Hendrix and Bohlen 2002; Hendrix et al. 2008), Australia (Baker et al. 2006). In South Africa earthworms have been introduced (Ljungström 1972; Reinecke and Visser 1980; Reinecke 1983; Plisko 2001, 2010; Haynes et al. 2003), as well as ants (Skaife 1955; Prins 1978; Witt and Gilliom 2004), termites (Mitchell 2002), isopods (woodlice) (Dangerfield and Telford 1994; 1995) and collembolans (springtails) (Janion-Scheepers et al. 2015). The pattern is basically the same for many other countries to which people migrated or with whom they trade. The question is, what are they doing to the endemic biodiversity and to soil processes? Are they all true invaders? The invasive biology of most soil invertebrates has not been studied thoroughly (Ehrenfeld and Scott 2001) because most of the research on invasions by terrestrial invertebrates has focused on economically important pest insects. Their ability to spread to large areas quickly as a result of their high mobility and fecundity has been researched intensively (Simberloff 1989).

Human migration and commerce over centuries have been the principal mechanisms for the introduction of

exotic species into new areas, also as far as earthworms are concerned (Gates 1967; Reinecke 1983; Hendrix and Bohlen 2002). Introductions were both unintentional in ships' ballast or with imported plants and soil, but also intentionally for the provision of fishing bait or as waste decomposers (for vermicomposting). Whether or not they become invasive depends on their inherent abilities to cope with conditions of the ecosystem they are introduced to. Also their interaction with other species will play a role.

Invasions by more cryptic and less mobile soil fauna appear to be qualitatively and quantitatively different from those of other invertebrates (Hendrix and Bohlen 2002) because of the more limited modes of transportation but it seems to emphasise the role of man in transporting them over vast distances and natural barriers. Certain species of exotic earthworms have the potential to invade new habitats and, once established, may affect other organisms and soil processes (Dalby et al. 1998; Hale et al. 2006). The earthworms *Pontoscolex corethrurus* and *Aporrectodea trapezoides* and some *Amyntas* species seem to be such candidates in southern Africa where their occurrence is widespread in disturbed soils where they may play an invasive role.

In North America, the most dramatic effects of exotic earthworm invasions on soil processes have been in areas previously devoid of earthworms (e.g. north of Pleistocene glacial margins) (Hendrix and Bohlen 2002). Gates (1967) reviewed an account of the exotic earthworm *Lumbricus terrestris* obliterating soil horizons quite deeply in the USA. Significant effects of exotic earthworms on soil profiles, on nutrient and organic matter dynamics, on other soil organisms, or on plant communities have been reported in southern California (Graham and Wood 1991) and New Zealand (Stockdill 1982). Several introduced lumbricid and megascolecid species survive and flourish in South Africa in gardens and irrigated agricultural soils where favourable conditions exist.

The mechanisms by which exotic earthworms become dominant in certain ecosystems (Stebbins 1962) have been heavily debated. In southern Africa, as in many other cases, exotic species invaded ecosystems previously devoid of earthworms (Reinecke and Ljungström 1969; Ljungström 1972) or disturbed areas (Reinecke and Visser 1980) or areas inhabited by native earthworms but disturbed by agricultural activities and forestry. No direct evidence of competitive exclusion of native earthworms by exotic ones is available (Hendrix and Bohlen 2002) but this could be because of a lack of evidence. In South Africa (Reinecke and Visser 1980) and India (Narayanan et al. 2016) the impression is that exotic species are more robust where agricultural activity entails mechanical and/or chemical disturbance. The important operational mechanism for displacement of native earthworm populations could therefore be the alteration of their habitat rather than direct competition, although the relative roles of these two should

be researched more fully. Irrigation of crops seemed to have favoured the establishment of exotic populations in otherwise dry land without indigenous earthworm species.

The possibility that the phenomenon of biotic resistance (Williamson and Fitter 1996) in the context of earthworm invasions could explain why some indigenous species are capable of maintaining their position in spite of the presence of introduced species, should be explored further by comparative physiological experiments. However, climate change may, for example, challenge their tolerance ranges increasingly and affect their future distribution.

Horn et al. (2007) undertook a qualitative survey of the leaf-litter earthworm fauna of 11 indigenous forests in South Africa. They identified five indigenous and 12 exotic species. This may be a worrying find of invasions that requires urgent attention. They did however not find evidence of an association between exotic and indigenous species richness but warned against an assumption of no impact on forest ecosystems. More, longer-term quantitative studies are clearly needed even though there is no evidence of a negative economic impact on soil productivity.

Species such as the earthworm *Pontoscolex correthurus*, that exhibit a wide range of environmental plasticity in their native habitats, are likely to be more successful as invaders than species with more restrictive environmental requirements (Williamson and Fitter 1996). The distinctive presence of *P. corethrurus* in various pristine eastern regions in southern Africa (Plisko 2001) confirms its adaptability.

The suggestion that European lumbricid species from northern latitudes and some Asian megascolecids are poor colonisers in tropical or subtropical climates (Hendrix and Bohlen 2002) also seems to hold true for southern Africa. Although several species have been introduced, their distribution seems to be limited in natural areas although they might flourish in disturbed soils. Of the introduced “vermicomposting” or “manure worms” such as *Eisenia fetida*, *E. andrei* (from Europe), *Perionyx excavatus* (from Asia) and *Eudrilus eugeniae* (from western Africa), only the first two are sometimes found in isolated, organically rich garden habitats where conditions are favourable in terms of moisture and high organic matter content but not in natural habitats. Reinecke et al. (1992), after studying the temperature requirements of these species, suggested that there are probably only very few south and eastern coastal areas in South Africa where the two tropical species, *P. excavatus* and *E. eugeniae*, may be able to survive low outdoor temperatures. Their potential to become invaders, outcompeting indigenous species or disturbing soil processes, would therefore be low in large areas where minimum temperatures fall well below their lower temperature tolerance limits. The same can't be said of all introduced, epigeic species from Asia simply because their specific habitat requirements and tolerance limits are unknown. A sound assessment of the impact of

introduced soil-dwelling invertebrates on the indigenous soil biodiversity and soil processes is therefore still a major challenge.

Urbanisation as driver of change

The earth's surface is rapidly being urbanised, creating a vast new habitat with small isolated islands or strips of the original habitat remaining (Radeloff et al. 2005, Grimm et al. 2008). With urbanisation come many secondary activities that can impact on soils. How soil invertebrates respond to urbanisation deserves attention because of their important ecological role in soil formation, decomposition of organic matter and soil fertility.

Landscapes are becoming increasingly heterogeneous and habitats more fragmented as a result of more and wider roads and building complexes. Organisms with limited means of dispersal such as, for example, mites, nematodes, springtails, isopods and earthworms, may have no links or bridges between separated landscape elements, in contrast to more mobile organisms. The inability of soil dwellers to cross these manmade barriers will prevent maintenance of gene flow networks. This will create small, isolated populations, with an already patchy distribution, that will undergo inbreeding depression. This may affect the soil ecosystem's resilience to recover from disturbances caused by phenomena such as fire, drought, salinisation and the effects of chemical or mechanical impacts. As suggested the introduction and maintenance of undisturbed green patches and parks can provide sanctuary for more mobile species such as flying insects. However, it may not be true for less mobile soil-dwellers with limited means of dispersal, unless sufficient so-called “green corridors” are provided. Future urbanisation projects should, in their design, include continuous areas, linking habitats.

Climate change as driver of change for soil organisms

The nature of the expected impact of climate change (Intergovernmental Panel on Climate Change 2014) on soil invertebrates is uncertain. The timing and magnitude of rainfall events are predicted to change over time, resulting in longer drought periods and larger rainfall events. Soil invertebrate community composition and function are both sensitive to changes in rainfall. The question is whether they can adopt strategies that can ensure sufficient fitness under changed conditions, as seems to be the case with microbial communities (Evans and Wallenstein 2014). Future genomic research will have to show whether genetically-based adaptation rather than mere acclimatisation had taken place as a result of the selection pressure.

Biological trends can't easily be linked causally to climate change because non-climatic influences dominate local, short-term biological changes (Parmesan and Yohe 2003) but evidence is mounting that biological trends correlate with climate change predictions. Also climate change is already

affecting living systems and the outlook for some parts of the world seems less encouraging. The responsiveness of fauna in many parts of the world to climate change events is poorly documented and not routinely incorporated into regional conservation planning (Erasmus et al. 2002); even more so, as far as subsurface soil invertebrates, other than surface-active arthropods, are concerned of which we know so little in spite of their diversity. Erasmus et al. (2002) modelled the likely range alterations of a representative suite of 179 animal species in South Africa, which, apart from vertebrates, included 19 butterfly species and 57 "other" species (which included termites, ant lions and beetles) to climate change brought about by the doubling of CO₂ concentrations with an expected mean temperature increase of 2 °C. Their predictions suggest that the Kruger National Park conservation area in South Africa may lose up to 66% of the species included in this analysis. This highlights the extent and severity of the predicted range shifts. It is expected that the conflicts between conservation and other land uses (that may impact on climate (such as industrial and mining activities) may escalate, should the effects of climate change become more severe and obvious to a wider range of stakeholders.

The current status of the truly soil-dwelling, soft-bodied invertebrates and the impact of a complex set of transforming environmental factors have not been considered much. Rising atmospheric CO₂ concentrations and temperatures are expected to have marked impacts on the carbon (C) turnover in agro-ecosystems through increased plant photosynthetic rates, leading to an enhanced biomass, and wider plant C/N ratios according to Sticht et al. (2006). Their results revealed significant effects of CO₂ enrichment on density and species diversity of collembolans. There is, however, much scope to explore this further in light of the expected climate change since it has been suggested that environmental changes of rising atmospheric CO₂ concentration, warming, and changed precipitation patterns, will increase the frequency of plant invasions. This is expected to exacerbate the negative effects of these events that are likely to be widespread (Kriticos et al. 2003).

It must be emphasised that generalisations about the effects of any single driver of change, such as for example climate change, should be done with great caution because there are so many diverse climatic zones ranging from temperate to arid to semi-desert to tropical that can be expected to respond differently.

How the expected changes will affect the soil ecosystem services remains a grand challenge to soil biologists. Researching the impacts of anthropogenic activities by executing ambitious monitoring programmes will require a well-coordinated cross-disciplinary approach taking all forms of life, at all levels, from molecule to community, both above as well as below the ground, into consideration.

Warming can, on the one hand, increase activity of microbial soil communities directly and on the other hand change

plant community composition and thereby indirectly alter the soil communities that depend on their energy inputs. Kardol et al. (2010) illustrated this experimentally with field studies of plants and nematodes and concluded that accurate assessments of climate-change impacts on organisms and soil ecosystem functioning require incorporating the concurrent changes in plant function and plant community composition, which will likely modify or counteract the direct impact of atmospheric and climate change on soil ecosystem functioning. Hence, these indirect effects should be taken into account when predicting how global change will alter ecosystem functioning. The need for a multi-disciplinary approach accounting for all physical, chemical and biological factors seems obvious and will require a wide spectrum of expertise.

Severe changes that can alter plant communities can be expected to have indirect and even direct effects on subsurface functions. Pritchard (2011) is of the opinion that the impact of indirect effects of increased temperatures may even be greater on individual soil-dwelling species because it will benefit some plants more than others. If plant communities should change drastically, the amount and quality of organic matter reaching the soil from plants will also change. Also Wardle et al. (2004) think that changes in the composition of plant communities could be more important for soil organisms than the direct effects of rising temperatures.

Should the overall impact of climate change on the soil fauna be as negative as that predicted for other species (Erasmus et al. 2002), the loss of this important component of a region's biodiversity may have more severe consequences than generally appreciated because it plays, in many respects, a fundamental service-providing role.

Summary and conclusions

The broader environmental literature shows that human impact on the natural environment and its ecosystems has reached a peak. We have highlighted several major drivers of change that are transforming the terrestrial environment and can be expected to impact severely on the underground fauna. The extent of this impact and its implications for the various soil-related ecosystem services remains to be unravelled, especially in the broader context of the aboveground versus belowground interaction. Although reliable evidence of the real impact of some of the changes is still scarce, human impact on the terrestrial environment can be seen in growing land use for agricultural and other purposes; the increase in built-up areas; the physical and chemical impact of mining and other industrial activities; the landfarming of different kinds of toxic waste and the invasion of exotic species.

It can on reasonable grounds be accepted that the transformation is already such that the ideal of rehabilitation and reverting of systems to their hypothetical "original state" will, in most, if not all, cases remain an unfulfilled

dream, especially since climate change, facilitated by anthropogenic activity, is continuing unabated. In the long run this will in any case lead to irreversible changes because organisms will respond and adapt due to the selection pressure being exerted on them.

The conservation and sustainable use of soil fauna depend on knowledge of their diversity and ecological roles as well as the threats they are facing and how they are responding. Without this knowledge and without focussed long-term protocols based upon it, the selection of taxons as indicators of anthropogenic impact on the biological environment will be of limited value (McGeogh 1998).

It has been suggested that the soil food web should be fairly resistant to environmental changes because of resilience and redundancy within the enormous biodiversity with so many functional groups (Laakso and Setälä 1999; Briones et al. 2009), but it may be more complicated than we expect. There may well be compensation by other groups of soil organisms (Hunt and Wall 2002; Briones et al. 2009) to replace the functions of affected ones, depending on factors such as trophic levels occupied and tolerance ranges. However, the evidence from the available literature provides both positive (Sticht et al. 2006) and negative effects depending on a combination of factors such as the taxa involved and the prevailing environmental conditions. Changing environmental factors are not necessarily operating singly and linkages with others are often the case.

From this review of the available information, it became evident that most of the published findings on the relationship between effects and their causes are based on observational evidence. This may show correlations, which are useful, but provide only associational evidence. Without controlled experimental observations, which are of course not always possible because of temporal and spatial constraints, causality between environmental changes and their observed effects is not firmly established. Careful interpretation of data and a multi-disciplinary approach (Brevik et al. 2015) is therefore imperative to ensure that alarmist conclusions are not made about the risks involved. There is room for improvement of our current assessment methodology and understanding of the risks.

This study confirmed that the effects of anthropogenic changes on soil biodiversity deserve more attention, not only in terms of the short-term implications but also in a longer-term evolutionary context.

Acknowledgement

We thank the University of Stellenbosch and the National Research Foundation (NRF) for financial support. Opinions and conclusions are those of the authors alone. This publication is dedicated to the memory of Prof PAJ Ryke who, in the late nineteen fifties of the previous century, played a leading role at Potchefstroom to stimulate soil zoological and acarological research in South Africa.

Authors' contributions

Both authors participated in the literature study and interpretation of the findings. The first author (AJR) wrote and translated the original manuscript and both authors participated in editing it.

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